



United States Department of Agriculture

Effects of Drought on Forests and Rangelands in the United States: A Comprehensive Science Synthesis



Photographs are provided courtesy of the U.S. Department of Agriculture (USDA) Forest Service, Agricultural Research Service, and Natural Resources Conservation Service; the U.S. Geological Survey; and other Federal and State agencies, universities, and nongovernmental organizations. Individual photo credits are provided.

Cover Photographs (from top to bottom):

J.S. Quick, Colorado State University, Bugwood.org

Ronald F. Billings, Texas Forest Service, Bugwood.org

U.S. Geological Survey



Forest Service

Research & Development

Gen. Tech. Report WO-93b

January 2016

Effects of Drought on Forests and Rangelands in the United States: A Comprehensive Science Synthesis

EDITORS

James M. Vose

James S. Clark

Charles H. Luce

Toral Patel-Weynand

J.M. Vose is a Research Ecologist, U.S. Department of Agriculture, Forest Service, Southern Research Station (SRS), Center for Integrated Forest Science (CIFS), North Carolina State University, Department of Forestry and Environmental Resources, Raleigh, NC 27695.

J.S. Clark is the Nicholas Professor of Environmental Science and Professor of Statistical Science, Nicholas School of the Environment, Duke University, Durham, NC 27708-0338.

C.H. Luce is a Research Hydrologist, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Boise, ID 83702.

T. Patel-Weynand is Director of the Forest Management Sciences' (SFMR) staff, U.S. Department of Agriculture, Forest Service, Research and Development (R&D), Washington, DC 20024.

Acknowledgments

The editors thank the authors who contributed to this report. We also thank the technical reviewers who provided comments and suggestions on earlier drafts. We thank Jennifer Plyler and Stephanie Laseter for their assistance with editing and formatting. We thank the Southern Research Station for its work to publish this report; specifically, we thank Donna Burnett for technical editing and ensuring compliance with the U.S. Government Publishing Office, Maureen Stuart for technical editing and leading the publication process, and Helen Robinson for graphic design. The U.S. Department of Agriculture, Forest Service, Southern Research Station (J.M. Vose), Rocky Mountain Research Station (C.H. Luce), and National Research and Development Washington Office (T. Patel-Weynand and James S. Clark) provided support for the editors and the publication process.

Abstract

This assessment provides input to the reauthorized National Integrated Drought Information System (NIDIS) and the National Climate Assessment (NCA), and it establishes the scientific foundation needed to manage for drought resilience and adaptation. Focal areas include drought characterization; drought impacts on forest processes and disturbances such as insect outbreaks and wildfire; and consequences for forest and rangeland values. Drought can be a severe natural disaster with substantial social and economic consequences. Drought becomes most obvious when large-scale changes are observed; however, even moderate drought can have long-lasting impacts on the structure and function of forests and rangelands without these obvious large-scale changes. Large, stand-level impacts of drought are already underway in the West, but all U.S. forests are vulnerable to drought. Drought-associated forest disturbances are expected to increase with climatic change. Management actions can either mitigate or exacerbate the effects of drought. A first principal for increasing resilience and adaptation is to avoid management actions that exacerbate the effects of current or future drought. Options to mitigate drought include altering structural or functional components of vegetation, minimizing drought-mediated disturbance such as wildfire or insect outbreaks, and managing for reliable flow of water.

Keywords: Climate change, drought, forest disturbances, natural disasters, water quantity and quality.



Contents

Acknowledgments	ii
Abstract	ii
Executive Summary	1
Overview and Purpose	1
Topics Addressed in This Assessment	2
Key Messages From the Report	3
Managing Forests and Rangelands To Increase Resiliency and Drought Adaptation.	7
1 Understanding and Anticipating Potential Drought Impacts	9
Literature Cited	11
2 Characterizing Drought for Forested Landscapes and Streams.	13
Introduction	14
What Is Drought?	14
Drought Classification	15
Drought Influences on Forest and Stream Ecosystems	17
Ecological Drought Characterization	17
Measures of Drought	20
Paleoclimatic Context for Evaluating Drought	23
Historical and Recent Drought	32
Climate Change Impacts on Drought Frequency and Severity	34
Summary	41
Literature Cited	41
3 Physiological Responses of Forests to Future Drought	49
Introduction	50
A Plant’s Perspective on Drought	50
Belowground Mechanisms to Survive Drought	52
The Interaction of Drought, Host Physiology, and Multi-Trophic Community Dynamics	54
Can CO ₂ Fertilization Mitigate Drought Impacts?	55
Do Ecosystem Models Include Plant Drought-Response Mechanisms?	55
Conclusions	56
Literature Cited	56
4 Impacts of Increasing Drought on Forest Dynamics, Structure, Diversity, and Management.	59
Introduction	60
Evidence for Drought Impacts on Forests	61
Drought-Mediated Biogeographic and Biome Shifts in U.S. Forests	70
Implications for Forest Management Practices	78
Research to Better Anticipate Drought Effects on U.S. Forests	82
Conclusions	83
Literature Cited	84

5	Forest Biogeochemistry in Response to Drought	97
	Introduction	98
	Drought and Forest Biogeochemistry	99
	Drought and Carbon Balance in Forests	103
	Management Implications	104
	Representation of Drought in Ecosystem and Global Models	105
	Summary and Conclusions	106
	Acknowledgments	106
	Literature Cited	106
6	Forest Insect and Fungal Pathogen Responses to Drought	113
	Introduction	114
	Tree Responses to Drought	114
	Insect and Pathogen Responses to Drought	116
	Regional and Sub-Regional Differences and Interactions	122
	Anticipating Impacts: Predictions of Future Drought-Related Insect and Disease Impacts	125
	Summary and Research Needs for Insects and Pathogens	126
	Conclusions	128
	Literature Cited	128
7	Fire and Drought	135
	Introduction and Historical Perspective	136
	Characterizing Drought: Metrics of Fire Risk	137
	Regional Differences in Fire and Interactions With Other Stressors	141
	Quantifying and Projecting Drought Effects on Wildfire: Biological and Physical Factors	146
	Management and Social Implications	150
	Literature Cited	150
8	Rangeland Drought: Effects, Restoration, and Adaptation	155
	Introduction	156
	Types and Patterns of Rangeland Drought	157
	Effects of Drought on Rangelands	163
	Drought Interactions With Other Disturbances and Stressors	169
	Effects of Drought on, or in Combination With, Human Uses and Practices	173
	Increasing Rangeland Ecosystem Resilience to Drought	177
	Conclusions	182
	Acknowledgments	183
	Literature Cited	183

9	Detecting and Monitoring Large-Scale Drought Effects on Forests: Toward an Integrated Approach	195
	Introduction	196
	Existing Approaches Used for Broad-Scale Drought Impact Detection and Monitoring	204
	Integrating Broad Monitoring With Assessment	214
	“Big Data” Integration: A Contextual Learning Approach to Drought	219
	Summary.	224
	Literature Cited.	225
10	Ecohydrological Implications of Drought	231
	Introduction	232
	Relationship Between Meteorological Drought and Hydrologic Drought.	233
	Species Composition, Vegetation Dynamics, and Drought Interactions With Streamflow.	235
	Range Shifts in Major Ecosystem Types in Response to Climate Change	238
	Groundwater Interactions With Drought	240
	Challenges to Predicting the Impacts of Drought on Hydrological Processes	240
	Drought Impacts on Water Quality	241
	Management Options for Minimizing the Impacts of Drought on Water Quantity and Quality	244
	Conclusions	244
	Literature Cited.	245
11	Economics and Societal Considerations of Drought	253
	Introduction	254
	General Economic and Social Effects of Drought in Forests and Rangelands	254
	Examples of Drought Effects on the Forest and Rangeland Sectors	260
	Conclusions	273
	Literature Cited.	275
	Appendix.	279
12	Summary and Conclusions	283
	Introduction	284
	Characterizing Drought	284
	Drought Effects on Wildlands	284
	Socioeconomic Impacts	285
	Critical Research Needs	286
	Management Responses	287
	Literature Cited.	288

Executive Summary

James M. Vose

James S. Clark

Charles H. Luce

Toral Patel-Weynand

J.M. Vose is a Research Ecologist, U.S. Department of Agriculture, Forest Service, Southern Research Station (SRS), Center for Integrated Forest Science (CIFS), North Carolina State University, Department of Forestry and Environmental Resources, Raleigh, NC 27695.

J.S. Clark is the Nicholas Professor of Environmental Science and Professor of Statistical Science, Nicholas School of the Environment, Duke University, Durham, NC 27708-0338.

C.H. Luce is a Research Hydrologist, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Boise, ID 83702.

T. Patel-Weynand is Director of the Forest Management Sciences' (SFMR) staff, U.S. Department of Agriculture, Forest Service, Research and Development (R&D), Washington, DC 20024.

Overview and Purpose

This assessment provides input to the reauthorized National Integrated Drought Information System (NIDIS) and the National Climate Assessment (NCA); it also establishes the scientific foundation needed to manage for drought resilience and adaptation. The NIDIS Act¹ was signed into law in 2006 and reauthorized by Congress in 2014.² NIDIS will be implemented through a network of agencies and partners to integrate drought monitoring and forecasting systems at multiple levels (Federal, State, and local). It will support research that focuses on drought risk assessment, forecasting, and monitoring. Produced every 4 years, the NCA evaluates the effects of global climate change on forests, agriculture, rangelands, land and water resources, human health and welfare, and biological diversity, and it projects major trends. The NCA is based on technical information produced by public agencies and nongovernmental organizations.

As drought regimes change, the ability to quantify and predict the impacts on forests and rangelands is critical to developing and implementing management actions to increase resiliency and adaptation. The U.S. Department of Agriculture (USDA), Forest Service, Research and Development scientists in partnership with Duke University authored this assessment, entitled, *Effects of Drought on Forests and Rangelands in the United States: A Comprehensive Science Synthesis*. The assessment is a collaborative effort authored by 77 scientists from the Forest Service and other Federal agencies, research institutions, and various universities across the United States. The authors identified key issues from a series of virtual workshops involving scientists and stakeholders. Focal areas in the assessment include drought characterization, drought impacts on forest processes and disturbances such as insect outbreaks and wildfire, and the consequences on forest and rangeland values. The assessment closely follows the Intergovernmental Panel on Climate Change (IPCC) process, which is organized with convening authors, lead chapter authors, and contributing authors. The convening authors for the assessment had the chapters individually peer reviewed, and the lead and contributing authors revised the text in response to reviewer comments.



This assessment establishes the scientific foundation needed to manage forests and rangelands for resilience and adaption to drought.

Photo credits (from top to bottom):
 Craig D. Allen, U.S. Geological Survey
 J.S. Quick, Colorado State University, Bugwood.org

¹ National Integrated Drought Information System Act of 2006. P.L. 109-430 (December 20, 2006). 15 U.S.C. § 313d.

² National Integrated Drought Information System Act of 2014. P.L. 113-86 (March 6, 2014).



Topics Addressed in This Assessment

- Characterizing Drought for Forested Landscapes and Streams
- Physiological Responses of Forests to Future Drought
- Impacts of Drought on Forest Dynamics, Structure, Diversity, and Management
- Forest Biogeochemistry in Response to Drought
- Insect and Pathogen Responses to Drought
- Fire and Drought
- Rangeland Drought: Effects, Restoration, and Adaptation
- Detecting and Monitoring Large-Scale Drought Effects on Forests: Toward an Integrated Approach
- Ecohydrological Implications of Drought
- Economics and Societal Considerations of Drought in Forests and Rangelands

This assessment focuses on drought characterization, the impacts on forest processes and disturbances, and the consequences on forest and rangeland values.

Photo credits (from top to bottom):
 Craig D. Allen, U.S. Geological Survey
 John M. Randall, The Nature Conservancy, Bugwood.org
 U.S. Geological Survey

Key Messages From the Report

Characterizing and Predicting Future Drought

In simple terms, drought is a lack of water over a given temporal and spatial scale. Drought can be a severe natural disaster with substantial social and economic consequences. Drought becomes most obvious when large-scale changes are observed (e.g., insect outbreaks or wildfires) or when water requirements for human or agricultural needs are not met; however, even moderate drought can have long-lasting impacts on the structure and function of forests and rangelands without these obvious large-scale changes. Droughts are generally identified as one of four types: (1) meteorological, (2) hydrologic, (3) agricultural, or (4) socioeconomic. Meteorological and hydrologic droughts relate water availability to a reference condition (e.g., long-term mean); agricultural and socioeconomic droughts relate to impacts. In agricultural systems producing annual crops, characterizing and assessing drought impacts can be fairly straight forward; however, in systems with perennial vegetation (both natural and agricultural systems), characterizing and assessing drought impacts is much more complex, as responses can vary in space, time, and among species.

Historical and paleoclimatic evidence shows that drought has always impacted the physical environment and will continue to do so. The direction of trends in recent history varies from region to region, with the Western United States showing a trend toward dry conditions while trends in the East are more variable and complex. Much of the variability in how drought is characterized depends on definitions for terms, for reference conditions, and for methods of averaging short-term weather into climate statistics. Predicting future changes in drought frequency and severity has proven difficult using General Circulation Models (GCMs), but recent trends are a growing global concern. Uncertainty arises primarily from limited capacity to predict future precipitation changes, particularly long-term lapses in precipitation. Despite this uncertainty, there is growing consensus that extreme precipitation events (e.g., lapses in precipitation and more intense storms) will increase in frequency, and warmer temperatures will exacerbate the impacts of drought on forests and rangelands in the future (chapter 2).



Drought becomes obvious when large-scale changes such as insect outbreaks, (top) or wildfires (center) are observed and when water requirements for human or agricultural needs are not met (bottom).

Photo credits (from top to bottom):
 USDA Forest Service, Bugwood.org
 National Interagency Fire Center, Bugwood.org
 Gerald Holmes, California Polytechnic State University,
 Bugwood.org



Ecosystem structure and processes are altered by drought. Cheatgrass (top) is a nonnative plant that invades burned sites. Dieback (bottom) can have global impacts on carbon cycles.

Photo credits (from top to bottom):
Craig D. Allen, U.S. Geological Survey
Chris Evans, Illinois Wildlife Action Plan, Bugwood.org

Understanding the Effects of Drought on Forests and Rangelands

There is a critical need to understand how drought affects forests and rangelands, in part because drought severity and drought-associated forest disturbances are expected to increase with climatic change. Drought affects forest and rangeland systems both directly and indirectly. In regions where seasonal droughts are common, forest and rangeland ecosystems respond through various physiological and morphological adaptations. In regions where drought is less common, responses can be substantial because ecosystems are not well adapted to drought conditions.

High evaporative demand, the combination of high temperature and low humidity, combines with low soil moisture to induce stress through closure of stomata, which can lead to carbon stress, loss of hydraulic function, and mortality. Species vary in their vulnerability to drought due to differences in their allocation to roots, mycorrhizal associations, and xylem anatomy (chapter 3). Large stand-level impacts of drought are already underway in the West, but all U.S. forests are vulnerable to drought. Changes in climate will continue to stress forests and alter suitable habitat. Combined field evidence and models suggest that climate change is causing relocation of habitats at rates much faster than populations of trees can migrate. Reorganizations of stand structure and species composition are expected to lag behind shifts in habitat caused by increasing drought and temperature change (chapter 4).

Droughts are predicted to accelerate the pace of invasion by some nonnative plant species into rangelands and grasslands. Drought can also promote plant invasion indirectly by modifying the environment to favor nonnative species. For example, opportunities for invasion are created when drought kills native plants leaving open niches and bare ground (chapter 8). Drought is also an important contributor to the invasive annual grass-wildfire loop that threatens ecosystems not adapted to fire (e.g., cheatgrass' positive feedback with fire in parts of western North America's sagebrush biome). In this self-perpetuating cheatgrass-fire loop, drought increases the frequency of wildfires, and nonnative plants (especially annual grasses) are likely to invade burned sites.

Drought alters ecosystem processes such as nutrient, carbon, and water cycling in ways that are not yet well understood (chapter 5). Drought tends to slow nutrient uptake by plants and reduce retranslocation of foliar nutrients with premature leaf senescence. Dieback that results from combinations of drought and natural enemies

can severely reduce carbon exchange between atmosphere and biosphere. Recent large diebacks have had global impacts on carbon cycles, including carbon release from biomass and reductions in carbon uptake from the atmosphere, although impacts may be offset by vegetation regrowth in some regions. Multi-year or severe droughts can have substantial impacts on hydrological and stream biogeochemical processes.

Indirect effects of drought on forests can be widespread and devastating. Notable recent examples include insect and pathogen outbreaks (chapter 6) and increased wildfire risk (chapter 7). Available evidence suggests a nonlinear relationship between drought intensity and bark beetle outbreaks; moderate drought reduces outbreaks whereas long, intense drought can increase it. As a consequence of long-term drought and warming in the Western United States, bark beetles are currently the most important biotic agent of tree mortality. Multiple large outbreaks have killed hundreds of millions of trees in recent decades. Host trees weakened by drought allow beetle populations to build. Warming facilitates northward range expansion. In contrast, there is little current evidence for a role of drought in bark beetle outbreaks in coniferous forests of the Eastern United States. Fungal pathogens are poorly understood, but available evidence suggest reduced pathogen performance and host impacts in response to drought for primary pathogens and pathogens whose lifecycle depends directly on moisture. In comparison, secondary pathogens that depend on stressed hosts for colonization are anticipated to respond to drought with greater performance and host impacts.

Historical and pre-settlement relationships between drought and wildfire have been well documented in much of North America, with forest fire occurrence and area burned clearly increasing in response to drought. This body of evidence indicates that the role of drought in historical and likely future fire regimes is an important contingency that creates anomalously high potential for ignition, fire spread, and large fire events. However, drought is only one aspect of a broader set of controls on fire regimes, and by itself is insufficient to predict fire dynamics or effects. Whereas the relationships between fire occurrence or area burned and drought are well documented, the relationship between drought and fire severity can be complex. For example, north-facing slopes might offer some degree of local protection during mild droughts, but even they become dry under extreme conditions, reducing fine-scale heterogeneity in vegetation consequences.



Drought can increase the intensity of insect and pathogen outbreaks including bark beetles (top), Dothistroma needle blight (center), and hemlock woolly adelgid (bottom).

Photo credits (from top to bottom):
 Ronald F. Billings, Texas Forest Service, Bugwood.org
 Robert L. James, USDA Forest Service, Bugwood.org
 Elizabeth Willhite, USDA Forest Service, Bugwood.org



Streamflow and groundwater recharge respond directly to drought through reductions in precipitation (rain and/or snowfall), and they respond indirectly via evapotranspiration responses to changing evaporative energy and water availability. Hydrologic responses to drought can be either mitigated or exacerbated by forest vegetation, depending on vegetation water use and how drought affects forest population dynamics (chapter 10). Drought affects water quality both directly and indirectly. Direct impacts are primarily physical, as reduced streamflow concentrates nutrients and sediment and warms more quickly. Indirect effects include a combination of terrestrial, riparian, and instream processes that impact sediment and nutrient concentrations and fluxes.

Detecting and Monitoring Future Droughts

The ability to detect drought effects on forest and rangelands over broad scales is limited, especially for episodic droughts of moderate severity. Compared to agricultural systems, detecting drought impacts on trees and other perennial vegetation may require a multi-year “memory” of antecedent conditions. With broad-scale monitoring, it is often not possible to detect drought effects, as moisture stress is not expressed uniformly across vegetation types.



Drought impacts streams (top) by concentrating sediments and nutrients. In rangelands, drought can reduce vegetative cover, leading to wind and water erosion (bottom).

Remote sensing approaches attempt to observe direct, secondary, and longer term effects of drought on vegetation (chapter 9). Remote sensing methods integrate across entire mixed-vegetation pixels and rarely distinguish the effects of drought on a single species, nor can they disentangle drought effects from those caused by various other disturbance agents. An integrated data-mining approach may hold the most promise for enhancing our ability to resolve drought impacts to forests. Efforts to integrate meteorological and remotely sensed data streams, together with other ancillary datasets such as vegetation type, wildfire occurrence, and pest activity, may help to identify and characterize drought effects.

Economic and Social Consequences of Drought

Drought has direct consequences to forest and rangeland production (chapter 11). Droughts can negatively impact forest inventories by increasing mortality and reducing growth. Drought in rangelands reduces forage and water available for livestock grazing. Reduced vegetative cover can lead to wind and water erosion. Drought-related disturbance, such as wildfire, can have protracted effects that include significant timber market losses.

Photo credits (from top to bottom):
Carol J. VanDyke, U.S. Geological Survey
Seth Munson, U.S. Geological Survey

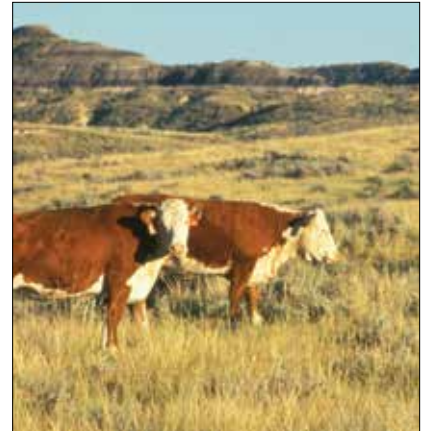
Reduced water yield from forests and rangelands during extended meteorological drought can have substantial impacts on domestic and agricultural water supplies, which often results in water markets implementing quantity controls. Drought can also have nonmarket effects on forests and rangelands. For example, drought affects outdoor recreation, where low reservoir levels can reduce availability of fishing, recreational boating, swimming, and camping (although some net benefit can result from more precipitation-free days). Low winter snow cover reduces economic benefits from skiing and related activities.

Ongoing drought in the Western United States, where most tribal lands exist, is expected to continue to affect tribal health, culture, economies, and infrastructure. Competing demands for dwindling water resources challenge Federal trust responsibilities. Complicating factors, including warming streams and hydrologic-cycle changes, affect fish populations important to tribal diets and ceremonies. Because of their natural resource dependence for income, employment, and cultural practices, many tribes are also vulnerable to higher rates of forest and rangeland disturbances, including invasive species spread, increased occurrences of epidemic pest populations and their associated damages, and wildfires.

Managing Forests and Rangelands To Increase Resiliency and Drought Adaptation

How can forest and rangeland practices adapt to changing drought regimes? Frequent low-severity drought may selectively favor more drought-tolerant species and create forests and rangelands better adapted to future conditions without the need for management intervention. By contrast, severe drought (especially in combination with insect outbreaks or fire), may threaten large-scale changes that warrant substantial management responses. Actions could range from reducing vulnerability, facilitating post-drought recovery, or facilitating a transition to a new condition.

Management actions can either mitigate or exacerbate the effects of drought. A first principal for increasing resilience and adaptation would be to avoid management actions that exacerbate the effects of current or future drought. Options can include altering structural or functional components of vegetation, minimizing drought-mediated disturbance



Drought in rangelands reduces forage and water available for livestock grazing (top). Lower reservoir and winter snow levels impact outdoor recreation activities (bottom).

Photo credits (from top to bottom):
Keith Weller, USDA Agricultural Research Service, Bugwood.org
U.S. Geological Survey



such as wildfire or insect outbreaks, and managing for reliable flow of water. Managers can implement structural changes by thinning or density management of planted forests. Thinned stands require less water and may be less vulnerable to water stress and insect outbreaks. Reduced fuel loads in thinned stands can also reduce wildfire risk.

Managers can also implement functional changes by favoring or planting more drought-adapted species. Management for a diversity of species can reduce stand vulnerability to drought, as uncertainty in future climate can encourage management for mixtures of drought-tolerant species and genotypes. Species diversity can also reduce intensity of insect attacks. In some regions of the United States, planting or favoring more drought-tolerant species may conflict with management objectives that favor rapid accumulation of biomass, as fast-growing woody species often use more water and exacerbate drought impacts.



Management strategies, such as thinning (top) and riparian buffer zone conservation (bottom), may help to mitigate the effects of drought.

Photo credits (from top to bottom):
Scott Roberts, Mississippi State University, Bugwood.org
USDA Natural Resources Conservation Service

While harvesting increases annual water yield in some forest ecosystems, a large reduction of forest cover is needed to have an appreciable effect on water yield. Hence, potential increases in streamflow through forest cutting are limited by the amount of land that managers can harvest. In addition, streamflow responses are often short term due to rapid forest regrowth, and the aggrading post-cut forest may actually have lower streamflow than the uncut forest. In contrast to management actions that are intended to augment streamflow, increasing drought stress in some forest ecosystems may warrant management strategies that retain water (and hence reduce streamflow) on the landscape in order to keep trees alive. Land managers may need to plan the timing of some management activities to ensure that ecosystems have optimal growing conditions and that these activities do not disturb streams during low-flow periods. Removal and alteration of riparian vegetation increases stream temperatures; therefore, maintaining or increasing shading from solar radiation through riparian buffer zone conservation and restoration may mitigate any changes in stream temperatures caused by drought.

In summary, this assessment synthesizes information from the published literature to better understand the impacts of drought on forests and rangelands in the United States. Our expectation is that this assessment will provide researchers, land managers, policymakers, and other stakeholders a set of realistic inferences of drought effects that can be applied to help predict future impacts and evaluate management options for adaptation and mitigation.

Understanding and Anticipating Potential Drought Impacts

James M. Vose

James S. Clark

Charles H. Luce

Toral Patel-Weynand

J.M. Vose is a Research Ecologist, U.S. Department of Agriculture, Forest Service, Southern Research Station (SRS), Center for Integrated Forest Science (CIFS), North Carolina State University, Department of Forestry and Environmental Resources, Raleigh, NC 27695.

J.S. Clark is the Nicholas Professor of Environmental Science and Professor of Statistical Science, Nicholas School of the Environment, Duke University, Durham, NC 27708-0338.

C.H. Luce is a Research Hydrologist, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Boise, ID, 83702.

T. Patel-Weynand is Director of the Forest Management Sciences' (SFMR) staff, U.S. Department of Agriculture, Forest Service, Research and Development (R&D), Washington, DC 20024.

Droughts have been a major factor influencing forests and rangelands in the United States for millennia (Cook and others 2007, Cook and others 2014), and they can have substantial social and economic consequences (Andreadis and others 2005, Wilhite and Buchanan-Smith 2005). Cook and others (2007) suggest that the Western United States has recently entered a period of protracted aridity, and drought has become more frequent and severe in the Southeastern United States since the 1980s (Melillo and others 2014, Pederson and others 2012, Seager and others 2009). In forests, these recent droughts have contributed to large-scale insect outbreaks (Weed and others 2013), forest die-off and reduced growth (Allen and others 2010, Breshears and others 2005, Klos and others 2009), and increased wildfire risk and area burned (Littell and others 2009, Westerling and others 2003), all of which impact forest biogeochemical cycling (Goetz and others 2012, Johnson and others 2007) and hydrologic processes (Guardiola-Clarmonte and others 2011, Holden and others 2012). In rangeland ecosystems, severe drought can limit production (Knapp and Smith 2001), alter nutrient cycling (Evans and Burke 2013), and increase wildfire risk and susceptibility to invasive plant species (Abatzoglou and Kolden 2011). Quantifying the economic and social impacts of drought on forests and rangelands is complex due to the wide array of ecosystem services impacted; however, impacts such as reduced forest growth and carbon (C) accumulation (Amiro and others 2010, Hicke and others 2012), increased wildfire suppression costs (Prestemon and others 2008), and degraded rangeland conditions (Polley and others 2013) are well documented.

Although it is clear that shifts in circulation patterns, energy for evapotranspiration (ET), and air temperatures are changing in ways that enhance the consequences of drought on forests and rangelands, there is less certainty about the effects of climate change on drought occurrence in the future (Seneviratne and others 2012, Trenberth and others 2014). Despite this uncertainty, many of the General Circulation Models predict that some regions of the United States (e.g., the Southwest) may experience a greater frequency of severe droughts (Swain and Hayhoe 2015). When combined with greater air temperatures, droughts could have a greater impact on forests and ranges (Adams and others 2009, Allen and others 2010), even if severity and occurrence is unchanged in the future. The prospect of increasing frequency and severity of future droughts motivates a fresh synthesis of evidence for changes underway now,

their cause, and how they may affect forest and range ecosystems and management responses.

Forest and rangeland ecosystems are inherently resilient to climate variability at time scales ranging from daily to millennia. This resiliency has ensured that ecosystems can endure short-term and minor climatic variation without substantial losses in structure and function. In areas where drought is common and ecosystems have some level of adaptive capacity (Breda and others 2006, Mariotte and others 2013, Milbau and others 2005), a key unknown is whether current species and associated ecosystem processes will be able to endure more severe (or different) droughts in the future. Tipping points may have already been reached in some ecosystems, with large-scale mortality resulting from “global-change-type” droughts (Adams and others 2009, Breshears and others 2005) in forests in the Southwestern United States. Less is known in more mesic regions, where observational data on the impacts of historical droughts are limited (Klos and others 2009); however, an increased frequency of episodic events such as severe droughts may have even greater impacts because some species are not as well adapted to increasing aridity (Pederson and others 2014). In this case, drought may favor more drought-tolerant species and alter successional pathways (Meinzer and others 2013). In either case, it is likely that drought will be a major disturbance force in the future and will present challenges for natural resource managers as they deal with the implications of changing forest conditions and disturbance regimes. A better understanding of drought impacts on forest and rangeland values will help land managers anticipate responses and inform management actions that increase adaptive capacity.

The need to better understand current changes and to anticipate potential impacts of drought on U.S. forests and rangelands is addressed in this assessment by science leaders from Government agencies, national labs, and the academic community. The assessment is divided into three main components: (1) characterizing drought, (2) understanding the effects of drought on forests and rangelands, and (3) assessing the consequences of drought on forest and rangeland values. The first component, characterizing drought, provides a thorough analysis of how drought is quantified and provides metrics and approaches best suited for forest and rangeland ecosystems. The second component addresses direct effects on growth, mortality, and biogeochemical cycling processes, as well as indirect effects on wildfires and insect and

pathogen outbreaks. The final component addresses impacts on water resources and economic and social systems. We developed inferences from the published literature that included results from direct observation, experiments, and modeling. Due to the uncertainty of future predictions of drought occurrence, we do not explicitly predict the impacts of future climate change on forest and rangeland ecosystems; however, observations from recent extended droughts in many regions of the United States may provide a realistic set of inferences that can be projected into the future.

Literature Cited

- Abatzoglou, J.T.; Kolden, C.A. 2011. Climate change in western U.S. deserts: potential for increased wildfire and invasive annual grasses. *Rangeland Ecology & Management* 64: 471-478.
- Adams, H.D.; Guardiola-Claramonte, M.; Barron-Gafford, G.A. [and others]. 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences*. 106(17): 7063-7066.
- Allen, C.D.; Macalady, A.K.; Chenchouni, H. [and others]. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*. 259(4): 660-684.
- Amiro, B.D.; Barr, A.G.; Barr, J.G. [and others]. 2010. Ecosystem carbon dioxide fluxes after disturbances in forests of North America. *Journal of Geophysical Research*. 115: 1-13.
- Andreadis, K.M.; Clark, E.A.; Wood, A.W. [and others]. 2005. Twentieth-century drought in the conterminous United States. *Journal of Hydrometeorology*. 6: 985-1001.
- Breda, N.; Huc, R.; Granier, A. [and others]. 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*. 63(6): 625-644.
- Breshears, D.D.; Cobb, N.S.; Rich, P.M. [and others]. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences*. 102: 15,144-15,148.
- Cook, E.R.; Seager, R.; Cane, M.A. [and others]. 2007. North American drought: reconstructions, causes, and consequences. *Earth-Science Reviews*. 81(1): 93-134.
- Cook, B.I.; Smerdon, J.E.; Seager, R. [and others]. 2014. Pan-continental droughts in North America over the last millennium. *Journal of Climate*. 27(1): 383-397.
- Evans, S.E.; Burke, I.C. 2013. Carbon and nitrogen decoupling under an 11-year drought in the shortgrass steppe. *Ecosystems*. 16:20-33.
- Goetz, S.J.; Bond-Lamberty, B.; Law, B.E. [and others]. 2012. Observations and assessments of forest carbon dynamics following disturbance in North America. *Journal of Geophysical Research*. 117: 1-17.
- Guardiola-Claramonte, M.; Troch, P.; Breshears, D. [and others]. 2011. Decreased streamflow in semi-arid basins following drought-induced tree die-off: a counter-intuitive and indirect climate impact on hydrology. *Journal of Hydrology*. 406(3-4): 225-233.
- Hicke, J.A.; Allen, C.D.; Desai, A. [and others]. 2012. The effects of biotic disturbances on carbon budgets of North American forests. *Global Change Biology*. 18: 7-34.
- Holden, Z.A.; Luce, C.H.; Crimmins, M.A. [and others]. 2012. Wildfire extent and severity correlated with annual streamflow distribution and timing in the Pacific Northwest, USA (1984–2005). *Ecohydrology*. 5(5): 677-684.
- Johnson, D.; Murphy, J.D.; Walker, R.F. [and others]. 2007. Wildfire effects on forest carbon and nutrient budgets. *Ecological Engineering*. 31: 183-192.
- Klos, R.J.; Wang, G.G.; Bauerle, W.L. [and others]. 2009. Drought impact on forest growth and mortality in the Southeast USA: an analysis using Forest Health and Monitoring data. *Ecological Applications*. 19(3): 699-708.
- Knapp, A.K.; Smith, M.D. 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science*. 291: 481-484.
- Littell, J.S.; McKenzie, D.; Peterson, D.L.; Westerling, A.L. 2009. Climate and wildfire area burned in western U.S. ecoregions, 1916-2003. *Ecological Applications*. 19(4): 1003-1021.
- Mariotte, P.; Vandenberghe, C.; Kardol, P. [and others]. 2013. Subordinate plant species enhance community resistance against drought in semi-natural grasslands. *Journal of Ecology*. 101: 763-773.
- Meinzer F.C.; Woodruff, D.R.; Eissenstat, D.M. [and others]. 2013. Above- and belowground controls on water use by trees of different wood types in an eastern U.S. deciduous forest. *Tree Physiology*. 33(4): 345-356.
- Melillo, J.M.; Richmond, T.; Yohe, G.W. 2014. Climate change impacts in the United States: the third national climate assessment: U.S. Global Change Research Program. 841 p. doi:10.7930/JOZ31WJ2. <http://nca2014.globalchange.gov>. [Date accessed: October 14, 2015].
- Milbau, A.; Scheerlinck, L.; Reheul, D. [and others]. 2005. Ecophysiological and morphological parameters related to survival in grass species exposed to an extreme climatic event. *Physiologia Plantarum*. 125: 500-512.
- Pederson, N.; Bell, A.; Knight, T.A. [and others]. 2012. A long-term perspective on a modern drought in the American Southeast. *Environmental Research Letters*. 7(1): 014034.
- Pederson, N.; Dyer, J.M.; McEwan, R.W. [and others]. 2014. The legacy of episodic climatic events in shaping temperate, broadleaf forests. *Ecological Monographs*. 84(4): 599-620. doi: 10.1890/13-1025.1. [Published online: August 1, 2015].
- Polley, H.W.; Briske, D.D.; Morgan, J.A. [and others]. 2013. Climate change and North American rangelands: trends, projections, and implications. *Rangeland Ecology & Management*. 66: 493-511.
- Prestemon, J.P.; Abt, K.; Gebert, K. 2008. Suppression cost forecasts in advance of wildfire seasons. *Forest Science* 54(4): 381-396.
- Seager, R.; Tzanova, A.; Nakamura, J. 2009. Drought in the Southeastern United States: causes, variability over the last millennium, and the potential for future hydroclimate change. *Journal of Climate*. 22(19): 5021-5045.
- Seneviratne, S.I.; Nicholls, N.; Easterling, D. [and others]. 2012. Changes in climate extremes and their impacts on the natural physical environment. In: Field, C.B.; Barros, V.; Stocker, T.F. [and others], eds. *Managing the risks of extreme events and disasters to advance climate change adaptation. A Special Report of Working Groups I and II of the Intergovernmental Panel on*

- Climate Change (IPCC). Cambridge, UK, and New York, NY, USA: Cambridge University Press: 109-230.
- Swain, S.; Hayhoe, K. 2015.** CMIP5 projected changes in spring and summer drought and wet conditions over North America. *Climate Dynamics*. 44(9-10): 2737-2750. doi: 10.1007/s00382-014-2255-9. [Published online: August 12, 2014].
- Trenberth, K.E.; Dai, A.; van der Schrier, G. [and others]. 2014.** Global warming and changes in drought. *Nature Climate Change*. 4(1): 17-22.
- Weed, A.S.; Ayres, M.P.; Hicke, J.A. 2013.** Consequences of climate change for biotic disturbances in North American forests. *Ecological Monographs*. 83: 441-470.
- Westerling, A.L.; Gershunov, A.; Brown, T.J. [and others]. 2003.** Climate and wildfire in the Western United States. *Bulletin of the American Meteorological Society*. 84(5): 595-604.
- Wilhite, D.A.; Buchanan-Smith, M. 2005.** Drought as hazard: understanding the natural and social context. In: Wilhite, D.A., ed. *Drought and Water Crises: Science, Technology and Management Issues*. Boca Raton, FL: Taylor and Francis: 3-29.

Characterizing Drought for Forested Landscapes and Streams

Charles H. Luce
Neil Pederson
John Campbell
Connie Millar
Patrick Kormos
James M. Vose
Ross Woods

C.H. Luce is a Research Hydrologist, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Boise, ID 83702.

N. Pederson is a Senior Ecologist, Harvard Forest, Petersham, MA 01366.

J. Campbell is a Research Ecologist, U.S. Department of Agriculture, Forest Service, Northern Research Station (NRS), Durham, NH 03824.

C. Millar is a Paleoecologist, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station (PSW), Albany, CA 94710.

P. Kormos is a Research Associate, U.S. Department of Agriculture, Agricultural Research Service (ARS), Boise, ID 83712.

J.M. Vose is a Research Ecologist, U.S. Department of Agriculture, Forest Service, Southern Research Station (SRS), Center for Integrated Forest Science (CIFS), North Carolina State University, Department of Forestry and Environmental Resources, Raleigh, NC 27695.

R. Woods is a Senior Lecturer, Faculty of Engineering, University of Bristol, Bristol, BS8 1TH, UK.

Introduction

The changing nature of drought is a growing global concern (Cook and others 2015, Dai 2011, Seneviratne and others 2010, Sheffield and Wood 2008b, Trenberth and others 2014, Wilhite and others 2014). Drought can be a severe natural disaster with substantial social and economic consequences affecting large areas with extended durations (Wilhite and Buchanan-Smith 2005). Although it is clear that shifts in circulation patterns, energy for evapotranspiration, and air temperatures are changing in ways that enhance the consequences of drought, there is only weak consensus about the effects of climate change on drought occurrence (IPCC 2013, Seneviratne and others 2012, Trenberth and others 2014). Some of that uncertainty stems from the complex nature of quantitatively defining drought, but also because some of the changes in drought characteristics are only partially reflected in traditional drought metrics [Palmer Drought Severity Index (PDSI) and the Standardized Precipitation Index (SPI)]. Furthermore, although these traditional metrics have adequately reflected the consequences of meteorologically derived moisture deficits on agricultural commodities and water supply, there is a poorer (although improving) understanding of how drought interacts with forests and rangelands and their associated aquatic habitats. Understanding the potential impacts of future drought on forests and rangelands requires knowledge of how droughts impact forest, shrub, and rangeland structure (covered in other chapters in this assessment) and how drought projections are characterized in the General Circulation Model (GCM) output.

The purpose of this chapter is to explore drought as a hydrometeorological phenomenon and reflect broadly on the characteristics of drought that influence forests, rangelands, and streams. It is a synthesis of understanding about drought processes, hydrology, paleoclimatology, and historical climate variability, and how this understanding can help predict potential future droughts and their consequences to forests and rangelands. It describes alternative approaches for characterizing drought and highlights additional work that could inform projection and adaptation for future droughts.

What Is Drought?

Drought is a lack of water. This simple wording implies potentially complex stories. The most important implication is that drought is characteristic of time, not

of place. A place can be dry or wet, but droughts occur in given locations over time. For example, the Sonoran Desert may have a lack of water for many purposes, but conceptually it has just the right amount of water for the Sonoran Desert, and it occasionally experiences droughts. Wet places, like the coastal rain forests in Washington State, also experience droughts when there is an unusually dry summer. Consistently dry seasons would not merit the designation of “drought” in and of themselves; however, variations in how dry or long the dry season is from year to year are relevant. In places like the Western United States, where there is a coincidence of the dry season with the growing season every year, it does not make sense to frame summer as a “drought” so much as to note the seasonal aridity of the location (Seneviratne and others 2012, Wilhite and Buchanan-Smith 2005).

Although drought is generally defined from a climatic perspective (precipitation levels that are much lower than the annual average), short-term moisture fluctuations also provide important ecological context. A wet period leading to a vegetation flush, followed by a long dry spell, for instance, may not constitute a “drought” relative to long-term averages, but the inability to meet the temporarily increased water demand would nonetheless represent a meaningful drought. From the perspective of a plant, it may look like a temporary enhancement of seasonal aridity contrasts. An example of this is seen in fire risks in rangeland ecosystems where wet springs can produce an overabundance of fine fuels from invasive annual grasses (Littell and others 2009, Swetnam and Betancourt 1998, Westerling and others 2003). Similarly, such fluctuations have been tied to forest mortality, with timing having an important influence on outcomes (Anderegg and others 2013).

This descriptive definition also speaks to a purpose for water. Lack of water is most relevant when water requirements for sustaining terrestrial and aquatic ecosystems or providing for human uses cannot be met. In natural ecosystems, those requirements broadly relate to climatological expectations (in a statistical sense) for water supply. Similarly, in rational agricultural management, climatological expectations should still provide a basic norm for distinguishing drought conditions, although sometimes drought is claimed when slightly dry conditions endanger marginally suited crops. Generally, drought is perceived as a concern during the growing season or warm season, as these are when there is a demand for water. However,

droughts can have substantial ecological consequence related to lack of snow cover, particularly for wildlife (McKelvey and others 2011) or plants that are protected from cold extremes by a layer of snow.

Drought Classification

Most of the indices applied to classify drought are tied to common meteorological measurements, like precipitation and temperature, because these are widely available with relatively long records. The long records make it possible to compare particular precipitation amounts or water-balance estimates to the local climatological distribution, in essence gauging risk or probability levels of current meteorological events. The meteorologically based indices are commonly applied for drought forecasting based on weather forecasts, given that weather is the most fundamental driver and also the most fundamental uncertainty in drought estimation. Despite common application, there is some concern about the utility of drought indices in understanding conditions related to changes in land cover, land use, or climate (Alley 1984, Sheffield and others 2012).

The context of utility or need for water frames much of the traditional way of defining and describing drought. Drought is most commonly thought of in

terms of the harm it can induce. It is broadly seen as one of the most potentially severe natural disasters in terms of either human lives or capital loss because it covers large areas and can lead to famine for large populations (Wilhite and Buchanan-Smith 2005). Drought has generally been framed in four classes or “types” (Wilhite and Glantz 1985): (1) meteorological drought, (2) hydrologic drought, (3) agricultural drought, and (4) socioeconomic drought (table 2.1). These four classes are not mutually independent, but refer to different ways to measure, identify, or conceptualize drought conditions. Almost all types of drought relate to meteorological conditions leading to a lack of water, such as a lack of precipitation or excess demand from evapotranspiration. Hydrologic, agricultural, and socioeconomic drought are filters placed on meteorological drought to frame how they affect human demands and values for water, ranging from food production to electrical power production, recreation, and wildlife management. Generally the context is economic, although environmental benefits of water are recognized as well. They also frame different time scales of response to meteorological forcing. Most of these drought types frame drought as an event. In this framing, a drought is a type of disturbance, or even disaster, with a distinct occurrence. This framing is particularly relevant to crops of limited lifespan, seasonal cycles of water

Table 2.1—The four drought classes

Drought class	Primary focus	Estimation
Meteorological	Dry weather	Indices built from weather station or weather forecast information targeted toward soil moisture and agricultural or hydrologic drought. Weather changes rapidly, but indices aggregate weather over time.
Hydrologic	Streamflow and reservoir levels	Measured or modeled runoff and reservoir levels. Some meteorological drought indices target this particular outcome.
Agricultural	Productivity and survival of crops	Measured or modeled crop yields. Some meteorological drought indices target this particular outcome.
Socioeconomic	Economic outcomes of drought	Measured and modeled financial consequences of water supply or agricultural production deficits.

demand (municipal supply, hydropower demand, water-oriented recreation), and other activities where short-term interruptions in water supply are economically relevant (e.g., manufacturing).

Meteorological Drought

Meteorological drought definitions refer to atmospheric components of the water balance, precipitation and evapotranspiration, where low precipitation and high evapotranspirative demand lead to a relative lack of water. In practice, estimates of these components or proxies for their estimation (e.g., temperature) are generally used. Despite the name, meteorological drought metrics use modeling or simple logic to reframe short-term meteorological measurements into indices of impacts to terrestrial and aquatic systems. Meteorological drought can be framed strictly in terms of the amount of precipitation over a time period, as with the SPI (McKee and others 1993), or processed with temperature information to estimate a soil water balance, as in the PDSI (Palmer 1965). The Keetch-Byram Index model (Keetch and Byram 1968) has a similar conceptualization (though with feedback between moisture level and loss rate) directed towards vegetation and fuel moisture levels. Details of these indices are discussed later in this chapter.

Hydrologic Drought

Hydrologic drought is focused more directly on water available as streamflow or in surface or near-surface storage, such as reservoirs or shallow aquifers. While hydrologic drought follows from meteorological drought, its measurement or estimation focuses primarily on the various uses of streamflow or reservoirs, such as aquatic habitat, irrigation, hydroelectric power generation, or recreation. There is a temporal lag between unusually dry meteorological conditions and actual stream and lake levels, and factors other than those indexing meteorological drought may influence actual outcomes for streams, shallow groundwater, lakes, or reservoirs. For instance, precipitation intensity or its distribution in time can markedly influence its potential for generation of runoff in both the short and long term. Multiple brief or small rainfall events may increase the amount of precipitation received, but much of that water would likely be returned to the atmosphere through subsequent evaporation after being intercepted in trees or only shallowly penetrating the soil. On the other hand, focusing an equivalent amount of water into a single, brief storm with high intensity may result in increased runoff but little recovery in soil or vegetation moisture levels.

For some purposes, a lack of streamflow represents a drought more than a lack of precipitation. A lack of water can yield profound impacts for stream fishes, as it affects volume of available fish habitat, stream temperature (Isaak and others 2012), and food supply to fishes (Harvey and others 2006). In western U.S. mountains, runoff from accumulated snowpacks feeds reservoirs and irrigation to downstream farms. Although these farms may get occasional rain in the summer months, that precipitation amount may never really be sufficient to support crops. In such a case, the local precipitation or water balance is not as relevant as the potential hydrologic drought of the stream providing irrigation water.

Simple meteorological indices of drought do not consistently predict the streamflow consequences of a drought. While there is a connection between a lack of precipitation and a lack of streamflow, there are subtleties of shift in precipitation characteristics, or even of changes in vegetation or soil characteristics that can change the runoff efficiency of precipitation events that occur within the context of a prolonged drought (Guardiola-Claramonte and others 2011, Potter and Chiew 2011). There can also be mismatches between return intervals of precipitation amounts (or index values) and streamflow volumes (Potter and Chiew 2011), reflective of the complexity of runoff generation processes.

Agricultural Drought

Agricultural drought, also termed soil moisture drought by Seneviratne and others (2012), is tied to productivity and mortality of crops. It is functionally related to the soil moisture reservoir. Once precipitation has stopped, soils dry through evaporation at the surface and via evapotranspiration of water through the crop. The contribution of direct evaporation at the surface to total evapotranspiration declines as the soil dries. As the soil moisture content drops, roots cannot uptake water as rapidly, and plant productivity falls off as stomata remain closed for a greater fraction of the time. Eventually, the water in the soil is bound so strongly by capillary and osmotic potentials that plant roots cannot extract more water. Crops can die before this level is reached simply if productivity falls below the needs for maintenance respiration. Metrics of agricultural drought (PDSI) were developed for annual crops or vegetation managed as an annual crop. As such, they are best suited for shallow-rooted plants and may overestimate drought experienced by deep-rooted perennial forest and shrub species.

Socioeconomic Drought

Socioeconomic drought follows from both agricultural and hydrologic drought. Agricultural losses from drought represent a fairly direct economic impact, but this also cascades into lack of materials for agricultural manufacturing and support industries and services. Similarly, a lack of water for municipal supply, manufacturing, irrigation, hydroelectric production, or recreation can reverberate through the economy. These economic impacts may substantially lag behind the meteorological drought event that triggers socioeconomic consequences. The relationship between drought and its economic consequences also varies with associated historical decisions (chapter 11). This complex interplay of drought, environmental consequences, and impacts to humans, followed by human-mediated responses to drought (e.g., technological advances and altered land values), leads to broadening economic ramifications over time and space.

Drought Influences on Forest and Stream Ecosystems

For forest and stream ecosystems, meteorological and hydrologic drought frameworks are useful for characterizing impacts of a given drought event. For example, meteorological or hydrologic drought may presage or correlate to fire events (chapter 7) or insect outbreaks (chapter 6). Most of the work in later chapters and information on drought changes in this chapter relate to the common metrics above. However, it is worthwhile to also reflect on ways that drought influences forest ecosystems outside of the traditional harm-oriented framework. It serves as context for drought metrics, trends, and projections described later.

Forests offer a unique challenge to the traditional framing of drought because they persist over long time scales. Forests have adapted to droughts both through their resilience to drought effects and resistance to drought occurrence. While fires, insect outbreaks, and other forest mortality events are tied to drought, it is generally only the most severe droughts that produce large-scale or landscape-scale changes. Most droughts reduce productivity or carbon fixation in trees rather than kill them. As the climate changes, drought may become a stronger driver for changes in vegetation species composition and life form (shrub, woodland, forest) (Dale and others 2001, Jentsch and others 2007, Luce and others 2012). Reframing drought as a driver that determines relative fitness among species

adds new context for characterizing drought. To address this, we can draw on ecological theory and our understanding of the hydrometeorological process to assess how long-term changes in drought climatology (frequency, severity, or spatiotemporal scaling) might drive large-scale changes in vegetation.

In addition to drought impacts on terrestrial vegetation, there are impacts to forest aquatic ecosystems. Forests are generally the largest source for high-quality water supplies, and they provide extensive habitat for coldwater fishes (Rieman and others 2003). Drought-related changes in forests cause changes in runoff generation, with the potential for immediate negative impacts on stream ecology. However, drought is also a fundamental driver of instream ecological processes, and some highly prized aquatic species are present because they are better adapted to drought-related effects to streams and surrounding forests than are other species. Changes in drought characteristics may consequently be a driver of long-term and large-scale changes to instream ecological processes. Fish species are substantially less long-lived than trees, but presence of a given population in a stream is a comparably persistent aspect of the problem. The interaction of drought with local population and metapopulation dynamics is a more important consideration than losses from a single generation. For example, increased drought-related disturbance may promote migratory life histories over resident life histories (Dunham and others 2003). Another example is the range of drought adaptations of some fishes in the Great Plains (Falke and others 2011, Fausch and others 2002). Local extirpations of some fishes could result if small streams become both more unpredictable in low flows and less productive (reducing the potential for migratory life histories).

Ecological Drought Characterization

The impacts of dry conditions on ecological processes are about tradeoffs. Some biota benefit from drought primarily because other biota are more negatively impacted. This view of drought ecology—where drought stress is viewed as a driver of ecosystem processes—is part of what makes application of traditional drought metrics difficult. Although indices with single values are easier to present and apply in quantitative analysis, ecological drought characterization is more complex and multidimensional. Some of the key dimensions are:

- **Severity**—defined as degree of moisture deficit
- **Frequency**—level of deficit, alternatively probability
- **Temporal patchiness**—autocorrelation in time that incorporates duration and short-term variability
- **Spatial coherence**—or spatial distribution across the landscape
- **Correlation with other factors** (e.g., season or temperature)

Some current metrics conflate one or more of the aforementioned dimensions. Calculation of PDSI, for example, incorporates lack of precipitation, air temperature, and duration of an event. SPI is a simple metric of severity, but the complete range of options for SPI values with varying temporal footprints reveals that it also can offer temporal autocorrelation information. It is likely that drought cannot be measured or characterized along any one of these dimensions absent some others; however, exploring the different dimensions can be informative for explaining component contributions in part for ecological drought.

The most natural and direct measures of drought severity for forest and stream ecosystems are probably reflected in measures such as soil moisture, streamflow, or fuel moisture. These measures have a particular value at a given time, but they reflect spatial and temporal integration of precipitation and evapotranspiration. Consequently, there is some need to explicitly recognize the role of time if only meteorological information is used. A day without precipitation occurs often, but multiple days without precipitation cause drier soils and reduced streamflow. Nonetheless, we can see that with an appropriately informative footprint (discussed briefly below), variations in the amount of precipitation received or precipitation less evapotranspiration are informative quantities.

Frequency of a given level of severity is critical in understanding the ecological role of drought because the relationship of the frequency of mortality-inducing drought to generation or recovery times is a fundamental descriptor of ecosystem dynamics. At one end of the spectrum, species that mature more slowly than the frequency at which mortality-inducing weather events occur are not well fit to the local climate. At the other end, species that take advantage of frequent disturbance may not compete well with species that

invest toward longer term gains when disturbance is infrequent. In most cases, disturbances will occur within a species lifetime, and there are different strategies and adaptations related to different frequencies. Relationships between frequency and severity are commonly embedded within those adaptations. It is unusual to have severe fire or insect outbreaks on a frequent basis, simply because it is hard to regrow adequate fuel or food to sustain the next severe event. Although fire, pathogen, and insect outbreaks are general examples in this area, trees adapted to low-productivity arid sites, such as bristlecone pine (*Pinus aristata*), offer another example where the isolation offered by frequent severe drought builds a degree of resilience to other mechanisms of mortality spread by abundance of neighbors.

The concept of *temporal patchiness* is a metric to describe how slowly moisture states vary. Broadly, high year-to-year autocorrelation in moisture reflects long-term dry states, whereas low autocorrelation reflects high variability in moisture states over short timeframes. Both ends of this spectrum can have substantial impacts on ecological processes and disturbance regimes. For example, high contrasts in moisture over relatively short (seasonal to interannual time scales) can increase the severity of drought-related stressors such as fire or insects. Such is the case in shrublands with wet winters and springs that promote heavy growth of annual grasses (e.g., *Bromus* spp.) and lead to more severe and larger fires during the following dry summer (Abatzoglou and Kolden 2011, Littell and others 2009). Substantial growth in a forest in a wet year contrasted to dry conditions the next year can lead to increased moisture stress because of increased leaf area. While duration is well captured by common drought indices, the high contrast risk is not, and the two are related in a given climate and soil. While the former is important to critical water supply levels and agricultural crops, the latter has greater context in less regulated systems.

Meteorological drought has substantial *spatial coherence*, with a footprint of much greater scale than is typical for landscape ecology. Severe meteorological droughts, sometimes termed “megadroughts” may encompass multiple regions of the United States at a given time (e.g., Coats and others 2014, Cook and others 2014a). While this scale has potential importance for distribution of fire suppression equipment or response to insect outbreaks, more-local scales are also relevant because a particular meteorological drought may play out differently within a landscape. North-facing

slopes retain moist conditions longer into the growing season than south-facing slopes, which is reflected in productivity and plant species. One consequence is that fire severity can vary substantially across topographic position, such as aspect or riparian proximity (Dillon and others 2011, Dwire and Kauffman 2003). The outcome for vegetation communities is that the spatial scales of drought-related mortality are related to the grain of topographic variation, or hillslope facets, in historical examinations (Hessburg and Agee 2003). The severity of the meteorological drought can, itself, have some influence on this patchiness, and topographic relationships to fire severity are damped in the driest years (Dillon and others 2011).

Correlation of drought to other meteorological characteristics is an increasingly important area of study. If we look through the list of key dimensions, there is a sense of increasing levels of information or organization (sensu Blöschl 1996) of outcomes for drought events. At the basic level, there is the question of how dry it is (*severity*), followed by how dry an event is relative to other events (*probability/frequency*), followed by how quickly or slowly the moisture levels transition (*temporal patchiness*), and how different places within a landscape experience a given meteorological drought (*spatial coherence*). The next level of organization is how drought might relate to other factors of importance in ecology. In the following section, we discuss the linkage between temperature and drought because it has substantial relevance to the broad discussion on climate change and drought (Dai 2011, Sheffield and others 2012, Trenberth and others 2014), particularly in the context of forest ecology (Adams and others 2009, Allen and others 2010, Breshears and others 2005).

The causal relationship between temperature and drought arises from interactions mediated by solar heating. Clearly, warmer air has lower relative humidity (given a fixed specific water content in the air), and warmer air has the capacity to impart more sensible heat to the energy balance. However, the great majority of the heat in the energy balance is incoming solar radiation. Some solar heating goes to evaporating water and some goes into heating soil, vegetation, and air. As a consequence, air temperature and evapotranspiration are correlated simply because they share the same driver (i.e., solar radiation), not because air temperature substantially adds to the energy available for evapotranspiration. This makes temperature a simple index for framing both the energy available for evapotranspiration and the capacity of air

to hold additional moisture. For example, temperature is a variable in the Thornthwaite equation (Thornthwaite 1948), which is used in calculation of the PDSI. When there is less water available (due to a lack of antecedent precipitation), more of the incoming solar energy goes into raising temperature; however, when conditions are dry, the increase in temperature is at the expense of evapotranspiration. Energy goes into warming, not evaporating. Under dry conditions, temperature becomes an index of the lack of water available for evapotranspiration. Thus, within historic contexts, temperature can be used as an index of dryness: dry is warm, and warm is dry.

Under a changing climate, in contrast, temperature will rise independently of aridity. Warmer temperatures will result from increased atmospheric emissivity and a changed energy balance of the air. Net radiation will increase, slightly increasing the energy available for evaporation, but the relationship between relative humidity (or vapor pressure deficit) and temperature for warming on that slow of a scale will not be the same as it is in current empirical contexts. In short, the correlation between air temperature and drought will still exist, but its value will not be in indexing drought conditions in relation to current conditions.

Instead, warmer temperatures paired to drought will represent a greater challenge for plants to cope with drought (Adams and others 2009). This context of drought being warmer has been termed “global-change-type drought” (Breshears and others 2005) to reflect the idea that whether or not “drought” is worse under a changing climate, the consequences of a given level of drought could be worse in combination with warmer temperatures. Because warmer temperatures elevate metabolism and respiration, a higher productivity will be required to match the demand. As plants shut down during moisture stress, they will exhaust carbon stores more quickly, and survival times between wetting events will shorten. The physiological mechanisms underlying drought mortality are discussed in chapter 3.

The correlation of drought to the season in which it occurs is another important characteristic that may also shift with warming. For example, if the period of common drought corresponds to the warm season (growing season), drought effects will be more severe, in a broad sense. Expansion of the growing season as temperatures warm could draw soil water down sooner as well, yielding deeper dryness in the soil earlier in the growing season; this would effectively increase

the duration of the summer drought and have potential consequences for wildfire (e.g., Westerling and others 2006). Where precipitation is more abundant during the growing season, the susceptibility to drought is related to interruptions in that precipitation supply.

Measures of Drought

The drought types mentioned earlier offer some distinction for classifying drought prediction tools. Some measures target characterizing drought for broad purpose based primarily on weather measurements, while others target understanding hydrologic drought. Given the general interest in forecasting drought, both approaches are based on meteorological measurements and meteorological model outputs. Meteorological drought indices are either directly tied to the measurements or placed in a context for convoluting precipitation and temperature with time to give a mixed drought and exposure index. Hydrologic drought is necessarily more local in nature as it depends on characteristics of the basin of concern. Some reporting tools, such as the U.S. Drought Monitor, use a blend of hydrologic and meteorological drought metrics along with expert guidance.

Fundamentally, every kind of drought is meteorological in nature, but outcomes are shaped through local topographic, geologic, and biotic filters. In so far as models correctly reflect the hydrologic processes of interest, weather forecasts or stochastic simulations contingent on seasonal climatological forecasts can provide useful information on potential outcomes. We briefly discuss the most common ones here (see Hayes and others 2011 for a more thorough listing).

Meteorological Drought Metrics

Three of the most common metrics in this class are the Standardized Precipitation Index (SPI) (McKee and others 1993), the Palmer Drought Severity Index (PDSI) (Palmer 1965), and the Keetch-Byram Drought Index (Keetch and Byram 1968). Although these metrics theoretically address potential outcomes of drought (such as soil moisture, streamflow, or crop productivity and mortality), they are approximate models.

The SPI is a relatively simple approach to characterizing a precipitation anomaly (McKee and others 1993). Precipitation totals are calculated for a given window of specific dates over a series of years. A cumulative density function (CDF) of the values is computed and the quantiles are mapped to a normal CDF, allowing the

probability of exceedance above and below the mean to be translated into approximate standard deviations of departure. The index is only applicable locally, and it is relative to the mean precipitation over the period of interest.

The PDSI and related derivatives are conceptually related to the water balance of a relatively thin, two-layer soil incorporating estimates of evaporation and runoff. The precipitation component is relatively straightforward, and runoff is computed based on the water-holding capacity of the soil column (porosity at field capacity). Evapotranspiration (ET) is drawn from the two layers of soil independently, with the thin top layer being available for direct evaporation, while the second soil layer retains water for transpiration. ET is calculated based on air temperature using the Thornthwaite method (Thornthwaite 1948). Because drier soils evapotranspire less than moist soils, there is a seasonal adjustment to the Thornthwaite estimate for well-watered soils. This seasonal adjustment does not respond to actual evolution of conditions, however, and close inspection reveals the adjustments to be relatively minor. A limit is ultimately placed on ET to prevent violation of the mass balance. To calculate the index, a convolution of the soil moisture estimated using this method over time provides a metric that combines both dryness and the length of time plants are exposed to the dryness. These calculations are then treated similarly to the SPI to derive a local dryness index.

The Keetch-Byram Index (Keetch and Byram 1968) is absolute in nature and not locally indexed. It is based on an exponential decay conceptualization of soil moisture in fuels. Precipitation less interception (constant) rewets fuels, and loss each day is calculated (in tables) as a function of the daily air temperature and the previous day's drought index. As the index approaches its driest extreme, the effect of further drying is diminished asymptotically.

Hydrologic Drought Metrics

Hydrologic drought metrics are generally based upon measurements of streamflow. Hydrologic drought may be defined as uncharacteristically low streamflows; however, values depend heavily on the averaging period for the quantification of flows (Vidal and others 2010). For example, annual-scale hydrologic drought is quantified by comparing total annual flow values among a series of years and finding quantiles of the distribution. Because there is a pronounced annual cycle, this averaging scale can be useful for a range of purposes.

For consequences that manifest at shorter time scales, shorter averaging periods are necessary and can be characterized by one of many methods of quantifying how low flows are in a particular low-flow period. In places with noted seasonality in runoff, such as those associated with seasonal precipitation or snowmelt-dominated runoff, season-scale averages can suffice. In places where precipitation and runoff do not show pronounced seasonality, a shorter time-scale average has greater utility.

Differences in seasonality related to presence and absence of snow and temperature-precipitation correlation form the basis for a comprehensive classification of hydrologic drought types (Van Loon and Van Lanen 2012). One example dichotomy is flows that are low because the warm season has low precipitation versus flows that are low because the precipitation is frozen in winter. Ecological considerations of how aquatic species respond to low flows in warm-dry versus frozen seasons might require examining these two types of hydrologic drought separately.

Common formal quantification of low flows occurs in two metrics: the 7Q10 metric and the return intervals of given percentile on the flow duration curve. The 7Q10 is the minimum weekly flow (drawn from the period of interest, such as winter or summer) in each year with a return period of 10 years. For example, with a record length of 20 years, the second to the lowest of the observed annual weekly minimum flow would be the 7Q10. Flow duration curves define the quantiles of flow in each year, and the 20th percentile daily flow would be that flow that is exceeded in 80 percent of the year (i.e. 292 days have higher flows, and 72 days have lower flows in that year). That value can be sampled from each year, and comparison can be made by way of quantiles of the distribution again (the 5- or 10-year return period, for example).

Physically Based Hydrologic Models as Metrics

Advances in computing have resulted in development of more computationally intensive, physically based hydrological models, which, like their computationally simpler predecessors, estimate soil moisture content. Although there is greater expectation or promise for precision and transferability, some of the promise of such models has yet to be realized (Blöschl and others 2013). Despite the availability of such models and example applications (e.g., Sheffield and Wood 2007), much work is still focused on use of common (less computationally intensive) drought metrics. Although

there is a range of reasons for such choices, a key point is that the basic inputs of precipitation and radiant energy inputs (or proxies) shared in common across various models and metrics means that the outputs are relatively well correlated (Williams and others 2014), making the indices a more practical and efficient approach.

This capacity to use indices in a correlative manner, however, may limit the advancement of causative modeling. Although short-term (within a year) drought forecasting is conceptually intended to look at potential future outcomes (e.g., river levels, soil moisture levels, crop mortality, or fire danger), the development and validation of the historical/conceptual drought forecasting models have not focused on prediction of these values, per se; rather, they have focused on correlation between the indices and local outcomes. This leaves us with the strongest predictive capacity for droughts that have been observed in the past, without necessarily providing the best information for predicting drought consequences under a changed climate. Identifying and revising those parameterizations within physically based models that intrinsically rely on empirical relationships could help advance understanding of drought risks in a changing climate.

Because of their more comprehensive set of calculations, more detailed water-balance models blur the line between meteorological drought forecasting and hydrologic drought forecasting. These models offer a more flexible approach in estimating persistence of moisture availability; therefore, they may eventually become more useful than current indices for characterizing forest-related drought.

Relationships Between Meteorological Drought and Hydrologic Drought

Although both are referred to as “drought,” the relationship between meteorological drought and hydrologic drought is not linear. Complex interactions among changes in precipitation, evapotranspiration, and streamflow (particularly at the extremes) result in lags and nonlinearities in responses. Understanding this complexity has similarities to understanding ecological consequences of meteorological drought.

While the basics are fairly clear (less input generally means less output), there are a number of aspects that make the problem more complex, and defined relationships offer some use in prediction of places and times of relative sensitivity. A number of statistical

and physically based modeling tools have been applied to the problem of relating weather to low streamflows (Laaha and others 2013). Analysis of the relationship is commonly framed within a sensitivity or similar modeling framework, such as the Budyko (1974) relationship between precipitation, net radiation (energy for evapotranspiration), and how precipitation is partitioned into evapotranspiration versus runoff, or simpler sensitivity/elasticity frameworks (sensu Schaake 1990) that empirically relate precipitation and temperature to streamflow.

The effects of precipitation variability on streamflow are fairly pronounced (Milly and Dunne 2002); generally, when there is less precipitation there is less runoff (e.g., fig. 2.1). Thus, meteorological drought results in hydrologic drought; however, the lag in streamflow response after precipitation stops means that hydrologic drought integrates precipitation inputs over time, and the lowest streamflows result from some combination of low initial soil/groundwater recharge, a long period since last precipitation, and evapotranspirative demand. Rapid evapotranspiration, at an event time scale, contributes to reduced flows in many circumstances, as it makes water unavailable for runoff. However, at long time scales (e.g., annual), evapotranspiration in many places is functionally limited by available soil moisture and tends to positively co-vary with streamflow (Milly and Dunne 2002). In other words, years with hydrologic drought may also experience reduced evapotranspiration.

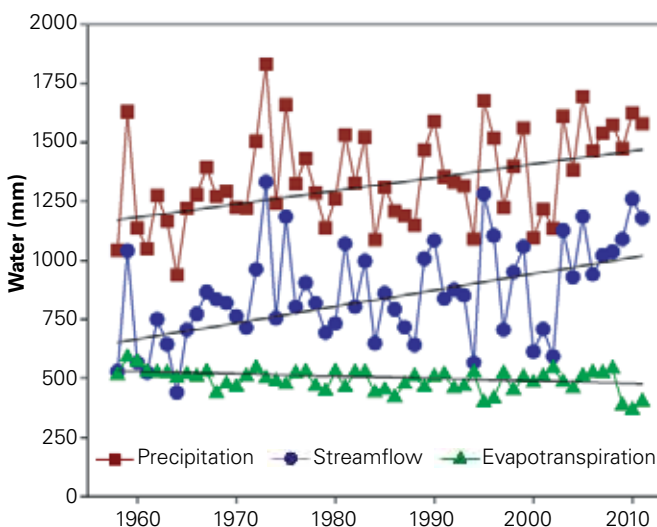


Figure 2.1—Streamflow variability as related to variations in precipitation and evapotranspiration at Hubbard Brook in the Northeastern United States.

One approach to understanding the relationships between meteorological drought and hydrologic drought is with direct correlations between flow data and indices such as PDSI, SPI, and variants (e.g., Haslinger and others 2014). These kinds of relationships often work best in rainfed agricultural catchments with limited snowpack, similar to validations where they were developed (Palmer 1965). Lag times from substantial snow accumulation or deep groundwater weaken relationships with these indices.

The water balance provides another approach, at least at interannual time scales. Using the water balance of soil (which is conceptually thin enough that we can ignore storage changes at interannual time scales) where Q represents both surface runoff and recharge to groundwater (from which it is assumed little evapotranspiration occurs, but which could store substantial recharge), we can write:

$$P = Q + ET \quad (1)$$

Precipitation (P) is the largest term and is split into Q and ET . When P goes down, both Q and ET tend to decrease as well. However, we expect the fraction of precipitation allocated to Q versus ET to be a function of the ratio of net radiation (energy available for ET) to P (Budyko 1974, Milly and Dunne 2002). The general expectation is that as conditions become drier, a greater fraction of the P becomes ET (fig. 2.2), exacerbating hydrologic drought as meteorological drought progresses.

Figure 2.2 describes the Budyko relationship, where the red and blue lines represent physical limits related to energy and water availability for evaporation. The bottom axis is an aridity index, which is the ratio of the incoming energy (which can evaporate water if it is available) to precipitation (normalized by the latent heat of evaporation to put it in energy units). The left axis is the ratio of actual evapotranspiration to precipitation. Note that while the bottom axis can range to large values (lots of energy and little water), the vertical axis is constrained to be less than one because you cannot evaporate water you do not have. The curved line is Budyko's (1974) empirically derived relationship from a large number of rivers around the World. The black and gray points represent potential river basins one might find. Some rivers plot above the curve; others, particularly the gray ones, plot below. Points below the line partition more water into runoff than average, while points above the line evaporate more water. Variations

above and below the line relate to factors, such as those discussed below, that enhance partitioning into runoff versus evapotranspiration.

The related climate elasticity of streamflow approach (Sankarasubramanian and others 2001, Schaake 1990) uses changes in precipitation or temperature to form estimates for annual streamflow changes. This method uses the relative (and interactive) roles of temperature and precipitation to understand variations in and mediation of streamflow (Fu and others 2007, Harman and others 2011, Potter and others 2011, Vano and others 2012).

In addition to aridity, a number of factors influence the partitioning of water into evapotranspiration rather than runoff/recharge (Woods 2003). A primary example is the soil depth or rooting depth. The more soil there is to hold water for trees to utilize, the greater the proportion that tends to evapotranspire. Similarly, coarse soils and steep slopes—both of which promote drainage of the soil profile—tend to reduce evapotranspiration. When more precipitation falls in cool months, interception losses are smaller than when it falls in warm months (Wolock and McCabe 1999). Runoff from basins where snowmelt dominates tends to be generated more efficiently than rain-related runoff (Berghuijs and others 2014). Forest cover and tree species may vary

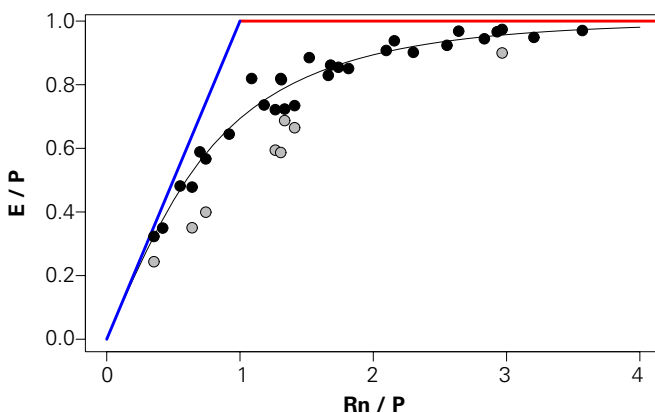


Figure 2.2—The Budyko (1974) relationship relating the aridity index given as the ratio of the net radiation (Rn , energy available for evapotranspiration) to precipitation (P) to the ratio of the actual evaporation (E) to precipitation. The blue line shows the energy limitation for potential evaporation where $Rn = P$. After there is sufficient net radiation to evaporate all precipitation, there is simply a limitation on evaporation given by the red line where $Ea = P$. Budyko's curve fits below these physical limits (black line) as an empirical relationship derived by plotting several of the World's rivers on these axes. The points (black and gray) represent some hypothetical streams. When equation 1 (see text) applies, the ratio of flow to precipitation (Q/P) is $1 - E/P$, or the distance between the red line and the point.

independent of the slightly more static features, and they can exert substantial control on partitioning as well (e.g., Zhang and others 2001). Soil and vegetation controls are covered in more detail in chapter 10, but are mentioned here to illustrate potential controls on drought responses related to site characteristics.

Changes in precipitation characteristics with prolonged or extensive droughts could be important as well. Circulation changes associated with large-scale drought may promote variations in intensity, duration, and volume statistics for storms; these variations alter a storm's runoff generation potential (Potter and Chiew 2011). For example, if storms have similar frequency, but each delivers less water, a greater fraction may be lost to interception.

Spatial differences also play a role in the relationships between drought characteristics and streamflow characteristics, and these differences have been explored through hydrologic modeling approaches. For example, in the Western United States, framing the low-flow response in terms of both the annual recharge and the length of the dry season can highlight the influence of bedrock geology on late summer low flows (e.g., Tague and Grant 2009). The sensitivity of low flows to timing and amount of recharge is a function of how much groundwater levels are drawn down through a given volume of evapotranspiration or runoff. A range of recession analysis techniques have been applied for periods without precipitation (e.g., Kirchner 2009, Tallaksen 1995).

There are a number of ways in which meteorological extremes may ultimately manifest in low streamflows or similar hydrologic outcomes (Van Loon and Van Lanen 2012). Increasingly, physically based hydrologic models are being applied to evaluate historical and potential future droughts (e.g., Sheffield and others 2004) as opposed to more simple approaches related to indices such as SPI or PDSI. Unfortunately, not all models are equally suited for drought prediction, and scientists are actively testing across multiple models (e.g., Tallaksen and Stahl 2014).

Paleoclimatic Context for Evaluating Drought

Historic climate can be reconstructed through the use of many types of proxy variables. Interpretations of past climates, including drought, have been developed using tree rings; pollen, chironomids, diatoms,

sediment, and isotopes taken from lake-sediment cores; records of Aeolian deposits in sand dunes; micro- and macrofossil remains in woodrat middens; speleothems; glacial and periglacial deposits; lake levels; and archaeological records (Bradley 1999). These records are able to reveal small- to broad-scale changes in climate from decades to millennia. Each of these has certain biases and strengths. For example, plant macrofossils (leaves, fruit, etc.) can place a species at a specific location, while microfossils (pollen) have a range of uncertainty including source region and limited botanical identification. The most robust reconstructions derive from use of multiple proxies. Together with the continual development of varying climate proxies from sediment cores (e.g., Booth 2002), reconstructions of past climates will improve.

Tree rings are an important and common source for understanding late-Holocene droughts. Trees from mid to high latitudes produce annual growth rings, and the variation in ring width is influenced by a multitude of factors, including water availability, at various time scales. When aggregated from stand to continental scales, ring-width measurements can reflect these factors at various spatial and temporal scales. Fundamental to dendrochronology is the identification of the pattern of large and small rings through time in a collection of tree cores (i.e., cross-dating), which affords the ability to precisely date rings to a calendar year. Cross-dating (Douglass 1920) allows scientists retrospective estimates of past climatic and ecological change. Separating the climatic influence from the effects of genetic diversity and ecological effects, or, more realistically, reducing the nonclimatic input on growth from the climatic signal in tree rings, requires sophisticated standardization. The process involves transforming raw ring widths into time series of radial indices that are most likely to be a proxy of past climates. Advances in dendrochronology over the last 60 years (including techniques to interpret past climate through ring density and stable isotope composition as well as width) have enabled researchers to reconstruct climate from the stand and regional scale to continental and hemispheric scales (Cook and others 2004, Cook and others 2007, Cook and others 2010, Fritts 1976, Jacoby and D'Arrigo 1989, Meko and others 1993). Besides inferences about climate from growth increments, tree rings are used to date environmental disturbances tied to drought, like fire (Heyerdahl and others 2008, Whitlock and others 2003) and canopy disturbance (Lorimer 1985, Rubino and McCarthy 2004). These advances aid in the understanding of

long-term spatiotemporal variations in drought and the atmospheric dynamics behind them.

The North American Drought Atlas (NADA) is the best source for understanding spatial and temporal patterns of tree-ring-reconstructed moisture variability over the last 500–1,000 years (Cook and Krusic 2004, Cook and others 2004). Chronology length and coverage varies in the atlas, with stronger fidelity in the Southwestern United States and weaker fidelity in New England and the Great Lakes region. The New England and Great Lakes regions generally show similar trends and patterns as other eastern regions, but more work is required to refine estimates of long-term drought severity and frequency. Another important note is that drought in the NADA is represented by different seasons in different regions. Winter precipitation is the primary signal reconstructed from tree rings from the Pacific Northwest to Northern Mexico and west Texas, while the eastern half of the atlas contains a summer moisture index (St. George and others 2010).

Continental and Subcontinental Patterns in Paleoclimate

Regional aridity and warmth was widely expressed during the middle Holocene. In many parts of southwestern and central North America, this was the warmest and driest interval of the past 10,000 years (Dean and others 1996, Spaulding 1991, Yu and others 1997). Proxy records from pollen, woodrat middens, tree-rings, lake levels, and Aeolian indicators document extensive warmth and aridity from 8 ka (kiloannus, or thousand years) to 3.8 ka, peaking at 6 ka (Benson and others 2002, Dean and others 1996, Holliday 1989, Mensing and others 2004). In contrast, the dry interval for the Pacific Northwest and parts of the northern Rocky Mountains was before 8ka (Brunelle and others 2005, Whitlock and others 2003).

In northeastern North America, various proxy records show that the mid-Holocene was a period of high aridity (Hardt and others 2010, Marsicek and others 2013, Menking and others 2012, Newby and others 2011, Newby and others 2014, Nichols and Huang 2012, Shuman and Donnelly 2006). Supporting earlier work by Webb and others (1993), these same studies indicate trends toward more moist conditions since the mid-Holocene aridity up to the 20th century. High hydroclimatic variability punctuated this trend, most notably between 3,900 and 5,200 years before present (e.g., Booth and others 2005, Foster and others 2006, Newby and others 2014).

Although pan-continental droughts were relatively rare during the last 1,000 years, the North American Drought Atlas indicates that they occurred more frequently during the Medieval Climate Anomaly (MCA) and could be related to defined climate modes (Cook and others 2014b). Notable pan-continental droughts include 1344–1353 C.E. (Common Era), 1661–1671 C.E., and 1818–1820 C.E. (Cook and others 2007). Cook and others (2014b) highlight the unusual nature of the 2012 pan-continental drought, but also indicate the potential for some predictability of these events as well as increased severity of pan-continental droughts as a result of greenhouse gas forcing.

Over the last 1,100 years, there have been several large-scale, hydroclimatic events in the conterminous United States. The MCA is widely recognized and regionally expressed as warm and/or dry (Bradley and others 2003, Lamb 1965, Mann and others 2009). Extensive periods of aridity characterized western North America during two centennial-scale arid periods, from 900 to 1100 C.E. and 1200 to 1350 C.E. (Cook and others 2010, MacDonald 2007, Stine 1994). In eastern North America, great droughts also characterize the MCA period, although the timing is shifted. Megadroughts (i.e., severe droughts of a decade or more) are seen in the extensive tree-ring record from the mid-Mississippi River Valley during the mid-900s C.E., 1100–1250 C.E., and then 1340–1400 C.E. (Cook and others 2010). Sediment core records document dry conditions during the MCA in the Eastern United States as well (Minckley and others 2011, Pederson and others 2005). These droughts come at the tail end of more-frequent drought conditions during the MCA across the Western United States (Cook and Krusic 2004, Cook and others 2004).

A persistent trend of increasing wetting was present across the Western United States during the Little Ice Age (Cook and others 2004). This trend was punctuated by severe droughts, such as the late 14th century and the 1805–1806 C.E. droughts centered on the Great American Desert (Cook and others 2007), the 1379–1388 C.E. drought centered on the Mississippi Valley, and the 16th century megadrought (Cook and others 2007, Stahle and others 2000). [The 16th century megadrought has been recently documented in the Northeastern United States (Ireland and Booth 2011) and is the most synchronous sustained drought in the Eastern United States of the last 500 years (Pederson and others 2013b).]

Regional Patterns in Paleoclimate

Eastern United States—As discussed previously, analyses of basin-scale streamflow records do not

show an increase in drought frequency over the past several decades; however, there are several important aspects of the changing hydroclimate in the Eastern United States (figs. 2.3–2.6). Notably, there is a recent divergence in moisture conditions between the Northeastern and Southeastern United States (Melillo and others 2014). Meteorological drought has become more frequent and severe in the Southeastern United States since the 1980s drought (Laseter and others 2012, Melillo and others 2014, Pederson and others 2012, Seager and others 2009). While the 1980s drought was one of the more severe droughts since 1700 (Cook and others 1988), reconstructions of PDSI from tree rings indicates that prior centuries were generally drier and had more severe and extended drought (figs. 2.3 and 2.5). The most recent severe droughts fall short of the more severe droughts in the last millennium (Stahle and others 2013b, Stahle and Cleaveland 1992).

The Northeastern United States is currently experiencing one of the wettest growing-season pluvials since 1531 C.E. (figs. 2.3, 2.4, and 2.6) (Pederson and others 2013b). Variation in reconstructed PDSI occurs at decadal to multi-decadal time steps with a positive shift in increased moisture availability and extreme events since the early 2000s (Matonse and Frei 2013, Melillo and others 2014, Pederson and others 2013b). These shifts are observed across New England in rising streamflow and groundwater tables (Dudley and Hodgkins 2013, Weider and Boutt 2010). Varved sediments also indicate the Northeast is undergoing one of the wettest periods in the last 1,000 years (Hubeny and others 2011). These findings are supported at even longer time scales. Lake levels across Massachusetts indicate a positive trend in effective moisture over the last 3,000 years resulting in “exceptionally high” levels of water in the recent era (Newby and others 2014). The centennial trend of increased moisture in the tree-ring reconstruction and various hydrological measures in the Northeast generally follow the trajectory of the Massachusetts lakes indicating that the current period could be one of the wettest of the last 3,000 years.

Plains and Midwest—Reconstructions of moisture in the Plains and Midwest contain many of the same trends described above (fig. 2.3), although there is some spatial complexity in trends during the most recent century. The northwestern portion of the Prairie Pothole Region of the upper Great Plains has become drier over the past century while the southeastern portion, bordering on the western edge of the eastern

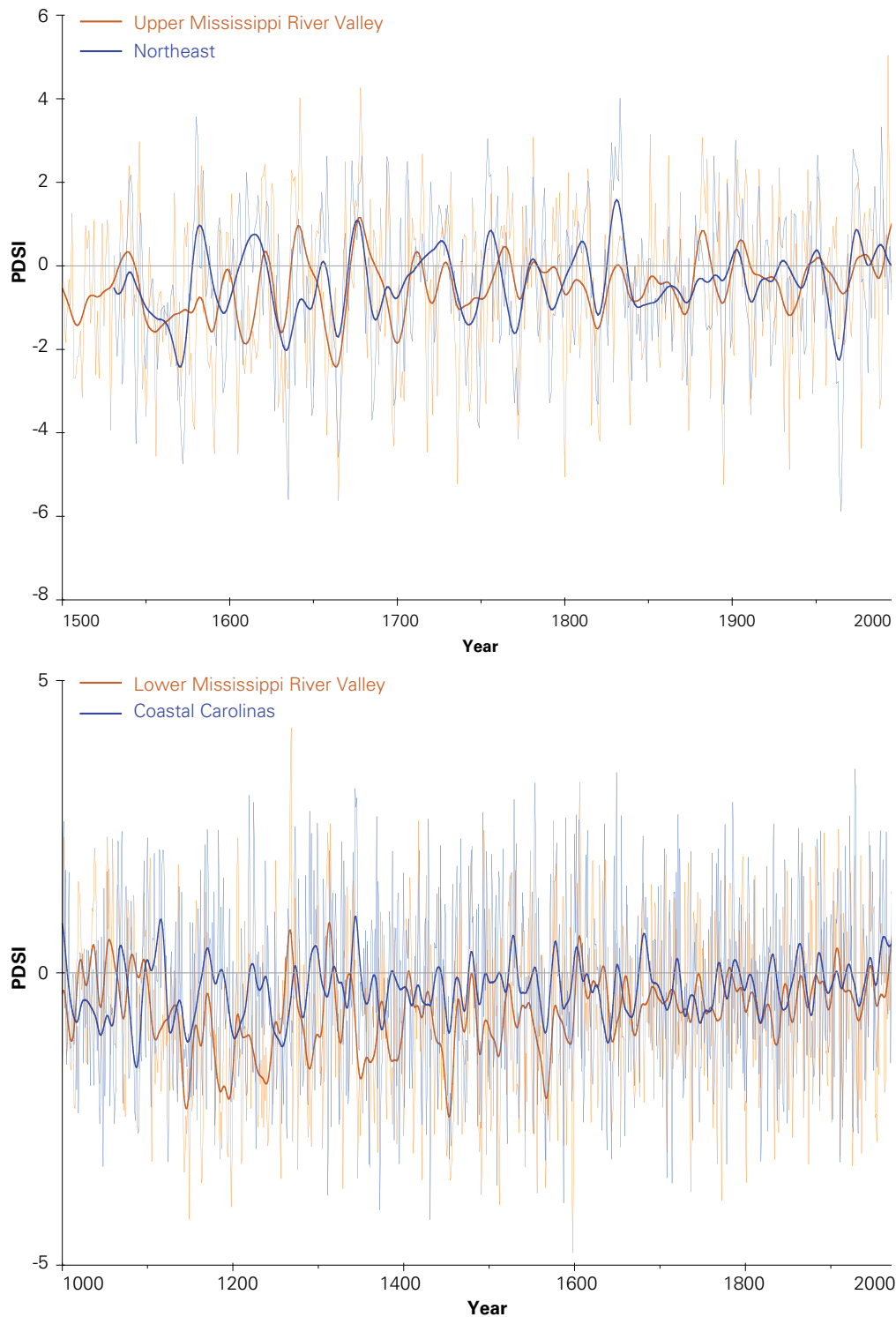


Figure 2.3—Time-series of Palmer Drought Severity Index (PDSI) over the last 500 years (Upper Mississippi River Valley and Northeast) and 1000 years (Lower Mississippi River Valley and Coastal Carolinas). Notable features in these series are the relative absence of annual values during the 16th century megadrought in the Upper Mississippi River Valley and Northeastern United States (upper panel) and similar features during the 12th and 13th centuries in regions to the south (lower panel). Annual values are shown in faint, thin lines, and 20-year smoothed data with the dark, thicker lines. The horizontal line at 0 represents the 1900–2005 mean. These data are drawn from reconstructions of PDSI from the North American Drought Atlas (Cook and others 2007) for the Upper Mississippi River Valley, Lower Mississippi River Valley, and Coastal Carolinas, and Pederson and others (2013b) for the Northeast.

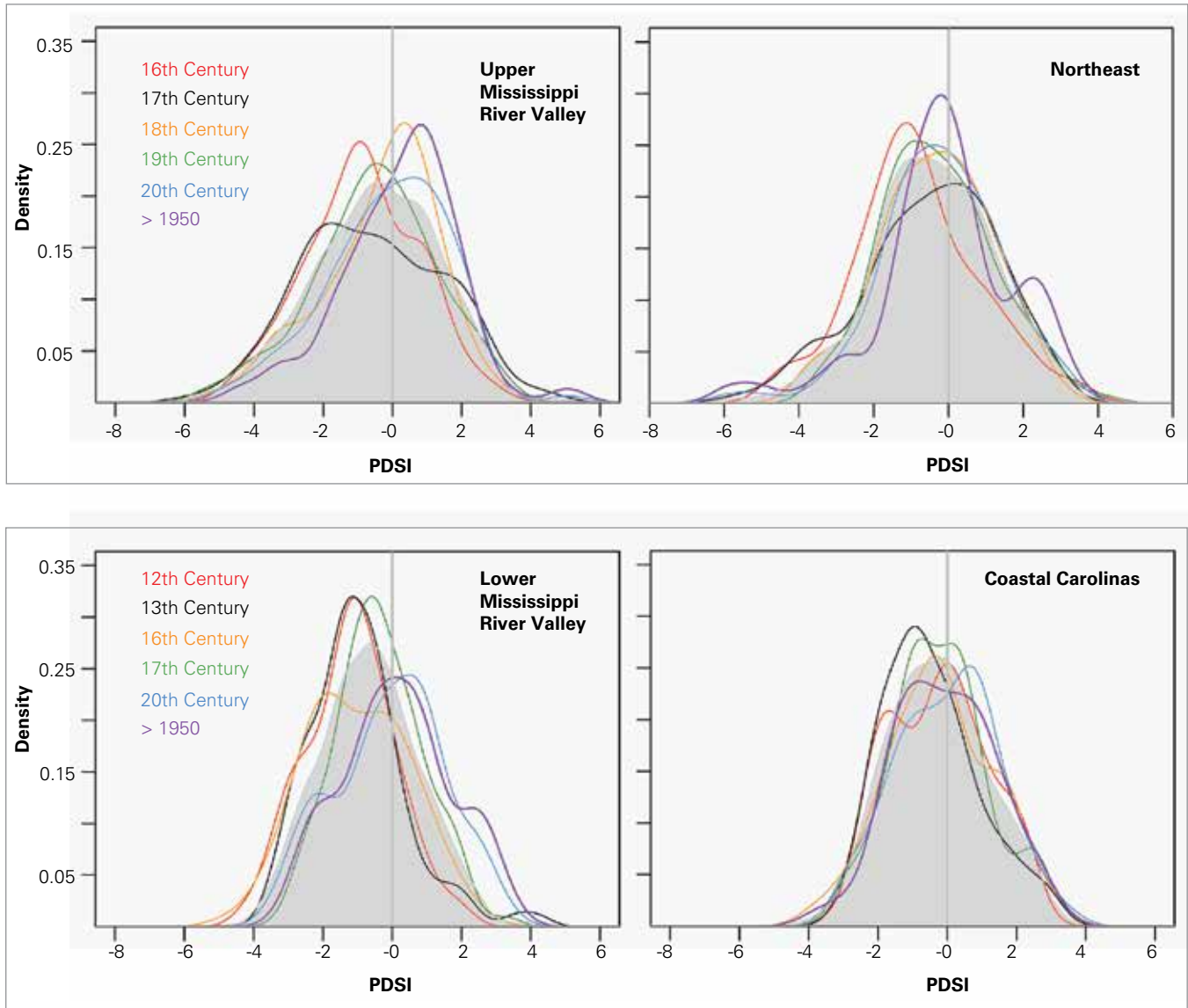


Figure 2.4—Density of Palmer Drought Severity Index (PDSI) over the last 500 years (Upper Mississippi River Valley and Northeast) and 1000 years (Lower Mississippi River Valley and Coastal Carolinas). The gray area represents the 1500–2005 and 1000–2005 distributions, respectively. The areas under the blue line and purple line represent the 1900–2000 and 1950–2005 periods, respectively. The end of the 20th century, a period of intense forest study, is generally one of the wettest periods in each region, indicating a general shift towards wetter conditions across the Eastern United States. The vertical line at 0 represents the 1900–2005 mean, so the values on the horizontal axis are departures from the mean. These data are drawn from reconstructions of PDSI from the North American Drought Atlas (Cook and others 2007) for the Upper Mississippi River Valley, Lower Mississippi River Valley, and Coastal Carolinas, and Pederson and others (2013b) for the Northeast.

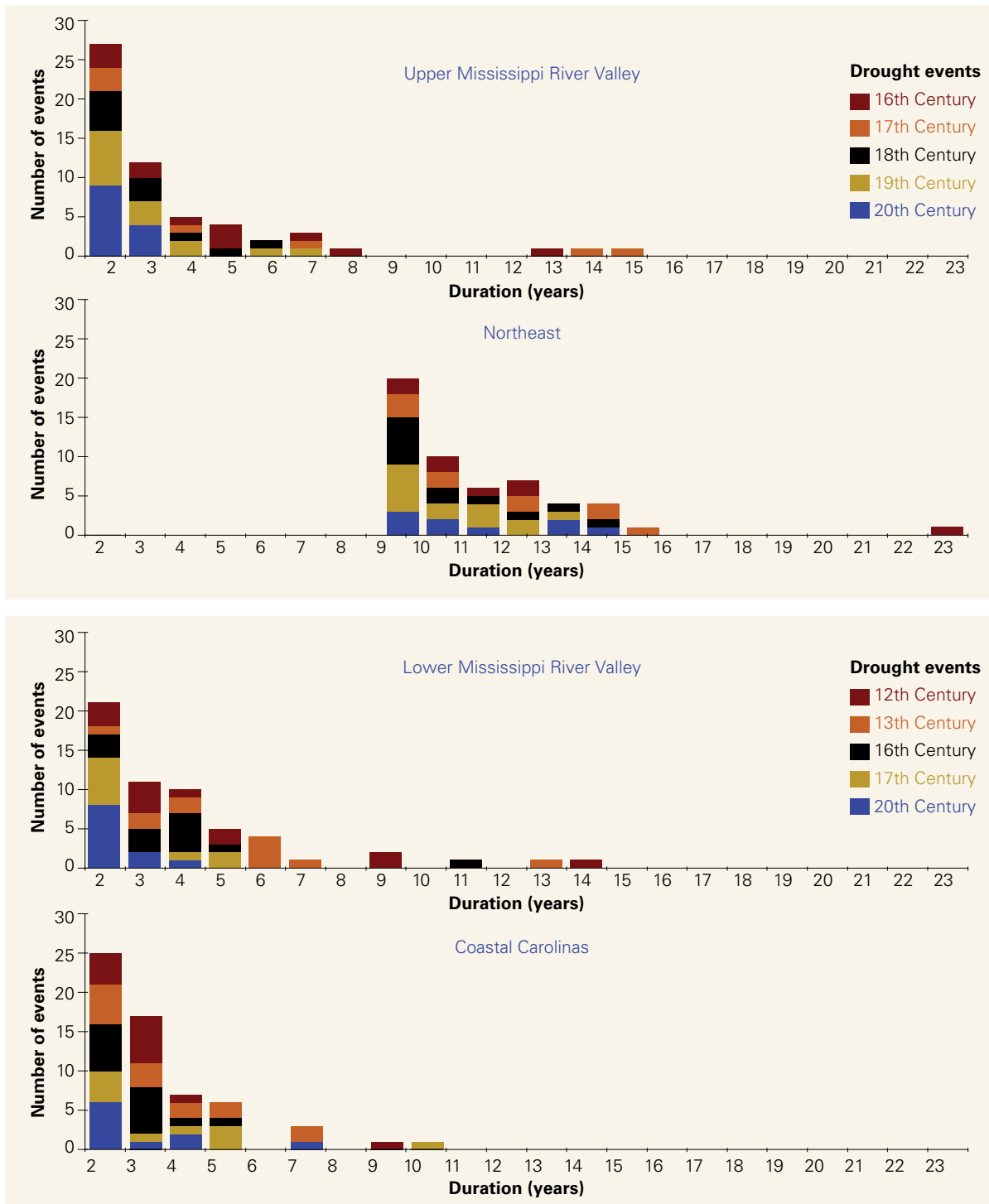


Figure 2.5—Frequency of discrete drought events of 2 years or more for key centuries over the last 500 years (Upper Mississippi River Valley and Northeast) and 1000 years (Lower Mississippi River Valley and Coastal Carolinas). In these four corners of the Eastern Deciduous Forest region, extended drought has been relatively unusual during the 20th century (blue). Droughts of the longest duration (>5 years) occur mostly in the 16th and 17th centuries in the north and the 12th and 13th centuries in the south. These data are drawn from reconstructions of PDSI from the North American Drought Atlas (Cook and others 2007) for the Upper Mississippi River Valley, Lower Mississippi River Valley, and Coastal Carolinas, and Pederson and others (2013b) for the Northeast.

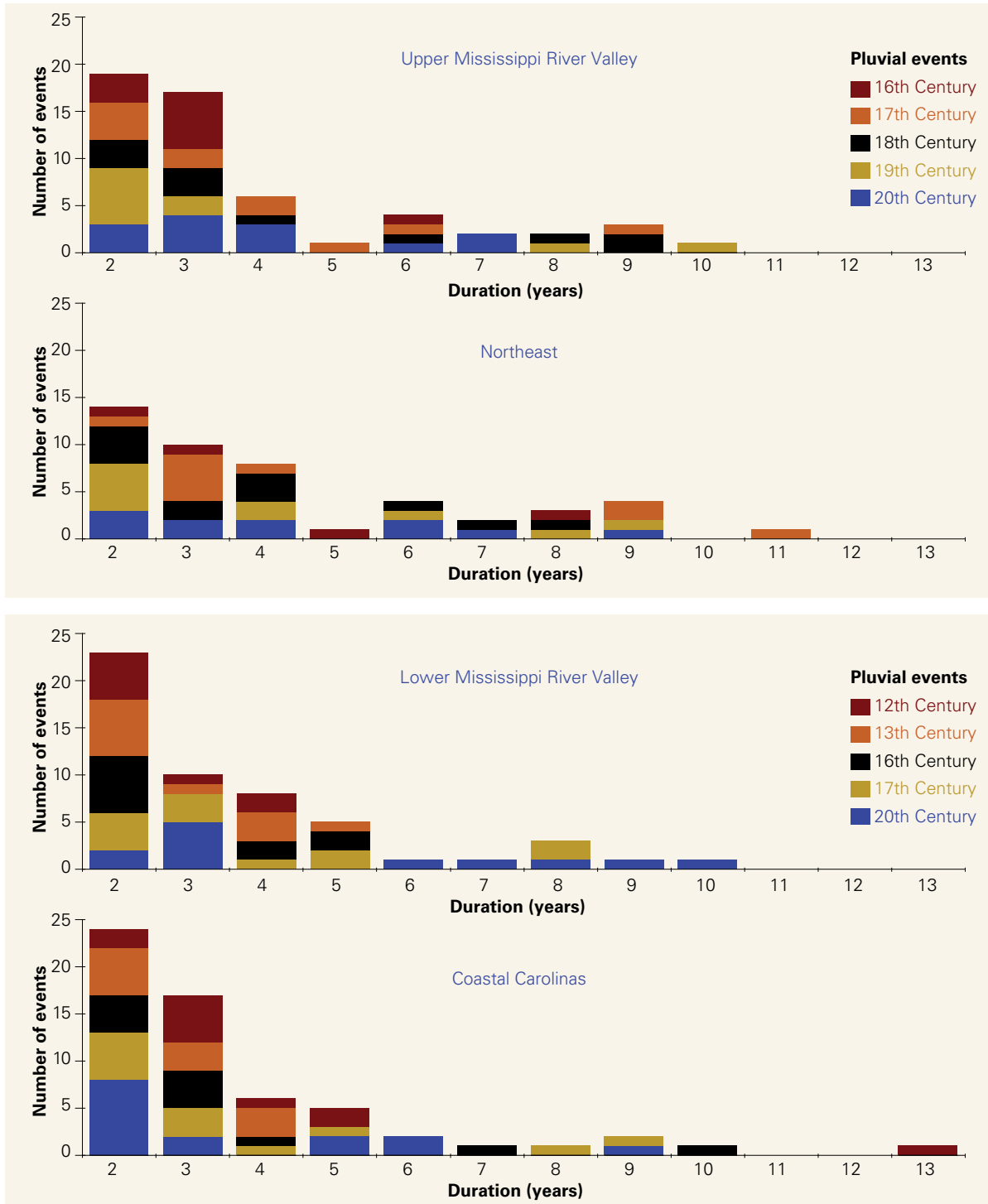


Figure 2.6—Frequency of discrete pluvial events of 2 years or more for key centuries over the last 500 years (Upper Mississippi River Valley and Northeast) and 1000 years (Lower Mississippi River Valley and Coastal Carolinas). In these four corners of the Eastern Deciduous Forest region, extended pluvials (>5 years) have been more frequent in the Lower Mississippi River Valley and the Northeast during the 20th century (blue). These data are drawn from reconstructions of PDSI from the North American Drought Atlas (Cook and others 2007) for the Upper Mississippi River Valley, Lower Mississippi River Valley, and Coastal Carolinas, and Pederson and others (2013b) for the Northeast.

U.S. forest, has become wetter (Millett and others 2009). Generally, droughts were more severe and of greater duration prior to the 20th century (figs. 2.5 and 2.6) (Cleaveland and Stahle 1989, Cook and others 2004, Cook and others 2010, Stahle and others 1985, Stahle and others 2007, Woodhouse and Overpeck 1998). Outstanding findings from reconstructed PDSI include more severe and extended droughts during the MCA (900s and 1100–1200), early Little Ice Age (late-1300s), and late 16th century (Cook and others 2010, Stahle and others 2007, Woodhouse and Overpeck 1998). During the past 500 years, however, the Dust Bowl drought was second only to the 16th century megadrought (Fye and others 2003). Since 1500 C.E., less extreme drought conditions (similar to the 1950s drought) have occurred 12 times; drought conditions that exceeded those of the 1950s drought have occurred 4 times during that same period (Fye and others 2003). Interestingly, there is a circa 600-year trend in wetting in the mid-Mississippi River Valley that peaks late in recent decades (fig. 2.3) (Cook and others 2010). Similar to the Northeastern United States, this trend towards increasing moisture is reflected in the southeastern Prairie Pothole Region, where a survey of ponds during the month of May suggests a substantial increase in the number of ponds since 1995 versus the period between 1974 and 1994 (Ballard and others 2014).

Southwestern United States Including California and the Great Basin—The Southwestern United States is an example of where understanding of long-term climate dynamics is crucial for sustainable management of environmental resources. Both an early and a recently updated reconstruction of streamflow in the Colorado River Basin indicate that water management agreements were developed during one of the wettest periods of the last 500 years (Stockton and Jacoby 1976, Woodhouse and others 2006). Creation of water distribution policies during such extreme periods (like the early 20th century pluvial) can lead to an over-expectation of water delivery when the climate system returns to “normal” or drought conditions. Since the early 20th century pluvial, there has been significant drying in the region.

Megadroughts were more common in the Southwest during the past several millennia. The most long-lasting and severe drought interval of the late Holocene is documented by multiple proxies across the central Great Basin extending to Great Salt Lake, and lasting from 2,800 to 1,850 years before present (Mensing

and others 2013). During this period, wetlands and meadows shrunk in size, lake levels decreased, and waters became more saline. Drought was zonally limited, and areas of the northern Great Basin remained or grew wetter. This pattern of dry in the southwest and wet in the northwest across the Great Basin is supported by large-scale spatial climate pattern hypotheses involving ENSO (El Niño-Southern Oscillation), PDO (Pacific Decadal Oscillation), AMO (Atlantic Multidecadal Oscillation), and the position of the Aleutian Low and North Pacific High, particularly during winter (Mensing and others 2013).

As elsewhere in North America, droughts were most notable during the MCA (Cook and others 2004). Reconstructed droughts during this period were not only relatively more severe versus those during recent centuries (Cook and others 2010, Meko and others 2007), but drought during the MCA also covered a considerably greater portion of the Western United States. Approximately 30 percent of the Western United States experienced annual drought during the 20th century versus approximately 41.3 percent between 900 and 1300 C.E. (Cook and others 2004). Treelines were elevated in the Sierra Nevada and White Mountains during the MCA (LaMarche 1973, Lloyd and Graumlich 1997), and growth patterns indicate extended warm and dry conditions (Graumlich 1993, Scuderi 1993).

Reconstructions of hydroclimate covering the last 2,000 years indicate the occurrence of drought equal to or greater in severity than those during the MCA. A reconstruction of the San Juan River from bristlecone pine indicates a severe, 51-year drought from 122 to 172 C.E. (Routson and others 2011). [Although this record has low tree replication during this period, comparison to other records of drought in and adjacent to this region substantiates the severity of second century drought (Cook and others 2004, Cook and others 2007, Knight and others 2010).] The extent of this drought, from southern New Mexico to Idaho, is similar to the 12th century megadrought (Routson and others 2011), suggesting perhaps a recurring forcing.

Over the past 2,740 years, oscillations in hydrologic balance are documented throughout the region, with droughts occurring about every 150 years and intervals between droughts ranging from 20 to 100 years (Benson and others 2002). Similar patterns of synchronous drought exist from the Great Basin through New Mexico and coincide with Ancient Puebloan withdrawals and abandonments in Arizona

and Colorado, documenting the likely wide extent and impact of these droughts (Benson and others 2002, Dean 1996, Grissino-Mayer 1996).

Insight into seasonal dynamics of precipitation delivery within the North American Monsoon region was recently revealed. Using indices of early-wood and late-wood widths from two tree species over a large region, Griffin and others (2013) reconstructed cool-season and monsoonal precipitation going back to 1539 C.E. The two records of reconstructed precipitation indicate periods of dry, cool-season conditions followed by a failure of the monsoon during the 1570s, 1660s, 1770s, and early 2000s. Similarly, the early 20th century pluvial was characterized by synchronous, dual-season surplus precipitation. Interestingly, much of the period during the instrumental record is characterized by a high frequency of asynchronous cool-season and monsoonal precipitation or “*opposing-sign precipitation anomalies*” (Griffin and others 2013). What this study reveals, however, is that this anti-phasing of cool-season and monsoonal precipitation is more of an exception rather than the rule during the 470-year reconstructions. Therefore, a fuller understanding of climate dynamics of the North American Monsoon region likely requires an understanding of the dynamics outside of the instrumental record.

More than half of California was in a state of moderate drought between June 2013 and June 2014, at which time 100 percent of the State reached that level of drought. The conditions in 2014 culminated in the driest 3-year period of the last century (Griffin and Anchukaitis 2014). To place this drought in a long-term context, tree-ring analysis of blue oak (*Quercus douglasii*) around the Central Valley of California was used to characterize annual variations of drought history over the past seven centuries (Meko and others 2001, Meko and others 2011, Stahle and others 2001, Stahle and others 2013a). Independent reconstructions of November–April precipitation for North and South Coast Ranges indicate strong annual correlations during the common period (1584–2003), although there were eras of asynchrony between the two regions during the 1770s, 1810s–1840s, and 1970s, for example (Stahle and others 2013a). Winter storm track position is thought to control the more extreme periods in the tree-ring records. An updated reconstruction of drought in this region using blue oak collected following the 2014 growing season indicates unprecedented drought conditions in 2014 compared to the prior 1,200 years (Griffin and Anchukaitis 2014).

Ecological Outcomes of Paleoclimate on Forests

Ecological responses at regional scales were widespread, with changes in ecosystem structure, composition, and range toward dry-adaptations and changes in disturbance patterns reflecting drier conditions. Forest response included, for example, conversion from mesic forest to prairie in the Midwest (Baker and others 1992), dominance of dry-adapted taxa (*Chrysolepis*, *Quercus*) at high elevations that are currently occupied by *Abies* and *Pinus* in the Sierra Nevada of California (Anderson and Smith 1994), and expansion of warm-adapted pines and oaks in the Colorado Plateau (Betancourt 1990). Regionally warm and dry climates evolved in the middle Holocene as a combined effect of insolation changes due to orbital relations, which affected the amount and seasonality of precipitation, and changes in the position of jet streams, storm tracks, and blocking of warm maritime air (Baker and others 1992, Dean and others 1996, Yu and others 1997).

The ecological impact of the Medieval Climate Anomaly droughts in the Western United States is reflected by the presence of in-situ stumps in present-day rivers and lakes (Kleppe and others 2011, Stine 1994); lowered lake levels (Stine 1990); decreased alpine treelines (LaMarche 1973, Lloyd and Graumlich 1997); decreased growth of trees (LaMarche 1974); and changes in species distributions, elevation zonation, and abundance (Lloyd and Graumlich 1997, Millar and others 2006). Shifts toward warm and dry conditions also altered fire regimes, such that fire activity was highest relative to the entire Holocene during the MCA in the Pacific Northwest and parts of the Northern Rocky Mountains (Brunelle and others 2005, Whitlock and others 2003), whereas changes in forest structure related to aridity (low fuel density, sparse stands) resulted in many small fires in the western Sierra Nevada relative to mesic intervals (Swetnam 1993). Mechanistic forcing for the dry centuries of the Medieval period has been related to changes in ocean circulation, in particular the development of persistent positive North Atlantic Oscillation conditions (Trouet and others 2009), and northward shifts in storm tracks across the eastern North Pacific with a contraction of the Aleutian Low (Graham and others 2007, MacDonald and Case 2005). More recent reconstructions suggest that the causes were more complex and that the MCA was characterized by an enhanced zonal Indo-Pacific Sea Surface Temperature (SST) gradient with resulting changes in Northern Hemisphere tropical and extra-tropical circulation patterns and hydroclimate regimes (Graham and others 2011).

An important hydroclimatic event with ecological implications in the Western United States is the early 20th century pluvial, one of the most contiguous pluvial events of the last 1,000 years (Cook and others 2011, Stahle and others 2007). This pluvial—a period of extended, above average moisture condition—covered about half of the continent and is thought to have been an important trigger in tree recruitment in the Southwestern United States (Savage and others 1996). Generally, the 20th century was a substantially wetter period across the United States versus the prior three to eight centuries (Cook and others 2004, Cook and others 2010, Stahle and Cleaveland 1992, Stahle and others 1988, Stahle and others 2007).

The ecological impact of historic droughts is well documented throughout the Holocene in the Eastern United States. Throughout the Holocene, drought has been an important contributor to forest change (Shuman and others 2009a). Drought variation during the MCA was an important factor contributing to the decline in American beech (*Fagus grandifolia*) in the Great Lakes region (Booth and others 2012). In a surprising contrast, drought is seen to be an important factor of deciduous forest expansion in Minnesota early in the Little Ice Age (Shuman and others 2009b). Abrupt hydroclimatic variability is attributed to peatland development in Pennsylvania (Ireland and Booth 2011). The 16th century megadrought likely influenced stand dynamics in a large wetland complex in the Mississippi Valley (Stahle and others 2006), while repeated droughts during the mid-18th century appear to be contributors of regional-scale canopy disturbance in the Southeastern United States (Pederson and others 2014). The latter finding follows observations of oak growth decline and mortality in the Midwestern United States during the late 20th century (Pedersen 1998).

Periods of abundant moisture could be key elements of forest dynamics in the mesic Eastern United States. An expansion of yellow birch (*Betula alleghaniensis*) occurs during a period of increased moisture and high lake levels (Jackson and Booth 2002). The rise of maple (*Acer* spp.) and other mesophytic species during the 20th century occurs towards the end of a centennial wetting trend (McEwan and others 2011, Pederson and others 2013b); however, given the complexity of factors in this region, it is yet to be determined whether this wetting is an important factor of this rise. However, if the trend in wetting over the last 2,000–3,000 years in the Northeastern United States (Newby and others 2014) is similar to the wetting trend over the Eastern

United States from the end of the Little Ice Age into the 20th century (Pederson and others 2013a), there is much to investigate regarding drought-forest dynamics over this mesic region across spatial and temporal scales. Greater detail on the ecological impact of drought on forests is found in chapter 4.

Historical and Recent Drought

Approaches to quantifying changes in drought depend on how “drought” is defined (Trenberth and others 2014). In this context, we suggest two important observations: (1) climate variability occurs at multiple time scales (Hurst 1951), and (2) widespread drought-related forest mortality is occurring (Allen and others 2010, Breshears and others 2005, van Mantgem and others 2009). The first point is that many hydrologic phenomena show cycles at a large range of time scales, some tied to known climatic modes (e.g., El Niño, PDO, AMO), and others at longer scales. The implication is that the ability to detect trends in hydrologic phenomena may depend upon whether the time period of interest encompasses one or more of these cycles. The primary value in finding hydrologic trends, then, is in relating different co-occurring trends to one another to learn about potential causal relationships.

The second point is that, in many regions of the World, large numbers of long-lived plants seemed to be dying at rates unprecedented in historical times, indicating that hydrologic processes may be changing in ways that are ecologically meaningful. Because of this, we require an understanding of what aspects of changing drought regimes are causing these significant ecological impacts. The drought metrics and understanding of forest physiology and ecology outlined above indicate water balance, temperature (both as index to ET and as it affects physiology), and time are three key ways drought may be changing. This is a complex mix, particularly considering that the interactions among these three are of fundamental importance. A rich literature on historical (relying on the instrumental record) changes tying variability to known climate modes can help us interpret some of the trends and patterns of change. The recent literature is rich on the topic of recent trends for many regions in the United States, but only two regions are discussed here as examples.

Eastern United States

Compared to most other areas of the United States, the East receives large amounts of precipitation, with

30-year (1981–2010) normals ranging from 80 to 200 cm across the region (PRISM 2013). Precipitation is spatially and temporally variable in the East due to a combination of many factors, including proximity to the Atlantic Ocean and Gulf Stream, influence of the Great Lakes, and orographic effects associated with mountains, including the Appalachian chain that extends from Alabama to north of Maine (Huntington and others 2009, Mulholland and others 1997). Broad-scale circulation patterns influence the eastern climate, contributing to patterns in precipitation. In the Southeast, precipitation is associated with El Niño/Southern Oscillation (ENSO), with dry conditions occurring during La Niña events (Piechota and Dracup 1996, Ropelewski and Halpert 1986, Roswintarti and others 1998). During the growing season, precipitation has been linked to the North Atlantic Subtropical High in the Southeast (Li and others 2011). Precipitation in the Northeast also suggests possible linkages with ENSO, as well as the North Atlantic Oscillation (NAO) (Bradbury and others 2003, Kingston and others 2007), with evidence of a relationship between negative NAO conditions and drought (Bradbury and others 2002, Seager and others 2012). A positive NAO promotes pluvial conditions (Seager and others 2012), although the ultimate causes of pluvials are complex (Ning and Bradley 2014, Seager and others 2012).

Despite the relatively abundant supply of precipitation in the East, droughts are a natural part of the climate system and occur with regularity. Over the last 100 years, eastern droughts generally last only 1–2 years, unlike arid regions of the Central and Western United States that experience more intense and prolonged meteorological droughts (Seager and others 2009). A notable example of a severe eastern drought is the drought of the early 1960s that lasted 4 years and affected a broad area, including New England, the Mid-Atlantic States, and parts of the Midwest (Namias 1966). The Southeastern United States has also experienced severe droughts over the last several decades, including one from 1984 to 1988 (Cook and others 1988) and more recently from 2006 to 2008 (Kam and others 2014).

Analyses of past occurrences of drought show no indication that they are becoming more frequent in the Eastern United States. In fact, precipitation has increased throughout the region, especially in the Northeast (Melillo and others 2014), which has resulted in an overall reduction in drought conditions (Andreadis and Lettenmaier 2006, Sheffield and Wood 2008a).

These increases in precipitation have led to documented regional increases in streamflow and are consistent with patterns observed in many other regions of the United States (Groisman and others 2001, McCabe and Wolock 2002). Although there are no apparent increasing trends in drought during the recent past (Patterson and others 2013, Sheffield and Wood 2008a), most models indicate that drought frequency in the Eastern United States will increase by the end of the century, despite projected concurrent increases in precipitation (Hayhoe and others 2007, Sheffield and Wood 2008b). This paradox is largely explained by enhanced future evapotranspiration associated with longer growing seasons and warmer air temperatures. This may already be occurring in some regions. For example, recent analyses suggest that although there are no observable trends towards increasing drought frequency over the past 70+ years, overall streamflow has decreased by about 7 percent in the South Atlantic region of the Eastern United States (Patterson and others 2013).

Although droughts in the Eastern United States are not as severe as those in the Southwest and Great Plains, the effects can be acute because of the high population density and associated demands for water (Patterson and others 2013). The southeastern drought of 2006 to 2008 caused societal and economic hardships, with agricultural losses exceeding a billion dollars (Manuel 2008). The drought also led to interstate disputes over water use as supplies diminished. Recent evidence suggests that severe, short-duration droughts in the East can also have lasting effects on forest ecosystems (Klos and others 2009, Pederson and others 2014). These events can alter the structure of forests for centuries, particularly if they are exacerbated by other broad-scale disturbances, such as frost, ice storms, and insect outbreaks. Understanding the effects of extreme climatic events, such as droughts, will help determine how eastern forests will respond to future climate change.

Northwestern United States

Temperature recorded at long-term stations has increased in the Northwest since the early 20th century, with some of the cause attributed to increased carbon dioxide (CO₂) (Abatzoglou and others 2014). Less certain, however, are precipitation trends and their causes, as suggested by the long-term instrumental record and modeling studies. Most of the data for these long-term studies come from stations at lower elevations, where they can be collected more reliably. Because much of the water in the Northwestern United

States comes out of mountains, further data collection and analysis is needed at high elevations to gain a better understanding.

One of the most frequently discussed changes to Northwest hydroclimatology is trends in snowpacks (e.g., Mote 2003). Summers are very dry compared to winters in much of the Northwest, although there are June peaks in precipitation in the Northern Rockies and some summer monsoonal moisture over southeastern Oregon and southern Idaho. Because of the general lack of summer precipitation, snowmelt is a critical part of the water supply in forests and rivers during the Northwest's growing season. A lack of snow for melt means that the snowpack ablates earlier and stream runoff occurs earlier (Cayan and others 2001, Stewart and others 2005) because a shallower snowpack takes less time to melt. What has previously been unclear is the relative contributions of temperature and precipitation to these snowpack trends (Luce and others 2013, Mote and others 2005), which has important consequences for leveraging current trend information for application to future projections.

Streamflow has been declining in the Northwest since the late 1940s (Clark 2010, Dai and Trenberth 2002, Luce and Holden 2009), particularly drought-year flows. The declines have been driven primarily by winter precipitation declines (Luce and others 2013). Streamflow declines have shown a pattern where the driest years (25th percentile), in particular, are showing the strongest trends, approaching a 50-percent decline in drought-year flows over the last 60+ years (Luce and Holden 2009). This pattern is consistent with other observations of increasing variance in runoff in the Western United States (Pagano and Garen 2005) and with expectations for increasing variance in runoff ($P - E$) with warming (Seager and others 2012). Previous work missed detecting changes in precipitation because it was based on analysis of low-elevation stations (Mote and others 2005, Regonda and others 2005), while the decreases in runoff were related to decreased high-elevation precipitation driven by reduced westerly wind speeds over the region.

The twin contexts of decreasing precipitation and warming temperatures, with consequent changes in snowpack, make evaluation of drought effects in the region multifaceted. For example, earlier work showed that wildfire was more prevalent in the region in association with earlier snowmelt, presumed to be a function of warming temperatures alone (e.g.,

Westerling and others 2006). An awareness of the declining precipitation, though, has revealed that the precipitation variability has historically been a more important control on interannual variability in burned area (Abatzoglou and Kolden 2013, Holden and others 2012, Riley and others 2013), and increasing wildfire area is consistent with increasing drought severity as indexed by the lower streamflow quartile.

Low flows during the dry summer months are also showing declines (Dittmer 2013, Leppi and others 2011, Lins and Slack 2005). Some of this is related to earlier runoff timing, as the time between recharge of the soil mantle and groundwater and the runoff increases; but some is also related to declining recharge volumes (Safeeq and others 2013). Again, most of the effect has been attributed to earlier snowmelt and reduced accumulation as a function of increasing temperatures, but the precipitation variations affect both timing and total annual streamflow (Holden and others 2012, Luce and Holden 2009). More work in this area is needed to identify the relative contributions in the historical record.

Drought in the Pacific Northwest is strongly tied to several modes of climate variability, ENSO, the Pacific North America Pattern (PNA), and the Pacific Decadal Oscillation (PDO). The most severe droughts generally occur during El Niño events (Cayan and others 1999, Piechota and Dracup 1996, Redmond and Koch 1991, Ropelewski and Halpert 1987). ENSO-mediated precipitation variations may disproportionately affect mountain watersheds (Dettinger and others 2004). Precipitation variations are also well correlated to the PNA at intraseasonal to interannual time scales (Abatzoglou 2011) and the PDO (Mantua and others 1997) at decadal time scales. Trends in these indices are weakly related to the observed trends in westerly winds over the region, and consequently with trends in runoff and precipitation (Luce and others 2013). The related changes in pressure pattern driving the wind changes are consistent with increased CO₂ content, but the change in winds and pressure exceed the average expectation for wind decreases by 2080.

Climate Change Impacts on Drought Frequency and Severity

Will drought be more or less frequent in the future? Will it be more or less severe in the future? These questions are very difficult to answer with climate change projections from GCMs (Dai 2013, Hoerling

and others 2012, Sheffield and Wood 2008b, Trenberth and others 2014). For example, some researchers have used the PDSI conceptualization of “drought,” which in a warming future may index temperature more than it indexes water balances (Cook and others 2014a, Hoerling and others 2012, Sheffield and others 2012, Trenberth and others 2014), leading to suggestions of alternative models or indices of drought that may be more indicative. A more relevant question for this report is: will forests and rangelands be more severely impacted by drought in the future? Answers for this question are more complex, but potentially more informative and certain. For example, warming means that the droughts we have now are more likely to produce tree mortality for a given level of water deficit (e.g., Adams and others 2009). Beyond that, answers to the question of whether other aspects of drought will change in the future, particularly those related to precipitation, are much more challenging to elicit from GCMs. Despite these challenges, the recent Intergovernmental Panel on Climate Change

(IPCC 2013) report provides some expectations of how climate change will impact drought frequency and severity in the United States.

General Drought Projection Information

A number of different projections are given in the IPCC (2013) Working Group 1 (WG1) report that relate to drought, such as changes in annual and seasonal precipitation (fig. 2.7) and associated changes in runoff and soil moisture (fig. 2.8). Except as specifically noted, in this chapter we discuss the multi-model means for RCP 8.5 2081–2100 compared to 1986–2005 averages from IPCC (2013) chapters 12 and 14. Generally, expected runoff patterns correlate strongly to expectations of future precipitation, but future soil moisture is expected to decline in most land areas. Theoretically, this is related to increased evapotranspiration, itself tied to increased downwelling longwave radiation. The combination of increased runoff, which is related to increased precipitation, and decreased soil moisture is intriguing. Usually soil

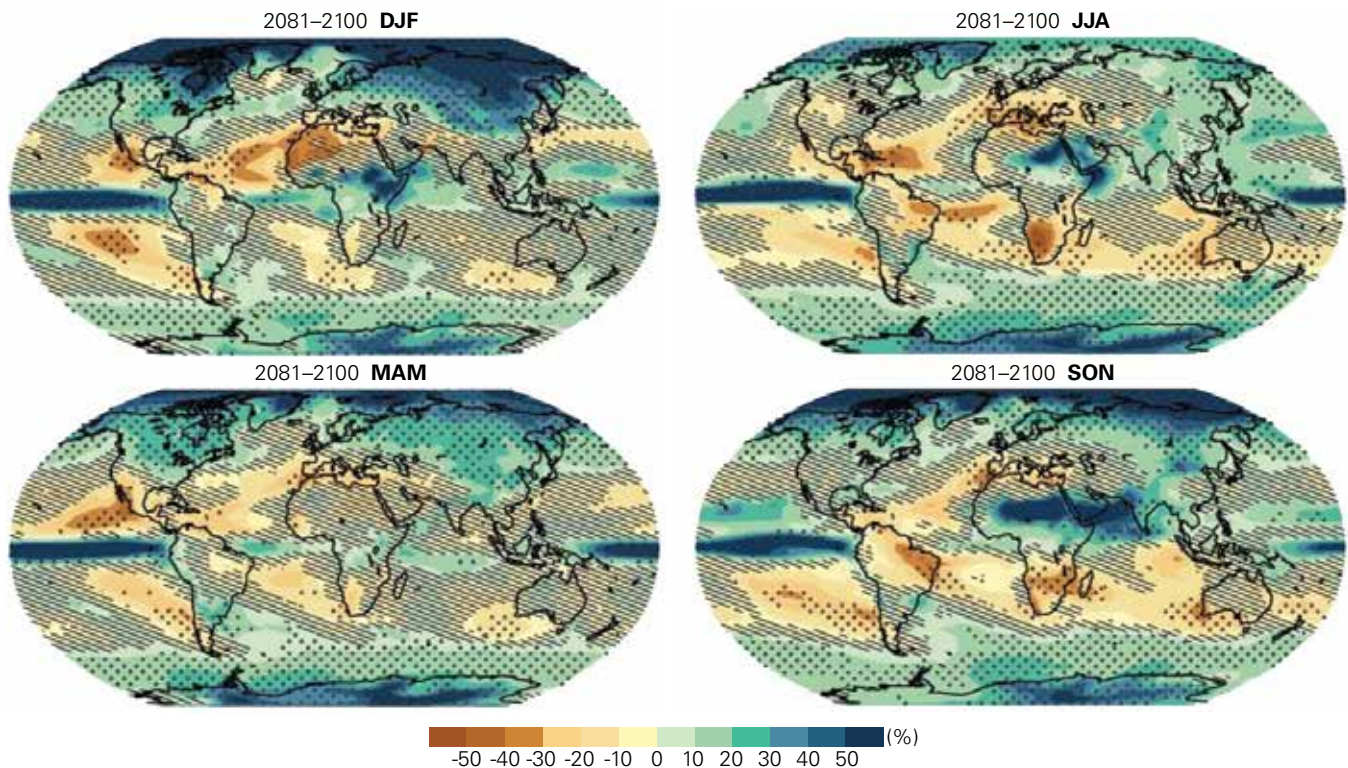


Figure 2.7—Coupled Model Intercomparison Project Phase 5 (CMIP5) multi-model average percentage change in seasonal mean precipitation relative to the reference period 1986–2005 averaged over the period 2081–2100 under the RCP 8.5 forcing scenario. Hatching indicates regions where the multi-model mean change is less than one standard deviation of internal variability. Stippling indicates regions where the multi-model mean change is greater than two standard deviations of internal variability and where at least 90 percent of models agree (from fig. 12.22 of IPCC 2013). Thirty-nine CMIP5 models were used for each panel. From top to bottom, the figures describe northern hemisphere winter (Dec.–Feb.), spring (Mar.–May), summer (Jun.–Aug.), and autumn (Sep.–Nov.). RCP means Representative Concentration Pathway.

moisture and runoff vary together in forested watersheds. The differential trends in soil moisture and runoff is explained conceptually by the fact that increased precipitation comes by way of increased precipitation intensity, meaning that more of the water might be expected to run off. It is not clear that this is an appropriate re-partitioning in forested landscapes, however, and might just be an artifact of the land surface model in the GCMs. An additional model output is also conceptually tied to increased precipitation intensity. The argument that similar or slightly increased total precipitation is delivered in higher intensity events yields an estimate that interstorm periods will be longer, increasing the number of consecutive dry days in most years, although the effect is minor across much of the continental United States (fig. 2.9).

Post-processing of GCM outputs has also been applied to examine how changes in precipitation amount, timing, and form (snow versus rain) interact with energy

available for ET to estimate details of potential future conditions (e.g., Cook and others 2015, Elsner and others 2010, Hamlet and others 2013, Sheffield and others 2004, Vano and others 2012, Wood and others 2004). Some of these are essentially more-detailed versions of the land-surface models used to describe the lower boundary condition of the GCMs. These approaches relatively directly disentangle a range of drought definitions to describe how the components of drought are likely to change in the future. An important consideration in interpreting output of these simulations is that they can double count the effects of increased incoming longwave radiation on ET (Milly 1992).

Other approaches directly estimate PDSI values with projected temperature and precipitation changes (e.g., Dai 2013). Whether the calculated changes in PDSI reflect actual changes in drought severity is a subject of substantial debate (Cook and others 2014a, Hoerling and others 2012, IPCC 2013, Sheffield and others

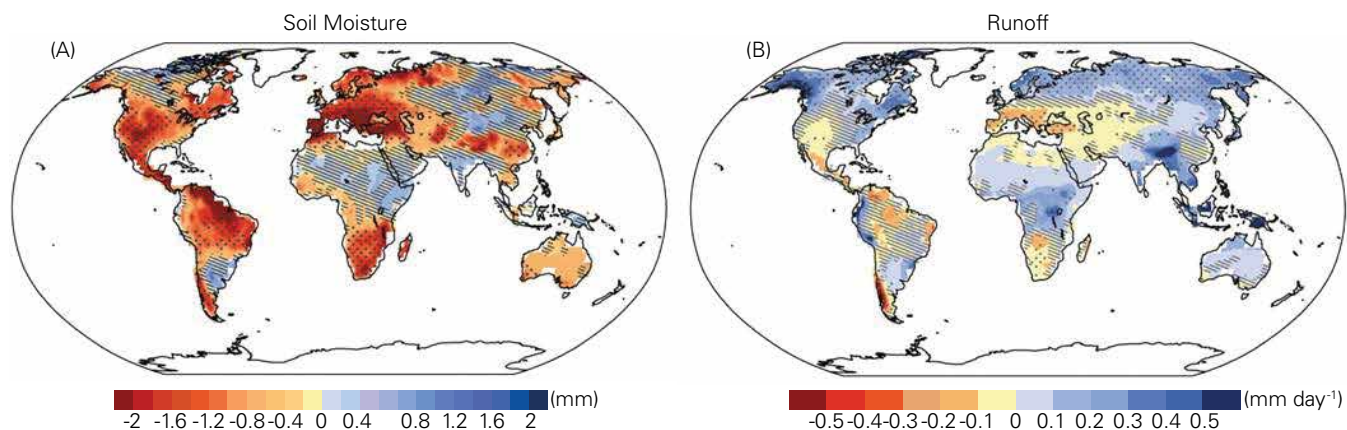


Figure 2.8—Change in annual mean (A) soil moisture (mass of water in all phases in the uppermost 10 cm of the soil) (mm), and (B) runoff relative to the reference period 1986–2005 projected for 2081–2100 under RCP 8.5 from the Coupled Model Intercomparison Project Phase 5 (CMIP5) ensemble. Hatching indicates regions where the multi-model mean change is less than one standard deviation of internal variability. Stippling indicates regions where the multi-model mean change is greater than two standard deviations of internal variability and where at least 90 percent of models agree. RCP means Representative Concentration Pathway. (From figs. 12.23 and 12.24 of IPCC 2013).

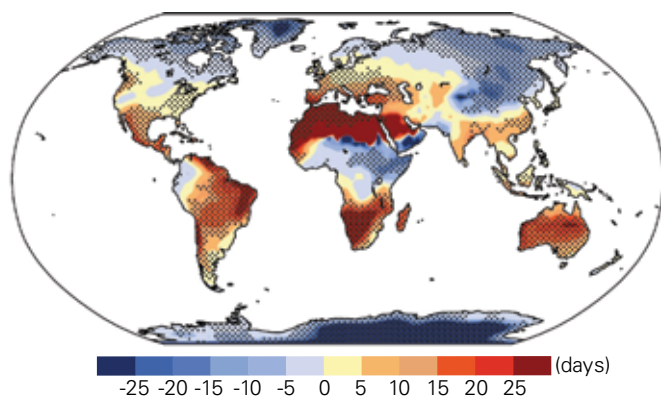


Figure 2.9—Projected change in the annual maximum number of consecutive dry days when precipitation is <1 mm, over the 2081–2100 period in the RCP 8.5 scenario (relative to the 1981–2000 reference period) from the Coupled Model Intercomparison Project Phase 5 (CMIP5) models. Stippling indicates gridpoints with changes that are significant at the 5-percent level using a Wilcoxon signed-ranked test. RCP means Representative Concentration Pathway. (From fig. 12.26 of IPCC 2013; updated from Sillmann and others 2013).

WHAT DOES RCP MEAN?

Representative concentration pathways (RCP) is a shorthand way of saying, *let us assume that the concentrations of anthropogenic greenhouse gases reach a certain level as indicated by the additional radiative forcing they cause by 2100*. Four levels were considered in the Intergovernmental Panel on Climate Change Fifth Assessment Report (IPCC 2013): 2.6, 4.5, 6, and 8.5 W/m² (Watts per square meter). Each “pathway” has a slightly different trajectory in greenhouse gas concentrations (and consequent forcing) over time, with the RCP 2.6 scenario, for example, showing higher forcing at mid-century and recovering toward the end of the century. The wattages associated with each RCP level are strictly related to the anthropogenic greenhouse gases, and increased water vapor that comes as feedback to the initial forcing may multiply the increased longwave radiation effect three- to four-fold. Thus, an RCP of 8.5 could yield a net increase in downwelling longwave radiation of 34 W/m².

2012, Trenberth and others 2014). Applicability of this index to future conditions and their consequences will depend in part on how the various components of the PDSI relate to the phenomenon of interest. For instance, applicability may vary depending upon whether forest die-off is more related to shallow soil versus how long it has been since precipitation has occurred. Most of the projections of increasing PDSI values in the United States are associated with increases in temperature, although an increase in the number of consecutive dry days during monsoon season may be important for areas affected by the North American Monsoon System (IPCC 2013). There is again the concern of double accounting of energy (first for heating and then for evapotranspiration) in using a temperature-based potential evaporation model (Milly 1992). This is increasingly well known for applications of the original formulation of the PDSI, which uses temperature explicitly through the Thornthwaite (1948) evaporation model. The Penman-Monteith potential evaporation formulation (Monteith 1965), which has been adapted for use in PDSI and as part of more complex water-balance models (Cook and others 2014a, Sheffield and others 2012), implicitly carries a strong temperature dependence in the calculation of the vapor pressure deficit term as well. Distinguishing between contributions in future drought caused by increased

evapotranspiration rates versus precipitation lapses may be helpful in interpreting this kind of work.

Projections of Relevant Factors

Temperatures are expected to increase 4–7 °C across the continental United States, with stronger increases in the interior than near the coasts. Summer relative humidity is expected to drop in the neighborhood of 4–8 percentage points, with weakest declines in the Southwest, where summer humidity is already low. Temperature increases in Alaska range from 4 to 9 °C, with greater increases farther north. Projected temperature increases around Hawaii are in the 3–4 °C range. Both Alaska and Hawaii have nearly no projected change in relative humidity.

Winter precipitation (DJF) increases on the order of 0–10 percent (with large differences among models) are expected over most of the continental United States, except for the Southwest where declines of 0–10 percent are projected. Alaska shows increases of 10–50 percent, increasing with latitude. Hawaii has a minor and uncertain decline. Summer precipitation (JJA) is projected to decline (0–20 percent) over most of the continental United States, except for the East and Gulf Coasts where 0–10 percent increases are projected. Alaska shows increases of 0–20 percent, increasing with latitude. Hawaii has a minor and uncertain increase.

Duration of dry spells is expected to increase in western U.S. mountains, where less snowpack accumulation and earlier melt combine to extend the dry summers (Barnett and others 2008, Westerling and others 2006). Some areas dependent on rainfall for moisture will also see increased dry-spell length. The maximum number of consecutive dry days (precipitation <1 mm) in a year is not projected to change substantially over most of the United States, except in the Southwestern United States (AZ, NM, TX) and Pacific Northwest (WA, OR, ID), which may see 5- to 10-day increases in dry-spell duration. In the Southwestern United States, the increases are expected to occur in summer months in association with changes in the North American Monsoon.

Teleconnections from tropical SST patterns are a primary control on drought occurrence in the United States (Dai 2011, Rajagopalan and others 2000). Despite substantial intermodel variability in projections of ENSO, it is expected to continue to be the dominant mode of climate variability. The interannual variability driven by ENSO provides some insights into future

drought, insofar as it reflects variance in precipitation. Broadly, the sense that wet places get wetter while the dry get drier can also be applied to temporal variations in precipitation as controlled by ENSO (Seager and others 2012). Because a warmer atmosphere can hold (and release) more water, circulation dynamics leading to greater runoff ($P - E$) will be enhanced in contrast to those that do not. An increase in interannual variability of $P - E$ of about 10–20 percent is expected across most of the continental United States, except the Southwestern United States where a decline in variance is expected (Seager and others 2012). Increases in interannual variability on the order of 30–40 percent are expected in Alaska.

Challenges for Interpreting Projections

Does a projected trend in precipitation or temperature portend a trend in drought? There are two important aspects of this question: (1) the time scale associated with the changes, and (2) whether the trends affect those extremes in weather that we term “drought.” The first point is mostly one of an appropriate datum from which to measure a shift or departure. If the future of a location is drier, does it also represent an increased drought condition? If we are conceptually contrasting two time periods as two separate ecological equilibriums, simply being drier does not necessarily imply increased drought conditions or severity if the water “needs” of the new landscape shift in conjunction with the availability. However, during the transition, as natural and human communities adjust to the shifting dryness, increased “droughtiness” is a possibility. For example, one could ask, “Is Nevada a dry place, or has it been in a drought since the end of the Pleistocene?” Sagebrush and bristlecone pine researchers may, appropriately, have different answers. Similarly, increased moisture may not preclude a future with more severe drought episodes. For example, increased variance in precipitation may produce years that are extremely challenging to a moist-adapted landscape. While this question could be taken as one of semantics, it is more appropriately applied in a quantitative context by tying characteristic time scales of processes of interest (e.g., life spans, age to reproduction, seed durability) to drought as a transient phenomenon with its own time scales associated with duration and frequency (for a given intensity). Recognizing this aspect calls for greater precision in specifying the nature of the kind of drought of concern rather than just identifying a comparatively dry period in a time series as a drought without reference to time scales.

Coupled to this concern is the lack of knowledge of how interannual to interdecadal scale climate modes (e.g., teleconnections such as ENSO, PDO, AMO) might shift in response to increased atmospheric CO_2 . There is evidence that the inability of GCMs to capture low-frequency modes of internal climate variability could lead to underestimation of risks of persistent drought (Ault and others 2014). Multiple years of drought may be more stressful to forests than single-year droughts, and the relative risks of reduced precipitation for several years to decades may not be well represented in GCMs.

The second point is that trends in means may or may not reflect changes in extremes. Projections specifically of changes in extremes or variance or identification of their trends is much more informative with respect to drought impacts (Seneviratne and others 2012). Drought is an extreme in moisture availability, and several recent studies show increased variance along with lower annual precipitation in some western U.S. mountains (Luce and others 2013, Luce and Holden 2009, Pagano and Garen 2005) (fig. 2.10). Shifts in extremes may result from shifts in the entire distribution without a change in variability, or they may result from a shift in the variability with no shift in the mean (e.g., “Summary for Policy Makers” in Field and others 2012) (fig. 2.11). A shift in variance or mean could change the probability of exceeding a threshold or proceeding into novel weather (Field and others 2012, Jentsch and others

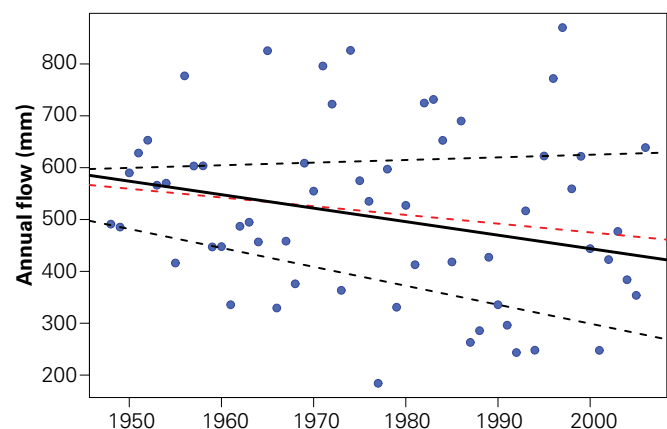


Figure 2.10—Annual runoff in the Boise River near Twin Springs, ID for water years 1948 to 2006. The dashed red line is the trend in the mean annual flow, and the solid black line is the trend in median annual flow. The upper and lower black dashed lines are the 75th and 25th percentile annual flows, respectively. Note that while the wetter years show nearly no trend, drought years (the 25th percentile) have trended significantly, with about a 30-percent decline over the period of record. This shows a shift from a narrow distribution in the 1950s to a wide one in the 2000s (this would appear as (C) in fig. 2.11).

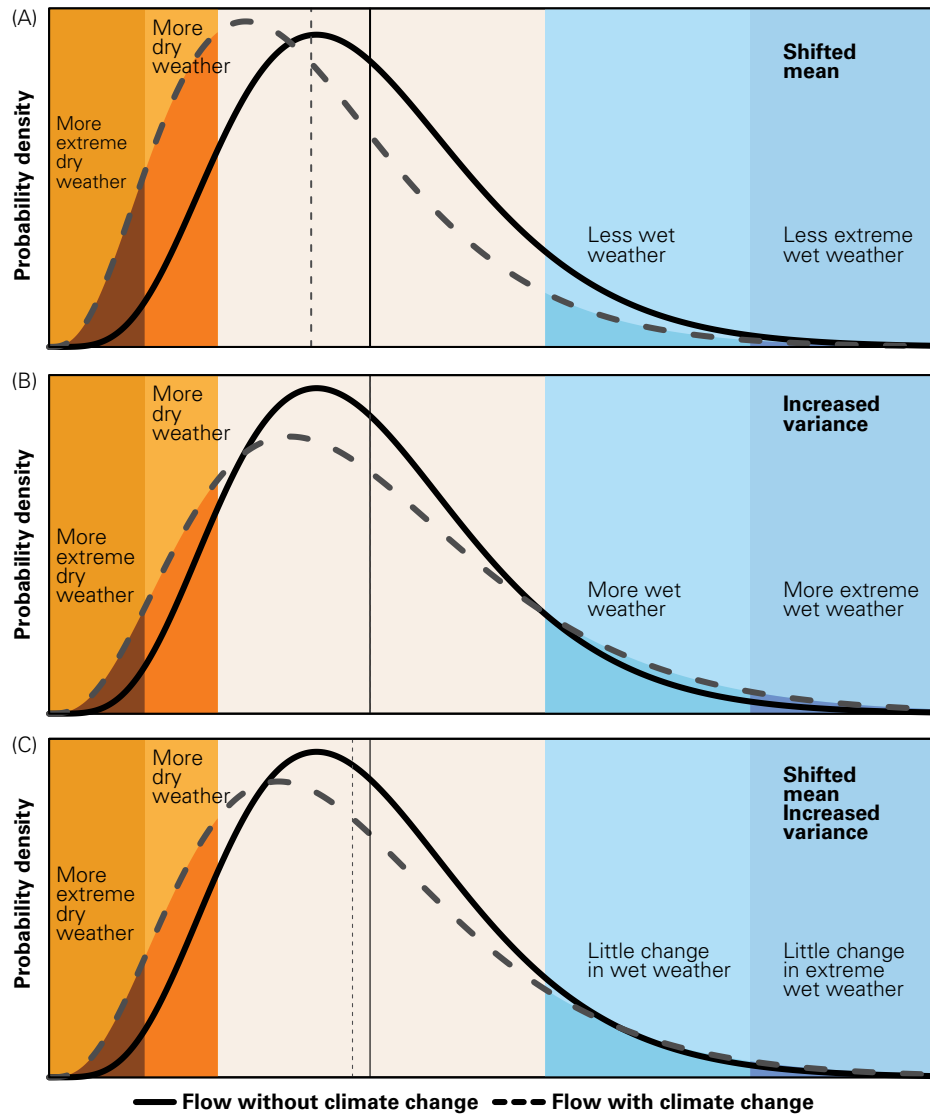


Figure 2.11—Different changes in runoff distributions between present and future climate and their effects on extreme values of the distributions: (A) effects of a simple shift of the entire distribution toward drier weather; (B) effects of an increase in runoff variability with no shift in the mean; (C) effects of an altered shape of the distribution, in this example a shift in mean weather toward drier conditions with an increase in variance. Vertical lines are means. [After fig. SPM.3 in Field and others (2012); also see Anderegg and others (2013)].

2007). These kinds of changes are important both in the context of a trend acting on existing vegetation, wherein a single crossing into unprecedented weather or drought severity is a critical concern, and in the context of potential future plant communities, which may be shaped more by the extremes in future climate than the means. Extremes, and the events associated with them, will likely be critical determinants of ecological change (Dale and others 2001, Easterling and others 2000, Jentsch 2007).

This sense of drought as an extreme is of particular concern with respect to GCM outputs, which are poor at representing interannual variability (e.g., Sperna Weiland and others 2010). Only a few GCMs accurately recreate the ENSO pattern, a driver of interannual scale variability in weather across much of the World (IPCC 2013, Seager and others 2012). Most outputs of GCM information are ensemble averages of several realizations from a given model and across models. This allows comparison of climatic averages across models, and maps of these average changes are the common maps of change shown in IPCC reports (e.g., figs. 2.7–2.9). Common downscaling procedures draw directly from this kind of information to specify an average difference for a given month or season for each GCM grid cell (Wood and others 2004). For example, interannual variability in Variable Infiltration Capacity (VIC) hydrologic projections (Vano and others 2012) is a legacy of the historical time series on which the changes in the averages are placed.

GCMs are also more challenged by precipitation estimates than other climate characteristics (Blöschl and Montanari 2010, Johnson and Sharma 2009). GCMs show substantial agreement with metrics like pressure and temperature, but notable discrepancies in precipitation, and the differences among the models are not well understood (IPCC 2013). Some of the issue is almost certainly that precipitation processes occur at scales much smaller than those of GCM grid cells (e.g., Rasmussen and others 2011). While GCMs can model general circumstances of temperature, temperature stratification, and vapor that are more or less encouraging of precipitation, they ultimately must rely on sub-grid-scale parameterizations to estimate precipitation. That is to say that semi-empirical equations or rules are applied instead of solution to partial differential equations derived from the basic physics, as is done for temperature and pressure. One consequence of the

large grid-cell size is also that most GCMs produce what amounts to a persistent drizzle (e.g., Gao and Sorooshian 1994, Pitman and others 1990), reflecting the general scale-related issue that it is almost always raining somewhere within a GCM cell, but it is usually a fairly small proportion of the area experiencing precipitation. As an addition to the problem, GCMs do not model the control that mountains place on precipitation generation, which has led to efforts to regionally downscale the GCMs to better reflect topographic influences on precipitation in mountainous areas using Regional Climate Models, which have higher spatial resolution (Rasmussen and others 2011, Salathé and others 2010).

Projections of the key climate phenomena feeding moisture to the continental United States in the summer—the North American Monsoon System (NAMS) and North Atlantic tropical cyclones—are uncertain (IPCC 2013); however, there appears to be a tendency toward drier conditions, according to the climate models with the strongest historical performance (Maloney and others 2014, Sheffield and others 2013). The most consistent projection for NAMS relevant to drought is an increase in the number of consecutive dry days by 15–40 percent (interquartile range). In the context of a warming future, an increase in the time between precipitation events could have substantial ecological importance (Adams and others 2009).

Applying Drought Projections To Predict Impacts

The overall consensus on drought projections is that there is a great deal of uncertainty, primarily because of uncertainty in projecting future precipitation; however, drought projections can be useful when placed in the proper context. Drought is a derived quantity with dimensions of severity, frequency, scale, and organization. It can be thought of as a collection of “extreme” events that must occur simultaneously to create a situation of concern, such as tree mortality or water scarcity. There is some sense that drought will intensify faster (or alternatively, drought effects will manifest more quickly during a dry spell) than it has in the past (Trenberth and others 2014). For example, “global-change-type drought” infers that drought is occurring in the context of much warmer weather (Adams and others 2009, Allen and others 2010) and, hence, the effects on forests are greater. When combined with projections of longer interstorm periods in some locations, impacts on terrestrial ecosystems could be substantial.

Summary

Historical and paleoclimatic evidence clearly shows that the nature of drought has always changed and continues to change. The direction of trends in recent history vary from region to region, with the western half of the United States indicating broadly drier conditions while the eastern regions show broadly wetter conditions. Although these patterns are often used to generalize about changing drought regimes (e.g., rarer, more frequent, more severe, or unchanging), individual findings can conflict with one another because the definitions or quantification methods for “drought” differ among many studies (Seneviratne and others 2012).

The relationship between forested landscapes and drought may differ substantially from that of the engineered or agricultural landscape. In particular, water supply thresholds may exist for particular crops or industries. In contrast, forest ecosystems often have mechanisms of resilience to drought, such that their ultimate response to drought may not relate to the *initial perturbation* after a drought event, but rather the context of that event and others like it in time and across landscapes and stream systems. While there is a well-developed science on how various biota respond to individual events, it is this longer term consequence that will have a lasting effect on species distributions.

Droughts severe enough to affect forest ecosystems may be driven primarily by periodic deficits in precipitation, as opposed to changes in potential evaporation (e.g., Abatzoglou and Kolden 2013, Holden and others 2012). Although incoming radiation is adequate in most places in the continental United States to evaporate a substantial fraction of the annual water balance (see fig. 2a in Sankarasubramanian and Vogel 2003), variation in annual precipitation is the dominant driver of variations in annual water balance (Milly and Dunne 2002). On longer time scales, however, the availability of warmer and drier air may more broadly shift many places to more consistently arid conditions. If drought is considered from the viewpoint of a global/absolute threshold, as might be the case for a particular plant or an engineered system, this broad shift could presage a drought from the point of view of system tolerance. However, if drought is defined in terms of variability over time (given a particular time-averaging window), which has substantial relevance to self-regulating or temporally dynamic systems, increasing potential evapotranspiration pressure primarily has relevance to the rapidity of drought onset after

precipitation stops. This variation in framing has been a central issue in debates on the kinds of metrics to apply in evaluating trends in droughts and making projections.

The future of drought is uncertain. One aspect of uncertainty is that precipitation projections in GCMs are fairly poor. A second aspect of uncertainty is that persistently wetter or drier conditions do not necessarily reflect drought risks in natural systems the same way that they might be observed in engineered or agricultural systems. In natural systems, there is adjustment to gradual shifts in means or even regimes; however, variability on the order of a few years to a few decades can have substantial impacts on ecosystems. These intermediate time scales pose the greatest challenge for GCM projections. Improving our understanding of temporal trends in teleconnections and climate indices may be a fruitful alternative in understanding future variations at these intermediate time scales.

Literature Cited

- Abatzoglou, J.T. 2011. Influence of the PNA on declining mountain snowpack in the Western United States. *International Journal of Climatology*. 31(8): 1135-1142.
- Abatzoglou, J.T.; Kolden, C.A. 2011. Climate change in western U.S. deserts: potential for increased wildfire and invasive annual grasses. *Rangeland Ecology & Management*. 64(5): 471-478.
- Abatzoglou, J.T.; Kolden, C.A. 2013. Relationships between climate and macroscale area burned in the Western United States. *International Journal of Wildland Fire*. 22(7): 1003-1020.
- Abatzoglou, J.T.; Rupp, D.E.; Mote, P.W. 2014. Seasonal climate variability and change in the Pacific Northwest of the United States. *Journal of Climate*. 27(5): 2125-2142.
- Adams, H.D.; Guardiola-Claramonte, M.; Barron-Gafford, G.A. [and others]. 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences*. 106(17): 7063-7066.
- Allen, C.D.; Macalady, A.K.; Chenchouni, H. [and others]. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*. 259(4): 660-684.
- Alley, W.M. 1984. The Palmer drought severity index: limitations and assumptions. *Journal of Climate and Applied Meteorology*. 23(7): 1100-1109.
- Anderegg, L.D.; Anderegg, W.R.; Berry, J.A. 2013. Not all droughts are created equal: translating meteorological drought into woody plant mortality. *Tree Physiology*. 33(7): 672-683.
- Anderson, R.S.; Smith, S.J. 1994. Paleoclimatic interpretations of meadow sediment and pollen stratigraphies from California. *Geology*. 22(8): 723-726.
- Andreadis, K.M.; Lettenmaier, D.P. 2006. Trends in 20th century drought over the continental United States. *Geophysical Research Letters*. 33(10): L10403. 4 p. doi:10.1029/2006GL025711. [Published online: May 26, 2004].

- Ault, T.R.; Cole, J.E.; Overpeck, J.T. [and others]. 2014. Assessing the risk of persistent drought using climate model simulations and paleoclimate data. *Journal of Climate*. 27(20): 7529-7549.
- Baker, R.G.; Maher, L.J.; Chumbley, C.A.; Van Zant, K.L. 1992. Patterns of Holocene environmental change in the Midwestern United States. *Quaternary Research*. 37(3): 379-389.
- Ballard, T.; Seager, R.; Smerdon, J.E. [and others]. 2014. Hydroclimate variability and change in the Prairie Pothole Region: the "duck factory" of North America. *Earth Interactions*. (18): 1-28.
- Barnett, T.P.; Pierce, D.W.; Hidalgo, H.G. [and others]. 2008. Human-induced changes in the hydrology of the Western United States. *Science*. 319: 1080-1083.
- Benson, L.; Kashgarian, M.; Rye, R. [and others]. 2002. Holocene multidecadal and multicentennial droughts affecting Northern California and Nevada. *Quaternary Science Reviews*. 21(4): 659-682.
- Berghuijs, W.; Woods, R.; Hrachowitz, M. 2014. A precipitation shift from snow towards rain leads to a decrease in streamflow. *Nature Climate Change*. 4: 583-596.
- Betancourt, J.L. 1990. Late Quaternary biogeography of the Colorado Plateau. In: Betancourt, J.; van Devender, T.R.; Martin, P.S., eds. *Packrat middens: the last 40,000 years of biotic change*. Chapter 12. Tucson, AZ: University of Arizona Press: 259-293.
- Blöschl, G. 1996. Scale and scaling in hydrology. *Habilitationschrift*. Wien: Weiner Mitteilungen Wasser Abwasser Gewässer. 346 p.
- Blöschl, G.; Montanari, A. 2010. Climate change impacts—throwing the dice? *Hydrological Processes*. 24(3): 374-381.
- Blöschl, G.; Sivapalan, M.; Wagener, T. [and others], eds. 2013. *Runoff prediction in ungauged basins: synthesis across processes, places and scales*. Cambridge: Cambridge University Press. 465 p.
- Booth, R.K. 2002. Testate amoebae as paleoindicators of surface-moisture changes on Michigan peatlands: modern ecology and hydrological calibration. *Journal of Paleolimnology*. 28(3): 329-348.
- Booth, R.K.; Jackson, S.T.; Forman, S.L. [and others]. 2005. A severe centennial-scale drought in midcontinental North America 4200 years ago and apparent global linkages. *The Holocene*. 15(3): 321-328.
- Booth, R.K.; Jackson, S.T.; Sousa, V.A. [and others]. 2012. Multi-decadal drought and amplified moisture variability drove rapid forest community change in a humid region. *Ecology*. 93(2): 219-226.
- Bradbury, J.A.; Dingman, S.L.; Keim, B.D. 2002. New England drought and relations with large scale atmospheric circulation patterns. 38(5): 1287-1299.
- Bradbury, J.A.; Keim, B.D.; Wake, C.P. 2003. The influence of regional storm tracking and teleconnections on winter precipitation in the Northeastern United States. *Annals of the Association of American Geographers*. 93(3): 544-556.
- Bradley, R.S. 1999. *Paleoclimatology: reconstructing climates of the Quaternary*. 2d ed. Vol. 68. Burlington, MA: Academic Press. 610 p.
- Bradley, R.S.; Hughes, M.K.; Diaz, H.F. 2003. Climate in medieval time. *Science*. 302(5644): 404-405.
- Breshears, D.D.; Cobb, N.S.; Rich, P.M. [and others]. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences*. 102: 15,144-15,148.
- Brunelle, A.; Whitlock, C.; Bartlein, P.; Kipfmüller, K. 2005. Holocene fire and vegetation along environmental gradients in the Northern Rocky Mountains. *Quaternary Science Reviews*. 24(20): 2281-2300.
- Budyko, M.I. 1974. *Climate and life*. International Geophysics Series. Vol. 18. San Diego, CA: Academic Press. 508 p.
- Cayan, D.R.; Kammerdiener, S.A.; Dettinger, M.D. [and others]. 2001. Changes in the onset of spring in the Western United States. *Bulletin of the American Meteorological Society*. 82(3): 399-415.
- Cayan, D.R.; Redmond, K.T.; Riddle, L.G. 1999. ENSO and hydrologic extremes in the Western United States. *Journal of Climate*. 12(9): 2881-2893.
- Clark, G.M. 2010. Changes in patterns of streamflow from unregulated watersheds in Idaho, western Wyoming, and northern Nevada. *Journal of the American Water Resources Association*. 46: 486-497.
- Cleaveland, M.K.; Stahle, D.W. 1989. Tree ring analysis of surplus and deficit runoff in the White River, Arkansas. *Water Resources Research*. 25(6): 1391-1401.
- Coats, S.; Cook, B.I.; Smerdon, J.E.; Seager, R. 2014. North American pan-continental drought in model simulations of the last millennium. *Journal of Climate*. 28(5): 2025-2043.
- Cook, B.I.; Ault, T.R.; Smerdon, J.E. 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. *Science Advances*. 1(1): 7 p. doi: 10.1126/sciadv.1400082. [Published online: February 1, 2015].
- Cook, B.I.; Cook, E.R.; Anchukaitis, K.J. [and others]. 2011. Forced and unforced variability of twentieth century North American droughts and pluvials. *Climate Dynamics*. 37(5-6): 1097-1110.
- Cook, B.I.; Smerdon, J.E.; Seager, R.; Coats, S. 2014a. Global warming and 21st century drying. *Climate Dynamics*. 43(9-10): 2607-2627.
- Cook, B.I.; Smerdon, J.E.; Seager, R.; Cook, E.R. 2014b. Pan-continental droughts in North America over the last millennium. *Journal of Climate*. 27(1): 383-397.
- Cook, E.R.; Kablack, M.A.; Jacoby, G.C. 1988. The 1986 drought in the Southeastern United States: how rare an event was it? *Journal of Geophysical Research: Atmospheres* (1984–2012). 93(D11): 14,257-14,260. doi: 10.1029/JD093iD11p14257. [Published online: September 21, 2012].
- Cook, E.R.; Krusic, P.J. 2004. The North American Drought Atlas [Homepage]. <http://iridl.ldeo.columbia.edu/SOURCES/LDEO/TRL/NADA2004/pdsi-atlas.html>. [Date accessed: August 27, 2014].
- Cook, E.R.; Seager, R.; Cane, M.A.; Stahle, D.W. 2007. North American drought: reconstructions, causes, and consequences. *Earth-Science Reviews*. 81(1): 93-134.
- Cook, E.R.; Seager, R.; Heim, R.R. [and others]. 2010. Megadroughts in North America: placing IPCC projections of hydroclimatic change in a long-term palaeoclimate context. *Journal of Quaternary Science*. 25(1): 48-61.
- Cook, E.R.; Woodhouse, C.A.; Eakin, C.M. [and others]. 2004. Long-term aridity changes in the Western United States. *Science*. 306(5698): 1015-1018.
- Dai, A. 2011. Drought under global warming: a review. *Wiley Interdisciplinary Reviews: Climate Change*. 2(1): 45-65.
- Dai, A. 2013. Increasing drought under global warming in observations and models. *Nature Climate Change*. 3(1): 52-58.

- Dai, A.; Trenberth, K.E. 2002. Estimates of freshwater discharge from continents: latitudinal and seasonal variations. *Journal of Hydrometeorology*. 3(6): 660-687.
- Dale, V.H.; Joyce, L.A.; McNulty, S. [and others]. 2001. Climate change and forest disturbances. *BioScience*. 51(9): 723-734.
- Dean, J.S. 1996. Kayenta Anasazi settlement transformations in northeastern Arizona, AD 1150 to 1350. In: Adler, M.A., ed. *The prehistoric Pueblo world, AD 1150-1350*. Tucson, AZ: University of Arizona Press: 29-47.
- Dean, W.E.; Ahlbrandt, T.S.; Anderson, R.Y.; Bradbury, J.P. 1996. Regional aridity in North America during the middle Holocene. *The Holocene*. 6(2): 145-155.
- Dettinger, M.; Redmond, K.; Cayan, D. 2004. Winter orographic precipitation ratios in the Sierra Nevada—large-scale atmospheric circulations and hydrologic consequences. *Journal of Hydrometeorology*. 5(6): 1102-1116.
- Dillon, G.K.; Holden, Z.A.; Morgan, P. [and others]. 2011. Both topography and climate affected forest and woodland burn severity in two regions of the Western U.S., 1984 to 2006. *Ecosphere*. 2(12): 130. 33 p. doi: 10.1890/ES11-00271.1. [Published online: December 12, 2011].
- Dittmer, K. 2013. Changing streamflow on Columbia Basin tribal lands—climate change and salmon. *Climatic Change*. 120(3): 627-641.
- Douglass, A.E. 1920. Evidence of climatic effects in the annual rings of trees. *Ecology*. 1(1): 24-32.
- Dudley, R.W.; Hodgkins, G.A. 2013. Historical groundwater trends in northern New England and relations with streamflow and climatic variables. *Journal of the American Water Resources Association*. 49(5): 1198-1212.
- Dunham, J.B.; Young, M.K.; Gresswell, R.E.; Rieman, B.E. 2003. Effects of fire on fish populations: landscape perspectives on persistence of native fishes and nonnative fish invasions. *Forest Ecology and Management*. 178(1-2): 183-196.
- Dwire, K.A.; Kauffman, J.B. 2003. Fire and riparian ecosystems in landscapes of the Western U.S.A. *Forest Ecology and Management*. 178: 61-74.
- Easterling, D.R.; Evans, J.L.; Groisman, P.Y. [and others]. 2000. Observed variability and trends in extreme climate events: a brief review. *Bulletin of the American Meteorological Society*. 81(3): 417-425.
- Elsner, M.M.; Cuo, L.; Voisin, N. [and others]. 2010. Implications of 21st century climate change for the hydrology of Washington State. *Climatic Change*. 102: 225-260.
- Falke, J.A.; Fausch, K.D.; Magelky, R. [and others]. 2011. The role of groundwater pumping and drought in shaping ecological futures for stream fishes in a dryland river basin of the western Great Plains, USA. *Ecology*. 4(5): 682-697.
- Fausch, K.D.; Torgersen, C.E.; Baxter, C.V.; Li, H.W. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes—a continuous view of the river is needed to understand how processes interacting among scales set the context for stream fishes and their habitat. *BioScience*. 52(6): 483-498.
- Field, C.B.; Barros, V.; Stocker, T.F. [and others], eds. 2012. *Managing the risks of extreme events and disasters to advance climate change adaptation (SREX)*. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change. New York: Cambridge University Press. 582 p.
- Foster, D.R.; Oswald, W.W.; Faison, E.K. [and others]. 2006. A climatic driver for abrupt mid-Holocene vegetation dynamics and the hemlock decline in New England. *Ecology*. 87(12): 2959-2966.
- Fritts, H.C. 1976. *Tree rings and climate*. New York: Academic Press. 567 p.
- Fu, G.; Charles, S.P.; Chiew, F.H. 2007. A two-parameter climate elasticity of streamflow index to assess climate change effects on annual streamflow. *Water Resources Research*. 43(11): W11419. 12 p. doi: 10.1029/2007WR005890. [Published online: November 24, 2007].
- Fye, F.K.; Stahle, D.W.; Cook, E.R. 2003. Paleoclimatic analogs to twentieth-century moisture regimes across the United States. *Bulletin of the American Meteorological Society*. 84(7): 901-909.
- Gao, X.; Sorooshian, S. 1994. A stochastic precipitation disaggregation scheme for GCM applications. *Journal of Climate*. 7(2): 238-247.
- Graham, N.; Ammann, C.; Fleitmann, D. [and others]. 2011. Support for global climate reorganization during the "Medieval Climate Anomaly." *Climate Dynamics*. 37(5-6): 1217-1245.
- Graham, N.E.; Hughes, M.K.; Ammann, C.M. [and others]. 2007. Tropical Pacific—mid-latitude teleconnections in medieval times. *Climatic Change*. 83(1-2): 241-285.
- Graumlich, L.J. 1993. A 1000-year record of temperature and precipitation in the Sierra Nevada. *Quaternary Research*. 39(2): 249-255.
- Griffin, D.; Anchukaitis, K.J. 2014. How unusual is the 2012–2014 California drought? *Geophysical Research Letters*. 41(24): 9017-9023.
- Griffin, D.; Woodhouse, C.A.; Meko, D.M. [and others]. 2013. North American monsoon precipitation reconstructed from tree-ring latewood. *Geophysical Research Letters*. 40(5): 954-958.
- Grissino-Mayer, H.D. 1996. A 2129-year reconstruction of precipitation for northwestern New Mexico, U.S.A. In: Dean, J.S.; Meko, D.M.; Swetnam, T.W., eds. *Tree rings, environment, and humanity*. *Radiocarbon*: 191-204.
- Groisman, P.Y.; Knight, R.W.; Karl, T.R. 2001. Heavy precipitation and high streamflow in the contiguous United States: Trends in the twentieth century. *Bulletin of the American Meteorological Society*. 82(2): 219-246.
- Guardiola-Claramonte, M.; Troch, P.; Breshears, D. [and others]. 2011. Streamflow response in semi-arid basins following drought-induced tree die-off: indirect climate impact on hydrology. *Journal of Hydrology*. 406: 225-233. doi:10.1016/j.jhydrol.2011.06.017. [Published online: July 7, 2011].
- Hamlet, A.F.; Elsner, M.M.; Mauger, G.S. [and others]. 2013. An overview of the Columbia Basin climate change scenarios project: approach, methods, and summary of key results. *Atmosphere-Ocean*. 51(4): 392-415.
- Hardt, B.; Rowe, H.D.; Springer, G.S. [and others]. 2010. The seasonality of east central North American precipitation based on three coeval Holocene speleothems from southern West Virginia. *Earth and Planetary Science Letters*. 295(3-4): 342-348.
- Harman, C.; Troch, P.; Sivapalan, M. 2011. Functional model of water balance variability at the catchment scale: 2. Elasticity of fast and slow runoff components to precipitation change in the continental United States. *Water Resources Research*. 47(2): W02523. 12 p. doi: 10.1029/2010WR009656. [Published online: February 16, 2011].

- Harvey, B.C.; Nakamoto, R.J.; White, J.L. 2006. Reduced streamflow lowers dry-season growth of rainbow trout in a small stream. *Transactions of the American Fisheries Society*. 135: 998-1005.
- Haslinger, K.; Koffler, D.; Schöner, W.; Laaha, G. 2014. Exploring the link between meteorological drought and streamflow: Effects of climate-catchment interaction. *Water Resources Research*. 50(3): 2468-2487.
- Hayes, M.; Svoboda, M.; Wall, N.; Widhalm, M. 2011. The Lincoln declaration on drought indices: universal meteorological drought index recommended. *Bulletin of the American Meteorological Society*. 92(4): 485-488.
- Hayhoe, K.; Wake, C.P.; Huntington, T.G. [and others]. 2007. Past and future changes in climate and hydrological indicators in the U.S. Northeast. *Climate Dynamics*. 28(4): 381-407.
- Hessburg, P.F.; Agee, J.K. 2003. An environmental narrative of inland northwest United States forests, 1800–2000. *Forest Ecology and Management*. 178(1-2): 23-59.
- Heyerdahl, E.K.; Morgan, P.; Riser II, J.P. 2008. Multi-season climate synchronized historical fires in dry forests (1650–1900), Northern Rockies, U.S.A. *Ecology*. 89(3): 705-716.
- Hoerling, M.P.; Eischeid, J.K.; Quan, X.-W. [and others]. 2012. Is a transition to semipermanent drought conditions imminent in the U.S. Great Plains? *Journal of Climate*. 25(24): 8380-8386.
- Holden, Z.A.; Luce, C.H.; Crimmins, M.A.; Morgan, P. 2012. Wildfire extent and severity correlated with annual streamflow distribution and timing in the Pacific Northwest, U.S.A (1984–2005). *Ecohydrology*. 5(5): 677-684.
- Holliday, V.T. 1989. Middle Holocene drought on the southern High Plains. *Quaternary Research*. 31(1): 74-82.
- Hubeny, J.B.; King, J.W.; Reddin, M. 2011. Northeast U.S. precipitation variability and North American climate teleconnections interpreted from late Holocene varved sediments. *Proceedings of the National Academy of Sciences*. 108(44): 17,895-17,900.
- Huntington, T.G.; Richardson, A.D.; McGuire, K.J.; Hayhoe, K. 2009. Climate and hydrological changes in the Northeastern United States: recent trends and implications for forested and aquatic ecosystems. *Canadian Journal of Forest Research* 39(2): 199-212.
- Hurst, H.E. 1951. Long-term storage capacity of reservoirs. *Transactions of the American Society of Civil Engineers*. 116: 770-799.
- Intergovernmental Panel on Climate Change (IPCC). 2013. *Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. New York: Cambridge University Press. 1535 p.
- Ireland, A.W.; Booth, R.K. 2011. Hydroclimatic variability drives episodic expansion of a floating peat mat in a North American kettlehole basin. *Ecology*. 92: 11-18.
- Isaak, D.J.; Wollrab, S.; Horan, D.; Chandler, G. 2012. Climate change effects on stream and river temperatures across the Northwest U.S. from 1980–2009 and implications for salmonid fishes. *Climatic Change*. 113: 499-524.
- Jackson, S.T.; Booth, R.K. 2002. The role of Late Holocene climate variability in the expansion of yellow birch in the western Great Lakes region. *Diversity and Distributions*. 8: 275-284.
- Jacoby, G.C., Jr.; D'Arrigo, R. 1989. Reconstructed Northern Hemisphere annual temperature since 1671 based on high-latitude tree-ring data from North America. *Climatic Change*. 14(1): 39-59.
- Jentsch, A. 2007. The challenge to restore processes in face of nonlinear dynamics—on the crucial role of disturbance regimes. *Restoration Ecology*. 15(2): 334-339.
- Jentsch, A.; Kreyling, J.; Beierkuhnlein, C. 2007. A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment*. 5(7): 365-374.
- Johnson, F.; Sharma, A. 2009. Measurement of GCM skill in predicting variables for hydroclimatological assessments. *Journal of Climate*. 22(16): 4373–4382.
- Kam, J.; Sheffield, J.; Wood, E.F. 2014. A multi-scale analysis of drought and pluvial mechanisms for the Southeastern United States. *Journal of Geophysical Research: Atmospheres*. 119(12): 7348-7367.
- Keetch, J.J.; Byram, G.M. 1968. A drought index for forest fire control. Res. Pap. SE-38. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 32 p.
- Kingston, D.G.; McGregor, G.R.; Hannah, D.M.; Lawler, D.M. 2007. Large-scale climatic controls on New England river flow. *Journal of Hydrometeorology*. 8(3): 367-379.
- Kirchner, J.W. 2009. Catchments as simple dynamical systems: catchment characterization, rainfall-runoff modeling, and doing hydrology backward. *Water Resources Research*. 45(2): W02429. 34 p. doi:10.1029/2008WR006912. [Published online: February 25, 2009].
- Kleppe, J.; Brothers, D.S.; Kent, G.M. [and others]. 2011. Duration and severity of Medieval drought in the Lake Tahoe Basin. *Quaternary Science Reviews*. 30(23): 3269-3279.
- Klos, R.J.; Wang, G.G.; Bauerle, W.L.; Rieck, J.R. 2009. Drought impact on forest growth and mortality in the Southeast U.S.A: an analysis using Forest Health and Monitoring data. *Ecological Applications*. 19(3): 699-708.
- Knight, T.A.; Meko, D.M.; Baisan, C.H. 2010. A bimillennial-length tree-ring reconstruction of precipitation for the Tavaputs Plateau, Northeastern Utah. *Quaternary Research*. 73(1): 107-117.
- Laaha, G.; Demuth, S.; Hisdal, H. [and others]. 2013. Prediction of low flows in ungauged basins. Chapter 8. In: Blöschl, G.; Sivapalan, M.; Wagener, T. [and others], eds. *Runoff prediction in ungauged basins synthesis across processes, places and scales*. United Kingdom: Cambridge University Press: 163-188.
- LaMarche, V.C. 1973. Holocene climatic variations inferred from treeline fluctuations in the White Mountains, California. *Quaternary Research*. 3(4): 632-660.
- LaMarche, V.C. 1974. Paleoclimatic inference from long tree-ring records. *Science*. 183: 1043-1048.
- Lamb, H.H. 1965. The early medieval warm epoch and its sequel. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 1: 13-37.
- Laseter, S.H.; Ford, C.R.; Vose, J.M.; Swift, L.W. 2012. Long-term temperature and precipitation trends at the Coweeta Hydrologic Laboratory, Otto, North Carolina, U.S.A. *Hydrology Research*. 43(6): 890.
- Leppi, J.C.; DeLuca, T.H.; Harrar, S.W.; Running, S.W. 2011. Impacts of climate change on August stream discharge in the Central-Rocky Mountains. *Climatic Change*. 112: 997-1014. doi: 10.1007/s10584-011-0235-1. [Published online: September 9, 2011].
- Li, W.; Li, L.; Fu, R. [and others]. 2011. Changes to the North Atlantic subtropical high and its role in the intensification of summer rainfall variability in the Southeastern United States. *Journal of Climate*. 24(5): 1499-1506.

- Lins, H.F.; Slack, J.R. 2005. Seasonal and regional characteristics of U.S. streamflow trends in the United States from 1940 to 1999. *Physical Geography*. 26(6): 489-501.
- Littell, J.S.; McKenzie, D.; Peterson, D.L.; Westerling, A.L. 2009. Climate and wildfire area burned in western U.S. ecoregions, 1916–2003. *Ecological Applications*. 19(4): 1003-1021.
- Lloyd, A.H.; Graumlich, L.J. 1997. Holocene dynamics of treeline forests in the Sierra Nevada. *Ecology*. 78(4): 1199-1210.
- Lorimer, C.G. 1985. Methodological considerations in the analysis of forest disturbance history. *Canadian Journal of Forest Research*. 15(1): 200-213.
- Luce, C.H.; Abatzoglou, J.T.; Holden, Z.A. 2013. The missing mountain water: slower westerlies decrease orographic enhancement in the Pacific Northwest U.S.A. *Science*. 342(6164): 1360-1364.
- Luce, C.H.; Holden, Z.A. 2009. Declining annual streamflow distributions in the Pacific Northwest United States, 1948–2006. *Geophysical Research Letters*. 36: L16401. 6 p. doi: 10.1029/2009GL039407. [Published online: August 22, 2009].
- Luce, C.; Morgan, P.; Dwire, K. [and others]. 2012. Climate change, forests, fire, water, and fish: building resilient landscapes, streams, and managers. Gen. Tech. Rep. RMRS-GTR-290. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 207 p.
- MacDonald, G.M. 2007. Severe and sustained drought in southern California and the West: present conditions and insights from the past on causes and impacts. *Quaternary International*. 173-174: 87-100.
- MacDonald, G.M.; Case, R.A. 2005. Variations in the Pacific Decadal Oscillation over the past millennium. *Geophysical Research Letters*. 32(8): L08703. 4 p. doi: 10.1029/2005GL022478. [Published online: April 20, 2005].
- Maloney, E.D.; Camargo, S.J.; Chang, E. [and others]. 2014. North American climate in CMIP5 experiments, part III: assessment of twenty-first-century projections. *Journal of Climate*. 27(6): 2230-2270.
- Mann, M.E.; Zhang, Z.; Rutherford, S. [and others]. 2009. Global signatures and dynamical origins of the Little Ice Age and Medieval Climate Anomaly. *Science*. 326(5957): 1256-1260.
- Mantua, N.; Hare, S.; Zhang, Y. [and others]. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorology Society*. 78: 1069-1079.
- Manuel, J. 2008. Drought in the Southeast: lessons for water management. *Environmental Health Perspectives*. 116(4): A168-71.
- Marsicek, J.P.; Shuman, B.; Brewer, S. [and others]. 2013. Moisture and temperature changes associated with the mid-Holocene Tsuga decline in the Northeastern United States. *Quaternary Science Reviews*. 80(0): 129-142.
- Matonse, A.H.; Frei, A. 2013. A seasonal shift in the frequency of extreme hydrological events in southern New York State. *Journal of Climate*. 26(23): 9577-9593.
- McCabe, G.J.; Wolock, D.M. 2002. A step increase in streamflow in the conterminous United States. *Geophysical Research Letters*. 29(24): 2185.
- McEwan, R.W.; Dyer, J.M.; Pederson, N. 2011. Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. *Ecography*. 34(2): 244-256.
- McKee, T.B.; Doesken, N.J.; Kleist, J. 1993. The relationship of drought frequency and duration to time scales. In: *Proceedings of the 8th Conference on Applied Climatology*. 17. Boston, MA: American Meteorological Society: 179-183.
- McKelvey, K.S.; Copeland, J.P.; Schwartz, M.K. [and others]. 2011. Climate change predicted to shift wolverine distributions, connectivity, and dispersal corridors. *Ecological Applications*. 21(8): 2882-2897.
- Meko, D.; Cook, E.R.; Stahle, D.W. [and others]. 1993. Spatial patterns of tree-growth anomalies in the United States and southeastern Canada. *Journal of Climate*. 6(9): 1773-1786.
- Meko, D.M.; Stahle, D.W.; Griffin, D.; Knight, T.A. 2011. Inferring precipitation-anomaly gradients from tree rings. *Quaternary International*. 235(1): 89-100.
- Meko, D.M.; Therrell, M.D.; Baisan, C.H.; Hughes, M.K. 2001. Sacramento River flow reconstructed to AD 869 from tree rings. *Journal of the American Water Resources Association*. 37(4): 1029-1039.
- Meko, D.M.; Woodhouse, C.A.; Baisan, C.A. [and others]. 2007. Medieval drought in the upper Colorado River Basin. *Geophysical Research Letters*. 34(10): L10705. 5 p. doi: 10.1029/2007GL029988. [Published online: May 24, 2007].
- Melillo, J.M.; Richmond, T.; Yohe, G.W. 2014. Climate change impacts in the United States: the third national climate assessment: U.S. Global Change Research Program. 841 p. doi:10.7930/J0Z31WJ2. <http://nca2014.globalchange.gov>. [Date accessed: October 14, 2015].
- Menking, K.M.; Peteet, D.M.; Anderson, R.Y. 2012. Late-glacial and Holocene vegetation and climate variability, including major droughts, in the Sky Lakes region of southeastern New York State. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 353-355(0): 45-59.
- Mensing, S.A.; Benson, L.V.; Kashgarian, M.; Lund, S. 2004. A Holocene pollen record of persistent droughts from Pyramid Lake, Nevada, U.S.A. *Quaternary Research*. 62(1): 29-38.
- Mensing, S.A.; Sharpe, S.E.; Tunno, I. [and others]. 2013. The late Holocene dry period: multiproxy evidence for an extended drought between 2800 and 1850 cal yr BP across the central Great Basin, U.S.A. *Quaternary Science Reviews*. 78: 266-282.
- Millar, C.I.; King, J.C.; Westfall, R.D. [and others]. 2006. Late Holocene forest dynamics, volcanism, and climate change at Whitewing Mountain and San Joaquin Ridge, Mono County, Sierra Nevada, CA, U.S.A. *Quaternary Research*. 66(2): 273-287.
- Millett, B.; Johnson, W.C.; Guntenspergen, G. 2009. Climate trends of the North American Prairie Pothole Region 1906–2000. *Climatic Change*. 93(1-2): 243-267.
- Milly, P.C.D. 1992. Potential evaporation and soil moisture in general circulation models. *Journal of Climate*. 5(3): 209-226.
- Milly, P.C.D.; Dunne, K.A. 2002. Macroscale water fluxes 2. Water and energy supply control of their interannual variability. *Water Resources Research*. 38(10): 1206. doi:10.1029/2001WR000760. [Published online: October 23, 2002].
- Minckley, T.A.; Booth, R.K.; Jackson, S.T. 2011. Response of arboreal pollen abundance to late-Holocene drought events in the upper Midwest, U.S.A. *The Holocene*. 22(5): 531-539.
- Monteith, J.L. 1965. Evaporation and environment. In: Fogg, G.E., ed. *Symposium of the Society for Experimental Biology: The State and Movement of Water in Living Organisms*, Vol. 19. New York: Cambridge University Press: 205-233.

- Mote, P.W. 2003.** Trends in snow water equivalent in the Pacific Northwest and their climatic causes. *Geophysical Research Letters*. 30: 1601-1604.
- Mote, P.W.; Hamlet, A.F.; Clark, M.P.; Lettenmaier, D.P. 2005.** Declining mountain snowpack in western North America. *Bulletin of the American Meteorological Society*. 86(11): 39-49.
- Mulholland, P.J.; Best, G.R.; Coutant, C.C. [and others]. 1997.** Effects of climate change on freshwater ecosystems of the South-eastern United States and the Gulf Coast of Mexico. *Hydrological Processes*. 11(8): 949-970.
- Namias, J. 1966.** Nature and possible causes of the Northeastern United States drought during 1962–65. *Monthly Weather Review*. 94(9): 543-554.
- Newby, P.E.; Shuman, B.N.; Donnelly, J.P. [and others]. 2014.** Centennial-to-millennial hydrologic trends and variability along the North Atlantic Coast, U.S.A., during the Holocene. *Geophysical Research Letters*. 41(12): 4300-4307.
- Newby, P.E.; Shuman, B.N.; Donnelly, J.P.; MacDonald, D. 2011.** Repeated century-scale droughts over the past 13,000 yr near the Hudson River watershed, U.S.A. *Quaternary Research*. 75(3): 523-530.
- Nichols, J.E.; Huang, Y. 2012.** Hydroclimate of the Northeastern United States is highly sensitive to solar forcing. *Geophysical Research Letters*. 39(4): 1-5.
- Ning, L.; Bradley, R.S. 2014.** Winter precipitation variability and corresponding teleconnections over the Northeastern United States. *Journal of Geophysical Research: Atmospheres*. 119(13): 7931-7945.
- Pagano, T.; Garen, D. 2005.** A recent increase in western U.S. streamflow variability and persistence. *Journal of Hydrometeorology*. 6: 173-179.
- Palmer, W.C. 1965.** Meteorological drought. Research Paper No. 45. Washington, DC: U.S. Department of Commerce, Weather Bureau. 58 p.
- Patterson, L.A.; Lutz, B.; Doyle, M.W. 2013.** Characterization of drought in the South Atlantic, United States. *Journal of the American Water Resources Association*. 49(6): 1-13.
- Pedersen, B.S. 1998.** The role of stress in the mortality of midwestern oaks as indicated by growth prior to death. *Ecology*. 79(1): 79-93.
- Pederson, D.; Peteet, D.; Kurdyla, D.; Guilderson, T. 2005.** Medieval warming, Little Ice Age, and European impact on the environment during the last millennium in the lower Hudson Valley, New York, U.S.A. *Quaternary Research*. 63(3): 238-249.
- Pederson, G.T.; Betancourt, J.L.; McCabe, G.J. 2013a.** Regional patterns and proximal causes of the recent snowpack decline in the Rocky Mountains, U.S. *Geophysical Research Letters* 40(9): 1811–1816.
- Pederson, N.; Bell, A.; Knight, T.A. [and others]. 2012.** A long-term perspective on a modern drought in the American Southeast. *Environmental Research Letters*. 7(1): 014034. 8 p. doi:10.1088/1748-9326/7/1/014034. [Published online: March 14, 2012].
- Pederson, N.; Bell, A.R.; Cook, E.R. [and others]. 2013b.** Is an epic pluvial masking the water insecurity of the greater New York City region? *Journal of Climate*. 26(4): 1339-1354.
- Pederson, N.; Dyer, J.M.; McEwan, R.W. [and others]. 2014.** The legacy of episodic climatic events in shaping temperate, broadleaf forests. *Ecological Monographs*. 84: 599-620.
- Piechota, T.C.; Dracup, J.A. 1996.** Drought and regional hydrologic variation in the United States: associations with the El Niño-Southern Oscillation. *Water Resources Research*. 32(5): 1359-1373.
- Pitman, A.; Henderson-Sellers, A.; Yang, Z. 1990.** Sensitivity of regional climates to localized precipitation in global models. *Nature*. 346(6286): 734-737.
- Potter, N.; Chiew, F. 2011.** An investigation into changes in climate characteristics causing the recent very low runoff in the southern Murray-Darling Basin using rainfall-runoff models. *Water Resources Research*. 47(12): W00G10. 12 p. doi: 10.1029/2010WR010333. [Published online: October 18, 2011].
- Potter, N.; Petheram, C.; Zhang, L. 2011.** Sensitivity of streamflow to rainfall and temperature in south-eastern Australia during the recent drought. In: MODSIM2011—19th International Congress on Modelling and Simulation. 12–16 December 2011. Perth, WA: Modelling and Simulation Society of Australia and New Zealand: 3636-3642.
- PRISM. 2013.** PRISM Climate Dataset. Corvallis, OR: PRISM Climate Group. <http://prism.oregonstate.edu>. [Date accessed: June 10, 2014].
- Rajagopalan, B.; Cook, E.; Lall, U.; Ray, B.K. 2000.** Spatiotemporal variability of ENSO and SST teleconnections to summer drought over the United States during the twentieth century. *Journal of Climate*. 13(24): 4244-4255.
- Rasmussen, R.; Liu, C.; Ikeda, K. [and others]. 2011.** High-resolution coupled climate runoff simulations of seasonal snowfall over Colorado: a process study of current and warmer climate. *Journal of Climate*. 24(12): 3015-3048.
- Redmond, K.T.; Koch, R.W. 1991.** Surface climate and streamflow variability in the Western United States and their relationship to large-scale circulation indices. *Water Resources Research*. 27(9): 2381-2399.
- Regonda, S.; Rajagopalan, B.; Clark, M.; Pitlick, J. 2005.** Seasonal cycle shifts in hydroclimatology over the Western United States. *Journal of Climate*. 18(2): 372-384.
- Rieman, B.E.; Lee, D.C.; Burns, D. [and others]. 2003.** Status of native fishes in the Western United States and issues for fire and fuels management. *Forest Ecology and Management*. 178(1-2): 197-211.
- Riley, K.L.; Abatzoglou, J.T.; Grenfell, I.C. [and others]. 2013.** The relationship of large fire occurrence with drought and fire danger indices in the Western U.S.A, 1984–2008: the role of temporal scale. *International Journal of Wildland Fire*. 22(7): 894-909.
- Ropelewski, C.F.; Halpert, M.S. 1986.** North American precipitation and temperature patterns associated with the El Niño/Southern Oscillation (ENSO). *Monthly Weather Review*. 114(12): 2352-2362.
- Ropelewski, C.F.; Halpert, M.S. 1987.** Global and regional scale precipitation patterns associated with the El Niño/Southern Oscillation. *Monthly Weather Review*. 115(8): 1606-1626.
- Roswintarti, O.; Niyogi, D.S.; Raman, S. 1998.** Teleconnections between tropical Pacific sea surface temperature anomalies and North Carolina precipitation anomalies during El Niño events. *Geophysical Research Letters*. 25(22): 4201-4204.
- Routson, C.C.; Woodhouse, C.A.; Overpeck, J.T. 2011.** Second century megadrought in the Rio Grande headwaters, Colorado: how unusual was medieval drought? *Geophysical Research Letters*. 38(22): L22703. 5 p. doi: 10.1029/2011GL050015. [Published online: November 19, 2011].

- Rubino, D.L.; McCarthy, B.C. 2004. Comparative analysis of dendroecological methods used to assess disturbance events. *Dendrochronologia*. 21(3): 97-115.
- Safeeq, M.; Grant, G.E.; Lewis, S.L.; Tague, C. 2013. Coupling snowpack and groundwater dynamics to interpret historical streamflow trends in the Western United States. *Hydrological Processes*. 27(5): 655-668.
- Salathé, E.P., Jr.; Leung, L.R.; Qian, Y.; Zhang, Y. 2010. Regional climate model projections for the State of Washington. *Climatic Change*. 102: 51-75.
- Sankarasubramanian, A.; Vogel, R.M. 2003. Hydroclimatology of the continental United States. *Geophysical Research Letters*. 30(7): 1363. 4 p. doi: 10.1029/2002GL015937. [Published online: April 3, 2003].
- Sankarasubramanian, A.; Vogel, R.M.; Limbrunner, J.F. 2001. Climate elasticity of streamflow in the United States. *Water Resources Research*. 37(6): 1771-1781.
- Savage, M.; Brown, P.M.; Feddema, J. 1996. The role of climate in a pine forest regeneration pulse in the Southwestern United States. *Ecoscience*. 3(3): 310-318.
- Schaake, J.C. 1990. From climate to flow. Chapter 8. In: Waggoner, P.E., ed. *Climate Change and U.S. Water Resources*. New York: John Wiley: 177-206.
- Scuderi, L.A. 1993. A 2000-year tree ring record of annual temperatures in the Sierra Nevada Mountains. *Science*. 259(5100): 1433-1436.
- Seager, R.; Naik, N.; Vogel, L. 2012. Does global warming cause intensified interannual hydroclimate variability? *Journal of Climate*. 25(9): 3355-3372.
- Seager, R.; Tzanova, A.; Nakamura, J. 2009. Drought in the Southeastern United States: causes, variability over the last millennium, and the potential for future hydroclimate change. *Journal of Climate*. 22(19): 5021-5045.
- Seneviratne, S.I.; Corti, T.; Davin, E.L. [and others]. 2010. Investigating soil moisture-climate interactions in a changing climate: A review. *Earth-Science Reviews*. 99(3): 125-161.
- Seneviratne, S.I.; Nicholls, N.; Easterling, D. [and others]. 2012. Changes in climate extremes and their impacts on the natural physical environment. In: Field, C.B.; Barros, V.; Stocker, T.F. [and others], eds. *Managing the risks of extreme events and disasters to advance climate change adaptation. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change (IPCC)*. New York: Cambridge University Press: 109-230.
- Sheffield, J.; Barrett, A.P.; Colle, B. [and others]. 2013. North American climate in CMIP5 experiments, part I: evaluation of historical simulations of continental and regional climatology. *Journal of Climate*. 26(23): 9209-9245.
- Sheffield, J.; Goteti, G.; Wen, F.; Wood, E.F. 2004. A simulated soil moisture based drought analysis for the United States. *Journal of Geophysical Research*. 109(D24): D24108. 19 p. doi:10.1029/2004JD005182. [Published online: December 29, 2004].
- Sheffield, J.; Wood, E.F. 2007. Characteristics of global and regional drought, 1950–2000: analysis of soil moisture data from off-line simulation of the terrestrial hydrologic cycle. *Journal of Geophysical Research*. 112(D17): D17115. 21 p. doi:10.1029/2006JD008288. [Published online: September 15, 2007].
- Sheffield, J.; Wood, E.F. 2008a. Global trends and variability in soil moisture and drought characteristics, 1950–2000, from observation-driven simulations of the terrestrial hydrologic cycle. *Journal of Climate*. 21(3): 432-458.
- Sheffield, J.; Wood, E.F. 2008b. Projected changes in drought occurrence under future global warming from multi-model, multi-scenario, IPCC AR4 simulations. *Climate Dynamics*. 31(1): 79-105.
- Sheffield, J.; Wood, E.F.; Roderick, M.L. 2012. Little change in global drought over the past 60 years. *Nature*. 491(7424): 435-438.
- Shuman, B.; Donnelly, J.P. 2006. The influence of seasonal precipitation and temperature regimes on lake levels in the Northeastern United States during the Holocene. *Quaternary Research*. 65(1): 44-56.
- Shuman, B.; Henderson, A.K.; Plank, C. [and others]. 2009a. Woodland-to-forest transition during prolonged drought in Minnesota after ca. AD 1300. *Ecology*. 90(10): 2792-2807.
- Shuman, B.N.; Newby, P.; Donnelly, J.P. 2009b. Abrupt climate change as an important agent of ecological change in the Northeast U.S. throughout the past 15,000 years. *Quaternary Science Reviews*. 28(17-18): 1693-1709.
- Spaulding, W.G. 1991. A middle Holocene vegetation record from the Mojave Desert of North America and its paleoclimatic significance. *Quaternary Research*. 35(3): 427-437.
- Sperna Weiland, F.; Van Beek, L.; Kwadijk, J.; Bierkens, M. 2010. The ability of a GCM-forced hydrological model to reproduce global discharge variability. *Hydrology and Earth System Sciences*. 14(8): 1595-1621.
- St. George, S.; Meko, D.M.; Cook, E.R. 2010. The seasonality of precipitation signals embedded within the North American Drought Atlas. *The Holocene*. 20(6): 983-988.
- Stahle, D.; Griffin, R.; Meko, D. [and others]. 2013a. The ancient blue oak woodlands of California: longevity and hydroclimatic history. *Earth Interactions*. 17(12): 1-23.
- Stahle, D.K.; Burnette, D.J.; Stahle, D.W. 2013b. A moisture balance reconstruction for the drainage basin of Albemarle Sound, North Carolina. *Estuaries and Coasts*. 36(6): 1340-1353.
- Stahle, D.W.; Cleaveland, M.K. 1992. Reconstruction and analysis of spring rainfall over the Southeastern U.S. for the past 1000 years. *Bulletin of the American Meteorological Society*. 73(12): 1947-1961.
- Stahle, D.W.; Cleaveland, M.K.; Griffin, R.D. [and others]. 2006. Decadal drought effects on endangered woodpecker habitat. *Eos Transactions American Geophysical Union*. 87(12): 121-125.
- Stahle, D.W.; Cleaveland, M.K.; Hehr, J.G. 1985. A 450-year drought reconstruction for Arkansas, United States. *Nature*. 316: 530-532.
- Stahle, D.W.; Cleaveland, M.K.; Hehr, J.G. 1988. North Carolina climate changes reconstructed from tree rings: AD 372 to 1985. *Science*. 240(4858): 1517-1519.
- Stahle, D.W.; Cook, E.R.; Cleaveland, M.K. [and others]. 2000. Tree-ring data document 16th century megadrought over North America. *Eos Transactions American Geophysical Union*. 81(12): 121-125.
- Stahle, D.W.; Fye, F.K.; Cook, E.R.; Griffin, R.D. 2007. Tree-ring reconstructed megadroughts over North America since AD 1300. *Climatic Change*. 83(1-2): 133-149.
- Stahle, D.W.; Therrell, M.D.; Cleaveland, M.K. [and others]. 2001. Ancient blue oaks reveal human impact on San Francisco Bay salinity. *Eos Transactions American Geophysical Union*. 82(12): 141-145.
- Stewart, I.T.; Cayan, D.R.; Dettinger, M.D. 2005. Changes toward earlier streamflow timing across Western North America. *Journal of Climate*. 18(8): 1136-1155.

- Stine, S. 1990. Late holocene fluctuations of Mono Lake, eastern California. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 78(3): 333-381.
- Stine, S. 1994. Extreme and persistent drought in California and Patagonia during medieval time. *Nature*. 369(6481): 546-549.
- Stockton, C.W.; Jacoby, G.C. 1976. Long-term surface-water supply and streamflow trends in the Upper Colorado River Basin based on tree-ring analyses. *Lake Powell Research Project Bulletin*. 18: 1-70.
- Swetnam, T.W. 1993. Fire history and climate change in giant sequoia groves. *Science*. 262 (5135): 885-885.
- Swetnam, T.W.; Betancourt, J.L. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *Journal of Climate*. (11): 3128-3147.
- Tague, C.; Grant, G.E. 2009. Groundwater dynamics mediate low-flow response to global warming in snow-dominated alpine regions. *Water Resources Research*. 45: W07421. 12 p. doi:10.1029/2008WR007179. [Published online: July 23, 2009].
- Tallaksen, L. 1995. A review of baseflow recession analysis. *Journal of Hydrology*. 165(1): 349-370.
- Tallaksen, L.M.; Stahl, K. 2014. Spatial and temporal patterns of large-scale droughts in Europe: model dispersion and performance. *Geophysical Research Letters*. 41(2): 429-434.
- Thorntwaite, C.W. 1948. An approach toward a rational classification of climate. *Geographical review*. 38(1): 55-94.
- Trenberth, K.E.; Dai, A.; van der Schrier, G. [and others]. 2014. Global warming and changes in drought. *Nature Climate Change*. 4(1): 17-22.
- Trouet, V.; Esper, J.; Graham, N.E. [and others]. 2009. Persistent positive North Atlantic Oscillation mode dominated the medieval climate anomaly. *Science*. 324(5923): 78-80.
- Van Loon, A.; Van Lanen, H. 2012. A process-based typology of hydrological drought. *Hydrology and Earth System Sciences*. 16(7): 1915-1946.
- van Mantgem, P.J.; Stephenson, N.L.; Byrne, J.C. [and others]. 2009. Widespread increase of tree mortality rates in the Western United States. *Science*. 523: 521-524.
- Vano, J.A.; Das, T.; Lettenmaier, D.P. 2012. Hydrologic sensitivities of Colorado River runoff to changes in precipitation and temperature. *Journal of Hydrometeorology*. 13(3): 932-949.
- Vidal, J.; Martin, E.; Franchistéguy, L. [and others]. 2010. Multilevel and multiscale drought reanalysis over France with the Safran-Isba-Modcou hydrometeorological suite. *Hydrology and Earth System Sciences Discussions*. 14(3): 459-478.
- Webb, R.S.; Anderson, K.H.; Webb, T. III. 1993. Pollen response-surface estimates of late-Quaternary changes in the moisture balance of the Northeastern United States. *Quaternary Research*. 40(2): 213-227.
- Weider, K.; Boutt, D.F. 2010. Heterogeneous water table response to climate revealed by 60 years of ground water data. *Geophysical Research Letters*. 37(24): L24405. doi: 10.1029/2010GL045561. [Published online: December 21, 2010].
- Westerling, A.L.; Gershunov, A.; Brown, T.J. [and others]. 2003. Climate and wildfire in the Western United States. *Bulletin of the American Meteorological Society*. 84(5): 595-604.
- Westerling, A.L.; Hidalgo, H.G.; Cayan, D.R.; Swetnam, T.W. 2006. Warming and earlier spring increases western U.S. forest wildfire activity. *Science*. 313(5789): 940-943.
- Whitlock, C.; Shafer, S.L.; Marlon, J. 2003. The role of climate and vegetation change in shaping past and future fire regimes in the Northwestern U.S. and the implications for ecosystem management. *Forest Ecology and Management*. 178(1-2): 5-21.
- Wilhite, D.A.; Buchanan-Smith, M. 2005. Chapter 1. Drought as hazard: understanding the natural and social context. In: Wilhite, D.A., ed. *Drought and water crises: science, technology and management issues*. Boca Raton: Taylor and Francis: 3-29.
- Wilhite, D.A.; Glantz, M.H. 1985. Understanding the drought phenomenon: the role of definitions. *Water International*. 10(3): 111-120.
- Wilhite, D.A.; Sivakumar, M.; Pulwarty, R. 2014. Managing drought risk in a changing climate: the role of national drought policy. *Weather and Climate Extremes*. (3): 4-13.
- Williams, A.P.; Seager, R.; Macalady, A.K. [and others]. 2014. Correlations between components of the water balance and burned area reveal new insights for predicting forest fire area in the Southwest United States. *International Journal of Wildland Fire*. 24: 14-26. doi: 10.1071/WF14023. [Published online: November 13, 2014].
- Wolock, D.M.; McCabe, G.J. 1999. Explaining spatial variability in mean annual runoff in the conterminous United States. *Climate Research*. 11(2): 149-159.
- Wood, A.W.; Leung, L.R.; Sridhar, V.; Lettenmaier, D. 2004. Hydrologic implications of dynamical and statistical approaches to downscaling climate model outputs. *Climatic Change*. 62(1-3): 189-216.
- Woodhouse, C.A.; Gray, S.T.; Meko, D.M. 2006. Updated streamflow reconstructions for the Upper Colorado River basin. *Water Resources Research*. 42(5): doi: 10.1029/2005WR004455. [Published online: May 11, 2006].
- Woodhouse, C.A.; Overpeck, J.T. 1998. 2000 years of drought variability in the central United States. *Bulletin of the American Meteorological Society*. 79(12): 2693-2714.
- Woods, R. 2003. The relative roles of climate, soil, vegetation and topography in determining seasonal and long-term catchment dynamics. *Advances in Water Resources*. 26(3): 295-309.
- Yu, Z.; McAndrews, J.H.; Eicher, U. 1997. Middle Holocene dry climate caused by change in atmospheric circulation patterns: evidence from lake levels and stable isotopes. *Geology*. 25(3): 251-254.
- Zhang, L.; Dawes, W.R.; Walker, G.R. 2001. Response of mean annual evapotranspiration to vegetation changes at catchment scale. *Water Resources Research*. 37(3): 701-708.

Physiological Responses of Forests to Future Drought

Nate McDowell

Paul J. Hanson

Inés Ibáñez

Richard P. Phillips

Michael G. Ryan

N. McDowell is a Staff Scientist, Earth and Environmental Sciences Division, Los Alamos National Lab, Los Alamos, NM 87545.

P.J. Hanson is a Corporate Fellow and Group Leader, Climate Change Science Institute and Environmental Science Division, Oak Ridge National Lab, Oak Ridge, TN 37830.

I. Ibáñez is an Associate Professor, School of Natural Resources and Environment, University of Michigan, Ann Arbor, MI 48109.

R.P. Phillips is an Associate Professor, Department of Biology, Indiana University, Bloomington, IN 47405.

M.G. Ryan is a Senior Research Scientist, Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523.

Introduction

Drought has long been viewed as a dominant factor regulating the distribution, productivity, and survival of plants (Running and others 2004). The nature of drought impacts is currently changing, however, due to a warming climate. As air warms, it can hold more water, making dry conditions relatively drier because the air extracts more water from the soil and from plant canopies (Held and Sodden 2006). In essence, a survivable drought of the past can become an intolerable drought under a warming climate (Williams and others 2013). In this chapter, we revisit the concept of drought from the perspective of plants and how they deal with droughts under warmer conditions, and we examine how models simulate future drought responses.

A Plant's Perspective on Drought

At the most basic level, drought for a plant is defined as a deficit in the amount of water available for transpiration relative to plant and atmospheric demand. Quantifying this imbalance requires understanding how much water is available to plants from subsurface reservoirs, the evaporative demand, and the plant's hydraulic conducting system. Thus, mechanistic measures of plant physiological responses to drought require an expression of "plant available" water.

Soil Water Potential

Water is generally most available for plant uptake when soils are between field capacity and species-specific wilting points (Kozłowski and Pallardy 2002). While the leaf wilting point is relatively fixed at species- and condition-specific values, variability in soil water, expressed as soil water potential, can drive a large amount of variation in transpiration (E) as seen from Fick's law

$$E = k_s (\Psi_{\text{leaf}} - \Psi_{\text{soil}}) \quad (1)$$

where k_s is plant hydraulic conductance, and Ψ_{leaf} and Ψ_{soil} are leaf and soil water potentials, respectively. As can be seen, variation in Ψ_{soil} is one of the critical parameters defining E .

Unfortunately, direct measures of the physiologically relevant Ψ_{soil} (and Ψ_{leaf}) are difficult to obtain in the field and are often replaced with either gravimetric or volumetric measures of the amount of water stored in

a given sample of soil volume or mass. It is possible to translate such data to soil matric potential, but the necessary nonlinear functions are not readily available for all sites and vary considerably across sites and with soil depth at a given site (Saxton and Rawls 2006). As a result, plant available soil water has often also been expressed as the relative amount of water stored in a soil with respect to its maximum saturated water capacity (Waring and Running 2010). The choice of the expression of soil water status impacts our impression and definition of drought. This is demonstrated using an example from a long-term study in Tennessee (see the text box on the following page).

Many models use relative water content as an expression of available water in soils (Hanson and others 2004), but such a metric does not account for the nonlinear nature of soil moisture availability with drying. Future assessments of drought effects on forests and the modeling of such effects should strive to employ soil water potential for various soil depths to better characterize drought severity across events and years. An integrated sum of daily water potential values (becoming more negative with drought severity) has been suggested as a metric for comparing the nature of one drought versus another (Hanson and others 2003).

Evaporative Demand

While soil moisture is critical for defining the ability of a plant to transpire, the evaporative demand placed upon the plant's canopy is equally important to defining drought impacts on plants. This is because of the application of Fick's law to transpiration (E) at the canopy scale:

$$E = g_s \cdot VPD \quad (2)$$

where VPD is vapor pressure deficit, or the difference in vapor pressure between the leaf and the atmosphere, and g_s is stomatal conductance. VPD rises with temperature (for a given absolute humidity) due to the greater water holding capacity of warmer air, and drought is often associated with high temperature extremes and lower relative and absolute humidity resulting in higher VPD . From a plant's perspective then, drought means not only periods of low soil water availability but can also include periods of warmer temperatures and higher VPD . High VPD impacts plants by either stressing the water conducting system or by eliciting stomatal closure (or a combination)—both mechanisms can negatively affect plants. If plants do not regulate g_s ,

THE WALKER BRANCH WATERSHED: Drought Characterization Varies as Different Metrics are Employed

The long-term record of soil water observations available for the Walker Branch Watershed in Tennessee (Hanson and others 2003) demonstrates the concept of how use of the water potential metric changes the “expression” of drought in a wet eastern forest, where years exist with both minimal and severe moisture stress. If soil water content below field capacity is chosen as the metric of water deficit associated with drought (fig. 3.1A), one might conclude that “drought” was occurring in approximately 11 of the 13 years. However, if soil matric potential is derived from soil water content using soil moisture release characteristics, a very different picture emerges. The soil matric potential data show reduced water availability in the surface soils for only 5 of 13 years, and perhaps for no more than 3 of 13 years when deeper soil water supplies are evaluated (fig. 3.1B). Matric or total soil water potential, the more mechanistic expression of what influences plant water status, provides a different view of soil water availability to plants than does soil water content. In this example for a wet eastern forest, the number of years characterized as “drought years” is appropriately reduced when the water potential metric is employed.

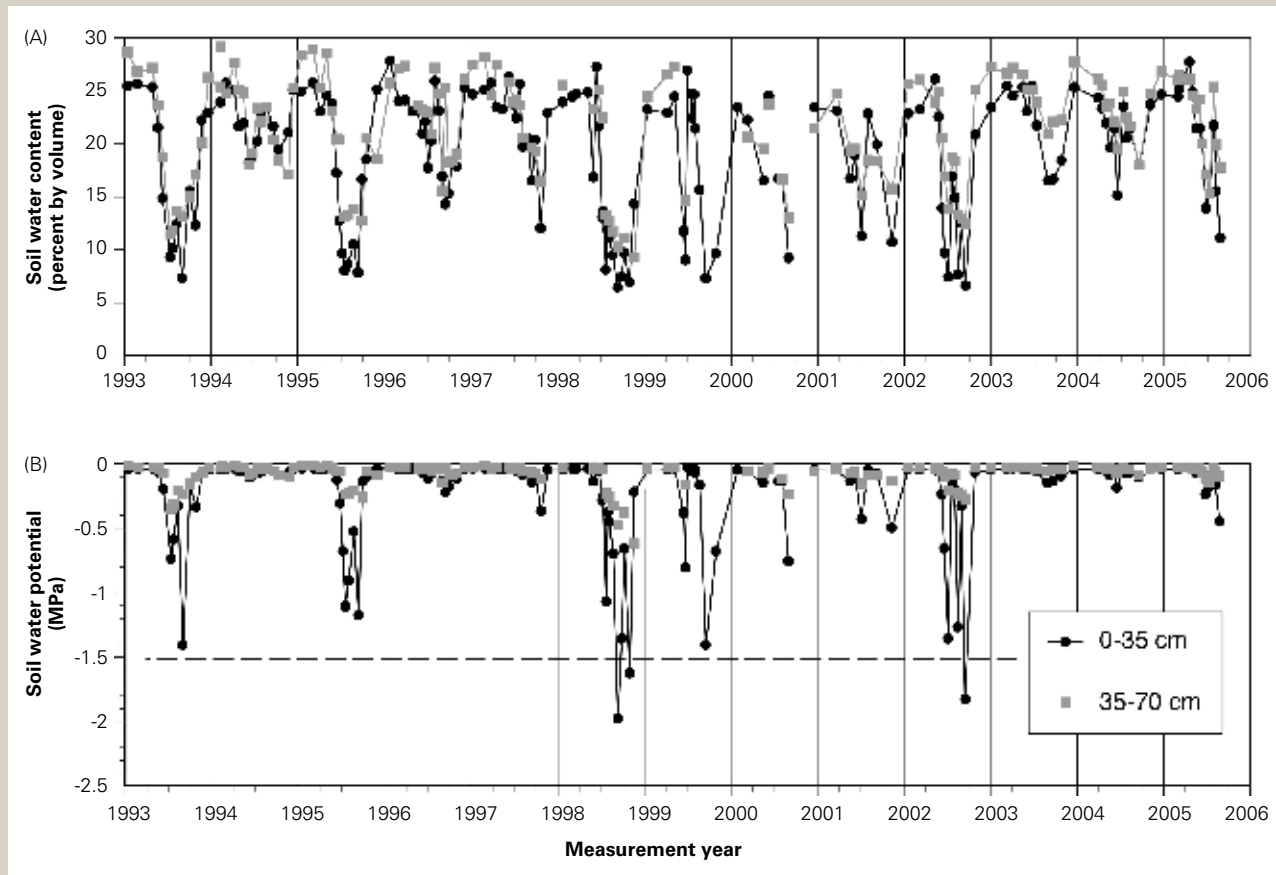


Figure 3.1—A 13-year record of (A) soil water content or (B) soil water potential at two measurement depths (0–35 and 35–70 cm) for the Walker Branch Watershed in Tennessee [modified from data in Hanson and others (2003)]. The dashed line in graph B represents a hypothetical threshold for critical plant water stress response. It is clear that similar surface water (0–35 cm depth) potentials are approaching critical drought thresholds while somewhat deeper soils (35–70 cm depth) retain ample soil water for plant function.

then high VPD can cause E to be higher than the plant can sustain because of low soil moisture and limits on the hydraulic conductance of the water transport pathway from soil to leaf. Excessively high E thus results in cavitation, or the nucleation of air bubbles within xylem, which blocks water transport (Sperry and others 1998). Cavitation can be repaired, but only when the demand for water is significantly less than soil moisture availability, which is unlikely to occur during severe drought. If left unchecked, cavitation can lead to hydraulic failure and subsequent desiccation of foliage (McDowell and others 2011). Plants can close their stomata by reducing g_s during periods of high VPD in order to minimize E (equation 2), thereby minimizing the risk of hydraulic failure. This comes at the cost of reduced photosynthesis, however, because of lower carbon dioxide (CO_2) supply to the foliage as the plant's stomata remain closed. If drought lasts sufficiently long, lowered photosynthesis can cause reductions in carbohydrate reserves because metabolic consumption of carbohydrates continues through respiration and other processes (McDowell and others 2011). Ultimately, this may cause carbon starvation, or the process leading to death from cessation of metabolism and inability to defend against pest attacks as the available carbohydrate supply declines (McDowell 2011). Thus, elevated VPD , as occurs during drought and with warming air temperature, is equally important to plant drought response as soil water availability (Breshears and others 2013).

In summary, the climatic conditions that are relevant to a plant during drought are largely dominated by Ψ_{soil} and VPD (and their influence on Ψ_{leaf}), with a key regulation existing within the hydraulic conducting pathway of the plant. Many drought indices exist (reviewed in Mu and others 2013), but we propose that future research consider plant-relevant drought indices that are most appropriate for management, prognostic forecasting, and ecological understanding. Indices that capture Ψ_{soil} and, or VPD duration and intensity would be most useful.

Belowground Mechanisms to Survive Drought

As highlighted in the material earlier, plant regulation of the hydraulic pathway is essential during drought. There are many above- and belowground aspects of hydraulic regulation to be considered during drought, with coordination among the plant hydraulic system being required for cavitation avoidance (Manzoni and others

2014). Among the most important regions of regulation is belowground. Plants have evolved a number of belowground traits and rooting strategies to cope with drought. These include morphological traits that are relatively fixed for a given species (root architecture, anatomy, depth, and type of mycorrhizal association) as well as more plastic physiological responses (shifts in belowground carbon (C) allocation, increased rhizodeposition, hydraulic redistribution) that depend on species and environmental context. Unfortunately, far more is known about interspecific and intraspecific differences in leaf-level responses to water stress than belowground responses (Breda and others 2006). Much of what is known about root traits and rooting strategies of trees comes from studies of seedlings and saplings grown under controlled conditions or in common gardens rather than from mature trees growing in forests (Hanson and Weltzin 2000); though a notable exception is the use of water isotopes to track depth of uptake (Dawson 1993). Hence, an important priority moving forward is to better quantify how root traits and belowground processes influence tree species' sensitivities to drought in mature forests.

Morphological Traits

Several morphological root traits are known to influence plant responses to water stress. Plants that produce small diameter absorptive roots (i.e., roots with high mass-specific length or mass-specific surface area) increase the amount of root surface area in contact with soil water, and thus minimize the impacts of drought by exploring a greater volume of soil (Comas and others 2013). Among the absorptive roots, those with small xylem diameters may be more tolerant of drought due to their reduced risk of cavitation and embolism, which is generally greater in roots relative to shoots (Jackson and others 1996, 2000). Root architecture and depth distribution (dimorphic distribution; presence/absence of a tap root) also influence plant responses to water stress, if roots growing deep into the soil profile can access subsurface sources of water that are uncoupled from recent precipitation events. Finally, the mycorrhizal status of a plant represents an additional "root trait" for coping with water stress. Nearly all plants' roots are colonized to some degree by mycorrhizal fungi. These fungi produce thin filamentous structures in soil (i.e., hyphae) that increase water uptake and transport by increasing absorptive surface area and by exploiting water in soil micropores.

Tree species' differences in root traits likely contribute to their drought tolerance. In theory, tree species

with an abundance of small-diameter absorptive roots should be better buffered from drought impacts than those with larger diameter fine roots. This is generally true across temperate tree species: oak trees (*Quercus* spp.) have smaller diameter absorptive roots than maple trees (*Acer* spp.) which have finer diameters than tulip poplar trees (*Liriodendron tulipifera*) (McCormack and others 2012, Pregitzer and others 2002), and such differences generally correspond to the drought tolerance of these species (Brzostek and others 2014). However, the greater drought tolerance of most oak trees also may relate to other factors such as deeper rooting depths and ring porous wood anatomy (Meinzer and others 2013).

The mycorrhizal association of tree species may influence their tolerance to drought. The two dominant types of mycorrhizal fungi that associate with trees are arbuscular mycorrhizal (AM) fungi and ectomycorrhizal (ECM) fungi. AM fungi promote drought resistance by synthesizing metabolites that act as osmolytes, thereby lowering the plant's water potential (Rapparini and Peñuelas 2014). ECM fungi may increase or decrease a tree's susceptibility to drought (Lehto and Zwiazek 2011) depending on the exploration type of the fungi and the ability of the fungi to produce aquaporins, or actively regulated water transport channels (Breda and others 2006, Lehto and Zwiazek 2011). While studies of dual colonists (i.e., tree species that can associate with both AM or ECM) suggest that AM tree roots are more drought-tolerant than ECM roots (Querejeta and others 2009), an analysis of the drought tolerance of the 20 most common deciduous tree species (>300,000 trees) in the Midwestern United States suggests that ECM trees may be more tolerant of water stress than AM trees (Brzostek and others 2014). Such opposite trends indicate the need for more research to better understand the role of mycorrhizal fungi and mycorrhizal association in facilitating water uptake and enhancing drought tolerance.

Physiological Responses

Optimal allocation (or partitioning) theory suggests that plants should increase C allocation to fine roots as soils dry down and water and nutrient limitation is exacerbated (Bloom and others 1985). While there is some evidence of this at the biome scale (Kozłowski and others 1991, Schenk and Jackson 2002), demonstrations of increases in fine root allocation during drought (either absolute or relative) in forest trees are inconsistent (Cudlin and others 2007, Eamus 2003, Gower and others 1992). In a multi-year throughfall

displacement study, Joslin and others (2000) found that 30-percent reductions in water input induced no changes in fine root biomass, fine root turnover, or root-to-shoot ratio. Additionally, in a study of 14 mature forest stands of European beech (*Fagus sylvatica* L.) across a precipitation gradient, Meier and Leuschner (2008) reported that fine root biomass (alone, or per unit leaf area) did not decline but rather increased with soil moisture, though root diameters generally decreased on drier soils (Hertel and others 2013). These findings suggest that fine root responses of trees may more closely parallel leaf-level responses, and that root allocation may depend on whole plant responses to water stress (Anderegg 2012). For example, anisohydric tree species maintain particularly negative water potentials via relatively open stomata and, hence, may be more likely to increase belowground C allocation during drought than isohydric species that close their stomata in response to water stress.

Despite the limited evidence that trees alter allocation to fine roots in response to water stress, there is support for the hypothesis that water-stressed trees increase allocation to roots growing deeper in the soil profile (Breda and others 2006, Schenk and Jackson 2002). Deeper rooting allows trees to access subsurface water resources in both saturated and unsaturated zones; if they possess the appropriate traits, trees may also transfer water from moist regions of soil to dry regions of soil through the nocturnal process of hydraulic redistribution (HR), which generally correlates with the degree of water limitation in an ecosystem (Schenk and Jackson 2002). While there is still some debate about the quantitative significance of HR (Neumann and Cardon 2012), the phenomenon appears to be widespread, occurring in plantation forests (Brooks and others 2002, Domec and others 2010), old growth forests (Brooks and others 2002, Oliveira and others 2005, Warren and others 2007), and in most tree species growing in savannas (Bleby and others 2010, Ludwig and others 2003). The ecological consequences of HR include enhanced understory growth during drought (Dawson 1993, Domec and others 2010), increased nutrient availability (McCulley and others 2004, Sardans and Peñuelas 2014), increased root life span (Bauerle and others 2008), and maintenance of the vitality of mycorrhizal fungi (Querejeta and others 2007). However, it is important to note that the amount of water transported through HR also depends on soil type and underlying geology (soil texture, depth to bedrock and water table, etc.). In shallow soils, for example, HR is likely to have limited effects on resilience to

drought. Thus, tree species that have the capacity to lift large quantities of subsurface water [e.g., sugar maple (Dawson 1993)] may still show strong growth decline in response to moderate water stress if soils are shallow (Brzostek and others 2014).

The Interaction of Drought, Host Physiology, and Multi-Trophic Community Dynamics

Large mortality events in forests are commonly associated with the incidence of several stressors (Allen and others 2010). Drought can modify trees' resilience and responses to diseases and herbivores by changing the tree's susceptibility to the biotic stressor or by combining the effects of multiple stressors (Anderegg and Callaway 2012). To certain extents, moderate water stress can stimulate tree defenses to resist insect attacks or diseases, but severe water stress decreases the individual's capacity to defend against those attacks (Herms and Mattson 1992, McDowell 2011). Thus, drought may compromise an individual's recovery from other stressors and may also promote their incidence or exacerbate their damage (Das and others 2013, Rouault and others 2006).

When several stressors affect individual trees simultaneously, such as drought and herbivory, the combined effects on the physiological functionality of the individual tree may be amplified (synergistic effects), accounting for more than the sum of the single stressors and potentially causing damage from which the individual cannot recover (Jactel and others 2012). In other cases, the combination of stressors may add up to less than the sum of the parts (positive or antagonistic effects), and the exposure to a previous stressor may ameliorate the effects of a subsequent one (Bansal and others 2013). For example, mild drought may reduce cell growth but enhance cell differentiation as more resources are then available for this process (Lorio 1986). This would result in thicker cell walls and higher concentrations of secondary products that would protect the plant from insect pests and diseases (Lorio 1986, Sharpe and others 1985).

Such disparate and *ad hoc* interactions make it very difficult to predict the outcome of multiple stressors and whether threshold-type responses may occur. Still, there are sufficient studies to allow for an informed assessment of the potential outcomes of the combined effect of drought and other biotic stressors.

In addition to the direct effects of drought on tree physiological performance, drought conditions can also promote the outbreak of forest pests (Ayres and Lombardero 2000, McDowell and others 2011, Raffa and Berryman 1983), exacerbating the effects of water-stress on the trees and ultimately on the whole ecosystem (Breshears and others 2005). The damage from insect pests under drought conditions seems to be related to both the intensity of the drought and the insect feeding guild (Jactel and others 2012). Typical outbreaks result in increased insect damage of water-stressed trees for chewing and galling insects, and decreased damage for sucking and boring pests.

Under drought conditions, the concentration of nitrogen compounds and sugars increase in plant tissue (Huberty and Denno 2004, Kramer 1983), especially in younger aboveground tissues (Mattson and Haack 1987), making plants more attractive to insect herbivores (Albert and others 1982, Haack and Slansky 1987, Mattson and Scriber 1987). The increase in concentrations of certain compounds and their volatilization may also change under drought conditions, promoting host acceptance and aiding insects in detection of stressed plants (Kimmerer and Kozlowski 1982, Mattson and Haack 1987, Visser 1986). These same physiological responses in the host plant could also explain how drought may promote mutualistic organisms associated with insect pests (Barras and Hodges 1969, Koricheva and others 1998) that could further favor the outbreak.

The link between drought and incidence of plant diseases is less documented, and only circumstantial evidence points to an increase in plant diseases with drought (Desprez-Loustau and others 2006; Maurel and others 2001a, 2001b). Commonly, disease agents that cause increased damage in plants under drought conditions are already present on or in their host as saprophytes or endophytes (Bachi and Peterson 1985; Blodgett and others 1997a, 1997b; Stanosz and others 2001).

The mechanism behind the interaction between drought and pathogen attack could be due to the water-stressed tissue of the plant being a better substrate for growth of the pathogen, or to water stress decreasing the plant's resistance to diseases (Boyer 1995). Trees can respond to drought by increasing glucose production and other compounds, which could then promote the attack and growth of pathogenic fungi (Belanger and others 1990, Popoola and Fox 2003, Wargo 1996). In other cases, the stress caused by drought jeopardizes the

plant's capacity to produce antifungal or antimicrobial compounds (Kruger and Manion 1994, Madar and others 1995).

As the responses to several stressors are activated by overlapping signaling systems, mild exposures to one stressor could induce resistance to succeeding stressors (Bowler and Fluhr 2000, Jactel and others 2011). There are instances when the attack of common soil pathogens has been reduced by drought and where dry soils have decreased the virulence of these pathogens (Marcais and others 1993). Resistance to drought could also be enhanced by *a priori* pathogenic infestation that conditions the plant to close the stomata and to produce stress-related hormones (Fujita and others 2006).

Can CO₂ Fertilization Mitigate Drought Impacts?

While rising CO₂ contributes to climate change and subsequently to higher intensity of droughts, it is important to note that elevated atmospheric CO₂ may also reduce plant water stress (Franks and others 2013). Higher atmospheric CO₂ increases the diffusion of CO₂ into leaves through the stomata, effectively increasing the availability of this critical resource to the plants. Most plants have been observed to increase their water-use efficiency (the ratio of CO₂ uptake to water loss) with increases in CO₂, and recent reports suggest that this may be sustaining the C sink of temperate forests (Keenan and others 2013). Additionally, elevated CO₂ generally increases root growth and rooting depth (Iversen 2010), which may help deep-rooted species overcome water stress. This short-term benefit of elevated CO₂ can yield sustained and significant increases in the growth of forests. However, multiple negative costs have also been observed. Increased growth results in higher leaf area of individual trees, which predisposes them to even greater drought stress (compared to a non-CO₂ fertilized stand) when and if a drought strikes (Warren and others 2011). This is because they hold greater transpiring leaf area, thus the consumption of water is higher from these larger canopies, requiring more water to maintain hydraulic function. This mechanism has been invoked as a primary driver of oak (*Quercus robur*) mortality in Europe (Levanič and others 2011).

At the global scale, CO₂ fertilization has been observed to increase growth in only 20 percent of forests (Geldanhoff and Berg 2010). The authors indicated that

the remaining 80 percent of forests were constrained from capitalizing on the CO₂ benefits by drought, and in some cases nutrient limitations. Furthermore, long-term studies of forest survival indicate that forests are dying at greater rates than they are regenerating (Peng and others 2011, van Mantgem and others 2009), and particularly large mortality events are being witnessed with increasing frequency (Allen and others 2010, Carnicer and others 2011). This increase in mortality is happening as atmospheric CO₂ is increasing, thus negating the inference that CO₂ is promoting greater forest survival (Franks and others 2013). Even in systems where growth is increasing, these benefits, which can take decades to manifest, are often wiped out in a single drought event (Allen and others 2010).

Do Ecosystem Models Include Plant Drought-Response Mechanisms?

Unfortunately, ecosystem biogeochemical cycling models contain a limited capacity to capture plant responses to drought. Model-data intercomparison summaries have emphasized that biogeochemical cycling models perform poorly under drought conditions (Hanson and others 2004) stemming largely from the lack of root and stem hydraulic characteristics in those models. Iversen (2010) characterized root traits and function within models dealing with elevated CO₂ response as ranging from being absent to being included as the presence of root mass density with depth. Warren and others (2015) further detail the role of roots within models and concluded that significant improvements need to be pursued to include root characteristics and function into ecosystem models. The lack of known drought response mechanisms within models limits their capacity for the prediction of plant and ecosystem response to current and future drought, and typically produces model results that overestimate the sensitivity of plants and ecosystems during drought. This error is perhaps greater in wetter ecosystems [eastern forests (Hanson and others 2004, Hanson and Weltzin 2000)] where models are "tuned" to nondrought conditions. Improved long-term assessments of forest responses to drought demand that ecosystem models include many of the drought mechanism described in this section. Major advances have been made in the representation of within-plan hydraulics and carbohydrate allocation (McDowell and others 2013). Parolari and others (2014) take further steps in this direction with a focus on capturing the process of forest mortality.

Conclusions

There are a number of aspects of the physiological responses of plants to drought that are clearly well understood, such as regulation of transpiration. In contrast, the response of the belowground system, ecosystem interactions across multiple trophic scales, and the interaction of drought with elevated CO₂ are less well understood and are critical areas for future research. Understanding these responses will greatly enhance our ability to simulate future forest responses to drought.

Literature Cited

- Albert, P.J.; Cearley, C.; Hanson, F.; Parisella, S. 1982. Feeding responses of eastern spruce budworm larvae to sucrose and other carbohydrates. *Journal of Chemical Ecology*. 8: 233-239.
- Allen, C.D.; Macalady, A.K.; Chenchouni, H. [and others]. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*. 259: 660-684.
- Anderegg, W.R.L. 2012. Complex aspen forest carbon and root dynamics during drought—a letter. *Climatic Change*. 111(3-4): 983-991.
- Anderegg, W.R.L.; Callaway, E.S. 2012. Infestation and hydraulic consequences of induced carbon starvation. *Plant Physiology*. 159(4): 1866-1874.
- Ayres, M.P.; Lombardero, M.J. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Science of the Total Environment*. 262: 263-286.
- Bachi, P.R.; Peterson, J.L. 1985. Enhancement of *Sphaeropsis sapinea* stem invasion of pines by water deficits. *Plant Disease*. 69(9): 798-799.
- Bansal, S.; Hallsby, G.; Löfvenius, M.O.; Nilsson, M.-C. 2013. Synergistic, additive and antagonistic impacts of drought and herbivory on *Pinus sylvestris*: leaf, tissue and whole-plant responses and recovery. *Tree Physiology*. 33(5): 451-463.
- Barras, S.J.; Hodges, J.D. 1969. Carbohydrates of inner bark of *Pinus taeda* as affected by *Dendroctonus frontalis* and associated microorganisms. *Canadian Entomologist*. 101: 489-493.
- Bauerle, T.L.; Richards, J.H.; Smart, D.R.; Eissenstat, D.M. 2008. Importance of internal hydraulic redistribution for prolonging the lifespan of roots in dry soil. *Plant Cell and Environment*. 31(2): 177-186.
- Belanger, R.R.; Manion, P.D.; Griffin, D.H. 1990. Amino acid content of water-stress plantlets of *Populus tremuloides* clones in relation to clonal susceptibility to *Hyposylon mammatum* in vitro. *Canadian Journal of Botany*. 68: 26-29.
- Blaby, T.M.; McElrone, A.J.; Jackson, R.B. 2010. Water uptake and hydraulic redistribution across large woody root systems to 20 m depth. *Plant, Cell & Environment*. 33(12): 2132-2148.
- Blodgett, J.T.; Kruger, E.L.; Stanosz, G.R. 1997a. Effects of moderate water stress on disease development by *Sphaeropsis sapinea* on red pine. *Phytopathology*. 87: 422-428.
- Blodgett, J.T.; Kruger, E.L.; Stanosz, G.R. 1997b. *Sphaeropsis sapinea* and water stress in a red pine plantation in central Wisconsin. *Phytopathology*. 87: 429-437.
- Bloom, A.J.; Stuart Chapin, F.; Mooney, H.A. 1985. Resource limitation in plants an economic analogy. *Annual Review of Ecology and Systematics*. 16: 363-392.
- Bowler, C.; Fluhr, R. 2000. The role of calcium and activated oxygens as signals for controlling cross-tolerance. *Trends in Plant Science*. 5: 241-246.
- Boyer, J.S. 1995. Biochemical and biophysical aspects of water deficits and the predisposition to disease. *Annual Review of Phytopathology*. 33: 251-274.
- Breda, N.; Huc, R.; Granier, A.; Dreyer, E. 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*. 63(6): 625-644.
- Breshears, D.D.; Adams, A.D.; Eamus, D. [and others]. 2013. The critical role of increasing atmospheric moisture demand on tree mortality and associated regional die-off. *Frontiers in Plant Science*. 4: 266-269.
- Breshears, D.D.; Cobb, N.S.; Rich, P.M. [and others]. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences*. 102(42): 15,144-15,148.
- Brooks, J.R.; Meinzer, F.C.; Coulombe, R.; Gregg, J. 2002. Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests. *Tree Physiology*. 22(15-16): 1107-1117.
- Brzostek, E.; Dragoni, D.; Schmid, H.P. [and others]. 2014. Chronic water stress reduces tree growth and the carbon sink of deciduous hardwood forests. *Global Change Biology*. 20(8): 2531-2539.
- Carnicer, J.; Coll, M.; Ninyerola, M. [and others]. 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the National Academy of Sciences*. 108(4): 1474-1478.
- Comas, L.H.; Becker, S.R.; Cruz, V.V. [and others]. 2013. Root traits contributing to plant productivity under drought. *Frontiers in Plant Science*. 4: 1-16.
- Cudlin, P.; Kieliszewska-Rojucka, B.; Rudawska, M. [and others]. 2007. Fine roots and ectomycorrhizas as indicators of environmental change. *Plant Biosystems*. 141(3): 406-425.
- Das, A.J.; Stephenson, N.L.; Flint, A. [and others]. 2013. Climatic correlates of tree mortality in water-and energy-limited forests. *PloS One*. 8(7): e69917.
- Dawson, T.E. 1993. Hydraulic lift and water-use by plants—implications for water-balance, performance and plant-plant interactions. *Oecologia*. 95(4): 565-574.
- Desprez-Loustau, M.-L.; Marçais, B.; Nageleisen, L.-M. [and others]. 2006. Interactive effects of drought and pathogens in forest trees. *Annals of Forest Science*. 63: 597-612.
- Domec, J.C.; King, J.S.; Noormets, A. [and others]. 2010. Hydraulic redistribution of soil water by roots affects whole-stand evapotranspiration and net ecosystem carbon exchange. *New Phytologist*. 187(1): 171-183.
- Eamus, D. 2003. How does ecosystem water balance affect net primary productivity of woody ecosystems? *Functional Plant Biology*. 30(2): 187-205.
- Franks, P.J.; Adams, M.A.; Amthor, J.S. [and others]. 2013. Sensitivity of plants to changing atmospheric CO₂ concentration: from the geological past to the next century. *New Phytologist*. 197(4): 1077-1094.

- Fujita, M.; Fujita, Y.; Noutoshi, Y. [and others]. 2006. Crosstalk between abiotic and biotic stress responses: a current view from the points of convergence in the stress signaling networks. *Current Opinion in Plant Biology*. 9: 436-442.
- Geldanhoff, Z.; Berg, A.A. 2010. Tree ring evidence for limited direct CO₂ fertilization of forests over the 20th century. *Global Biogeochemical Cycles*. 24(3): GB3027/1-GB3027/6. doi: 10.1029/2009GB003699. [Published online: September 30, 2010].
- Gower, S.T.; Vogt, K.; Grier, C.C. 1992. Carbon dynamics of Rocky Mountain Douglas-fir: influence of water and nutrient availability. *Ecological Monographs*. 62(1): 43-65.
- Haack, R.A.; Slansky, F. 1987. Nutritional ecology of wood-feeding Coleoptera, Lepidoptera and Hymenoptera. In: Slansky, F.; Rodriguez, J.G., eds. *The nutritional ecology of insects, mites and spiders*. New York: John Wiley: 449-486.
- Hanson, P.J.; Weltzin J.F. 2000. Drought disturbance from climate change: response of United States forests. *Science of the Total Environment*. 262(3): 205-220.
- Hanson, P.J.; Huston, M.A.; Todd, D.E. 2003. Walker Branch Throughfall Displacement Experiment (TDE). In: Hanson P.J.; Wullschlegel, S.D., eds. *North American temperate deciduous forest responses to changing precipitation regimes*. New York: Springer: 8-31.
- Hanson, P.J.; Amthor, J.S.; Wullschlegel, S.D. [and others]. 2004. Oak forest carbon and water simulations: model intercomparisons and evaluation against independent data. *Ecological Monographs*. 74(3): 443-489.
- Held, I.M.; Soden, B.J. 2006. Robust responses of the hydrological cycle to global warming. *Journal of Climate*. 19(21): 5686-5699. doi: 10.1175/JCLI3990.1. [Published online: November 1, 2006].
- Hertel, D.; Strecker, T.; Muller-Haubold, H.; Leuschner, C. 2013. Fine root biomass and dynamics in beech forests across a precipitation gradient—is optimal resource partitioning theory applicable to water-limited mature trees? *Journal of Ecology*. 101(5): 1183-1200.
- Herms, D.A.; Mattson, W.J. 1992. The dilemma of plants: to grow or defend. *Quarterly Review of Biology*. 67: 283-335.
- Huberty, A.F.; Denno, R.F. 2004. Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology*. 85: 1383-1398.
- Iversen, C.M. 2010. Digging deeper: fine-root responses to rising atmospheric CO₂ concentration in forested ecosystems. *New Phytologist*. 186: 346-357.
- Jackson, R.B.; Sperry, J.S.; Dawson, T.E. 2000. Root water uptake and transport: using physiological processes in global predictions. *Trends in Plant Science*. 5: 482-488. doi:10.1016/S1360-1385(00)01766-0. [Published online: November 1, 2000].
- Jackson, R.B.; Canadell, J.; Ehleringer, J.R. [and others]. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia*. 108(3): 389-411.
- Jactel, H.; Petit, J.; Desprez-Loustau, M-L. [and others]. 2012. Drought effects on damage by forest insects and pathogens: a meta-analysis. *Global Change Biology*. 18(1): 267-276.
- Joslin, J.D.; Wolfe, M.H.; Hanson, P.J. 2000. Effects of altered water regimes on forest root systems. *New Phytologist*. 147(1): 117-129.
- Keenan, T.F.; Hollinger, D.Y.; Bohrer, G. [and others]. 2013. Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. *Nature*. 499: 324-327.
- Kimmerer, T.W.; Kozlowski, T.T. 1982. Ethylene, ethane, acetaldehyde, and ethanol production by plants under stress. *Plant Physiology*. 69: 840-847.
- Koricheva, J.; Larsson, S.; Haukioja, E.; Keinanen, M. 1998. Regulation of woody plant secondary metabolism by resource availability: hypothesis testing by means of meta-analysis. *Oikos*. 83: 212-226.
- Kozlowski, T.T.; Kramer, P.J.; Pallardy, S.G. 1991. *The physiological ecology of woody plants*. San Diego: Academic Press. 657 p.
- Kozlowski, T.T.; Pallardy, S.G. 2002. Acclimation and adaptive responses of woody plants to environmental stresses. *The Botanical Review*. 68(2): 270-334.
- Kramer, P.J. 1983. *Water relations of plants*. New York: Academic Press. 489 p.
- Kruger, B.M.; Manion, P.D. 1994. Antifungal compounds in aspen: effect of water stress. *Canadian Journal of Botany*. 72: 454-460.
- Lehto, T.; Zwiarek, J.J. 2011. Ectomycorrhizas and water relations of trees: a review. *Mycorrhiza*. 21(2): 71-90.
- Levanič, T.; Čater, M.; McDowell, N.G. 2011. Associations between growth, wood anatomy, carbon isotope discrimination and mortality in a *Quercus robur* forest. *Tree Physiology*. 31(3): 298-308. doi: 10.1093/treephys/tpq111. [Published online: March 1, 2011].
- Lorio, Peter L. 1986. Growth-differentiation balance: a basis for understanding southern pine beetle-tree interactions. *Forest Ecology and Management*. 14(4): 259-273.
- Ludwig, F.; Dawson, T.E.; de Kroon, H. [and others]. 2003. Hydraulic lift in *Acacia tortilis* trees on an East African savanna. *Oecologia*. 134(3): 293-300.
- Madar, Z.; Solel, Z.; Riov, J.; Szejnberg, A. 1995. Phytoalexin production by cypress in response to infection by *Diplodia pinea* f. sp. *cupressi* and its relation to water stress. *Physiological and Molecular Plant Pathology*. 47: 29-38.
- Manzoni, S.; Katul, G.; Porporato, A. 2014. A dynamical system perspective on plant hydraulic failure. *Water Resources Research*. 50(6): 5170-5183.
- Marcais, B.; Dupuis, F.; Desprez-Loustau, M-L. 1993. Influence of water stress on susceptibility of red oak (*Quercus rubra*) to *Phytophthora cinnamomi*. *European Journal of Forest Pathology*. 23: 295-305.
- Mattson, W.J.; Haack, R.A. 1987. The role of drought stress in provoking outbreaks of phytophagous insects. In: Barbosa, P.; Schultz, J., eds. *Insect outbreaks: ecological and evolutionary perspectives*. New York: Academic Press: 365-407.
- Mattson, W.J.; Scriber, J.M. 1987. Nutritional ecology of insect folivores of woody plants: water, nitrogen, fiber, and mineral considerations. In: Slansky, F.; Rodriguez, J.G., eds. *The nutritional ecology of insects, mites, and spiders*. New York: John Wiley: 105-146.
- Maurel, M.; Capron, R.C.; Desprez-Loustau, M-L. 2001a. Effects of root damage associated with *Phytophthora cinnamomi* on water relations, biomass accumulation, mineral nutrition and vulnerability to water deficit of five oak and chestnut species. *Forest Pathology*. 31: 353-369.
- Maurel, M.; Robin, C.; Capdevielle, X. [and others]. 2001b. Effects of variable root damage caused by *Phytophthora cinnamomi* on water relations of chestnut saplings. *Annals of Forest Science*. 58: 639-651.

- McCormack, M.L.; Adams, T.S.; Smithwick, E.A.H.; Eissenstat, D.M. 2012. Predicting fine root lifespan from plant functional traits in temperate trees. *New Phytologist*. 195(4): 823-831.
- McCulley, R.L.; Jobbagy, E.G.; Pockman, W.T.; Jackson, R.B. 2004. Nutrient uptake as a contributing explanation for deep rooting in arid and semi-arid ecosystems. *Oecologia*. 141(4): 620-628.
- McDowell, N.G. 2011. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiology*. 155(3): 1051-1059. <http://dx.doi.org/10.1104/pp.110.170704>. [Published online: January 2011].
- McDowell, N.G.; Beerling, D.; Breshears, D.D. [and others]. 2011. Interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology and Evolution*. 26: 523-532.
- McDowell, N.G.; Fisher, R.A.; Xu, C. [and others]. 2013. Evaluating theories of drought-induced vegetation mortality using a multi-model-experiment framework. *New Phytologist*. 200(2): 304-321.
- Meier, I.C.; Leuschner, C. 2008. Belowground drought response of European beech: fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient. *Global Change Biology*. 14(9): 2081-2095.
- Meinzer, F.C.; Woodruff, D.R.; Eissenstat, D.M. [and others]. 2013. Above- and belowground controls on water use by trees of different wood types in an eastern U.S. deciduous forest. *Tree Physiology*. 33(4): 345-356.
- Mu, Q.Z.; Zhao, M.S.; Kimball, J.S. [and others]. 2013. A remotely sensed global terrestrial drought severity index. *Bulletin of the American Meteorological Society*. 94: 83-98.
- Neumann, R.B.; Cardon, Z.G. 2012. The magnitude of hydraulic redistribution by plant roots: a review and synthesis of empirical and modeling studies. *New Phytologist*. 194(2): 337-352.
- Oliveira, R.S.; Dawson, T.E.; Burgess, S.S.; Nepstad, D.C. 2005. Hydraulic redistribution in three Amazonian trees. *Oecologia*. 145(3): 354-363.
- Parolari, A.J.; Katul, G.G.; Porporato, A. 2014. An ecohydrological perspective on drought-induced forest mortality. *Journal of Geophysical Research-Biogeosciences*. 119: 965-981. doi:10.1002/2013JG002592. [Published online: May 29, 2014].
- Peng, C.; Ma, Z.; Lei, X. [and others]. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change*. 1(9): 467-471.
- Popoola, T.O.S.; Fox, R.T.V. 2003. Effect of water stress on infection by species of honey fungus (*Armillaria mellea* and *A. gallica*). *Journal of Arboriculture*. 27: 139-154.
- Pregitzer, K.S.; DeForest, J.L.; Burton, A.J. [and others]. 2002. Fine root architecture of nine North American trees. *Ecological Monographs*. 72(2): 293-309.
- Querejeta, J.I.; Egerton-Warburton, L.M.; Allen, M.F. 2007. Hydraulic lift may buffer rhizosphere hyphae against the negative effects of severe soil drying in a California oak savanna. *Soil Biology & Biochemistry*. 39(2): 409-417.
- Querejeta, J.I.; Egerton-Warburton, L.M.; Allen, M.F. 2009. Topographic position modulates the mycorrhizal response of oak trees to interannual rainfall variability. *Ecology*. 90(3): 649-662.
- Raffa, K.F.; Berryman, A.A. 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). *Ecological Monographs*. 53: 27-49.
- Rapparini, F.; Peñuelas, J. 2014. Mycorrhizal fungi to alleviate drought stress on plant growth. In: Miransari, M., ed. *Use of microbes for the alleviation of soil stresses*. New York: Springer: 21-42. Vol. 1.
- Rouault, G.; Candau, J-Noël; Lieutier, F. [and others]. 2006. Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. *Annals of Forest Science*. 63(6): 613-624.
- Running, S.W.; Nemani, R.R.; Heinsch, F.A. [and others]. 2004. A continuous satellite-derived measure of global terrestrial primary production. *Bioscience*. 54(6): 547-560.
- Sardans, J.; Peñuelas, J. 2014. Hydraulic redistribution by plants and nutrient stoichiometry: Shifts under global change. *Ecohydrology*. 7(1): 1-20.
- Saxton, K.E.; Rawls, W.J. 2006. Soil water characteristic estimates by texture and organic matter for hydrologic solutions. *Soil Science Society of America Journal*. 70(5): 1569-1578.
- Schenk, H.J.; Jackson, R.B. 2002. The global biogeography of roots. *Ecological Monographs*. 72(3): 311-328.
- Sharpe, P.J.J.; Wu, H.I.; Gates, R.G.; Goeschl, J.D. 1985. Energetics of pine defense systems to bark beetle attack. Gen. Tech. Rep. SO-56. In: Branham, S.J.; Thatcher, R.C., eds. *Integrated Pest Management Research symposium: the proceedings*. New Orleans: U.S. Department of Agriculture, Forest Service: 206-223.
- Sperry, J.S.; Adler, F.R.; Campbell, G.S.; Comstock, J.P. 1998. Limitation of plant water use by rhizosphere and xylem conductance: results from a model. *Plant, Cell & Environment*. 21(4): 347-359.
- Stanosz, G.R.; Blodgett, J.T.; Smith, D.R.; Kruger, E.L. 2001. Water stress and *Sphaeropsis apineae* as a latent pathogen of red pine seedlings. *New Phytologist*. 149: 531-538.
- van Mantgem, P.J.; Stephenson, N.L.; Byrne, J.C. [and others]. 2009. Widespread increase of tree mortality rates in the Western United States. *Science*. 323(5913): 521-524.
- Visser, J.H. 1986. Host odor perception in phytophagous insects. *Annual Review of Entomology*. 31: 121-144.
- Wargo, P.M. 1996. Consequences of environmental stress on oak: predisposition to pathogens. *Annals of Forest Science*. 53: 359-368.
- Waring, R.H.; Running, S. 2010. *Forest ecosystems: analysis at multiple scales*. 3rd ed. Burlington, VT: San Diego: Elsevier Academic Press. 440 p.
- Warren, J.M.; Meinzer, F.C.; Brooks, J.R. [and others]. 2007. Hydraulic redistribution of soil water in two old-growth coniferous forests: quantifying patterns and controls. *New Phytologist*. 173(4): 753-765.
- Warren, J.M.; Norby, R.J.; Wullschlegel, S.D. 2011. Elevated CO₂ enhances leaf senescence during extreme drought in a temperate forest. *Tree Physiology*. 31(2): 117-130. doi: 10.1093/treephys/tpr002. [Published online: March 22, 2011].
- Warren, J.M.; Hanson, P.J.; Iversen, C.M. [and others]. 2015. Root structural and functional dynamics in terrestrial biosphere models-evaluation and recommendations. *New Phytologist*. 205(1): 59-78.
- Williams, A.; Park, C.D.; Allen, A.K. [and others]. 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change*. 3(3): 292-297.

Impacts of Increasing Drought on Forest Dynamics, Structure, Diversity, and Management

James S. Clark
Louis Iverson
Christopher W. Woodall

CONTRIBUTORS

Craig D. Allen, David M. Bell, Don C. Bragg, Tony D'Amato,
 Frank W. Davis, Michelle Hersh, Inés Ibáñez, Stephen T. Jackson,
 Stephen Matthews, Neil Pederson, Matthew Peters, Mark Schwartz,
 Kristen Waring, and Niklaus E. Zimmermann

J.S. Clark is the Nicholas Professor of Statistical Science at Duke University, Nicholas School of the Environment, Durham, NC 27708.

L. Iverson is a Landscape Ecologist, U.S. Department of Agriculture, Forest Service, Northern Research Station (NRS), Delaware, OH 43015.

C.W. Woodall is a Research Forester, U.S. Department of Agriculture, Forest Service, Northern Research Station (NRS), St. Paul, MN 55108.

C.D. Allen is a Research Ecologist in Ecosystem Dynamics, Jemez Mountain Field Station, Bandelier National Monument, U.S. Geological Survey (USGS), Los Alamos, NM 87544;

D.M. Bell is a Research Forester, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station (PNW), Corvallis, OR 97331; **D.C. Bragg** is a Research Forester, U.S. Department of Agriculture, Forest Service, Southern Research Station (SRS), Monticello, AR 71656; **T. D'Amato** is an Associate Professor in Silviculture and Applied Forest Ecology, University of Vermont, Burlington, VT 05405; **F.W. Davis** is a Professor of Landscape Ecology and Conservation Planning, Bren School of Environmental Science and Management, University of California, Santa Barbara, CA 93106; **M. Hersh** is a Professor of Biology, Sarah Lawrence College, Yonkers, NY 10708; **I. Ibáñez** is an Associate Professor, School of Natural Resources and Environment, University of Michigan, Ann Arbor, MI 48109; **S.T. Jackson** is Director of Southwest Climate Science Center, U.S. Geological Survey (USGS), Tucson, AZ 85719; **S. Matthews** is an Ecologist, U.S. Department of Agriculture, Forest Service, Northern Research Station (NRS), Delaware, OH 43015; **N. Pederson** is a Senior Ecologist, Harvard Forest, Petersham, MA 01366; **M. Peters** is a Geographic Information System (GIS) Technician, U.S. Department of Agriculture, Forest Service, Northern Research Station (NRS), Delaware, OH 43015; **M. Schwartz** is a Professor of Conservation Science for Climate Change Adaptation, Department of Environmental Science and Policy, University of California at Davis, Davis, CA 95616; **K. Waring** is an Associate Professor, School of Forestry, Northern Arizona University, Flagstaff, AZ 86001; **N.E. Zimmermann** is a Senior Scientist, Swiss Federal Research Institute WSL, Zurich, Switzerland.

Introduction

At the time of this writing in 2015, drought conditions have sustained over much of the continental United States for up to 4 years. Drought, a moisture limitation resulting from below average precipitation, high temperatures, or both, represents a departure from the “mean climate” of a region—and more frequent and severe droughts change this mean climate. Multi-year droughts have occurred throughout history (chapter 2); recent concern about prolonged drought has arisen because the increasing

rainfall variation of recent decades (Janssen and others 2014, Li and others 2011) was a predicted consequence of greenhouse gas-driven warming (IPCC 1995, Overpeck and others 1990). While combined warming and variable precipitation have amplified forest drought severity in the last two decades (Allen and others 2015, Millar and Stephenson 2015) across the country (see text box below), the Western United States in particular has experienced numerous and widespread drought-related stand replacement events (e.g., Allen and others 2010, Breshears and others 2005, Ganey and Vojta 2011).

FOREST DROUGHTS HAVE INCREASED IN RECENT DECADES

What changes in drought are in progress now? Drought severity and frequency have been especially high during the last few decades in the West, Southeast, and Lake States, and are at least part of the explanation for tree mortality (fig. 4.1). The Cumulative Drought Severity Index (CDSI) shows the sum of monthly Palmer Drought Severity Index (PDSI) drought classes (1–moderate, 2–severe, 3–extreme) from 1987–2013. Values are aggregated by climate division and shown for the 21 forest cover types defined by the USDA Forest Service (2000). Locations of documented drought-related mortality generally correspond with locations of high CDSI. Compared with the previous 27-year period (1960–1987), the West saw increases in all drought classes and only minor change in the East (fig. 4.2).

Severe multi-year drought episodes in the West are linked to drought-related tree mortality. There are fewer documented examples of recent drought-induced tree mortality in eastern U.S. forests. Note that the map of cumulative drought over 27 years does not always capture short-term intense drought events.

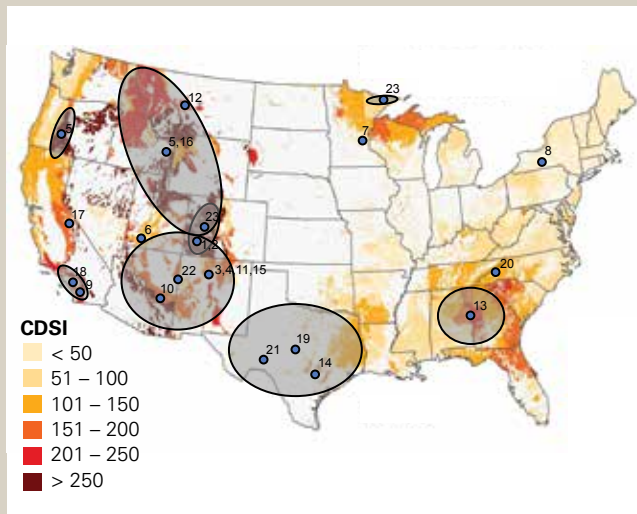


Figure 4.1—Cumulative drought severity index (CDSI) for forested lands from 1987–2013 with selected locations of drought- and heat-induced tree mortality indicated by blue circles and dots.

Numbers on map correspond to the following supporting references: 1—Anderegg and others (2012); 2—Anderegg and others (2013b); 3—Breshears and others (2005); 4—Breshears and others (2009); 5—Creeden and others (2014); 6—DeRose and Long (2012); 7—Faber-Langendoen and Tester (1993); 8—Fahey (1998); 9—Fellows and Goulden (2012); 10—Ganey and Vojta (2011); 11—Garrity and others (2013); 12—Kaiser and others (2012); 13—Klos and others (2009); 14—Kukowski and others (2012); 15—Macalady and Bugmann (2014); 16—Meddens and others (2012); 17—Millar and others (2012); 18—Minnich (2007); 19—Moore and others (In press); 20—Olano and Palmer (2003); 21—Twidwell and others (2014); 22—Williams and others (2013); 23—Worrall and others (2013). (modified from Peters and others 2014).

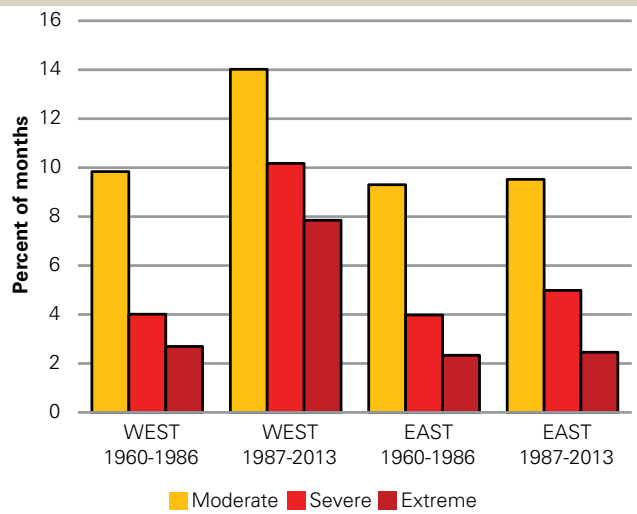


Figure 4.2—Drought for forested land of the conterminous United States for two 27-year periods from 1960 to 2013. For each forest type, drought conditions were summarized as the percentage of months during the 324-month period (27 years) among climate divisions that contained the forested land. (Peters and others 2014).

The work that follows examines not only these well-publicized western forest diebacks, but also considers inherent forest vulnerabilities to drought; it also highlights how little we actually know about the consequences of drought at all levels. Understanding how climatic changes already in progress will impact forests can help us anticipate socioeconomic impacts (chapter 11) and consequences for biodiversity. This synthesis of current understanding begins with an evaluation of the data available, followed by a synopsis of studies ranging from short-term observations, paleoecological research, and modeling work across a range of scales from individual trees to forest stands, landscapes, and regions. For example, there are numerous drought-related observations that generally hold for individual trees, such as drought tolerance increasing with tree size and age in many species (Cavender-Bares and Bazzaz 2000). We then translate how changes to plant-available moisture may affect the distributions of species, the biodiversity of landscapes, wildfire, net primary production, and virtually all goods and services provided by forests, including the development of a better understanding of tree biogeography. Finally, we provide advice for how management practices might be adapted to more frequent drought and address research needed to expand our understanding of forest response to drought.

Evidence for Drought Impacts on Forests

An Assessment of Available Data

To date, much of what we know about the effects of drought on the structure, composition, and function of forests in the United States has arisen from observations and data-driven interpretations of resource gradients, providing valuable if limited insights. Data sets that span sufficient temporal variation in climate are improving. Two censuses can be used to generate estimates of (1) mortality rates from numbers of trees that die during the interval (Dietze and Moorcroft 2011, Lines and others 2010); (2) recruitment rates from individuals appearing in a census not present previously (Zhu and others 2014); and (3) growth rates from changes in size (Vanderwel and others 2013). However, estimates of change over time, including forest demographic responses to climate change, require a minimum of three censuses. Forest Inventory and Analysis (FIA) data provide two consistent censuses for most of the Eastern United States (a third census is now available for some locations), but only one census for most of the West because nationally consistent

sample design and plot protocols were not adopted by FIA until the late 1990s (Goeking 2015). This uneven coverage makes it possible to consider the geographic correlation of climate effects on demographic rates (Dietze and Moorcroft 2011, Lines and others 2010, Purves 2009, Vanderwel and others 2013), but using them to understand change over time is difficult.

In addition, potentially long plot observation periods complicate the interpretation of specific climate effects. FIA inventory plots have been resampled at intervals of 4 to 10 or more years, which means data derived from them could encompass exceptionally warm, cold, dry, and wet years (Williams and others 2013). An individual tree contributes to a growth study one observation for each year of growth. By contrast, one tree contributes to a survival study a single event (survival or not). However, attribution of tree responses to drought based on observational studies is challenging because many factors can contribute to morbidity (Adams and others 2009, Allen and others 2010, Manion 1981, McDowell and others 2011, Radtke and others 2012, Wang and others 2006). Even the most complete inventories are hampered by inconsistent temporal coverage of observed droughts. As an example, droughts are predicted to increase in the Northeast (Melillo and others 2014), a region with droughts evident in the paleorecord (Pederson and others 2013) (chapter 2) but lacking severe events in recent decades when much of the most reliable forest inventory data was collected.

The previous point on inconsistent contemporary observations highlights the fact that many other types of important data are also uneven in their coverage. For example, many studies of the paleorecord on vegetative responses to climate come from wet environments, and thus overrepresent wetland species. Similarly, tree-ring data come primarily from trees expected to be most sensitive to climate (Fritts 1976)—often dry, sparsely forested locations. In these tree-ring-based climate reconstructions, old canopy trees are preferred, but these individuals respond differently to drought and heat stress than younger trees and may not reflect genetic selection pressures that may influence the responsiveness of future forests to drought stress.

Although inferences using spatiotemporal variation have long provided some of the most valuable insights on how forests respond to moisture and temperature gradients, those effects can be confounded by land use, management history, soils, complex hydrological patterns, and atmospheric chemistry change. For

example, inferences on drought impacts to different landowners are confounded by who owns what forest where. In the Pacific Northwest, private landowners primarily control productive low-elevation forests managed for timber production, whereas State and Federal agencies usually manage the less-productive and high-elevation old-growth forests of this region (Ohmann and Spies 1998) less intensively (if at all). Hence, Pacific Northwest forests reflect a multi-dimensional set of climatic, geological, and land-use gradients that are both driven and influenced by their composition, meaning that predicting future drought effects will be very difficult. In the Piedmont Plateau of the Southeast, moisture gradients are confounded by land use and stand age: wet bottomlands were left uncultivated and hence tend to have mature forests with older trees, while younger forests established on previously cultivated sites about a century ago and xeric sites were grazed and often remain in pasture (Oosting 1942, Quarterman and Keever 1962). Attributing forest changes to climate can be challenging when they are simultaneously experiencing rising levels of atmospheric ozone (O_3) and carbon dioxide (CO_2), greater nitrogen (N) deposition, and increasing overall stand age (McMahon and others 2010).

As a consequence of these factors and many others, observational data may not yield unambiguous relationships, and they offer only a subset of conditions that may prevail in the future. Hence, observational data are poorly suited for predicting how forests may respond to droughts because they provide a phenomenological, not mechanistic, interpretation of change. Experimentation addresses some of the limitations of observational data by providing controlled manipulations of the environment. However, to date, relatively few experiments have been conducted at a scale that provides general insight for climate changes that affect diverse habitats. For example, there are still only a few rainfall exclusion and redistribution experiments on mature forests (e.g., Hanson and Weltzin 2000, McDowell and others 2013). In addition, species will outrun some of their mutualists, competitors, and natural enemies, and encounter new ones. Some of these processes are too slow, too small, or too large to observe directly or manipulate experimentally; others do not become apparent until thresholds are crossed and dramatic shifts in composition and structure are witnessed (Millar and Stephenson 2015). Experiments sufficiently large and long-term to determine effects on stand composition and structure are also costly. Because of these constraints, future combinations of

climate, competition, and natural enemies cannot be fully anticipated by controlled experiments.

Influence of Drought on Individual Trees

Drought and tree growth—Many conifers and some hardwoods show growth responses to temperature at high elevations and at northern range margins (Bhuta and others 2009, Brubaker 1980, Cook and others 1998, Littell and others 2008, Salzer and others 2009). Tree-ring studies support the interpretation that growth in moist cove sites of the Southern Appalachians is sensitive to moisture variation (Martin-Benito and Pederson 2015, Maxwell and others 2011, Pederson and others 2012) (fig. 4.3). Not surprisingly, growth sensitivity to drought differs between species. Tree-ring studies from the Hudson River Valley in New York ranked growth responses to spring-summer Palmer Drought Severity Index (PDSI) as eastern hemlock (*Tsuga canadensis*) > tuliptree (*Liriodendron tulipifera*) > pignut hickory (*Carya glabra*) > chestnut oak (*Quercus montana*) > northern red oak (*Quercus rubra*) > black oak (*Quercus velutina*) (Pederson and others 2013). A 13-year study in Indiana found tuliptree and sassafras (*Sassafras albidum*) to be more sensitive to drought than oaks (Brzostek and others 2014). However, in southern Indiana, white oak (*Quercus alba*) responded more to summer PDSI variation than did tuliptree, whereas northern red oak responded less than either species (Brzostek and others 2014, Maxwell and others 2014). Even in mesic sites, tuliptree can experience larger growth sensitivity to drought than co-occurring white oak and black oak (Orwig and Abrams 1997). Evidence for drought effects on species of many of the same genera in Europe appears consistent with these observations. In central Germany, growth responses to PDSI ranked as European beech (*Fagus sylvatica*) > Scots pine (*Pinus sylvestris*) > durmast oak (*Quercus petraea*), with greatest sensitivity on the site with low rainfall (Friedrichs and others 2009). Durmast oak survival exceeded that of European beech over the 1976 drought in England (Cavin and others 2013).

Drier than normal conditions tend to have less impact on growth rates of oaks than other species (Clark and others 2011, 2014a; Elliot and Swank 1994; Klos and others 2009), probably related to physiology and deep rooting (Abrams 1990, Abrams and Kubiske 1990, Iverson and others 2008b) (chapter 3). The rank order of growth sensitivity of mesic hardwood > pine > oak from Clark and others (2014b) is consistent with growth and mortality trends reported for the 1999–2001 drought from analysis of FIA data (Klos and others 2009). Despite low growth sensitivity to drought on average,

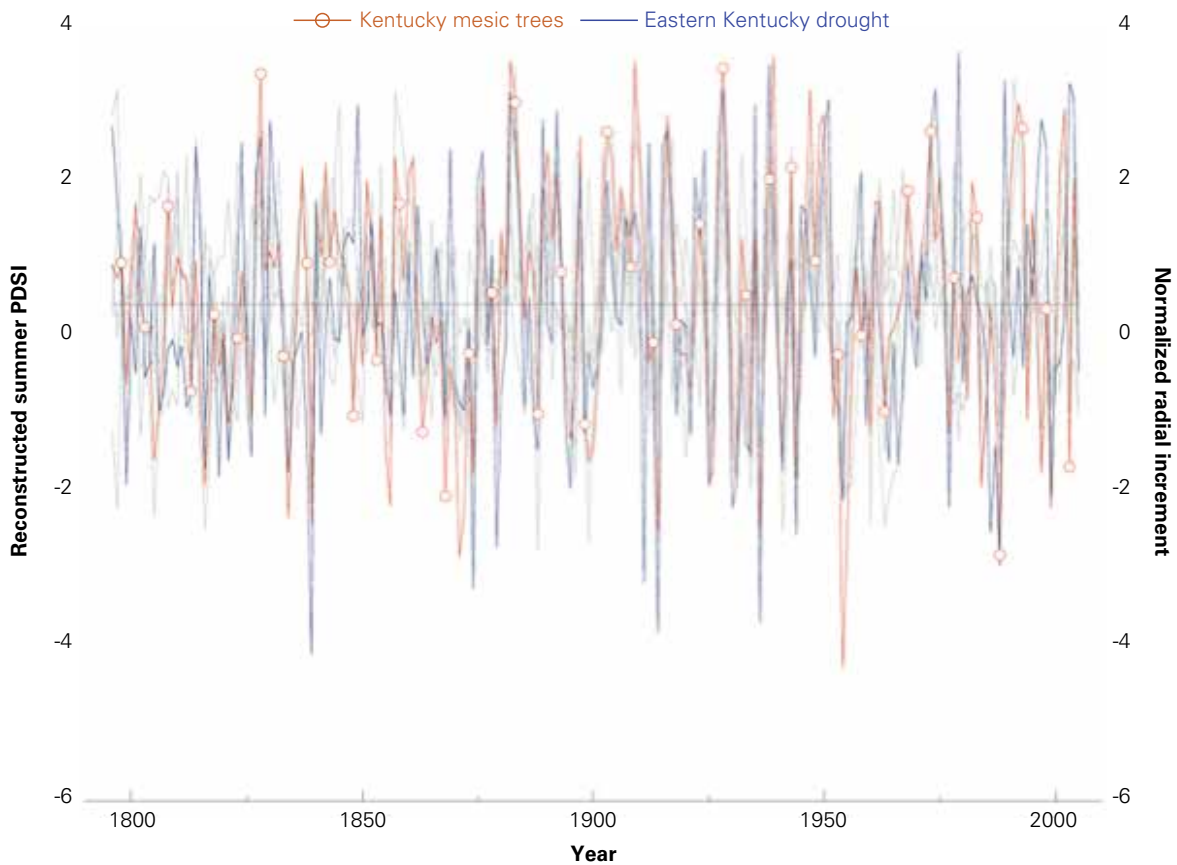


Figure 4.3—Growth responses to summer drought on mesic sites in Kentucky, 1796-2005. Average tree growth (orange line with circles) correlates with an independent reconstruction of summer Palmer Drought Severity Index (PDSI) (June, July, August) ($r = 0.55$, blue line). Chronologies plotted in light gray include eastern hemlock (*Tsuga canadensis*), tuliptree (*Liriodendron tulipifera*), chinquapin oak (*Quercus muehlenbergii*), and blue ash (*Fraxinus quadrangulata*). Despite differences in collections and land-use histories, they show a similar change in direction during specific PDSI conditions: positive growth during wet conditions ($\text{PDSI} \geq 2$) and vice-versa (adapted from Pederson and others 2012).

white oak growth rates can be correlated with moisture available early in the growing season, particularly in dry climates (LeBlanc and Terrell 2009, Pasho and others 2011). A combination of high temperatures and a reduction in moisture could further benefit oaks because many nonoak hardwoods display intermediate drought sensitivity for growth (Clark and others 2013, Klos and others 2009). Although oaks in the red oak subgenera can be susceptible to mortality during drought (Clinton and others 1993, Elliott and Swank 1994, Haavik and others 2011, Hursh and Haasis 1931, Jenkins and Pallardy 1995, Pedersen 1998, Starkey and others 1988, Voelker and others 2008), white oaks can show stronger growth responses.

Local environmental conditions further mediate drought impacts on individual tree growth. For most species of the southeastern Piedmont and Appalachians, the

largest growth sensitivity to drought occurs for trees at high light levels, a positive light-drought interaction. This positive interaction has been shown for juvenile growth of loblolly pine (*Pinus taeda*) (fig. 4.4), but it is not evident for adult growth or for fecundity. The interaction between localized soil moisture conditions and drought has implications for whether or not moist sites can provide a refuge for some species if droughts intensify. Short-term responses in mesic sites could be important for the drought-sensitive species dependent on such habitats. Furthermore, specific edaphic characteristics also influence the severity of droughts. For example, fragipan soils in some pine flatwoods of the Southeast restrict root depth and access to deep moisture (Rahman and others 2006, Wackerman 1929).

Large growth and fecundity responses to drought in southeastern forests could occur initially for trees

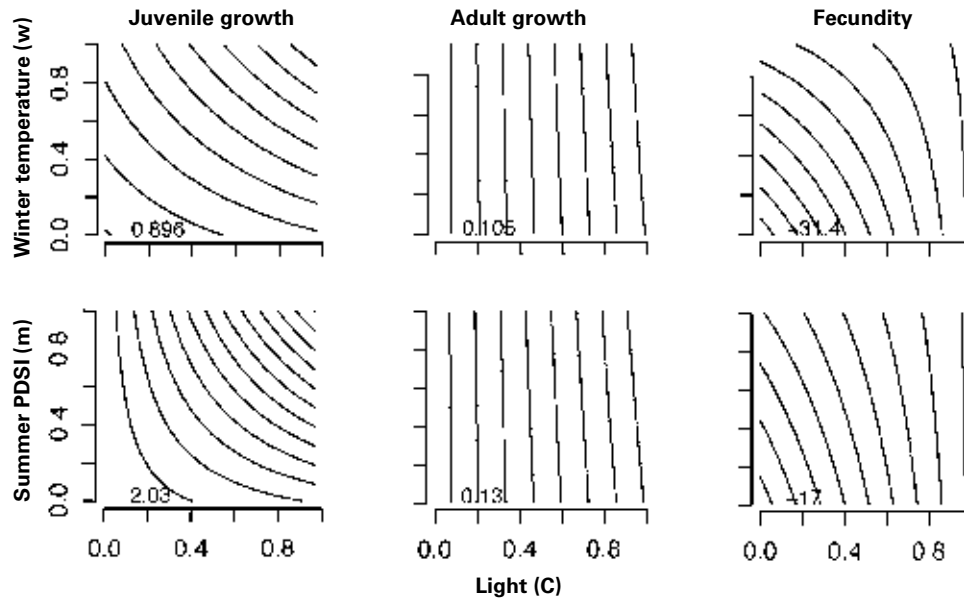


Figure 4.4—A joint distribution of three demographic responses is obtained when all responses are fitted simultaneously, as part of the same model. This example shows interactions that control responses of loblolly pine (*Pinus taeda*) to winter temperature (above) and summer Palmer Drought Severity Index (PDSI) (below) with light availability. Effects differ for growth and fecundity, in juveniles and adults. Amplifying positive interactions (growth) and buffering negative interactions (fecundity) are both evident. In all panels, contours increase from low at lower left to high at upper right (Clark and others 2013).

at high moisture levels, where leaf area, and thus, moisture demand is greatest (fig. 4.5) (Clark and others 2014b). Mesic sites might see more dramatic transitions because they often support sensitive species dependent on abundant moisture (Clark and others 2014b, Elliot and Swank 1994). Still another possibility is that sensitivity could be highest on sites of intermediate moisture (Dormana and others 2013). Moreover, the sign of the interaction between drought index and local drainage might shift from short-term positive (loss of moisture-demanding species on mesic sites) to negative (eventually the moist sites provide refuges for some species). Both phenomena could occur simultaneously. Stand response to sequential drought impacts will differ from individual events (Miao and others 2009).

Drought and tree health—Opportunistic reports of mortality following drought are common (Hough and Forbes 1943, Parshall 1995), but connections between drought and tree death are more difficult to quantify than those for tree growth. For example, extensive drought across much of the Western United States and adjoining Canada coincides with declining tree growth, which can anticipate mortality (Allen and others 2010, Hicke and others 2013, Joyce and others 2014,

O'Connor 2013, Williams and others 2013). Extended morbidity can precede death, a legacy of low vigor spanning decades (Wyckoff and Clark 2002), potentially related not only to repeated drought (Pedersen 1998, Pederson and others 2014, Voelker and others 2008) but also to any other risk factors that occur during the interval. Mortality rates in some old-growth forests during nondrought years have increased since the 1970s, attributed in part to warming temperatures in southwestern forests (van Mantgem and others 2009) and boreal forests in western Canada (Luo and Chen 2013, Peng and others 2011). Even where adequate moisture is available, rising temperatures could affect the health of individual trees.

Juvenile sensitivity to warming may restrict future habitats to mesic sites (McLaughlin and Zavaleta 2012). For trees beyond the seedling stage, Luo and Chen (2013) argue that warming has greatest impact on mortality rates of young trees, but there are also reports that old white spruce (*Picea glauca*) (Wang and others 2006) and English oak (*Quercus robur*) (Rozas 2005) show the strongest response to climate. Decreased vigor of trees due to drought and/or heat stress makes them more vulnerable to secondary mortality events. Pathogen-drought interaction studies

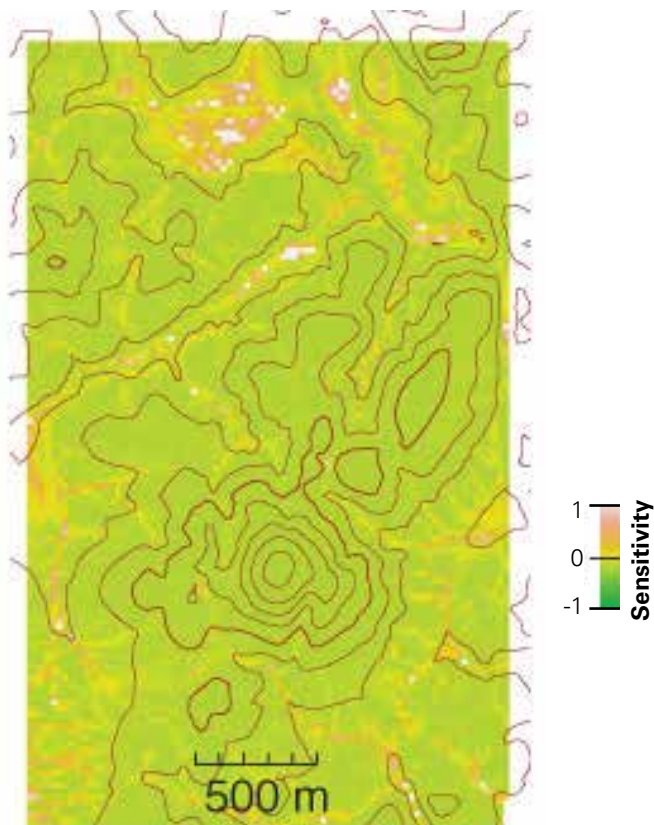


Figure 4.5—Drought effects on growth interact with soil moisture. For American elm (*Ulmus americana*) on the Piedmont Plateau in North Carolina, growth is most sensitive to drought on wet sites at low elevation (see contours), potentially contrary to the intuition that xeric stands are at greatest risk of drought. This is a positive moisture index/Palmer Drought Severity Index (PDSI) interaction, with the largest response to PDSI occurring on moist sites (Clark and others 2014b).

have thus far focused on cankers and root pathogens, with less emphasis on foliar diseases and biotrophic pathogens (Desprez-Loustau and others 2006). Many pathogens can tolerate a greater range of water stress than the plants they infect, and the combination of pathogen infection and moisture stress on host trees can increase disease severity (Desprez-Loustau and others 2006). Fungi that commonly occur in plant tissue may become pathogenic with reduced resistance from a water-stressed host (Desprez-Loustau and others 2006). Drought conditions can increase damage from secondary pathogens (those infecting tissue in poor physiological condition) while reducing damage from primary pathogens (those infecting healthy tissue) (Jactel and others 2012). Some examples of the interactions include increased mortality of holly oak (*Quercus ilex*) seedlings from the pathogenic oomycete *Phytophthora cinnamomi* (Corcobado and

others 2014) and the transition from quiescent to pathogenic *Sphaeropsis sapinea* on red pine (*Pinus resinosa*) seedlings (Stanosz and others 2001) under water stress. Such interactions are also reported in the tropics (Brenes-Arguedas and others 2009). Conversely, mutualistic associations with mycorrhizae and other beneficial microbes may mitigate the effects of drought. Drought can decrease mycorrhizal colonization (Compant and others 2010) and alter structure and function of rhizosphere microbial communities in ways that are not yet well understood (Evans and others 2014, Hawkes and others 2011). Many fungal and oomycete pathogens require moisture for spore dispersal, germination, or infection (Desprez-Loustau and others 2006). The moisture-pathogen interaction is complicated by the fact that moist conditions that promote fungal infection can also benefit the host plant (Hersh and others 2012). Combined effects may depend on the pathogen's mode of attack and on the degree of host stress (Desprez-Loustau and others 2006, Jactel and others 2012).

Drought and tree recruitment—This synthesis emphasizes growth and mortality, not because they are more important than recruitment, but rather due to the fact that recruitment is poorly understood. Indeed, recruitment warrants special consideration, both for its central role in decade-scale responses to drought, and because it has been especially difficult to study at the regional scale, to represent in models, and to predict. Drought can impact future forest composition through reduced fecundity, limited seed germination, and mortality of shallow-rooted seedlings that have limited carbohydrate and water storage (chapter 3). Unfortunately, most empirical studies of climate effects on seed production are limited to a few years (or less) and a few small study plots (Clark and others 1999). Some of the longer studies focus on interannual variation, but few provide evidence for decade-scale effects of increasing drought.

Drought effects on fecundity are complicated by feedbacks with other factors that contribute to masting cycles and recruitment success, and the interactions involving weather and seed production can span several years, thereby precluding simple generalizations on effects of drought. For instance, the development of moisture limitation over successive years appears especially important for fecundity. In general, female function in trees is stimulated by resources, including moisture (Perez-Ramos and others 2010), CO₂ (LaDeau and Clark 2001), and light availability (Clark and others

2014b). Seed production of many species shows positive interactions between moisture and light, with trees at high light levels showing the greatest response to moisture availability (Clark and others 2014b). Warm, dry weather may be beneficial during flower induction the year before seeds ripen (Houle 1999, Pucek and others 1993), a situation imposed artificially by water restriction in some fruit crops (Owens 1995). This effect may be enhanced if dry conditions follow a wet year (Piovesan and Adams 2001). Drought-induced increases in fecundity may be followed by reduced seed production up to several years thereafter (Bréda and others 2006, Innes 1994). In Mediterranean oaks, moisture availability is critical during the time when seeds are maturing; masting cycles can be disrupted by low rainfall (Koenig and Knops 2013, Perez-Ramos and others 2010).

Not all drought influences on tree recruitment should be construed as negative. Seedling recruitment and resprouting may increase following drought-related disturbances that impact the local environment, often for many years (Cooper-Ellis and others 1999, Dietze and Clark 2008, Kayes and Tinker 2012). Interactions with canopy structure and hydrology are important for tree recruitment in many different forests. On xeric sites in the Western United States, recruitment can benefit from a facilitation effect of the canopy on seedlings and saplings, an effect that is reduced by drought-related reductions in leaf area (Caldeira and others 2014, Royer and others 2011). On mesic sites, increased light penetration could promote recruitment and sapling growth (Galiano and others 2013, McCarthy-Neumann and Ibáñez 2012). First-year seedling mortality can be high due to damping-off fungi, particularly in cool, wet, shaded understories (Hood and others 2004, Ichihara and Yamaji 2009); hence, drier conditions may reduce these losses on some sites.

Drought-influenced processes that occur within individuals can affect organismal resource allocation, growth, maturation rates, fecundity, and survival, each of which can react to drought in different ways dependent on the responses of others (fig. 4.4). Taken together, the studies summarized in these sections clearly demonstrate individual tree vulnerability to drought, but they only hint at the complex biotic interactions that help determine where on a forested landscape drought will have the most profound impacts. While we have built on our current understanding of climate effects on individual trees (chapter 3), our intent is to anticipate consequences for forest structure

and composition. After all, many factors contribute to the challenge of forecasting how increasing drought will affect forest structure and diversity. Changing temperature and precipitation are producing climate combinations that alter frequency, intensity, and seasonality of drought (Allen and others 2015, Dai 2012, Wehner and others 2011). As a result, novel forest assemblages will emerge as individual trees respond and populations shift their landscape positions and migrate geographically. For example, it is possible that moist sites will provide refuges if climate becomes more xeric and an alternative positive interaction could result from competition—the water-demanding species on wet sites fully utilize more abundant moisture supply and thus are especially vulnerable when moisture availability declines (Frelich and Reich 2010). This transition is a collective response of individuals in the context of the populations and communities found in their local environment.

Influence of Drought on Stands and Landscapes

Many of the open questions summarized in the previous sections arise from the challenge of translating improved understanding of demographic consequences for trees to predictions of change in forests. Because of the complex interactions between organisms, populations, communities, sites, and other environmental determinants, many of the observations on individual trees (fig. 4.3) only poorly translate to predictions of stand-level responses. The following sections emphasize drought impacts on the forest stand, long considered the fundamental scale both for management and community ecology (e.g., O'Hara and Nagel 2013).

Interactions and the size-species distribution—

Some interactions occur between individuals, such as competition in crowded stands, and represent one of the most influential determinants of tree growth and survival. Drought may operate differently in stands of different density and age (Esper and others 2008). Stands with open canopies or ones in which leaf area index decreases during drought (chapter 3) could experience increased understory irradiance and transpiration demand. Klos and others (2009) likewise found that the effects of drought on growth and survival might increase with stand age in the Southeastern United States. Due to the large sample interval in many climate-mortality studies, evidence is equivocal. The disparate results could also indicate the importance of unobserved variables that co-vary with density and stand age (D'Amato and others 2013).

Climate variation that promotes growth or survival of individual trees usually has similar effects on their neighboring competitors, depending on the size-species distribution (SSD) of the stand. The SSD is the distribution of trees across species and size classes. The SSD results from interactions of individuals, as each tree responds to local conditions and weather. Competition and climate affect the species and size classes that make up stands in different ways. There is feedback—the structure itself determines how the SSD will respond to drought

through shading and transpiration. Biogeographic patterns in distribution and abundance emerge as individual responses translate to SSDs across heterogeneous landscapes. Management aims to modify SSDs (for example, via thinning and encouraging regeneration) to meet specific objectives, including controlling the SSD of stands to regulate bark beetle outbreaks (chapter 6). The fact that the SSD responds to climate change as a joint distribution of species and size classes has challenged our ability to anticipate the impact of drought.

MOISTURE AND SIZE-SPECIES DISTRIBUTIONS

How can the effects of drought on forest structure and diversity be quantified? Conversely, what can structure and diversity tell us about past and potential future responses? Such questions require effective summaries of how temperature, precipitation, and day and season length together influence forest demography—changes in the size-species distribution (SSD) of stands. Annual temperature and precipitation partly explain biodiversity and productivity gradients at sub-continental scales. But their combined effects depend on stand structure and on seasonal timing, more like the hydrothermal surplus (HTS) and hydrothermal deficit (HTD) in the degree-hours during months with positive and negative water balance, respectively (fig. 4.6). Unlike annual values, HTS and HTD describe the seasonal convergence of factors that affect competition between size-species classes. High temperatures and precipitation contribute to long, warm, wet growing seasons along the Gulf Coast. The resultant high HTS values extend up the moist Southern Appalachians, declining to the north and west, but different from either temperature or precipitation alone, in part due to summer deficits. The HTD is especially large in the Piedmont Plateau, Coastal Plain, and western Gulf Coast. The length of the growing season is short in the Northern United States, but during the growing season days are long. At this time, moisture is more available in the Northeast than the upper Midwest.

The hydrothermal surplus and deficit (see figs. 4.6 and 4.7 on the next page) and PDSI (the basis for CDSI of the text box on page 60) are two examples of variables used to explain forest properties. Note agreement between CDSI (fig. 4.1) and HTD (fig. 4.6) in the South, but disagreement in the upper Midwest. One reason for this difference is the fact that CDI counts every month when PDSI is low, progressively amplifying their effects from month to month, whereas HTD considers the entire growing season as a unit.

Perhaps most important are changes in surpluses and deficits, shown as a different map in Figure 4.7. Despite the fact that deficits dominate in specific regions (the West and Southeast), forests throughout the East are exposed to increasing deficits (fig. 4.7).

The SSD is a *stand-level variable*, a distribution of species and sizes, related through history, climate, and competition (histograms in fig. 4.6). Knowledge of the SSD is required for understanding demography, biodiversity, competitive interactions, fuel structure, and response to moisture stress. SSDs are a focus of management practice. For a given stand there is a distribution of stems across species (vertical axes) and size classes (horizontal axes). Disturbance and succession affect the species composition of large and small size classes. Advance regeneration in small classes provides clues to future stand composition. SSDs vary geographically with climate, soils, and time. For example, species present in the largest size classes can have disproportionate access to light and moisture, thereby suppressing competitors. Crowding affects canopy architecture of individuals, thus influencing their vulnerabilities to drought (fig. 4.12). Thus, different SSDs are expected to respond to drought differently. For this reason, physiology and tree-ring studies of individuals do not directly translate to the forest stand. Thus far, models used to anticipate forest response to drought are based on estimates of how individuals respond to climate. We suggest new efforts to quantify the SSD response.

(continued next page)

(continued from previous page)

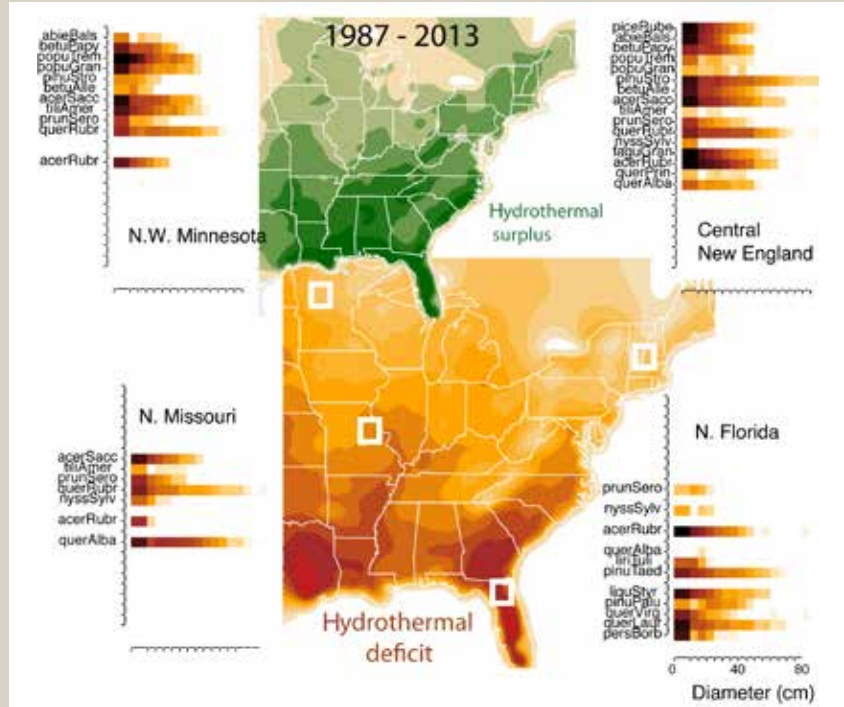
MOISTURE AND SIZE-SPECIES DISTRIBUTIONS

Figure 4.6—Expressed on a relevant scale for trees, such as the number of degree hours at positive (hydrothermal surplus, HTS) and negative (hydrothermal deficit, HTD) water balance, large geographic contrasts contribute to size-species distributions (histograms). Surplus (above) and deficit (below) both reach maximum values near 3000 degree hours, but in different locations. With sufficient moisture, high temperature (up to a point) increases development. Long days and growing seasons combined with moisture (high HTS) benefit species capable of exploiting these conditions in competition with individuals of other species. Conversely, a large number of degree hours at negative water balance benefits species capable of tolerating drought. In the Southeast, surpluses and deficits are both common. The upper Midwest has much lower precipitation, but also lower temperatures and shorter growing seasons. The Northeast benefits from infrequent deficits, despite lower temperatures. Size-species distributions (SSD), shown for four different regions, reflect climate differences and stand history (Clark and others, In press).

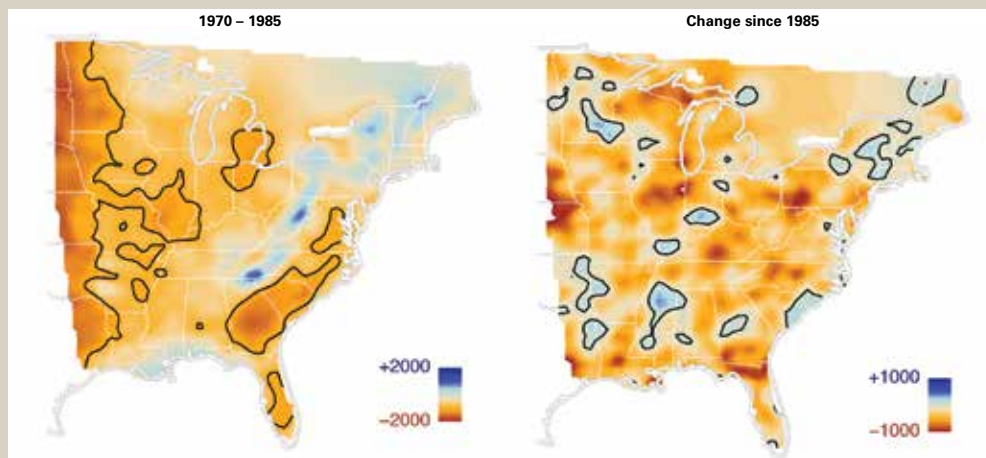


Figure 4.7—Deficits commonly develop throughout the Eastern United States each growing season, particularly in the Midwest and Southeast. At left is the difference between surplus and deficit (black isohydrotherm is drawn at -1000 degree hours) from 1970 to 1985. The recent shift to larger deficits is nearly ubiquitous in the Eastern United States (black line is drawn at zero difference before and after 1985). (Clark and others, In press).

Understanding why individual responses do not readily extrapolate to the SSDs of stands is related to how the SSD mediates a climate response. For instance, when using an analysis of FIA data specifically targeting the 1999–2001 drought in the Southeast, Klos and others (2009) found a weak relationship between stand diversity and drought impacts, suggesting that the partitioning of resources occurring in many stands buffered at least some drought effects. For codominant trees in crowded stands (trees with crowns in the main canopy), growth and mortality rates are dominated by competition. Canopy individuals that might respond positively to a moist growing season are constrained by the fact that the competing neighbors largely benefit at the same times. At the stand level, mortality can increase as a result of favorable conditions, because thinning rates increase with growth rates, despite the fact that conditions have improved on average.

Hence, the interdependence of individual responses that make up the stand response is harder to measure, replicate, and quantify than the response of an individual tree. For example, drought impacts depend on the species and size classes of individuals competing for moisture and light (see Moisture and Size-Species Distributions text box on pages 67 and 68). Soil moisture depends on an interaction that involves climate, redistribution by local drainage, and uptake by competing trees (fig. 4.5) (Ackerly and others 2010, Loik and others 2004). Conversely, drought that depresses growth of individual trees can also decrease crowding effects, reducing the competitive pressure on growth and survival. In fact, the competition interaction with climate can reverse the apparent effect of climate, depending on whether the focus is the individual tree or the stand (Clark and others 2014b). In contrast to codominant trees that experience high competition for light, the tallest (dominant) trees with emergent crowns may respond more directly to climate. The rare individuals that make up the right-most extremes in the preceding text box are the focus of many tree-ring studies, but they would almost never appear in small [0.0672-ha (hectare)] FIA plots (note that trees are sampled on the larger 0.4-ha macroplots in Western States). Best represented in plot-based studies are the smallest size classes, which in crowded stands can be limited by both light and moisture. The large number of positive interactions between light and drought result from the fact that individuals not severely light-limited can respond most to climate variation (Clark and others 2014b).

Interactions that occur within stands mean that stand-level responses to drought will not necessarily agree with studies of individual growth and survival. Responses of individual trees at low moisture availability do not tell us how the abundances of different species will change as a result of drought. Response of size-species structure depends on how these individual responses translate to population growth rates, each population being an aggregate across individuals of all size classes, competitive environments, and microhabitats (see Moisture and Size-Species Distributions text box on pages 67 and 68). If species that can tolerate xeric conditions progressively increase in abundance within stands that lose productivity and have lower transpiration demand, then the moisture for which trees compete becomes a competition feedback (D'Amato and others 2013). Development of better methods to combine the evidence from different scales is a goal of biodiversity research. The uncertainty that comes from climate-competition interaction effects on SSDs at the landscape scale must be met with studies that evaluate responses at both scales.

For example, climate-competition interactions are evident in several studies at the individual-tree scale (Cescatti and Piutti 1998, Martin-Benito and others 2011), at the stand scale (D'Amato and others 2013), and even across plot networks (Clark and others 2011, 2014b). However, climate variables often emerge as weak predictors of large-scale mortality, at best (Dietze and Moorcroft 2011, Gustafson and Sturtevant 2013, Lines and others 2010), and any patterns may be hard to interpret. A tendency toward higher mortality rates in warmer climates is expected on the basis of higher productivity in warmer climates—partly explained by the fact that high growth is attended by rapid thinning (Assmann 1970, Clark 1990). Some of the largest studies involving FIA data provide relationships that are geographic, rather than change over time. For example, a synthesis of plot data on 48,000 trees spanning 50 years over 4 Midwestern States did not find a link between precipitation and mortality, but rather highlighted the importance of competition (Yaussy and others 2013). While increased rainfall variability in recent decades (Li and others 2011, Melillo and others 2014) may influence geographic variation in mortality rates, the relationship between temperature and mortality does not necessarily constitute a threat of climate change—a study of geographic variation in mortality rate with average temperature did not necessarily find a vulnerability to temperature (Zhu and others 2014). Dieback events are also attributed to combinations

of physiological stress (Breshears and others 2009, Williams and others 2013), insect outbreaks (Gaylord and others 2013, Raffa and others 2008), and increased extent and severity of wildfire (Littell and others 2009, Westerling and others 2006, Williams and others 2013). Recruitment failure (Bell and others 2014, Brown and Wu 2005), growth decline (Chen and others 2010, Hogg and others 2008, Williams and others 2013), loss of canopy cover (Rehfeldt and others 2009, Worrall and others 2013), and extensive mortality (Allen and others 2010, Breshears and others 2005) have all played different roles in specific dieback episodes.

Even when drought does not directly kill trees, its effects on reduced vigor on competitive ability has implications for forest composition and structure. The critical roles of recruitment response to drought for future forests range from effects on migration potential to recolonization of diebacks. The relationship between diversity and resilience to drought may also vary among ecosystems (Grossiord and others 2014). Year-to-year volatility and high spatial variation that comes with the many feedbacks involving weather, competitors, fungal symbionts, and pathogens make it difficult to quantify. For example, ecologists have long suspected that pathogens mediate competition between trees of the same species when that species is at high density (Connell 1970, Janzen 1970), commonly termed density-dependence. Increases in natural enemies that occur where a host is abundant decrease the likelihood of any one species becoming dominant. If the host tree-pathogen relationships that promote diverse community structure are modulated by moisture availability, then drought effects could be unpredictable (Benítez and others 2013, Hersh and others 2012).

Evidence that temperate forest stands may see a long-term increase in oaks (Bachelet and others 2003, Clark and others 2014b) presents an apparent paradox, given that oak recruitment has declined in many regions (Abrams 2003, Fei and others 2011) (fig. 4.11). Advantages for oak trees under more xeric conditions are consistent with the population-scale tendency for oaks to expand in regions of low rainfall, but recruitment response remains questionable. In part, this may arise because seedling germination, establishment, and early survival are especially susceptible to environmental variation (Grubb 1977, Harper 1977, Ibáñez and others 2007, Silvertown 1987). The increased susceptibility of juvenile trees may be particularly acute in dry regions where interannual climatic variation is associated with episodic recruitment (Brown and Wu 2005, Jackson and others 2009). High

mortality of seedlings relative to adults suggests a bottleneck on population growth rate, but direct evidence for its effects on fitness of many interacting species is lacking. For example, competition in the years following seedling establishment may sometimes blur the impacts of high interannual variability on recruitment.

Increasing attention to interactive relationships among demographic processes is moving in the direction of more comprehensive synthesis, involving both individual growth (Bugmann 2001) and mortality (Allen and others 2010, Breshears and others 2005, van Mantgem and Stephenson 2007, van Mantgem and others 2009). The fact that drought impacts depend on interactions highlights the need to study both individual- and stand-level responses. For instance, those interactions involving drought and the biotic environment contribute to recruitment variation following disturbance, canopy gaps, fires, landslides, ice storms, timber harvesting, and pest outbreaks (Brown and Wu 2005, Hubbell and others 1999, Pederson and others 2008, Savage and others 1996). Specific examples of the interactions that can occur between disturbance and moisture availability include the increased recruitment near the prairie-forest ecotone in Minnesota during the 1930s drought (Shuman and others 2009) and in the Great Basin following fire suppression, livestock introduction, and wet climatic conditions in the late 1800s (Miller and Rose 1999). Thus far, there is much more information available on responses of individual trees than of stands, and the important interactions that will control stand responses to drought remain poorly understood. Questions remain if we can anticipate which effects of anticipated drought-mediated change are likely to be most severe, in what ways, and on which parts of the landscape.

Drought-Mediated Biogeographic and Biome Shifts in U.S. Forests

This section extends stand-level effects to biogeographic responses at regional to subcontinental scales. Biogeographic change in forests can include migration (change in distribution) and changing abundances within current ranges. While much of the literature on climate change and species migration does not focus specifically on effects of drought, this literature is relevant to increasing drought, which depends on interactions between temperature and precipitation (chapter 3). Evidence that species distributions are responding to climate change has been

both a source of concern and a reassurance that species may have the capacity to migrate to new locations. The climate change-species migration studies suggesting that potential distributions of many species are shifting faster than are the populations themselves could apply not only to temperature but also to drought.

Evidence Regarding Changes in Species Distributions

Forests respond to drought through both changes to the SSD and to immigration and local extinction (Chen and others 2011, Parmesan and Yohe 2003). Changes in species distributions occur when regeneration is successful beyond the current population frontier or when regeneration fails in a portion of the current range. In some cases, drought may relocate suitable habitats within the geographic range, such as shifts from areas of low to high moisture availability—for instance, at higher or lower elevations or adjacent to wetlands or bodies of water. Migration studies usually combine knowledge of species traits, paleo evidence for past spread, and modern landscape heterogeneity (Prasad and others 2013). However, migration occurs at and beyond range limits, where local heterogeneity in recruitment success (Ibáñez and others 2007, Morin and others 2007, Pitelka and others 1997), low population density, the potential importance of rare dispersal and establishment events over broad regions, and a lack of good distributional data on most species make migration difficult to detect and to quantify (Clark and others 2003).

Further complicating matters is that the concept of migration is not applied consistently. For plants, “migration” most often refers to accumulated gains and losses in the area occupied by a species, typically at a regional scale. Poleward or upslope expansions in response to warming climate are examples of this usage. A different definition of migration refers to latitude- or elevation-weighted abundance or performance (Feeley and others 2011, 2013; Gottfried and others 2012). Such weighted averages can be calculated for samples where observations are individual organisms, abundances of species on plots, or a performance measure (Lenoir and others 2008, Woodall and others 2009). For example, growth rates of trees can be used to calculate performance-weighted mean latitude for the species. The mean latitude calculated by this approach can change from one survey to the next, regardless of whether or not the population moves—even if the range is static, the mean will change if individuals in different parts of the range grow faster/slower than before. Like weighted averages, parametric functions fitted to occurrence, abundance, or demographic rates (Canham and Thomas 2010, Clark and others 2014a, Mok and others 2012, Vanderwel and others 2013, Zhu and others 2014) can be dominated by samples where the species is abundant and insensitive to range margins. The smooth declines in performance near species distribution limits assumed in many models are not widely observed in demographic data (fig. 4.8). Hence, metrics that focus on population

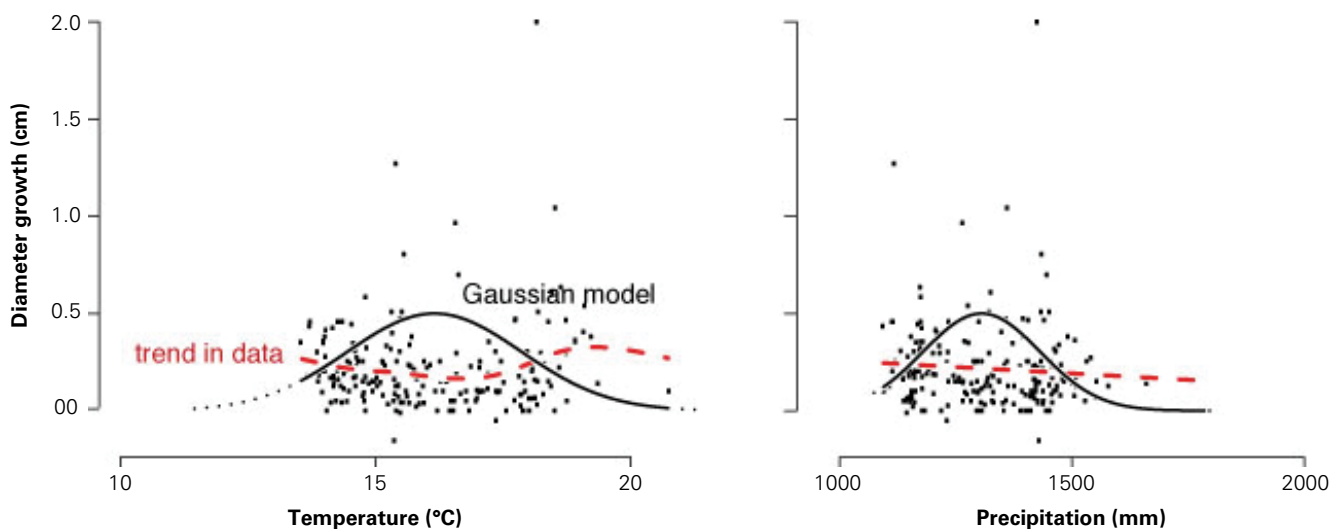


Figure 4.8—Models of distribution and abundance impose unrealistic relationships on Forest Inventory and Analysis data from the Eastern United States. The ubiquitous assumption that abundance and performance decline at range boundaries (e.g., a Gaussian model) contrasts with a spline smoothing (dashed red) of data (dots). Example shown here is red maple (*Acer barbatum*) (Clark and others, In press).

centroids can provide valuable insight on geographic patterns and migration trends, but it is important not to interpret them as a change in distribution of the species.

Although latitudinal migration in response to warming could be occurring for some species, evidence of poleward movement of trees is even less obvious than upslope migration. Warming over the last century in the continental United States has been most rapid in the upper Midwest and Northeast, due to the combination of regional climate change and low relief (chapter 2). Poleward migration would be identified by establishment of new recruitment out ahead of established range boundaries, especially in these areas of rapid change. This pattern is not evident in FIA data (Zhu and others 2012). It is important to point out that there are only a few examples of rapid contemporary natural tree migrations (Fastie 1995, Pitelka and others 1997). The paleo record may also provide examples of rapid spread in response to climate change, such as hazelnut (*Corylus*) expansion into western Europe in the early Holocene (Huntley and Birks 1983). However, many paleorecords are not well suited for determining rates of species migration or localized responses to short-term drought. For example, the sporadic occurrence of fossils in lake sediments can mean that a few trees are nearby or that many trees are far away, making it difficult to infer when a population arrives or disappears from a region. Interpretations of paleorecords to suggest rapid tree migrations, which were common in the past, are inconsistent with current understandings of species dispersal and life history observations (McLachlan and others 2005). Pollen records tend to lack fine-scale temporal resolution and can be ambiguous about the relationships between climate and vegetation patterns, especially when data are limited (e.g., Minckley and others 2008).

While some latitudinal migration may be underway, it is likely sporadic and difficult to detect—a pattern predicted by some models (Clark and others 2001). For example, FIA data failed to detect the southern magnolia (*Magnolia grandiflora*) expansion in the southeastern Piedmont (Gruhn and White 2011). The spread of this species is facilitated by horticultural practice, but populations are clearly capable of invading shaded understories of Piedmont forests. One of the few examples suggesting rapid spread from the Zhu and others (2012) analysis is American holly (*Ilex opaca*), which has ripe berries available for northward migrating birds in spring. Loss of paper birch (*Betula papyrifera*) and black spruce (*Picea mariana*) from

the Blackrock Forest in New York could be explained not only by increasing temperatures, but also by successional trends in these aging forests (Schuster and others 2008). However, new arrivals at that site in this century include some that are near or beyond their commonly recognized range limits, including southern catalpa (*Catalpa bignonioides*), cockspur hawthorn (*Crataegus crus-galli*), red mulberry (*Morus rubra*), cottonwood (*Populus deltoids*), and slippery elm (*Ulmus rubra*). In each of these cases, researchers found that migrations are difficult to detect due to the fact that establishment is sporadic. Although researchers could argue that migrations are simply undetected, it appears clear that waves of rapid spread exceeding 10^3 meters per year that would be required to match the pace of shifting habitats are not occurring.

Opportunities for migration to track changing potential distributions are also found in landscapes with topographic relief and, thus, variable drainage and a range of suitable microclimates. The most effective migration could be expected in mountainous regions of compact climate gradients, where habitat shifts might not require long distances. For example, Beckage and others (2008) found that northern hardwood species invaded plots at a lower boundary of boreal forest in the Green Mountains of Vermont over the last half century. In this location, the ecotone is sharp, concentrated within 200 m of elevation. The mountainous terrain of the West can provide nearby upslope locations with lower temperature and higher precipitation (Jump and others 2009). Species in the Rocky Mountains that are not already at high elevations may lose much of their current habitat but could potentially find suitable habitats at different elevations (Bell and others 2014). Coops and Waring (2011) predict a large distributional shift and reduction in range extent for lodgepole pine (*Pinus contorta*) in the Pacific Northwest due to a projected increase in late summer drought. Using the same approach, Coops and others (2011) discuss why western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) may expand their ranges, whereas ponderosa pine (*Pinus ponderosa*), lodgepole pine, grand fir (*Abies grandis*), and noble fir (*Abies procera*) ranges may contract. Still, even in such topography where dispersal is probably not limiting, tree upslope shifts appear to lag climate change in the Alps (Gehrig-Fasel and others 2007) and Andes (Feeley and others 2011).

Large-scale disturbance could accelerate migration, opening stands for invasion by propagules that would otherwise fail to invade competitive understories

(Dukes and others 2009, Weed and others 2013). Changes in land cover and diebacks resulting from combinations of climate, disease, and human action can all contribute to expanding or contracting ranges (Man 2013). Expansion of chaparral at the expense of forest is predicted for the San Francisco Bay Area (Cornwell and others 2012). Franklin and others (2013) predict changing distributions of 13 tree and 29 shrub species in California, with moisture being the most important cause. Declines in conifers and broadleaf deciduous trees and increases in grasses and shrubs are projected in parts of the West (Jiang and others 2013). Because many drought-tolerant species are also tolerant of fire, new range limits can depend on changes in fire regime. Increased fire frequency, size, and/or intensity (all of which have increased in the Western United States over the past 30 years) (Miller and others 2009) in forest types that are fire-maintained can rapidly shift composition, structure, and function of forests. Replacement of conifer forest by mixed evergreen forest and conversion of shrubland to grassland may be accelerated by fire (Lenihan and others (2008). Declines in the extents of valley oak (*Quercus lobata*) and blue oak (*Quercus douglasii*) are possible in California (Kueppers and others 2005).

However, the extent to which large diebacks could promote migration remains uncertain (Kane and others 2011, Linares and others 2009). In part, this is because future range shifts are difficult to anticipate due to limited evidence on the combinations of variables that control current range limits. For example, there is no clear indication that demographic rates, such as growth, survival, and reproduction (in other words, the patterns that would allow us to estimate factors that control distributions), decline near population frontiers (Abeli and others 2014, Tardiff and others 2006) (fig. 4.5). Yet the capacity for drought-induced dieback to accelerate change, including interactions involving fire and insects, suggests that change could occur at different rates, over centuries, and may be punctuated by episodic transitions. Tracking potential distributions could also depend on fire and other disturbances that accelerate migration. Therefore, the combination of large projected habitat shifts with limited evidence for the rapid migration that would be needed to track it suggests that biogeographic patterns could substantially lag climate change.

Our desire to anticipate the effects of increased drought on species diversity highlights the challenge of understanding an inherently stand-level consequence

that can vary regionally. In an example from the Eastern United States, Clark and others (2014a) found that the strongest relationship between species diversity and climate resides in the upper Midwest for precipitation and in the upper Midwest and Northeast for temperature. In western forests, especially those in warm and dry climates at low elevations, increasing drought could result in loss of some species, and this loss could be accelerated by dieback (Bell and others 2014, Kelly and Goulden 2008). The following sections take a more regional perspective on some of the likely biogeographic consequences of increasing drought in forests.

Drought-Related Changes in Eastern Forests

The last century does not include droughts as severe as some of those in previous centuries in some parts of the East (Cook and others 2010, McEwan and others 2011, Pederson and others 2013, Stahle and Cleaveland 1992, Stahle and others 1988). Drought effects on tree growth and survival in eastern forests are important not only in upland habitats (Abrams 1990, Graumlich 1993, Pederson and others 2012) but also in bottomlands and coastal wetlands (Cook and others 1999, Stahle and Cleaveland 1992). Drought effects also include coincidental events that could impact growth and mortality. For example, fires in the Eastern United States have increased in frequency and area burned during periods of low precipitation, high temperatures, or both (Clark 1989, Lafon and Quiring 2012, Lynch and Hessler 2010).

Regionally based growth-related drought responses of nonoak hardwood and conifer species are diverse. High temperatures appear to limit tree growth in many species, perhaps more in the South and Midwest (St. George and Ault 2014, Williams and others 2011) than in the North (Martin-Benito and Pederson 2015, St. George and Ault 2014, Williams and others 2011). Growing-season moisture deficits are common in the southeastern Piedmont and Southern Appalachians, and drought sensitivity of some pine species is high in this region (fig. 4.9) (Clark and others 2014a, Cook and others 2001, Henderson and Grissino-Mayer 2009, Schumacher and Day 1939), with possible exceptions at northern range margins and higher elevations (Bhuta and others 2009, Cook and others 1998, DeWeese and others 2010). Loblolly pine plantations along the coasts of Florida, Georgia, and the Carolinas may benefit from more consistent late-summer rainfall, a longer growing season, and a higher water table than is common in the more deficit-prone Piedmont (Jordan and others 2008).

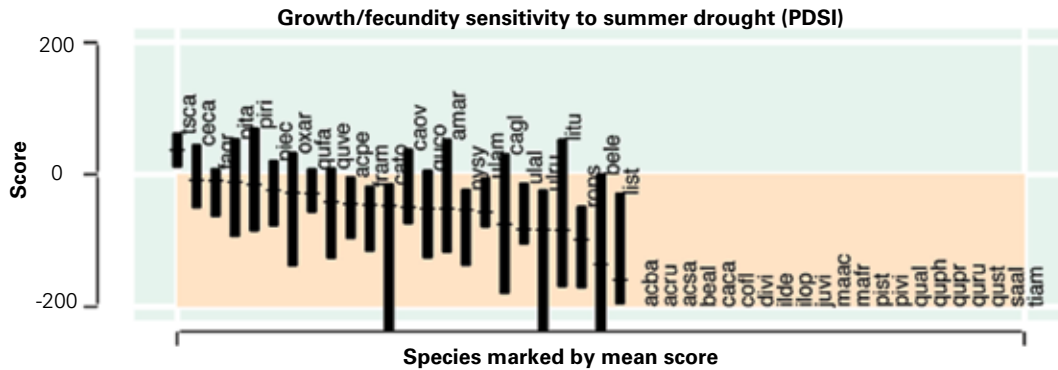


Figure 4.9—The joint distribution of growth and fecundity provides a sensitivity estimate to drought for southeastern tree species. High prediction scores on the vertical axis indicate high sensitivity (relative rather than absolute scores are meaningful). Species without bars at right are off the scale and insensitive relative to those at left (Clark and others 2013).

The interactions involving competition and drought could contribute to habitat shifts in the Eastern United States. Klos and others (2009) suggested that dense stands may experience the most severe impacts of drought, which agrees with the positive interaction between drought and competition found in studies of single species in Europe (Cescatti and Piutti 1998, Martin-Benito and others 2011), at the stand level in the upper Midwest (fig. 4.12), and at the tree scale for many species in the Eastern United States (Clark and others 2011, 2014b). In the upper Midwest and Lake States, stand composition may shift as drought-tolerant pines and oaks potentially expand relative to drought-intolerant quaking aspen (*Populus tremuloides*), bigtooth aspen (*Populus grandidentata*), and paper birch (*Betula papyrifera*) (Handler and others 2014, Scheller and Mladenoff 2008). Boreal and lowland conifers, northern hardwoods, aspen-birch, and riparian communities may decline with increased drought predicted for this region (Handler and others 2014). Eastern oak-hickory forests could potentially expand as other species become less competitive (Handler and others 2014).

Taken together, many species are vulnerable to drought in eastern forests. How this vulnerability at the individual scale translates to future forest composition and structure remains uncertain. Geographic variation with species occurrence is in many cases clearly linked to regional climate. However, few studies show direct connections between species distributions and geographic variation in mortality as opposed to, say, recruitment success. The effects of climate variation, such as drought, could differ for a species that is absent from a region because individuals cannot establish or established individuals cannot survive. The unclear role of mortality in species distributions (as opposed to recruitment) and how it is affected by drought complicates predictions of future forest responses to drought.

Drought-Related Changes in Western Forests

Unlike the Eastern United States, where large-scale drought effects are less well documented than the physiological responses of individual trees, the Western United States has experienced a number of catastrophic, widespread, stand-replacement events that are directly or indirectly related to drought (Allen and others 2010, Breshears and others 2005, Ganey and Vojta 2011, Gitlin and others 2006, Mueller and others 2005, van Mantgem and others 2009, Worrall and others 2013) (see Forest Droughts have Increased in Recent Decades text box on page 60). Since 1996, about 20 percent of southwestern forest area has been affected by high levels of tree mortality from combinations of drought stress, bark-beetle attacks, and fire (Williams and others 2010). In Arizona and New Mexico, high temperatures combined with droughts coincide with widespread mortality of diverse mesic montane tree species (Ganey and Vojta 2011, Gitlin and others 2006, Mueller and others 2005) and patchy die-off in two-needle pinyon (Breshears and others 2005, 2009). Other prominent examples of large die-offs include spruce in Alaska (Berg and others 2006) and Utah (DeRose and Long 2012); juniper, oaks, and pines in Texas in 2011 (Kukowski and others 2012, Twidwell and others 2014); whitebark pine (*Pinus albicaulis*) in the Sierra Nevada Mountains (Millar and others 2012); southern California conifers (Minnich 2007); and millions of hectares of lodgepole pine from Colorado (Creeden and others 2014) and Montana (Kaiser and others 2012) to British Columbia (Kurz and others 2008). An increase in drought-related quaking aspen mortality, sometimes termed sudden aspen decline, extends from Alberta to Colorado (Anderegg and others 2012, 2013a; Hogg and others 2008; Worrall and others 2013).

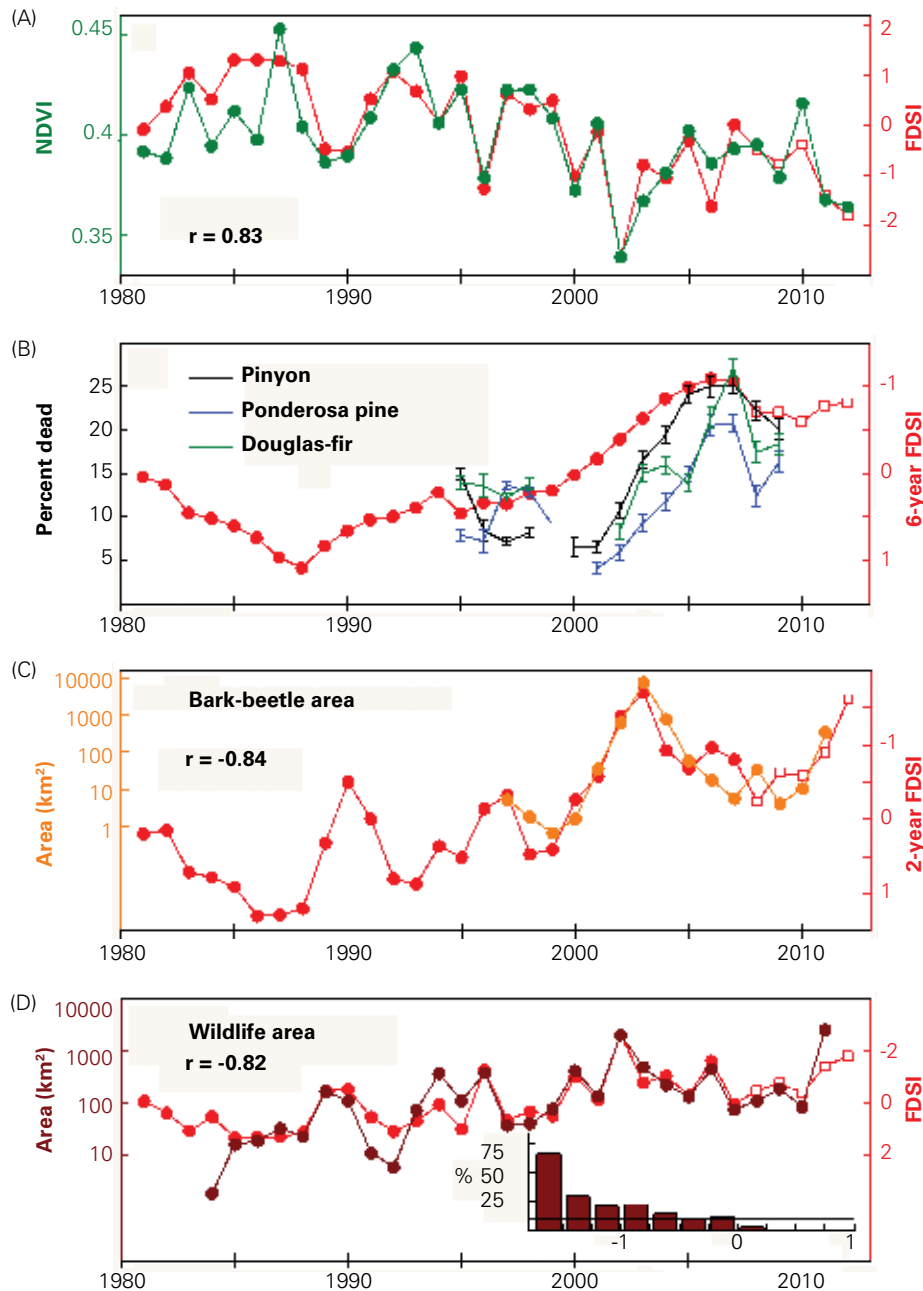


Figure 4.10—Forest productivity and mortality and the Forest Drought Severity Index (FDSI) (see text). (A) Annual average late-June to early-August Normalized Difference Vegetation Index (NDVI). (B) Percent standing dead trees from FIA plot data for the three most common southwestern conifer species. (C) Aerial estimates of area having 10 trees per acre killed by bark-beetle attack. (D) Satellite-derived moderately and severely burned forest and woodland in the Southwest. Inset shows percent of years within a given FDSI class that were top 10 percent fire-scar years during AD 1650–1899 (the horizontal line is at the expected frequency of 10 percent, bins are 0.25 FDSI units wide). Note the inverted axes for FDSI in B–D. (Graphic from Williams and others 2013).

The combination of low species diversity, low forest cover in some extensive forest types (for example, ponderosa pine and pinyon-juniper woodlands), low moisture availability on average, and frequent fire in the West shifts attention from the complexities of climate-competition interactions to the more immediate threats of stand-level replacement at regional scales. These transformations involve many of the dominant species. In addition, large diebacks have the potential to change species distributions more rapidly than has occurred in the past (Fellows and Goulden 2012, Millar and others 2012, Swetnam and Betancourt 1998). Drought-induced mortality in the 1950s is probably responsible for extensive upslope retreat of ponderosa pine in New Mexico (Allen and Breshears 1998) and alligator juniper (*Juniperus deppeana*) in southeast Arizona (Brusca and others 2013). Rapid redistribution of coniferous and broadleaf species occurred in southern California mountains during droughts of the early 2000s (Fellows and Goulden 2012).

Experimental evidence suggests that high temperatures can sometime increase drought-induced mortality in pinyon (Adams and others 2009). In many cases, high temperatures are thought to have a relatively minor direct effect on tree growth in western forests (although high surface temperatures can be lethal for seedlings) (Chmura and others 2011, Kolb and Robberecht 1996). Instead, warming is generally considered more important for phenology (Cayan and others 2001), seasonal soil-water balance due to changes in snowpack dynamics or evapotranspiration (Williams and others 2013), and insect populations (Bentz and others 2010). Changes in actual evapotranspiration and water deficit appear to be primary drivers of historical variations in tree recruitment and background as well as episodic tree mortality (Rapacciuolo and others 2014). A combination of high temperatures and low winter-spring precipitation of the previous year can explain much of the variation in conifer growth rates in the Southwest [primarily two-needle pinyon (*Pinus edulis*), ponderosa pine, and Douglas-fir (*Pseudotsuga menziesii*)] (fig. 4.10) and northern California [white fir (*Abies concolor*), red fir (*Abies magnifica*), sugar pine (*Pinus lambertiana*), ponderosa pine, and Douglas-fir] (Yeh and Wensel 2000). Similar relationships between moisture, heat, and growth variation are observed for white spruce in interior Alaska (Barber and others 2000), for Douglas-fir in the central and southwest Rocky Mountains and Mexico (Chen and others 2010), and for quaking aspen in western Canada (Hogg and others 2005).

Contributions From Regional-Scale Models of Biogeographic Change

Models are an important part of the research on climate effects. They continue to improve, but all are subject to important limitations. First is the uncertainty in climate itself. Two recent versions of three General Circulation Models (GCMs) project 2100 climates that differ by up to 4 °C for mean annual temperature and 60 percent for precipitation over North America (McKenney and others 2011). Additional uncertainty comes from the heterogeneity not captured in GCM output, from redistribution of precipitation within local drainages (wet and dry sites occupy the same grid cell for regional climate prediction), and from variation in temperature with local topography and vegetation cover. Second, many, if not most, models of forest response to climate change rely on parameters fitted independently to recruitment, growth, and mortality, and primarily from observations on individual trees. This narrow derivation may not adequately capture larger scale biotic interactions critical to understanding and predicting drought-related biogeographic shifts. Third, regional models of climate effects on forests are of several types and thus subject to critical limitations of scale, applicability, and compatibility. Some models represent individual trees, while others aggregate to species, life form, functional type, life stage, or patch structure. Some are static calibration-prediction models (species distribution models), while others are dynamic and vary in resolution from small plots (Shuman and others 2011) to patchy landscapes (Medvigy and Moorcroft 2012) and lattice grids (Franklin and others 2013), and yet others focus on abundance in nonspatial settings (Guisan and Thuiller 2005, Scheller and Mladenoff 2007).

Even with these limitations, models have significantly contributed to our understanding of the large-scale impacts of increasing drought on U.S. forests. Species distribution models (SDMs) have been used to map potential future species habitats under predicted climate scenarios (Franklin 2010, Guisan and Thuiller 2005, Matthews and others 2011, Prasad and others 2013, Rehfeldt and others 2006). To accomplish this, species distributions are first calibrated to climate, and then the fitted models are combined with climate predictions to identify regions of future suitable climate. Whether or not populations can move to regions of future suitable climate depends on migration. Potential distributions predicted from SDMs can be bracketed by two extremes: (1) no migration (species lose but do not gain habitat) and (2) unlimited migration (species

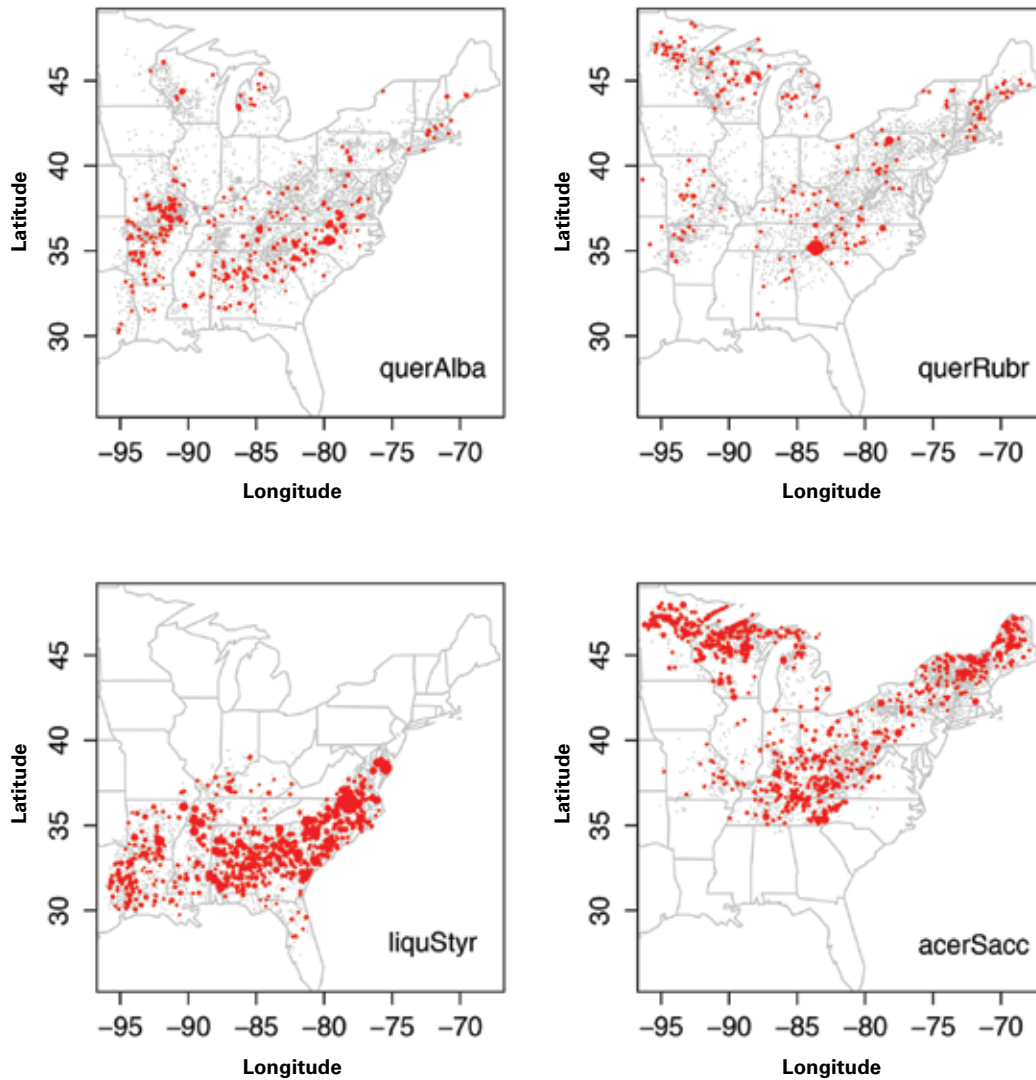


Figure 4.11—New recruits to FIA plots are relatively rare for oaks (upper panels) in comparison to other species having similar abundances in adult size classes (below). This comes at a time when moisture deficits are becoming more severe throughout the East (fig. 4.7) and despite the fact that many models predict increasing oaks. Red circles are in proportion to density of new recruits per ha. Gray shading shows the same for large size classes. Quantiles are shown for 98 percent of observations at sites where adults occur (Clark and others, In press).

occupy all suitable habitat) (Iverson and others 2008c, Meier and others 2012, Thuiller and others 2005). Some SDMs incorporate simple population dynamics (Cabral and Schurr 2010, Dullinger and others 2012, Iverson and others 2004, Meier and others 2012, Pagel and Schurr 2012, Prasad and others 2013, Saltre and others 2013). SDMs that assume climate effects on establishment and mortality (Crookston and others 2010, Sork and others 2010) have been used to interpret potential risks for eastern (Iverson and others 2008b, Potter and others 2010) and western forest species (Dobrowski and others 2011, Notaro and others 2012, Rehfeldt and others 2009). Current efforts seek to include a better understanding of species interactions (Fitzpatrick and Hargrove 2009, Ibáñez and others 2006, Wiens and others 2009) and ways to incorporate multiple species into models (Baselga and Araújo 2010, Clark and others 2014b, Guisan and Rahbek 2011).

SDMs have provided some of the strongest evidence that *potential distributions* of tree species are changing (McKenney and others 2007, 2011). In the Eastern United States, with its typically low relief, modest changes in climate can translate to large geographic shifts in suitable habitat (IPCC 2014, Loarie and others 2009, Zhu and others 2012), in agreement with models suggesting large reductions in potential range in the East (Potter and others 2010, Potter and Hargrove 2013). By 2100, mean latitudes are predicted to move northeastward from 400 km (kilometers) for a less CO₂-sensitive model (PCM) with high energy-resource efficiency (B1) to 800 km for a more sensitive model (HadleyCM3) with a “business as usual” scenario (A1F1) (Iverson and others 2008b). For the latter case, habitats for 66 species gain and 54 species lose about 10 percent of their current distributions. Species in Lake States and central hardwoods are predicted to be most vulnerable in the northern parts of their ranges (Brandt and others 2014, Handler and others 2014, Swanston and others 2011). Other drought-related predictions for the end of the 21st century include savanna-like conditions and loss of boreal forests from the Great Lakes region (Bachelet and others 2008).

Two other types of models have also contributed significantly to our understanding of drought impacts. In the nonspatial Dynamic Global Vegetation Models (DGVMs) (e.g., Daly and others 2000, Jiang and others 2013, Sitch and others 2003), species are aggregated as functional types, such as coniferous forests, deciduous forests, mixed forests, savannas and woodlands, or grasslands and shrublands (Bachelet and others 2003).

Some DGVMs also incorporate fire, atmospheric CO₂ (King and others 2013, Lenihan and others 2008), establishment mechanisms (Song and Zeng 2014), and patch age structure (Medvigy and Moorcroft 2012). Forest landscape models (FLMs) simulate forest demography on landscapes that may include drought, fire, land use, and pathogens. FLMs have been used to examine the stand-level consequences of species differences in vulnerability of individuals, with some FLM-based studies explicitly focusing on climate change impacts (Loehman and others 2011, Scheller and Mladenoff 2008), including migration (Gustafson and Sturtevant 2013, Lischke and others 2006, Nabel and others 2013, Scheller and Mladenoff 2008, Snell 2014).

Implications for Forest Management Practices

Timber harvest and land use are at least as influential in shaping forests as natural disturbances, particularly in the Southeastern and Northwestern United States (Masek and others 2011). As stated earlier, management practices modify the SSD and related forest elements (see Moisture and Size-Species Distributions text box on pages 67 and 68), which in turn influence a broad range of ecosystem services. Drought, especially prolonged and/or severe drought, similarly directly and indirectly impacts most of the ecosystem services provided by forests, including timber yield (Woodall and others 2013b), carbon storage (chapter 5), recreational value (Sheppard and Picard 2006), wildlife habitat (Banko and others 2013), and water yield and quality (Brown and others 2008) (chapter 10). Forestry practices that target one or more of these ecosystem services should be capable of addressing droughts, particularly in areas expected to receive more frequent and longer term drought events. To this end, we consider changes that may occur within stands as a function of drought as influenced by management practices and their potential biogeographic consequences.

Stand Density and Structural Management

Management actions can mitigate or exacerbate effects of drought, and effects can differ at both the tree and stand level. Most thinning treatments are designed to increase individual tree growth; increase stand resiliency to droughts, insects, and disease; and reduce standing fuels. For example, in dense red pine (*Pinus resinosa*) stands undergoing substantial self-thinning (fig. 4.12), some trees are under severe moisture limitation due to the combined effects of

competition and drought (D'Amato and others 2013). Thinning overstocked stands can provide short-term benefits through a variety of mechanisms. Harvesting stands to limit crown competition (Gyenge and others 2011, McDowell and others 2006) also reduces canopy interception of precipitation, thus increasing moisture that reaches the forest floor (Aussenac 2000, Stogsdili and others 1992). Likewise, trees in thinned stands usually expand their root systems to take advantage of improved soil moisture availability (Dawson 1996). Slow growth in older, denser (and often water-limited) stands has long been associated with beetle outbreaks (Fettig and others 2007, Hicks and others 1979); slow-growing, stressed host trees have diminished defenses to insect pests (Fettig and others 2007, Shaw and others 2005).

However, silvicultural practices intended to reduce vulnerability of remaining trees to drought can increase future (long-term) vulnerability through alterations to tree architecture and physiology. For instance,

increased leaf-to-sapwood area ratios following thinning can increase individual tree water demand (Kolb and others 2007, McDowell and others 2006). Therefore, even if stand-level water use declines following thinning, the high leaf-to-sapwood ratio promoted by reduced post-treatment competition may be disadvantageous during future drought. For this same reason, even though thinning beetle-affected stands usually increases residual tree growth (Fettig and others 2007, Kolb and others 1996, Skov and others 2004, Thomas and Waring 2014, Zausen and others 2005) and vigor over the short-term, it may also increase vulnerability to post-thinning droughts. Thinning also indirectly increases stand vulnerability to drought. Stands thinned and/or burned to promote regeneration (Covington and others 1997, Moore and others 1999) may increase vulnerability to drought due to increased evaporative losses (Aussenac 2000) and increased understory competition for soil moisture (Nilsen and others 2001, Zahner 1958).

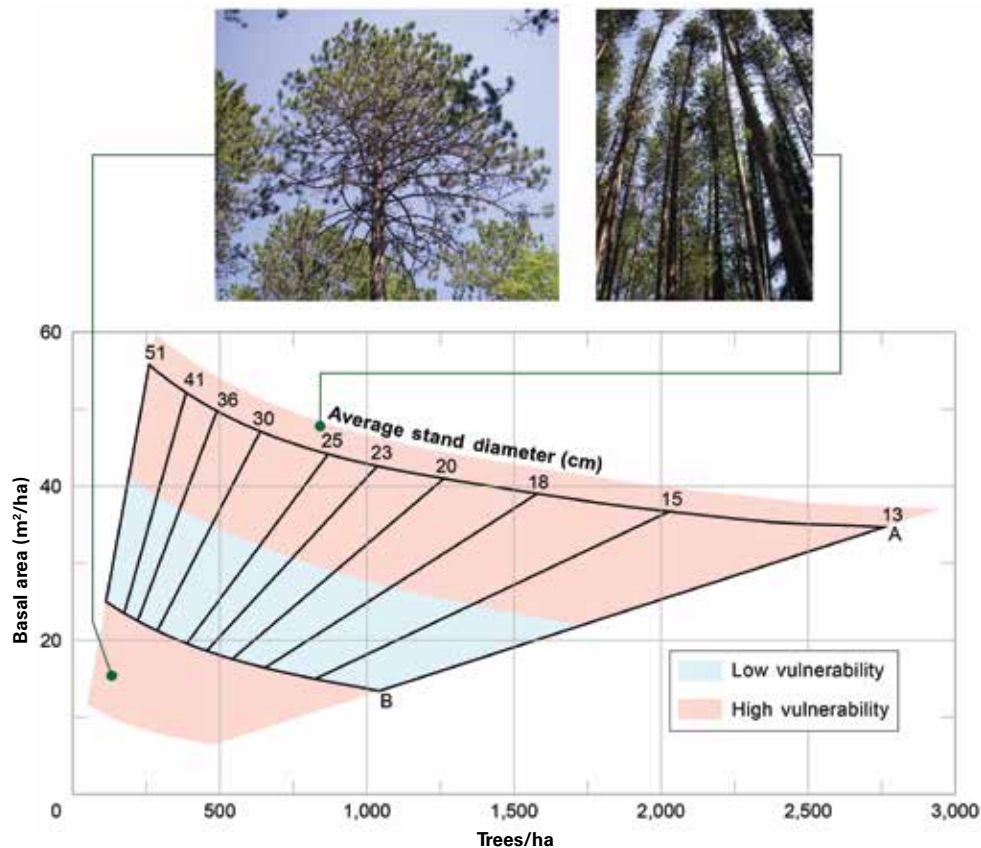


Figure 4.12—Hypothetical zones of drought susceptibility within a size/density management diagram for red pine. Trees may be susceptible to drought in two size/density situations: (1) at high density of large trees, with intense competition, and (2) at low density and high leaf-area to sapwood-area ratios, which promote canopy and root architecture that can put individual trees at risk.

Managers may want to adjust their silvicultural practices in stands expected to face increasing drought frequencies and durations. For example, thinning to manage for SSDs targeted to control those structural attributes sensitive to drought can improve stand resistance and resilience (Guldin 2014). Managers often take steps to maximize belowground development prior to and immediately after planting (Burdett 1990), or to shelter future crop trees during this vulnerable phase (Aussenac 2000). Recently planted seedlings with limited root development are particularly vulnerable to desiccation. Though more expensive, the better-developed and protected root systems of containerized nursery stock tend to survive and grow better than bare-root seedlings on xeric sites (Grossnickle 2005, Nilsson and Örlander 1995), and hence may be needed when drought is expected during planting. If bare-root seedlings are to be used, those with large root systems (shoot-to-root ratios below 2:1) are preferred (Haase and Rose 1993, Pinto and others 2012). Tree shelters can also enhance seedling survival on moisture-limited sites (Taylor and others 2009).

Maintenance of two- or uneven-aged stands may reduce stand-wide vulnerability to drought by spreading the risk across ages/sizes of different vulnerabilities. Uneven-aged management can reduce the microclimate extremes that limit regeneration following clearcuts (Aussenac 2000). Where management objectives require even-aged stands, shelterwoods can provide partial shading for regeneration (Castro and others 2004). However, there are drought-related complications associated with managing for multi-storied stands. Competition for moisture may be important enough to warrant understory control only during drought years (Carter and others 1984). In eastern forests, even-aged pine stands with a hardwood understory can experience greater soil moisture depletion than stands where the understory is reduced through prescribed burns or by other means (Zahner 1968).

Species Composition Management

Species composition is another silviculturally controllable aspect of U.S. forests. Some have called for the long-term strategy of managing for a diversity of genotypes and species to reduce stand-level vulnerability to drought, particularly in light of the uncertainty in future climate (Guldin 2014, Ledig and Kitzmiller 1992). There are also short-term options, such as the alteration of species composition through the selective removal of moisture-demanding species. The loss of less drought-tolerant species can release established

but suppressed individuals of more drought-tolerant species, as is currently being witnessed in the drought-induced dieback of the pinyon-juniper ecosystem of the Western United States (Floyd and others 2009). Managers can also encourage the natural regeneration of more drought-tolerant trees by exploiting their propensity to resprout, a characteristic of some species with extensive root systems [for example, post oak (*Quercus stellata*), Gambel oak (*Quercus gambelii*), or alligator juniper] (Larsen and Johnson 1998, Savage and others 2013). Indeed, such targeted treatments to favor sprouters can be most effective during droughts, as their extensive established root systems give them an advantage to those species that can only establish via seed. However, note that not all sprouters can take advantage of droughts. Quaking aspen, a prolific sprouter under favorable moisture conditions, is susceptible to drought and declines can be magnified by other factors such as ungulate browsing (Bartos and others 2014, Rogers and Mittanck 2014, Rogers and others 2014).

It is worth noting that species management through regeneration may prove more costly as droughts become more frequent (Nyland 2007). Despite some advantages of natural regeneration (including lower costs), drought may increase reliance on artificial regeneration (in other words, plantings) and/or seed-bed amelioration (e.g., seedling shelters). Artificial regeneration may become especially important for conifers that fail to regenerate or are out-competed by sprouting species (Feddema and others 2013, Haire and McGarigal 2008, Zhang and others 2008). Knowledge of how different species and genotypes respond on different sites (Blazier and others 2004, Erickson and others 2012, Will and others 2010) should guide decisions regarding how to manage forests for drought resistance. Regardless of stand origin, successful regeneration during drought depends on microsite conditions, including competition from less desirable species, so more intervention may be needed to help ensure the desired silvicultural outcomes. For example, competition control may become vital during prolonged droughts, particularly on sites with pronounced moisture limitations due to xeric conditions (Pinto and others 2012, Powers and Reynolds 1999, Wagner and Robinson 2006) or aggressive competitors. Additional steps, such as exposing mineral soil (Wagner and Colombo 2001) or mulching to increase moisture availability using harvest residues (Roberts and others 2005, Trottier-Picard and others 2014), may become increasingly important on some sites. These treatments

can add to the expense of silvicultural practices and could negatively impact other ecosystem services.

Fire and Fuels Management

In the Western United States, fire and harvest practices have contributed to increased fuel loads and a shift to high-density/small-diameter stands (e.g., Brown and Wu 2005, Covington and Moore 1994, Dolanc and others 2013, Fulé and others 2009, Lutz and others 2009, Mast and Wolf 2006, Parsons and DeBenedetti 1979). Prescribed fire can be used to manage complex stand structures following initial mechanical restoration treatments (Covington and others 2007, Roccaforte and others 2010), although extended droughts have reduced opportunities to conduct prescribed burns. Tree regeneration in western pine forests is resilient to surface fire in sustainable uneven-aged stands (Bailey and Covington 2002) except where regeneration is sufficiently dense to increase crown fire risk (Bailey and Covington 2002, Roccaforte and others 2010).

There are regional differences in the role of interactions between drought, fire, climate change, and human suppression of fire (Allen 2007, Joyce and others 2014, Littell and others 2009, Westerling and others 2006). In the Eastern United States, fire suppression may have led to “mesophication” as forest canopies closed, fuel conditions changed, and sites became increasingly more mesic (Nowacki and Abrams 2008). In recent decades, this combination of climate, land use, plant-animal interactions, and fire suppression may have contributed to recent increases in red maple (*Acer rubrum*) and sugar maple (*Acer saccharum*) recruitment at the expense of oak (Abrams 1998, Brose and others 2013, Fei and others 2011, Hutchinson and others 2008, Iverson and others 2008a). Similarly, decreased flammability may have followed the replacement of American chestnut (*Castanea dentata*) by maples in many eastern stands (Engber and Varner 2012, Kreye and others 2013), although historic alterations to fire regimes and fuel loads make it difficult to characterize presettlement fire regimes (Clark and Royall 1996, Guyette and others 2006, Parshall and Foster 2003). Some have speculated that elevated maple recruitment in the East could be reversed by increasingly dry conditions (Belden and Pallardy 2009, McEwan and others 2011, Woodall and others 2009); however, if fire suppression is primarily responsible for reduced oak regeneration in the East, then climatic trends favoring oak, including warmer temperatures and less rainfall, could be offset by mesophication.

Assisted Migration

SDMs suggest that shifts in potential distributions may occur faster than many tree populations can accommodate through migration. While there is substantial evidence that more mobile terrestrial and aquatic invertebrates, birds, and herbaceous plants are changing their distributions sufficiently to keep pace with rapid warming (Chen and others 2011, Parmesan and Yohe 2003), many tree populations are moving northward (Zhu and others 2012) and upward (Gehrig-Fasel and others 2007) much slower than changes in climate. Fearful of local extinctions, some have proposed that managers engage in “assisted migration” or “managed relocation” to establish species outside their historic distributions as a biological diversity conservation measure (Schwartz and others 2012). Assisted migration is a deliberate effort to establish populations in areas that are expected to have a suitable climate in the future, including populations sensitive to drought, to at least partially offset losses on sites no longer suitable. However, the effectiveness of widespread assisted migration is not yet known (Williams and Dumroese 2013), and some have expressed concerns about the risk of introducing invasive species (Mueller and Hellman 2008).

Centuries of horticultural and decades of silvicultural practices show that growth and establishment (reproductive success) of many tree species is possible well outside of their native ranges. Many commercial (e.g., loblolly pine) and ornamental species have had their ranges greatly expanded across the Southeastern United States. The widespread plantings of the southern magnolia in the southeastern Piedmont (Gruhn and White 2011) and upper Coastal Plain, and bois d’arc (*Maclura pomifera*) across the Eastern United States (Burton 1990) are examples of such facilitated migrations, helping to establish these species well beyond their native ranges. While these cultivated successes could be viewed as examples of the potential conservation value of assisted migration, far less is known about the likelihood of success of this management practice for the species most directly threatened by climate-induced environmental change. Efforts are currently underway to see if assisted migration can help with the federally endangered Florida torreya (*Torreya taxifolia*) as well as a number of other tree species imperiled by the anticipated impacts of increased drought and higher temperatures on their limited native distributions (McLachlan and others 2007, Williams and Dumroese 2013).

Research to Better Anticipate Drought Effects on U.S. Forests

Anticipated impacts of increasing drought, possibly leading to more xeric conditions in general, currently depend on a legacy of observational evidence along natural climate and hydrologic gradients. The value of such relationships is widely recognized and they provide the foundations for species distribution modeling and paleoclimate reconstructions (e.g., tree-ring studies). Despite many important insights from observational evidence, their lack of experimental control and uncertainties in future climate change poses new challenges and suggests some possible research directions.

Perhaps the greatest obstacle to understanding impacts of future drought on U.S. forests is the limited understanding of drought consequences at stand-to-landscape scales. We need more research to better understand the connections from individual tree to stand, based on both empirical (observational) and theoretical (modeling) evidence. For example, how does decline in individual tree health translate to population structure and abundance of a species, when individuals of all species are responding to climate, often in similar ways (Clark and others 2011)? The climate changes that place individuals at risk can have unpredictable effects on the stand, so empirical evidence is needed to evaluate both the individual responses and how they propagate to stand dynamics. At the individual scale, long-term data with regional coverage are needed to infer demographic processes under a range of climates and to detect early signs of change (Breshears and others 2009). While there exists a wealth of information on seed dispersal of common tree species in North America (e.g., Brown and others 1988, Chambers and MacMahon 1994, Farmer 1997, Matlack 1987) and Europe (e.g., Jensen 1985, Matlack 1987, Stöcklin and Bäumler 1996), many species are poorly studied, especially those with limited commercial value. The studies that are available on more abundant species show large variation in fecundity (Clark and others 2004, Koenig and Knops 2013) and recruitment (Ibáñez and others 2007)—what can be expected from rare taxa? Furthermore, even detailed knowledge of dispersal is not necessarily predictive of migration rates because of the influence of rare, long-distance dispersal events on population spread (Clark and others 2003, Higgins and Richardson 1999, Kot and others 1996, Schwartz 1993). However, predicting changes in stands also requires

stand-level inference. The observable physiological responses to temperature and moisture stress must be linked to demographic potential of individuals and to stand attributes, such as SSDs and abundance. Additional insight might be gained from more research on natural gradients in regions expected to differ in sensitivity to moisture and temperature, particularly that emphasizing the connections from individuals to stands and landscapes.

Interpretation of Holocene tree migration will remain the subject of considerable research—insights gained from this work may allow researchers to determine how paleo droughts may have influenced forest patterns. Understanding biogeographic patterns would likewise benefit from a better understanding of how current biogeography emerges from the responses of individual trees to climate (Murphy and others 2006, Rehfeldt and others 2006). Habitat interactions make it important to consider entire landscapes (e.g., Guisan and Zimmermann 2000), and recognizing past and present range limits is key to determine migration potential (Gaston 2009). For example, the range limits mapped for many North American vascular plants by Little (1971, 1976, 1977) can be updated with FIA data (and combined, perhaps, with habitat and/or climate envelope models) to better identify current distributions, recent trends, and limitations in knowledge (Murphy and others 2006, Peters and others 2013, Purves 2009, Rehfeldt and others 2006, Woodall and others 2013a). Understanding whether or not species can expand or retreat from population frontiers requires experimental evidence, with sufficient replication and control to evaluate competition-climate interactions. Currently, only a few experimental studies have addressed controls on recruitment near population frontiers (Ibáñez and McCarthy-Neumann 2014, McCarthy-Neumann and Ibáñez 2012); this work suggests the value of more extensive networks of such experiments.

In addition to a better understanding of tree range dynamics, more research on genetic variation of planting stock and the facilitation of regeneration in the context of drought is critical. As suggested earlier, some managers are moving ahead with assisted migration even though success is far from assured, and science has not comprehensively studied the ecological and socioeconomic implications of this practice. For example, the scarcity of information on tree regeneration in rare species constrains our ability to determine if assisted migration will prove to be a cost-effective option for biological conservation (Williams and Dumroese 2013).

Undoubtedly, we will benefit from developing a better understanding of the factors that control establishment of seeds that are moved to new locations (Bugmann 2001, Lischke and others 2006). Further research is also needed on the effectiveness of conventional silvicultural treatments in established stands to determine both the short- and long-term consequences of increasing droughts, particularly if they become more severe (drier and longer) than recent history suggests. To date, very little proactive silviculture has been implemented across the United States with regards to the worsening droughts and higher temperatures anticipated under most climate change scenarios—the socioeconomic implications of drought-related catastrophic failures in the heretofore more-mesic “woodbaskets” of the United States have not been fully considered.

These challenges (and many others) highlight the need for models that accommodate environmental change and forest response as a coherent joint distribution of species and sizes which respond to drought with feedbacks and interactions. The decade-old “scaling problem” (Levin 1992, Luo and others 2011) persists despite proliferation of bigger models, faster processing, and increased computer memory. Complex models can provide only limited guidance without the empirical basis for translating fine-scale to aggregate behavior, in the form of allocation constraints, species interactions, and feedbacks. These constraints are needed in models when they are fitted to field and experimental data. Not surprisingly, models combining these estimates predict migration rates that are highly uncertain due to large variability in these processes (Clark and others 2003), and land cover provides additional variability (Iverson and others 2004, Prasad and others 2013). Limited evidence of migration during the 21st century, a time when scientists have verified that climate change has been substantial in the Northern United States (Zhu and others 2012), diverges from predictions of rapid spread—and we need to understand why.

Dynamic stand models have become increasingly sophisticated, but they still lack a connection to stand-level data under different climate settings. Stand simulators, including forest gap (Botkin and others 1972, Bugmann 2001, Dixon 2002, Pacala and others 1996) and succession models (Mladenoff and others 1996, Scheller and Mladenoff 2008), recognize the importance of interactions among individuals. Efforts to connect physiology to stand dynamics in more general ways have increased in recent years (Keenan and others

2008, Ogle and Pacala 2009, Scherstjanoi and others 2014) but are still insufficient in many regards. For example, numerous models have examined the effects of disturbance (Caldwell and others 2013, Menard and others 2002, Papaik and Canham 2006, Reinhardt and Holsinger 2010, Saunders and Arseneault 2013, Uriarte and others 2009) and several have included drought (Gustafson and Shinneman 2015, Gustafson and Sturtevant 2013). However, unlike some types of disturbance that can be treated as an extrinsic force, drought involves a feedback with water use by the stand and thus is more difficult to model (Miller and others 2008, Morales and others 2005).

Indeed, all calibration-prediction and simulation approaches are challenged by the fact that parameters relating drought to recruitment, growth, and survival typically come from separate studies of individual trees across a range of spatial and temporal scales. Concerns include the need for better estimates of climate-mediated mortality (McDowell and others 2011) and recruitment (Ibáñez and others 2006). The interactions that affect the combined responses of individuals (fig. 4.4) and size-species structure of stands (see *Moisture and Size-Species Distributions* text box on pages 67 and 68) could benefit from estimates of the SSD as a joint distribution. Furthermore, to better model migration, we must enhance our understanding of how drought affects seed production, seed banks, and seedling establishment near range limits, and in particular, their role in local extinctions and re-colonization (Jackson and others 2009, Zimmermann and others 2009).

Conclusions

The widespread nature of recent droughts and their impacts on U.S. forests suggest transformations that will have far-reaching consequences. In addition to the declining growth rates with increasing drought conditions that may be expected during the 21st century, the extent and severity of drought impacts on western forests raises concern for biodiversity and carbon storage if these trends continue. Some of this change will occur following alterations to disturbance regimes. For instance, recent drought-related increases of high-severity fire in stands that historically were subject to high-frequency but low-severity fires may contribute to the loss of forests (Barton 2002, Goforth and Minnich 2008, Savage and Mast 2005, Savage and others 2013). A similar forest loss has also been suggested as a possible consequence of climate

change in the historically infrequent but high-severity fires for lodgepole pine forests in the Yellowstone region (Westerling and others 2011). In addition to direct losses to drought, increasing frequency or severity of related disturbances may increase prevalence of early successional species (e.g., bark-beetle infestations or wildfire), possibly leading to widespread forest-type conversions (Pelz and Smith 2013, Shinneman and others 2013).

Observational studies remain the largest source of information on drought effects, but they are difficult to extrapolate. Experimental studies are still few, small, and relatively short term. Taken together, the evidence for drought effects on forest structure and composition remains mostly indirect. Because individual trees can be studied experimentally more readily than forest stands, there is more evidence of drought effects on trees than on stand-level attributes, such as SSD. Indeed, in the Eastern United States, drought effects are still primarily observed as individual tree responses. At this scale, much is known about the differences among species that make some especially vulnerable to increased drought and other taxa less so. However, it is not clear how these species differences translate to future stand structure and composition. This is because observations are limited of stand-level responses that evaluate how changes in climate relate to changing effects of competitors, mutualists, and natural enemies, which are also responding to climate change. In the West, stand-level forest transformations are currently in progress, thus highlighting interactions among warming temperatures, drought, insect attacks, and fire. Recent western droughts show some of the drastic impacts that can occur when drought overwhelms other factors that contribute to the structure and diversity of more mesic forests.

There is broad consensus from modeling studies, increasingly supported by observations, that combinations of heat and moisture limitation, and their corresponding indirect effects, will change the health, dynamics, abundance, and distribution of tree species—changes that may accelerate in coming decades. This provides a sense of urgency for many forest managers who would like to proactively treat their forests. After all, management decisions regarding the size, age, and compositional conditions of any given stand have important implications for the degree of functional resistance and resilience to future drought (e.g., Guldin 2014). Although drought-based advice is context-dependent, in general management

strategies expecting increasing drought should benefit from developing more resilient forests by promoting tree (genotypic) diversity (especially drought-tolerant species or families) in lower density stands. Assisted migration, or drawing on species or genotypes outside their current geographic ranges, remains an option but needs to be better understood before it is widely implemented.

Research should be prioritized to include more attention on effects of drought beyond the individual; for example, it should focus on the combined size-species interactions that control diversity and productivity of stands. It remains difficult to quantify controls on range limits of species. Opportunistic or designed experiments are needed to better understand geographic variation in the effects of drought. Models will continue to play an important role, one that depends on improved understanding of stand-level responses and the acquisition of suitable, long-term data for detection, parameterization, calibration, and validation.

Literature Cited

- Abeli, T.; Gentili, R.; Mondoni, A. [and others]. 2014. Effects of marginality on plant population performance. *Journal of Biogeography*. 41: 239–249.
- Abrams, M.D. 2003. Where has all the white oak gone? *Bioscience*. 53: 927–939.
- Abrams, M.D. 1990. Adaptations and responses to drought in *Quercus* species of North America. *Tree Physiology*. 7: 227–238.
- Abrams, M.D. 1998. The red maple (*Acer rubrum*) paradox. *BioScience*. 48: 355–364.
- Abrams, M.D.; Kubiske, M.E. 1990. Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: influence of light regime and shade tolerance rank. *Forest Ecology and Management*. 31: 245–253.
- Ackerly, D.D.; Loarie, S.R.; Cornwell, W.K. [and others]. 2010. The geography of climate change: implications for conservation biogeography. *Diversity and Distributions*. 16: 476–487.
- Adams, H.D.; Guardiola-Claramonte, M.; Barron-Gafford, G.A. [and others]. 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences*. 106: 7063–7066.
- Allen, C.D. 2007. Interactions across spatial scales among forest dieback, fire, and erosion in northern New Mexico landscapes. *Ecosystems*. 10: 797–808.
- Allen, C.D.; Breshears, D.D. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences, U.S.A.* 95: 14,839–14,842.
- Allen, C.D.; Breshears, D.D.; McDowell, N.G. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*. 6(8): article 129.

- Allen, C.D.; Macalady, A.K.; Chenchouni, H. [and others]. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*. 259: 660-684.
- Anderegg, W.R.L.; Beryy, J.A.; Smith, D.D. [and others]. 2012. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *Proceedings of the National Academy of Sciences*. 109: 233-237.
- Anderegg, W.R.L.; Plavcová, L.; Anderegg, L.D.L. [and others]. 2013a. Drought's legacy: multi-year hydraulic deterioration underlies widespread aspen forest die-off and portends increased future risk. *Global Change Biology*. 19: 1188-1196.
- Anderegg, W.R.L.; Kane, J.M.; Anderegg, L.D.L. 2013b. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change*. 3: 30-36.
- Assmann, E. 1970. *The principles of forest yield study*. Oxford, UK: Pergamon Press. 16 p.
- Aussenac, G. 2000. Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. *Annals of Forest Science*. 57: 287-301.
- Bachelet, D.; Lenihan, J.M.; Drapek, R.J.; Neilson, R.M. 2008. VEMAP vs VINCERA: a DGVM sensitivity to differences in climate scenarios. *Global and Planetary Change*. 64: 38-48.
- Bachelet, D.; Neilson, R.P.; Hickler, T. [and others]. 2003. Simulating past and future dynamics of natural ecosystems in the United States. *Global Biogeochemical Cycles*. 17(2): 14-1.
- Bailey, J.D.; Covington, W.W. 2002. Evaluating ponderosa pine regeneration rates following ecological restoration treatments in northern Arizona, U.S.A. *Forest Ecology and Management*. 155: 271-278.
- Banko, P.C.; Camp, R.J.; Farmer, C. [and others]. 2013. Response of palila and other subalpine Hawaiian forest bird species to prolonged drought and habitat degradation by feral ungulates. *Biological Conservation*. 157: 70-77.
- Barber, V.A.; Juday, B.P.; Finney, B.P. [and others]. 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature*. 405: 668-673.
- Barton, A.M. 2002. Intense wildfire in southeastern Arizona: transformation of a Madrean pine-oak forest to oak woodland. *Forest Ecology and Management*. 165: 205-212.
- Bartos, D.L.; Tshireletso, K.; Malechek, J.C. 2014. Response of aspen suckers to simulated browsing. *Forest Science*. 60(2): 402-408.
- Baselga, A.; Araújo, M.B. 2010. Do community models fail to project community variation effectively? *Journal of Biogeography*. 37(10): 1842-1850. doi: 10.1111/j.1365-2699.2010.02341. [Published online: June 21, 2010].
- Beckage, B.; Osborne, B.; Pucko, C. [and others]. 2008. An upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont, U.S.A. *Proceedings of the National Academy of Sciences*. 105(11): 4197-4202.
- Belden, A.C.; Pallardy, S.G. 2009. Successional trends and apparent *Acer saccharum* regeneration failure in an oak-hickory forest in central Missouri, U.S.A. *Plant Ecology*. 204: 305-322.
- Bell, D.M.; Bradford, J.B.; Lauenroth, W.K. 2014. Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the Western United States. *Global Ecology and Biogeography*. 23: 168-180.
- Benitez, S.B.; Hersh, M.; Vilgalys, R. [and others]. 2013. Pathogen regulation of plant diversity via effective specialization. *Trends in Ecology and Evolution*. 12: 705-711.
- Bentz, B.J.; Régnière, J.; Fettig, C.J. [and others]. 2010. Climate change and bark beetles of the Western United States and Canada: direct and indirect effects. *BioScience*. 60: 602-613.
- Berg, E.E.; Henry, J.D.; Fastie, C. [and others]. 2006. Spruce beetle outbreaks in spruce forests on the western Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: relationships with summer temperature and regional differences in disturbance regimes. *Forest Ecology and Management*. 227: 219-232.
- Bhuta, A.A.R.; Kennedy, L.M.; Pederson, N. 2009. Climate-radial growth relationships of northern latitudinal range margin longleaf pine (*Pinus palustris* P. Mill) in the Atlantic Coastal Plain of Southeastern Virginia. *Tree Ring Research*. 65: 105-115.
- Blazier, M.A.; Hennessey, T.C.; Lynch, T.B. [and others]. 2004. Productivity, crown architecture, and gas exchange of North Carolina and Oklahoma/Arkansas loblolly pine families growing on a droughty site in southeastern Oklahoma. *Forest Ecology and Management*. 194: 83-94.
- Botkin, D.B.; Janak, J.F.; Wallis, J.R. 1972. Some ecological consequences of a computer model of forest growth. *Journal of Ecology*. 60: 849-872.
- Brandt, L.; He, H.; Iverson, L. [and others]. 2014. Central Hardwoods ecosystem vulnerability assessment and synthesis: a report from the Central Hardwoods Climate Change Response Framework project. Gen. Tech. Rep. NRS-124. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 254 p.
- Bréda, N.; Huc, R.; Granier, A.; Dreyer, E. 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*. 63: 625-644.
- Brenes-Arguedas, T.; Coley, P.D.; Kursar, A. 2009. Pests vs. drought as determinants of plant distribution along a tropical rainfall gradient. *Ecology*. 90: 1751-1761.
- Breshears, D.D.; Cobb, N.S.; Rich, P.M. [and others]. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences, U.S.A.* 102(42): 15,144-15,148.
- Breshears, D.D.; Myers, O.B.; Meyer, C.W. [and others]. 2009. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Frontiers in Ecology and the Environment*. 7: 185-189.
- Brose, P.H.; Dey, D.C.; Phillips, R.J.; Waldrop, T.A. 2013. A meta-analysis of the fire-oak hypothesis: does prescribed burning promote oak reproduction in Eastern North America? *Forest Science*. 59: 322-334.
- Brown, K.R.; Zobel, D.B.; Zasada, J.C. 1988. Seed dispersal, seedling emergence, and early survival of *Larix laricina* (DuRoi) K. Koch in the Tanana Valley, Alaska. *Canadian Journal of Forest Research*. 18: 306-314.
- Brown, P.M.; Wu, R. 2005. Climate and disturbance forcings of episodic tree recruitment in a southwestern ponderosa pine landscape. *Ecology*. 86: 3030-3038.
- Brown, T.C.; Hobbins, M.T.; Ramirez, J.A. 2008. Spatial distribution of water supply in the coterminous United States. *Journal of the American Water Resources Association*. 44: 1474-1487.
- Brubaker, L. 1980. Spatial patterns of tree growth anomalies in the Pacific Northwest. *Ecology*. 61: 798-807.
- Brusca, R.; Wiens, J.F.; Meyer, W.M. [and others]. 2013. Dramatic response to climate change in the Southwest: Robert Whittaker's 1963 Arizona Mountain plant transect revisited. *Ecology and Evolution*. 3(10): 3307-3319. doi: 10.1002/ece3.720. [Published online: August 13, 2013].

- Brzostek, E.R.; Dragoni, D.; Schmid, H.P. [and others]. 2014. Chronic water stress reduces tree growth and the carbon sink of deciduous hardwood forests. *Global Change Biology*. 20(8): 2531-2539. doi: 10.1111/gcb.12528. [Published online: February 21, 2014].
- Bugmann, H. 2001. A review of forest gap models. *Climatic Change*. 51: 259-305.
- Burdett, A.N. 1990. Physiological processes in plantation establishment and the development of specifications for forest planting stock. *Canadian Journal of Forest Research*. 20: 415-427.
- Burton, J.D. 1990. Osage-orange. In: Burns, R.M.; Honkala, B.H., tech. coord. *Silvics of North America: Volume 2, hardwoods*. Agric. Handb. 654. U.S. Department of Agriculture, Forest Service, Washington Office: 426-432.
- Cabral, J.S.; Schurr, F.M. 2010. Estimating demographic models for the range dynamics of plant species. *Global Ecology and Biogeography*. 19: 85-97.
- Caldeira, M.C.; Ibáñez, I.; Nogueira, C. [and others]. 2014. Direct and indirect effects of tree canopy facilitation in the recruitment of Mediterranean oaks. *Journal of Applied Ecology*. 51: 349-353.
- Caldwell, M.K.; Hawbaker, T.J.; Briggs, J.S. [and others]. 2013. Simulated impacts of mountain pine beetle and wildfire disturbances on forest vegetation composition and carbon stocks in the Southern Rocky Mountains. *Biogeosciences*. 10: 8203-8222.
- Canham, C.D.; Thomas, R.Q. 2010. Frequency, not relative abundance, of temperate tree species varies along climate gradients in eastern North America. *Ecology*. 91: 3433-3440.
- Carter, G.A.; Miller, J.H.; Davis, D.E. [and others]. 1984. Effective of vegetative competition on the moisture and nutrient status of loblolly pine. *Canadian Journal of Forest Research*. 14: 1-9.
- Castro, J.; Zamora, R.; Hódar, J.A. [and others]. 2004. Seedling establishment of a boreal tree species (*Pinus sylvestris*) at its southernmost distribution limit: consequences of being in a marginal Mediterranean habitat. *Journal of Ecology*. 92: 266-277.
- Cavender-Bares, J.; Bazzaz, F.A. 2000. Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. *Oecologia*. 124: 8-18.
- Cavin, L.; Mountford, E.P.; Peterken, G.F.; Jump, A.S. 2013. Extreme drought alters competitive dominance within and between tree species in a mixed forest stand. *Functional Ecology*. 27: 1424-1435.
- Cayan, D.R.; Kammerdiener, S.A.; Dettinger, M.D. [and others]. 2001. Changes in the onset of spring in the Western United States. *Bulletin-American Meteorological Society*. 82: 399-416.
- Cescatti, A.; Piutti, E. 1998. Silvicultural alternatives, competition regime and sensitivity to climate in a European beech forest. *Forest Ecology and Management*. 102: 213-223.
- Chambers, J.C.; MacMahon, J.A. 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. *Annual Review of Ecology and Systematics*. 25: 263-292.
- Chen, I.C.; Hill, J.K.; Ohlemüller, R. [and others]. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science*. 333: 1024-1026.
- Chen, P.Y.; Welsh, C.; Hamann, A. 2010. Geographic variation in growth response of Douglas-fir to interannual climate variability and projected climate change. *Global Change Biology*. 16: 3374-3385.
- Chmura, D.J.; Anderson, P.D.; Howe, G.T. [and others]. 2011. Forest responses to climate change in the Northwestern United States: ecophysiological foundations for adaptive management. *Forest Ecology and Management*. 261: 1121-1142.
- Clark, J.; Royall, P. 1996. Local and regional sediment charcoal evidence for fire regimes in presettlement north-eastern North America. *Journal of Ecology*. 84: 35-382.
- Clark, J.S. 1989. Water balance and fire occurrence during the last 160 years in northwestern Minnesota. *Journal of Ecology*. 77: 989-1004.
- Clark, J.S. 1990. Integration of ecological levels: individual plant growth, population mortality, and ecosystem dynamics. *Journal of Ecology*. 78: 275-299.
- Clark, J.S.; Beckage, B.; Camill, P. [and others]. 1999. Interpreting recruitment limitation in forests. *American Journal of Botany*. 86: 1-16.
- Clark, J.S.; Bell, D.M.; Hersh, M.H.; Nichols, L. 2011. Climate change vulnerability of forest biodiversity: climate and resource tracking of demographic rates. *Global Change Biology*. 17: 1834-1849.
- Clark, J.S.; Bell, D.M.; Kwit, M. [and others]. 2013. Dynamic inverse prediction and sensitivity analysis with high-dimensional responses: application to climate-change vulnerability of biodiversity. *Journal of Biological, Environmental, and Agricultural Statistics*. 18: 376-404.
- Clark, J.S.; Bell, D.M.; Kwit, C.; Zhu, K. 2014a. Competition-interaction landscapes for the joint response of forests to climate change. *Global Change Biology*. 20(6): 1979-1991. doi: 10.1111/gcb.12425. [Published online: April 10, 2014].
- Clark, J.S.; Gelfand, A.E.; Woodall, C.W.; Zhu, K. 2014b. More than the sum of the parts: forest climate response from joint species distribution models. *Ecological Applications*. 24(5): 990-999.
- Clark, J.S.; Iverson, L.; Woodall, C.W. [and others]. [In press]. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. *Global Change Biology*.
- Clark, J.S.; LaDeau, S.; Ibáñez, I. 2004. Fecundity of trees and the colonization-competition hypothesis. *Ecological Monographs*. 74: 415-442.
- Clark, J.S.; Lewis, M.; Horvath, L. 2001. Invasion by extremes: variation in dispersal and reproduction retards population spread. *American Naturalist*. 157: 537-554.
- Clark, J.S.; Lewis, M.; McLachlan, J.S.; Hille Ris Lambers, J. 2003. Estimating population spread: what can we forecast and how well? *Ecology*. 84: 1979-1988.
- Clinton, B.D.; Boring, L.R.; Swank, W.T. 1993. Canopy gap characteristics and drought influences in oak forests of the Coweeta Basin. *Ecology*. 74: 1551-1558.
- Comita, L.S.; Queenborough, S.A.; Murphy, S.J. [and others]. 2014. Testing predictions of the Janzen-Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *Journal of Ecology*. 102: 845-856.
- Compant, S.; Van Der Heijden, M.G.A.; Sessitsch, A. 2010. Climate change effects on beneficial plant-microorganism interactions: Climate change and beneficial plant-microorganism interactions. *FEMS Microbiology Ecology*. 73(2): 197-214.
- Connell, J.H. 1970. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: den Boer, P.J.; Graadwell G.R., eds. *Dynamics of Populations: Proceedings of the Advanced Study Institute on Dynamics of Numbers in Populations*. Wageningen, Netherlands: Centre for Agricultural Publishing and Documentation: 298-312.

- Cook, E.R.; Glitzenstein, J.S.; Krusic, P.J.; Harcombe, P.A. 2001. Identifying functions groups of trees in west Gulf Coast forests (U.S.A.): a tree-ring approach. *Ecological Applications*. 11: 883–903.
- Cook, E.R.; Meko, D.M.; Stahle, D.W.; Cleaveland, M.K. 1999. Drought reconstructions for the continental United States. *Journal of Climate*. 12: 1145–1162.
- Cook, E.R.; Nance, W.L.; Krusic, P.; Grissom, J. 1998. Modeling the differential sensitivity of loblolly pine to climatic change using tree rings. In: Mickler, R.A.; Fox, S., eds. *The productivity and sustainability of southern forest ecosystems in a changing environment*. New York: Springer-Verlag: 717–739.
- Cook, E.; Seager, R.; Heim, R.J. [and others]. 2010. Megadroughts in North America: placing IPCC projections of hydroclimatic change in a long-term palaeoclimate context. *Journal of Quaternary Science*. 25:48–61.
- Cooper-Ellis, S.; Foster, D.R.; Carlton, G.; Lezberg, A. 1999. Forest response to catastrophic wind: results from an experimental hurricane. *Ecology*. 80: 2683-2696.
- Coops, N.C.; Waring, R.H. 2011. A process-based approach to estimate lodgepole pine (*Pinus contorta* Dougl.) distribution in the Pacific Northwest under climate change. *Climatic Change*. 105: 313-328.
- Coops, N.C.; Waring, R.H.; Beier, C. [and others]. 2011. Modeling the occurrence of 15 coniferous tree species throughout the Pacific Northwest of North America using a hybrid approach of a generic process based growth model and decision tree analysis. *Applied Vegetation Science*. 14: 402-414.
- Corcobado, T.; Cubera, E.; Juárez, G. [and others]. 2014. Drought events determine performance of *Quercus ilex* seedlings and increase their susceptibility to *Phytophthora cinnamomi*. *Agricultural and Forest Meteorology*. 4: 192-193: 1–8.
- Cornwell, W.K.; Stuart, S.A.; Ramirez, A. [and others]. 2012. Climate change impacts on California vegetation: physiology, life history, and ecosystem change. Publication number: CEC-500-2012-023. Sacramento, CA: California Energy Commission. 79 p.
- Covington, W.W.; Fulé, P.Z.; Moore, M.M. [and others]. 1997. Restoring ecosystem health in ponderosa pine forests of the Southwest. *Journal of Forestry*. 95: 23-29.
- Covington, W.W.; Moore, M.M. 1994. Southwestern ponderosa pine forest structure: changes since Euro-American settlement. *Journal of Forestry*. 92: 39-47.
- Creeden, E.P.; Hicke, J.A.; Buotte, P.C. 2014. Climate, weather, and recent mountain pine beetle outbreaks in the Western United States. *Forest Ecology and Management*. 312: 239-251.
- Crookston, N.L.; Rehfeldt, G.E.; Dixon, G.E.; Weiskittel, A.R. 2010. Addressing climate change in the forest vegetation simulator to assess impacts on landscape forest dynamics. *Forest Ecology and Management*. 260: 1198-1211.
- D'Amato, A.W.; Bradford, J.B.; Fraver, S.; Palik, B.J. 2013. Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. *Ecological Applications*. 23: 1735-1742.
- Dai, A. 2012. Increasing drought under global warming in observations and models. *Nature Climate Change*. 3(1): 52-58.
- Daly, C.; Bachelet, D.; Lenihan, J.M. [and others]. 2000. Dynamic simulation of tree-grass interactions for global change studies. *Ecological Applications*. 10: 449-469.
- Dawson, T.E. 1996. Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: the roles of tree size and hydraulic lift. *Tree Physiology*. 16: 263-272.
- DeRose, R.J.; Long, J.N. 2012. Drought-driven disturbance history characterizes a southern Rocky Mountain subalpine forest. *Canadian Journal of Forest Research*. 42(9): 1649–1660.
- Desprez-Loustau, M.L.; Marçais, B.; Nageleisen, L.M. [and others]. 2006. Interactive effects of drought and pathogens in forest trees. *Annals of Forest Science*. 63: 597-612.
- DeWeese, G.G.; Grissino-Mayer, H.D.; Lafon, C.W.; Aldrich, S.R. 2010. Evaluating the dendroclimatological potential of central Appalachian Table Mountain pine (*Pinus pungens* Lamb.). *Dendrochronologia*. 28: 173-186.
- Dietze, M.; Clark, J.S. 2008. Rethinking gap dynamics: the impact of damaged trees and sprouts. *Ecological Monographs*. 78: 331-347.
- Dietze, M.C.; Moorcroft, P.R. 2011. Tree mortality in the Eastern and Central United States: patterns and drivers. *Global Change Biology*. 17: 3312–3326.
- Dixon, G.E., comp. 2002. *Essential FVS: a user's guide to the Forest Vegetation Simulator*. Internal Rep. Revised: February 25, 2015. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Forest Management Service Center. 226 p.
- Dobrowski, S.Z.; Thorne, J.H.; Greenberg, J.A. [and others]. 2011. Modeling plant ranges over 75 years of climate change in California, U.S.A: temporal transferability and species traits. *Ecological Monographs*. 81: 241-257.
- Dolanc, C.R.; Thorne, J.H.; Safford, H.D. 2013. Widespread shifts in the demographic structure of subalpine forests in the Sierra Nevada, California, 1934 to 2007. *Global Ecology and Biogeography*. 22: 264 –276.
- Dormana, M.; Svoray, T.; Perevolotsky, A.; Sarris, D. 2013. Forest performance during two consecutive drought periods: diverging long-term trends and short-term responses along a climatic gradient. *Forest Ecology and Management*. 310: 1-9.
- Dukes, J.S.; Pontius, J.; Orwig, D. [and others]. 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: what can we predict? *Canadian Journal of Forest Research*. 39: 231-248.
- Dullinger, S.; Gattlinger, A.; Thuiller, W. [and others]. 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. *Nature Climate Change*. 2: 619-622.
- Elliott, K.J.; Swank, W.T. 1994. Impact of drought on tree mortality and growth in a mixed hardwood forest. *Journal of Vegetation Science*. 5: 229–236.
- Engber, E.A.; Varner, J.M. 2012. Patterns of flammability of the California oaks: the role of leaf traits. *Canadian Journal of Forest Research*. 42: 1965–1975.
- Erickson, V.; Aubry, C.; Berrang, P. [and others]. 2012. Genetic resource management and climate change: genetic options for adapting national forests to climate change. Washington, DC: U.S. Department of Agriculture, Forest Service, Forest Management, Genetic Resource Management Program. [Internal white paper]. 20 p. http://www.nrcs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb1077125.pdf. [Date accessed: September 14, 2015].
- Esper, J.; Niederer, R.; Bebi, P.; Frank, D. 2008. Climate signal age effects—evidence from young and old trees in the Swiss Engadin. *Forest Ecology and Management*. 255: 3783–3789.
- Evans, S.E.; Wallenstein, M.D.; Burke, I.C. 2014. Is bacterial moisture niche a good predictor of shifts in community composition under long-term drought? *Ecology*. 95: 110–122.
- Faber-Langendoen, D.; Tester, J.R. 1993. Oak mortality in sand savannas following drought in east-central Minnesota. *Bulletin of the Torrey Botanical Club*. 248-256.

- Fahey, T.J. 1998. Recent changes in an upland forest in south-central New York. *Journal of the Torrey Botanical Society*. 125: 51-59.
- Farmer, R.E., Jr. 1997. Seed ecophysiology of temperate and boreal zone forest trees. Delray Beach, FL: St. Lucie Press. 253 p.
- Fastie, C.L. 1995. Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology*. 76(6): 1899–1916.
- Feddema, J.J.; Mast, J.N.; Savage, M. 2013. Modeling high-severity fire, drought and climate change impacts on ponderosa pine regeneration. *Ecological Modelling*. 253: 56-69.
- Feeley, K.J.; Hurtado, J.; Saatchi, S. [and others]. 2013. Compositional shifts in Costa Rican forests due to climate-driven species migrations. *Global Change Biology*. 19(11): 3472-3480.
- Feeley, K.J.; Silman, M.R.; Bush, M. [and others]. 2011. Upslope migration of Andean trees. *Journal of Biogeography*. 38: 783-791.
- Fei, S.; Kong, N.; Steiner, K.C. [and others]. 2011. Change in oak abundance in the Eastern United States from 1980 to 2008. *Forest Ecology and Management*. 262: 1370–1377.
- Fellows, A.W.; Goulden, M.L. 2012. Rapid vegetation redistribution in Southern California during the early 2000s drought. *Journal of Geophysical Research*. 117(G3): G03025. 11 p. doi:10.1029/2012JG002044. [Published online: August 31, 2012].
- Fettig, C.J.; Klepzig, K.D.; Billings, R.F. [and others]. 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the Western and Southern United States. *Forest Ecology and Management*. 238: 24-53.
- Fitzpatrick, M.C.; Hargrove, W.W. 2009. The projection of species distribution models and the problem of non-analog climate. *Biodiversity and Conservation*. 18: 2255-2261.
- Floyd, M.L.; Clifford, M.; Cobb, N.S. [and others]. 2009. Relationship of stand characteristics to drought-induced mortality in three Southwestern piñon-juniper woodlands. *Ecological Applications*. 19(5): 1223-1230.
- Franklin, J. 2010. Moving beyond static species distribution models in support of conservation biogeography. *Diversity and Distributions*. 16: 321-330.
- Franklin, J.; Davis, F.W.; Ikagami, M. [and others]. 2013. Modeling plant species distributions under future climates: how fine-scale do climate models need to be? *Global Change Biology*. 19: 473-483.
- Frelich, L.E.; Reich, P.B. 2010. Will environmental changes reinforce the impact of global warming on the prairie-forest border of central North America? *Frontiers in Ecology and the Environment*. 8: 371–378.
- Friedrichs, D.A.; Trouet, V.; Büntgen, U. [and others]. 2009. Species-specific climate sensitivity of tree growth in Central-West Germany. *Trees*. 23: 729-739.
- Fritts, H.C. 1976. *Tree rings and climate*. New York: Academic Press. 567 p.
- Fulé, P.Z.; Korb, J.E.; Wu, R. 2009. Changes in forest structure of a mixed conifer forest, southwestern Colorado, U.S.A. *Forest Ecology and Management*. 258 (7): 1200-1210.
- Galiano, L.; Martínez-Vilalta, J.; Eugenio, M. [and others]. 2013. Seedling emergence and growth of *Quercus* spp. following severe drought effects on a *Pinus sylvestris* canopy. *Journal of Vegetation Science*. 24: 580–588.
- Ganey, J.L.; Vojta, S.C. 2011. Tree mortality in drought-stressed mixed-conifer and ponderosa pine forests, Arizona, U.S.A. *Forest Ecology and Management*. 261(1): 162–168.
- Garrity, S.R.; Allen, C.D.; Brumby, S.P. [and others]. 2013. Quantifying tree mortality in a mixed species woodland using multitemporal high spatial resolution satellite imagery. *Remote Sensing of Environment* 129: 54-65.
- Gaston, K.J. 2009. Geographic range limits: achieving synthesis. *Proceedings of The Royal Society B*. 276: 1395-1406.
- Gaylord, M.L.; Kolb, T.E.; Pockman, W.T. [and others]. 2013. Drought predisposes piñon-juniper woodlands to insect attacks and mortality. *New Phytologist*. 198: 567-578.
- Gehrig-Fasel, J.; Guisan, A.; Zimmermann, N.E. 2007. Treeline shifts in the Swiss Alps: climate change or land abandonment? *Journal of Vegetation Science*. 18: 571-582.
- Gitlin, A.R.; Sthultz, C.M.; Bowker, M.A. [and others]. 2006. Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. *Conservation Biology*. 20: 1477-1486.
- Goeking, S.A. 2015. Disentangling forest change from forest inventory change: a case study from the U.S. interior west. *Journal of Forestry* 113(5): 475-483.
- Goforth, B.R.; Minnich, R.A. 2008. Densification, stand-replacement wildfire, and extirpation of mixed conifer forest in Cuyamaca Rancho State Park, southern California. *Forest Ecology and Management*. 256: 36-45.
- Gottfried, M.; Pauli, H.; Futschik, A. [and others]. 2012. Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*. 2: 111–115.
- Graumlich, L. 1993. Response of tree growth to climatic variation in the mixed conifer and deciduous forests of the upper Great Lakes region. *Canadian Journal of Forest Research*. 23: 133–143.
- Grossiord, C.; Granier, A.; Ratcliffe, S. [and others]. 2014. Tree diversity does not always improve resistance of forest ecosystems to drought. *Proceedings of the National Academy of Sciences*. 111: 14,812-14,815.
- Grossnickle, S. 2005. Importance of root growth in overcoming planting stress. *New Forests*. 30: 273-294.
- Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews, Cambridge Philosophical Society*. 52: 102-145.
- Gruhn, A.J.; White, P.S. 2011. *Magnolia grandiflora* L. range expansion: a case study of a North Carolina Piedmont forest. *Southeastern Naturalist*. 10(2): 275-288.
- Guisan, A.; Rahbek, C. 2011. SESAM – a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. *Journal of Biogeography*. 38: 1433-1444.
- Guisan, A.; Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters*. 8: 993-1009.
- Guisan, A.; Zimmermann, N.E. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling*. 135:147-186.
- Guldin, J.M. 2014. Adapting silviculture to a changing climate in the southern United States. In: Vose, J.M.; Klepzig, K.D., eds. *Climate change for adaptation and mitigation management options: a guide for natural resource managers in southern forest ecosystems*. Boca Raton, FL: CRC Press: 173-192.
- Gustafson, E.J.; Shinneman, D.J. 2015. Approaches to modeling landscape-scale drought-induced forest mortality. In: Perera, A.; Sturtevant, B.; Buse, L., eds. *Simulation modeling of forest landscape disturbances*. New York: Springer: 45-71.

- Gustafson, E.J.; Sturtevant, B.R. 2013. Modeling forest mortality caused by drought stress: implications for climate change. *Ecosystems*. 16: 60–74.
- Guyette R.P.; Spetich, M.A.; Stambaugh, M.C. 2006. Historic fire regime dynamics and forcing factors in the Boston Mountains, Arkansas, USA. *Forest Ecology and Management*. 234: 293–304.
- Gyenge, J.; Fernández, M.; Sarasola, M.; Schlichter, T. 2011. Stand density and drought interaction on water relations of *Nothofagus antarctica*: contribution of forest management to climate change adaptability. *Trees—Structure and Function*. 25: 1111–1120.
- Haase, D.L.; Rose, R. 1993. Soil moisture stress induces transplant shock in stored and unstored 2+0 Douglas-fir seedlings of varying root volumes. *Forest Science*. 39: 275–294.
- Haavik, L.; Stahle, D.; Stephen, F. 2011. Temporal aspects of *Quercus rubra* decline and relationship to climate in the Ozark and Ouachita Mountains, Arkansas. *Canadian Journal of Forest Research*. 781: 773–781.
- Haire, S.I.; McGarigal, K. 2008. Inhabitants of landscape scars: succession of woody plants after large, severe forest fires in Arizona and New Mexico. *The Southwestern Naturalist*. 53(2): 146–161.
- Handler, S.D.; Matthew, J.; Iverson, J. [and others]. 2014. Minnesota Forest Ecosystem Vulnerability Assessment and Synthesis: a report from the Northwoods Climate Change Response Framework. Gen. Tech. Rep. NRS-133. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 228 p.
- Hanson, P.J.; Weltzin, J.F. 2000. Drought disturbance from climate change: response of United States forests. *Science of the Total Environment*. 262: 205–220.
- Harper, J.L. 1977. Population biology of plants. London: Academic Press. 892 p.
- Hawkes, C.V.; Kivlin, S.N.; Rocca, J.D. [and others]. 2011. Fungal community responses to precipitation. *Global Change Biology*. 17: 1637–1645.
- Henderson, J.P.; Grissino-Mayer, H.D. 2009. Climate–tree growth relationships of longleaf pine (*Pinus palustris* Mill.) in the Southeastern Coastal Plain, U.S.A. *Dendrochronologia*. 27: 31–43.
- Hersh, M.H.; Vilgalys, R.; Clark, J.S. 2012. Evaluating the impacts of multiple generalist fungal pathogens on temperate tree seedling survival. *Ecology*. 93: 511–520.
- Hicke, J.A.; Meddens, A.J.H.; Allen, C.D.; Kolden, C.A. 2013. Carbon stocks of trees killed by bark beetles and wildfire in the Western United States. *Environmental Research Letters*. 8(3): 035032. 8 p. doi:10.1088/1748-9326/8/3/035032. [Published online: August 29, 2013].
- Hicks, R.R., Jr.; Howard, J.E.; Watterston, K.G.; Coster, J.E. 1979. Rating forest stand susceptibility to southern pine beetle in east Texas. *Forest Ecology and Management*. 2: 269–283.
- Higgins, S.I.; Richardon, D.M. 1999. Predicting plant migration rates in a changing world: the role of long-distance dispersal. *The American Naturalist*. 153: 464–475.
- Hogg, E.T.; Brandt, J.P.; Kochtubajda, B. 2005. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951–2000. *Canadian Journal of Forest Research*. 35: 610–622.
- Hogg, E.T.; Brandt, J.P.; Michaelian, M. 2008. Impacts of a regional drought on productivity, dieback, and biomass of western Canadian aspen forests. *Canadian Journal of Forest Research*. 38: 1373–1384.
- Hood, L.A.; Swaine, M.D.; Mason, P.A. 2004. The influence of spatial patterns of damping-off disease and arbuscular mycorrhizal colonization on tree seedling establishment in Ghanaian tropical forest soil. *Journal of Ecology*. 92: 816–823.
- Hough, A.F.; Forbes, R.D. 1943. The ecology and silvics of forests in the High Plateau of Pennsylvania. *Ecological Monographs*. 13: 299–320.
- Houle, G. 1999. Mast seeding in *Abies balsamea*, *Acer saccharum* and *Betula alleghaniensis* in an old growth, cold temperate forest of north-eastern North America. *Journal of Ecology*. 87: 413–422.
- Hubbell, S.P.; Foster, R.B.; O'Brien, S.T. [and others]. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science*. 283: 554–557.
- Huntley, B.; Birks, H.J.B. 1983. An atlas of past and present pollen maps for Europe: 0–13000 years ago. Cambridge, UK: Cambridge University Press. 688 p.
- Hursh, C.R.; Haasis, F.W. 1931. Effects of 1925 summer drought on southern Appalachian hardwoods. *Ecology*. 12: 380–386.
- Hutchinson, T.; Long, R.; Ford, R.; Sutherland, E.K. 2008. Fire history and the establishment of oaks and maples in second-growth forests. *Canadian Journal of Forestry Research*. 38: 1184–1196.
- Ibáñez, I.; Clark, J.S.; Dietze, M.C. [and others]. 2006. Predicting biodiversity change: outside the climate envelope, beyond the species-area curve. *Ecology*. 87: 1896–1906.
- Ibáñez, I.; Clark, J.S.; LaDeau, S.; Hille Ris Lambers, J. 2007. Exploiting temporal variability to understand tree recruitment response to climate change. *Ecological Monographs*. 77(2): 163–177.
- Ibáñez, I.; McCarthy-Neumann, S. 2014. Integrated assessment of the direct and indirect effects of resource gradients on tree species recruitment. *Ecology*. 95: 364–375.
- Ichihara, Y.; Yamaji, K. 2009. Effect of light conditions on the resistance of current-year *Fagus crenata* seedlings against fungal pathogens causing damping-off in a natural beech forest: fungus isolation and histological and chemical resistance. *Journal of Chemical Ecology*. 35: 1077–1085.
- Innes, J.L. 1994. The occurrence of flowering and fruiting on individual trees over 3 years and their effects on subsequent crown condition. *Trees Structure and Function*. 8: 139–150.
- Intergovernmental Panel on Climate Change (IPCC). 1995. IPCC Second Assessment: Climate Change 1995. <http://ipcc.ch/pdf/climate-changes-1995/ipcc-2d-assessment/2d-assessment-en.pdf>. [Date accessed: August 2015].
- Intergovernmental Panel on Climate Change (IPCC). 2014. Climate change 2014: impacts, adaptation, and vulnerability. Part B: regional aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK: Cambridge University Press. 688 p.
- Iverson, L.R.; Hutchinson, T.F.; Prasad, A.M.; Peters, M.P. 2008a. Thinning, fire, and oak regeneration across a heterogeneous landscape in the eastern U.S.: 7-year results. *Forest Ecology and Management*. 255: 3035–3050.
- Iverson, L.R.; Prasad, A.M.; Matthews, S.N.; Peters, M. 2008b. Estimating potential habitat for 134 eastern U.S. tree species under six climate scenarios. *Forest Ecology and Management*. 254: 390–406.
- Iverson, L.R.; Prasad, A.M.; Matthews, S.N.; Peters, M. 2008c. Estimating potential habitat for 134 eastern U.S. tree species under six climate scenarios. *Forest Ecology and Management*. 254: 390–406.

- Iverson, L.R.; Schwartz, M.W.; Prasad, A.M. 2004. How fast and far might tree species migrate in the Eastern United States due to climate change? *Global Ecology and Biogeography*. 13: 209-219.
- Jackson, S.T.; Betancourt, J.L.; Booth, R.K.; Gray, S.T. 2009. Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Science*. 106(2): 19,685-19,692.
- Jactel, H.; Petit, J.; Desprez-Loustau, M.L. [and others]. 2012. Drought effects on damage by forest insects and pathogens: a meta-analysis. *Global Change Biology*. 18: 267-276.
- Janssen, E.; Wuebbles, D.J.; Kunkel, K.E. [and others]. 2014. Observational- and model-based trends and projections of extreme precipitation over the contiguous United States. *Earth's Future*. 2: 99-113.
- Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist*. 104: 501-528.
- Jenkins, M.A.; Pallardy, S.G. 1995. The influence of drought on red oak group species growth and mortality in the Missouri Ozarks. *Canadian Journal of Forest Research*. 25: 1119-1127.
- Jensen, T.S. 1985. Seed-seed predator interactions of European beech, *Fagus sylvatica*, and forest rodents, *Clethrionomys glareolus* and *Apodemus flavicollis*. *Oikos*. 44: 149-156.
- Jiang, X.; Rauscher, S.A.; Ringler, D.M. [and others]. 2013. Projected future changes in vegetation in Western North America in the twenty-first century. *Journal of Climate*. 26: 3671-3687.
- Jordan, L.; Clark, A., III.; Schimleck, L.R. [and others]. 2008. Regional variation in wood specific gravity of planted loblolly pine in the United States. *Canadian Journal of Forest Research*. 38: 698-710.
- Joyce, L.A.; Running, S.W.; Breshears, D.D. [and others]. 2014. Ch. 7: forests. In: Melillo, J.M.; Richmond, T.; Yohe, G.W., eds. *Climate change impacts in the United States: the third national climate assessment*. U.S. Global Change Research Program: 175-194. Available at: doi:10.7930/JOZ60KZC. <http://nca2014.globalchange.gov/report/sectors/forests>. [Date accessed: November 2015].
- Jump, A.S.; Matyas C.; Penuelas, J. 2009. The altitude-for-latitude disparity in the range retractions of woody species. *Trends in Ecology & Evolution*. 24: 694-701.
- Kaiser, K.E.; McGlynn, B.L.; Emanuel, R.E. 2012. Ecohydrology of an outbreak: mountain pine beetle impacts trees in drier landscape positions first. *Ecohydrology*. 6(3): 444-454.
- Kane, J.M.; Meinhardt, K.A.; Chang, T. [and others]. 2011. Drought-induced mortality of a foundation species (*Juniperus monosperma*) promotes positive afterlife effects in understory vegetation. *Plant Ecology*. 212: 733-741.
- Kayes, L.J.; Tinker, D.B. 2012. Forest structure and regeneration following a mountain pine beetle epidemic in southeastern Wyoming. *Forest Ecology and Management*. 263: 57-66.
- Keenan, T.; Sabate, S.; Gracia, C.A. 2008. Forest eco-physiological models and carbon sequestration. In: Bravo, F.; LeMay, V.; Jandl, R.; von Gadow K., eds. *Managing forest ecosystems: the challenge of climate change*. Berlin: Springer: 83-102.
- Kelly, A.E.; Goulden, M.L. 2008. Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Science*. 105: 11,823-11,826.
- King, D.A.; Bachelet, D.M.; Symstad, A.J. 2013. Climate change and fire effects on a prairie-woodland ecotone: projecting species range shifts with a dynamic global vegetation model. *Ecology and Evolution*. 3(15): 5076-5097.
- Klos, R.J.; Wang, G.G.; Bauerle, W.L.; Rieck, J.R. 2009. Drought impact on forest growth and mortality in the southeast U.S.A: an analysis using Forest Health and Monitoring data. *Ecological Applications*. 19: 699-708.
- Koenig, W.D.; Knops, V. 2013. Large-scale spatial synchrony and cross-synchrony in acorn production by two California oaks. *Ecology*. 94: 83-93.
- Kolb, T.E.; Agee, J.K.; Fulé, P.Z. [and others]. 2007. Perpetuating old ponderosa pine. *Forest Ecology and Management*. 249: 141-157.
- Kolb, P.F.; Robberecht, R. 1996. High temperature and drought stress effects on survival of *Pinus ponderosa* seedlings. *Tree Physiology*. 16: 665-672.
- Kot, M.; Lewis, M.A.; van den Driessche, P. 1996. Dispersal data and the spread of invading organisms. *Ecology*. 77: 2027-2042.
- Kreye, J.K.; Varner, J.M.; Hiers, J.K.; Mola, J. 2013. Toward a mechanism for eastern North American forest mesophication: differential litter drying across 17 species. *Ecological applications: a publication of the Ecological Society of America*. 23: 1976-86.
- Kueppers, L.M.; Snyder, M.A.; Sloan, L.C. [and others]. 2005. Modeled regional climate change and California endemic oak ranges. *Proceedings of the National Academy of Sciences*. 102(45): 16,281-16,286.
- Kukowski, K.R.; Schwinning, S.; Schwartz, B.F. 2012. Hydraulic responses to extreme drought conditions in three co-dominant tree species in shallow soil over bedrock. *Oecologia*. 171(4): 819-830. doi 10.1007/s00442-012-2466-x. [Published online: October 2, 2012].
- Kurz, W.A.; Dymond, C.C.; Stinson, G. [and others]. 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature*. 452: 987-990.
- LaDeau, S.L.; Clark, J.S. 2001. Rising CO₂ levels and the fecundity of forest trees. *Science*. 292: 95-98.
- Lafon, C.W.; Quiring, S.M. 2012. Relationships of fire and precipitation regimes in temperate forests of the Eastern United States. *Earth Interactions*. 16: 1-15.
- Larsen, D.R.; Johnson, P.S. 1998. Linking the ecology of natural oak regeneration to silviculture. *Forest Ecology and Management*. 106: 1-7.
- Le Blanc, D.C.; Terrell, M.A. 2009. Radial growth response of white oak to climate in eastern North America. *Canadian Journal of Forest Research*. 39: 2180-2192.
- Ledig, F.T.; Kitzmiller, J.H. 1992. Genetic strategies for reforestation in the face of global climate change. *Forest Ecology and Management*. 50: 153-169.
- Lenihan, J.M.; Bachelet, D.; Neilson, R.P.; Drapek, R. 2008. Response of vegetation distribution, ecosystem productivity, and fire to climate change scenarios for California. *Climatic Change*. 87: 215-230.
- Lenoir, J.; Gégout, J.C.; Marquet, P.A. [and others]. 2008. A significant upward shift in plant species optimum elevation during the 20th century. *Science*. 320(5884): 1768-1771.
- Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology*. 73: 1943-1967.
- Li, W.; Li, L.; Fu, R. [and others]. 2011. Changes to the North Atlantic subtropical high and its role in the intensification of summer rainfall variability in the Southeastern United States. *Journal of Climate*. 24(5): 1499-1506. doi: 10.1175/2010JCLI3829.1. [Published online: March 1, 2011].

- Lin, L.X.; Comita, L.S.; Zheng, Z.; Cao, M. 2012. Seasonal differentiation in density-dependent seedling survival in a tropical rain forest. *Journal of Ecology*. 100: 905–914.
- Linares, C.J.; Camarero, J.; Carreira, A. 2009. Interacting effects of changes in climate and forest cover on mortality and growth of the southernmost European fir forests. *Global Ecology and Biogeography*. 18: 485–497.
- Lines, E.R.; Coomes, D.A.; Purves, D.W. 2010. Influences of forest structure, climate and species composition on tree mortality across the eastern U.S. *PLoS ONE*. 5(10): e13212. 12 p. doi: 10.1371/journal.pone.0013212. [Published online: October 13, 2010].
- Lischke, H.; Zimmermann, N.E.; Bolliger, J. [and others]. 2006. TreeMig: A forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. *Ecological Modelling*. 199: 409–420.
- Littell, J.S.; McKenzie, D.; Peterson, D.L.; Westerling, A.L. 2009. Climate and wildfire area burned in western U.S. ecoprovinces, 1916–2003. *Ecological Applications*. 19: 1003–1021.
- Littell, J.; Peterson, D.; Tjoelker, M. 2008. Douglas-fir growth in mountain ecosystems: water limits tree growth from stand to region. *Ecological Monographs*. 78: 349–368.
- Little, E.L., Jr. 1971. Atlas of United States trees: volume 1, conifers and important hardwoods: U.S. Department of Agriculture Misc. Publ. 1146. Washington, DC: U.S. Department of Agriculture, Forest Service. 9 p. 200 maps.
- Little, E.L., Jr. 1976. Atlas of United States trees, volume 3, minor Western hardwoods: U.S. Department of Agriculture Misc. Publ. 1314. Washington, DC: U.S. Department of Agriculture, Forest Service. 13 p. 290 maps.
- Little, E.L., Jr. 1977. Atlas of United States trees, volume 4, minor Eastern hardwoods: U.S. Department of Agriculture Misc. Publ. 1342. Washington, DC: U.S. Department of Agriculture, Forest Service. 17 p. 230 maps.,
- Loarie, S.R.; Duffy, P.B.; Hamilton, H. [and others]. 2009. The velocity of climate change. *Nature*. 462: 1052–1055.
- Loehman, R.A.; Corrow, A.; Keane, R.E. 2011. Modeling climate changes and wildfire interactions: Effects on whitebark pine (*Pinus albicaulis*) and implications for restoration, Glacier National Park, Montana, U.S.A. *Forests*. 2(4): 832–860.
- Loik, M.E.; Breshears, D.D.; Lauenroth, W.K.; Belnap, J. 2004. A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western U.S.A. *Oecologia*. 14: 269–281.
- Luo, Y.; Chen, H.Y.H. 2013. Observations from old forests underestimate climate change effects on tree mortality. *Nature Communications*. 4: 1655. 6 p. doi: 10.1038/ncomms2681. [Published online: April 3, 2013].
- Luo, Y.; Ogle, K.; Tucker, C. [and others]. 2011. Ecological forecasting and data assimilation in a data-rich era. *Ecological Applications*. 21: 1429–1442.
- Lutz, J.A.; van Wagtendonk, J.W.; Franklin, J.F. 2009. Twentieth-century decline of large-diameter trees in Yosemite National Park, California, U.S.A. *Forest Ecology and Management*. 257: 2296–2307.
- Lynch, C.; Hessl, A. 2010. Climatic controls on historical wildfires in West Virginia, 1939–2008. *Physical Geography*. 31: 254–269.
- Macalady, A.K.; Bugmann, H. 2014. Growth-mortality relationships in piñon pine (*Pinus edulis*) during severe droughts of the past century: shifting processes in space and time. *PLoS One* 9(5): e92770. doi: 10.1371/journal.pone.0092770. [Published online: May 2, 2014].
- Man, G., comp. 2013. Major forest insect and disease conditions in the United States: 2012. FS-1023. Washington, DC: U.S. Department of Agriculture, Forest Service, Forest Health Protection. 44 p. http://www.fs.fed.us/foresthealth/current_conditions.shtml. [Date accessed: September 14, 2015].
- Manion, P. 1981. *Tree disease concepts*, 2d ed. Englewood Cliffs, NJ: Prentice Hall. 399 p.
- Martin-Benito, D.; Kint, V.; del Río, M. [and others]. 2011. Growth responses of West-Mediterranean *Pinus nigra* to climate change are modulated by competition and productivity: past trends and future perspectives. *Forest Ecology and Management*. 262: 1030–1040.
- Martin-Benito, D.; Pederson, N. 2015. Convergence in drought stress, but a divergence of climatic drivers across a latitudinal gradient in a temperate broadleaf forest. *Journal of Biogeography*. 42: 925–937. doi: 10.1111/jbi.12462. [Published online: January 13, 2015].
- Masek, J.G.; Cohen, W.B.; Leckie, D. [and others]. 2011. Recent rates of forest harvest and conversion in North America. *Journal Geophysical Research: Biogeosciences*. 116(G4): G00K03. 22 p. doi:10.1029/2010JG001471. [Published online: April 15, 2011].
- Mast, J.N.; Wolf, J. 2006. Spatial patch patterns and altered forest structure in middle elevation versus upper ecotonal mixed-conifer forests, Grand Canyon National Park, Arizona, U.S.A. *Forest Ecology and Management*. 236: 241–250.
- Matlack, G.R. 1987. Diaspore size, shape, and fall behavior in wind-dispersed plant species. *American Journal of Botany*. 74: 1150–1160.
- Matthews, S.N.; Iverson, L.R.; Prasad, A.M. [and others]. 2011. Modifying climate change habitat models using tree species-specific assessments of model uncertainty and life history-factors. *Forest Ecology and Management*. 262: 1460–1472.
- Maxwell, J.T.; Harley, G.L.; Matheus, T.J. 2014. Dendroclimatic reconstructions from multiple co-occurring species: a case study from an old-growth deciduous forest in Indiana, U.S.A. *International Journal of Climatology*. 35(6): 860–870.
- Maxwell, R.S.; Hessl, A.E.; Cook, E.R.; Pederson, N. 2011. A multispecies tree ring reconstruction of Potomac River streamflow (950–2001). *Water Resources Research*. 47: W05512. 12 p. doi:10.1029/2010WR010019. [Published online: May 12, 2011].
- McCarthy-Neumann, S.; Ibáñez, I. 2012. Tree range expansion may be enhanced by escape from negative plant-soil feedbacks. *Ecology*. 93: 2637–2649.
- McDowell, N.G.; Adams, H.D.; Bailey, J.D. [and others]. 2006. Homeostatic maintenance of ponderosa pine gas exchange in response to stand density changes. *Ecological Applications*. 16: 1164–1182.
- McDowell, N.G.; Beerling, D.J.; Breshears, D.D. [and others]. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology and Evolution*. 26: 523–532.
- McDowell, N.G.; Fisher, R.A.; Xu, C.; Domec, J.C. [and others]. 2013. Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework. *New Phytologist*. 200: 304–321.
- McEwan, R.W.; Dyer, J.M.; Pederson, N. 2011. Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. *Ecography*. 34: 244–256.
- McKenney, D.W.; Pedlar, J.H.; Lawrence, K. [and others]. 2007. Potential impacts of climate change on distribution of North American trees. *BioScience*. 57: 939–948.

- McKenney, D.W.; Pedlar, J.H.; Rood, R.B.; Price, D. 2011. Revisiting projected shifts in the climate envelopes of North American trees using updated general circulation models. *Global Change Biology*. 17: 2720-2730.
- McLachlan, J.; Clark, J.S.; Manos, P.S. 2005. Molecular indicators of tree migration capacity under rapid climate change. *Ecology*. 86: 2088-2098.
- McLachlan, J.S.; Hellman, J.J.; Schwartz, M.W. 2007. A framework for debate of assisted migration in an era of climate change. *Conservation Biology*. 21(2): 297-302.
- McLaughlin, B.; Zavaleta, E.S. 2012. Predicting species' responses to climate change: demography and climate microrefugia in California valley oak. *Global Change Biology*. 18: 2301-2312.
- McMahon, S.M.; Parker, G.C.; Miller, D.R. 2010. Evidence for a recent increase in forest growth. *Proceedings of the National Academy of Sciences*. 107: 3611-3615.
- Meddens, A.J.H.; Hicke, J.A.; Ferguson, C.A. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the Western United States. *Ecological Applications*. 22(7): 1876-1891.
- Medvigy, D.; Moorcroft, P.R. 2012. Predicting ecosystem dynamics at regional scales: an evaluation of a terrestrial biosphere model for the forests of northeastern North America. *Philosophical Transactions of the Royal Society B-Biological Sciences*. 367: 222-235.
- Meier, E.S.; Lischke, H.; Schmatz, D.R.; Zimmermann, N.E. 2012. Climate, competition and connectivity affect future migration and ranges of European trees. *Global Ecology and Biogeography*. 21: 164-178.
- Melillo, J.M.; Terese, T.C.; Richmond, T.C.; Yohe, G.W., eds. 2014. Climate change impacts in the United States: the third national climate assessment. U.S. Global Change Research Program. 841 p. Available at: doi: 10.7930/J0Z31WJ2. <http://nca2014.globalchange.gov/report/regions/northeast> [Date accessed: November 2015].
- Menard, A.; Dube, P.; Bouchard, A. [and others]. 2002. Evaluating the potential of the SORTIE forest succession model for spatio-temporal analysis of small-scale disturbances. *Ecological Modelling*. 153: 81-96.
- Miao, S.; Zou, C.B.; Breshears, D.D. 2009. Vegetation responses to extreme hydrological events: sequence matters. *The American Naturalist*. 173: 113-118.
- Millar, C.I.; Stephenson, N.L. 2015. Temperate forest health in an era of emerging megadisturbance. *Science*. 349(6250): 823-826.
- Millar, C.I.; Westfall, R.D.; Delany, D.L. [and others]. 2012. Forest mortality in high-elevation whitebark pine (*Pinus albicaulis*) forests of eastern California, U.S.A.; influence of environmental context, bark beetles, climatic water deficit, and warming. *Canadian Journal of Forest Research*. 42(4): 749-765.
- Miller, J.; Safford, H.; Crimmins, M.; Thode, A. 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, U.S.A. *Ecosystems*. 12: 16-32.
- Miller, P.A.; Giesecke, T.; Hickler, T. [and others]. 2008. Exploring climatic and biotic controls on Holocene vegetation change in Fennoscandia. *Journal of Ecology*. 96: 247-259.
- Miller, R.F.; Rose, J.A. 1999. Fire history and western juniper encroachment in sagebrush steppe. *Journal of Rangeland Management*. 52(6): 550-559.
- Minckley, T.A.; Bartlein, P.J.; Whitlock, C. [and others]. 2008. Associations among modern pollen, vegetation, and climate in western North America. *Quaternary Science Reviews*. 27: 1962-1991.
- Minnich, R.A. 2007. Southern California conifer forests. In: Barbour, M.G.; Keeler-Wolf, T.; Schoenherr, A.S., eds. *Terrestrial vegetation of California*, 3rd ed. Los Angeles: University of California Press: 502-538. Chapter 18.
- Mladenoff, D.J.; Host, G.E.; Boeder, J.R.; Crow, T.R. 1996. LANDIS: a spatial model of forest landscape disturbance succession, and management. In: *GIS and Environmental Modeling: Progress and Research Issues*. Fort Collins, CO: GIS World Books: 175-179.
- Mok, H.F.; Arndt, S.K.; Nitschke, C.R. 2012. Modelling the potential impact of climate variability on species regeneration potential in SE Australia. *Global Change Biology*. 18: 1053-1072.
- Moore, G.W.; Edgar, C.B.; Vogel, J. [and others]. (In press). Tree mortality from an exceptional drought spanning mesic to semiarid ecoregions. *Ecological Applications*.
- Moore, M.M.; Covington, W.W.; Fulé, P.Z. [and others]. 1999. Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. *Ecological Applications*. 9: 1266-1277.
- Morales, P.; Sykes, M.T.; Prentice, I.C. [and others]. 2005. Comparing and evaluating process-based ecosystem model predictions of carbon and water fluxes in major European forest biomes. *Global Change Biology*. 11: 2211-2233.
- Morin, X.; Augspurger, C.; Chuine, I. 2007. Process-based modeling of species' distributions: what limits temperate tree species' range boundaries. *Ecology*. 88: 2280-2291.
- Mueller, J.M.; Hellman, J.J. 2008. An assessment of invasion risk from assisted migration. *Conservation Biology*. 22(3): 562-567.
- Mueller, R.C.; Scudder, C.M.; Porter, M.E. [and others]. 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. *Journal of Ecology*. 93: 1085-1093.
- Murphy, H.T.; VanDerWal, J.; Lovett-Doust, J. 2006. Distribution of abundance across the range in eastern North American trees. *Global Ecology and Biogeography*. 15: 63-71.
- Nabel, J.; Zurbriggen, N.; Lischke, H. 2013. Interannual climate variability and population density thresholds can have a substantial impact on simulated tree species' migration. *Ecological Modelling*. 257: 88-100.
- Newbery, D.M.; Stoll, P. 2013. Relaxation of species-specific neighborhood effects in Bornean rain forest under climatic perturbation. *Ecology*. 94: 2838-2851.
- Nilsen, E.T.; Clinton, B.D.; Lei, T.T. [and others]. 2001. Does *Rhododendron maximum* L. (Ericaceae) reduce the availability of resources above and belowground for canopy tree seedlings? *American Midland Naturalist*. 145: 325-343.
- Nilsson, U.; Örlander, G. 1995. Effects of regeneration methods on drought damage to newly planted Norway spruce seedlings. *Canadian Journal of Forest Research*. 25: 790-802.
- Notaro, M.; Mauss, A.; Williams, J.W. 2012. Projected vegetation changes for the American Southwest: combined dynamic modeling and bioclimatic-envelope approach. *Ecological Applications*. 22: 1365-1388.
- Nowacki, G.J.; Abrams, M.D. 2008. The demise of fire and "Mesophication" of forests in the Eastern United States. *Bioscience*. 58: 123-138.
- Nyland, R.D. 2007. *Silviculture: concepts and applications*. Long Grove, IL: Waveland Press. 704 p.

- O'Connor, C.D. 2013. Spatial and temporal dynamics of disturbance interactions along an ecological gradient. School of Natural Resources and the Environment, Tucson, AZ: University of Arizona. 204 p. Ph.D. Dissertation.
- Ogle, K.; Pacala, S.W. 2009. A modeling framework for inferring tree growth and allocation from physiological, morphological, and allometric traits. *Tree Physiology*. 29: 587-605.
- O'Hara, K.L.; Nagel, L.M. 2013. The stand: revisiting a central concept in forestry. *Journal of Forestry*. 111(5): 335-340.
- Ohmann, J.L.; Spies, T.A. 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. *Ecological Monographs*. 68: 151-182.
- Olano, J.M.; Palmer, M.W. 2003. Stand dynamics of an Appalachian old-growth forest during a severe drought episode. *Forest Ecology and Management*. 174: 139-148.
- Oosting, H.J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. *American Midland Naturalist*. 28: 1-126.
- Orwig, D.A.; Abrams, M.D. 1997. Variation in radial growth responses to drought among species, site, and canopy strata. *Trees*. 11: 474-484.
- Overpeck, J.T.; Rind, D.; Goldberg, R. 1990. Climate-induced changes in forest disturbance and vegetation. *Nature*. 343: 51-53.
- Owens, J.N. 1995. Constraints to seed production: temperate and tropical trees. *Tree Physiology*. 15: 477-484.
- Pacala, S.W.; Canham, C.D.; Saponara, J. [and others]. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs*. 66: 1-43.
- Pagel, J.; Schurr, F.M. 2012. Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. *Global Ecology and Biogeography*. 21: 293-304.
- Papaik, M.J.; Canham, C.D. 2006. Species resistance and community response to wind disturbance regimes in northern temperate forests. *Journal of Ecology*. 94: 1011-1026.
- Parmesan, C.; Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature*. 421: 37-42.
- Parshall, T. 1995. Canopy mortality and stand-scale change in a northern hemlock-hardwood forest. *Canadian Journal of Forestry Research*. 25: 1466-1478.
- Parshall, T.; Foster, D. 2003. Fire on the New England landscape: regional and temporal variation, cultural and environmental controls. *Journal of Biogeography*. 29: 1305-1317.
- Parsons, D.J.; DeBenedetti, S.H. 1979. Impact of fire suppression on a mixed-conifer forest. *Forest Ecology and Management*. 2: 21-33.
- Pasho, E.; Camarero, J.J.; de Luis, M.; Vicente-Serrano, S.M. 2011. Impacts of drought at different time scales on forest growth across a wide climatic gradient in north-eastern Spain. *Agricultural and Forest Meteorology*. 151: 1800-1811.
- Pedersen, B. 1998. The role of stress in the mortality of midwestern oaks as indicated by growth prior to death. *Ecology*. 79: 79-93.
- Pederson, N.; Bell, A.R.; Cook, E.R. [and others]. 2013. Is an epic pluvial masking the water insecurity of the greater New York City region? *Journal of Climate*. 26: 1339-1354.
- Pederson, N.; Bell, A.R.; Knight, T.A. [and others]. 2012. Long-term perspective on a modern drought in the American Southeast. *Environmental Research Letters*. 7. 014034. 8 p. doi:10.1088/1748-9326/7/1/014034. [Published online: 14 March 2012].
- Pederson, N.; Dyer, J.M.; McEwan, R.W. [and others]. 2014. The legacy of episodic climatic events in shaping broadleaf-dominated forests. *Ecological Monographs*. 84(4): 599-620.
- Pederson, N.; Varner, J.M., III; Palik, B.J. 2008. Canopy disturbance and tree recruitment over two centuries in a managed longleaf pine landscape. *Forest Ecology and Management*. 254: 85-95.
- Pelz, K.A.; Smith, F.W. 2013. How will aspen respond to mountain pine beetle? A review of literature and discussion of knowledge gaps. *Forest Ecology and Management*. 299: 60-69.
- Peng, C.H.; Ma, Z.H.; Lei, X.D. [and others]. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change*. 1: 467-471.
- Perez-Ramos, I.M.; Ourcival, J.M.; Limousin, J.M.; Rambal, S. 2010. Mast seeding under increasing drought: results from a long-term data set and from a rainfall exclusion experiment. *Ecology*. 91: 3057-3068.
- Peters, M.P.; Iverson, L.R.; Matthews, S.N. 2014. Spatio-temporal trends of drought by forest type in the conterminous United States, 1960-2013. Res. Map NRS-7. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. [scale 1:12,000,000].
- Peters, M.P.; Matthews, S.N.; Iverson, L.R.; Prasad, A.M. 2013. Delineating generalized species boundaries from species distribution data and a species distribution model. *International Journal of Geographical Information Science*. 28(8): 1547-1560. doi:10.1080/13658816.2013.840381. [Published online: November 1, 2013].
- Pinto, J.R.; Marshall, J.D.; Dumroese, R.K. [and others]. 2012. Photosynthetic response, carbon isotopic composition, survival, and growth of three stock types under water stress enhanced by vegetative competition. *Canadian Journal of Forest Research*. 42: 333-344.
- Piovesan G.; Adams, J.M. 2001. Masting behaviour in beech: linking reproduction and climatic variation. *Canadian Journal of Botany*. 79: 1039-1047.
- Pitelka, L.F.; Gardner, R.H.; Ash, J. [and others]. 1997. Plant migration and climate change. *American Scientist*. 85: 464-473.
- Potter, K.M.; Hargrove, W.W. 2013. Quantitative metrics for assessing predicted climate change pressure on North American tree species. *Mathematical and Computational Forestry and Natural Resources Sciences*. 5(2): 151-169.
- Potter, K.M.; Hargrove, W.W.; Koch, F.H. 2010. Predicting climate change extirpation risk for central and southern Appalachian forest tree species. In: Rentch, J.S.; Schuler, T.M., eds. *Proceedings from Conference on Ecology and Management of High-Elevation Forests of the Central and Southern Appalachian Mountains*. Gen. Tech. Rep. NRS-P-64. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station: 179-189.
- Powers, R.F.; Reynolds, P.E. 1999. Ten-year responses of ponderosa pine plantations to repeated vegetation and nutrient control along an environmental gradient. *Canadian Journal of Forest Research*. 29: 1027-1038.
- Prasad, A.M.; Gardiner, J.; Iverson, L. [and others]. 2013. Exploring tree species colonization potentials using a spatially explicit simulation model: implications for four oaks under climate change. *Global Change Biology*. 19: 2196-2208.
- Pucek, Z.; Jedrzejewski, W.; Jedrzejewska, B.; Pucek, M. 1993. Rodent population dynamics in a primeval deciduous forest (Bialowieza National Park) in relation to weather, seed crop, and predation. *Acta Theriologica*. 38: 199-232.

- Purves, D.W. 2009. The demography of range boundaries versus cores in Eastern U.S. tree species. *Proceedings of the Royal Society B*. 276: 1477-1484.
- Quarterman, E.; Keever, C. 1962. Southern mixed hardwood forest: climax in the Southeastern Coastal Plain, U.S.A. *Ecological Monographs*. 32: 167-185.
- Radtke, P.J.; Herring, N.D.; Loftis, D.L.; Keyser, C.E. 2012. Evaluating Forest Vegetation Simulator predictions for Southern Appalachian upland hardwoods with a modified mortality model. *Southern Journal of Applied Forestry*. 36: 61-70.
- Raffa K.F.; Aukema, B.H.; Bentz, B.J. [and others]. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience*. 58: 501-517.
- Rahman, M.S.; Messina, M.G.; Fisher, R.F. 2006. Intensive forest management affects loblolly pine (*Pinus taeda* L.) growth and survival on poorly drained sites in southern Arkansas. *Southern Journal of Applied Forestry*. 30(2): 79-85.
- Rapacciuolo, G.; Maher, S.P.; Schneider, A.C. [and others]. 2014. Beyond a warming fingerprint: individualistic biogeographic responses to heterogeneous climate change in California. *Global Change Biology*. 20: 2841-2855.
- Rehfeldt, G.E.; Crookston, N.L.; Warwell, M.V.; Evans, J.S. 2006. Empirical analyses of plant-climate relationships for the Western United States. *International Journal of Plant Sciences*. 167(6): 1123-1150.
- Rehfeldt, G.E.; Ferguson, D.E.; Crookston, N.L. 2009. Aspen, climate, and sudden aspen decline in western U.S.A. *Forest Ecology and Management*. 258: 2353-2364.
- Reinhardt, E.; Holsinger, L. 2010. Effects of fuel treatments on carbon-disturbance relationships in forests of the northern Rocky Mountains. *Forest Ecology and Management*. 259: 1427-1435.
- Roberts, S.D.; Harrington, C.A.; Terry, T.A. 2005. Harvest residue and competing vegetation affect soil moisture, soil temperature, N availability, and Douglas-fir seedling growth. *Forest Ecology and Management*. 205: 333-350.
- Roccaforte, J.P.; Fulé, P.Z.; Covington, W.W. 2010. Monitoring landscape-scale ponderosa pine restoration treatment implementation and effectiveness. *Restoration Ecology*. 18(6): 820-833.
- Rogers, P.C.; Landhäuser, S.M.; Pinno, B.D.; Ryel, R.J. 2014. A functional framework for improved management of western North American aspen (*Populus tremuloides* Michx.). *Forest Science*. 60(2): 345-359.
- Rogers, P.C.; Mittanck, C.M. 2014. Herbivory strains resilience in drought-prone aspen landscapes of the Western United States. *Journal of Vegetation Science*. 25(2): 457-469.
- Royer, P.D.; Cobb, N.S.; Clifford, M.J. [and others]. 2011. Extreme climatic event-triggered overstory vegetation loss increases understory solar input regionally: primary and secondary ecological implications. *Journal of Ecology*. 99: 714-723.
- Rozas, V. 2005. Dendrochronology of pedunculate oak (*Quercus robur* L.) in an old-growth pollarded woodland in northern Spain: tree-ring growth responses to climate. *Annals of Forest Science*. 62: 209-218.
- Saltre, F.; Saint-Amant, R.; Gritti, E.S. [and others]. 2013. Climate or migration: what limited European beech post-glacial colonization? *Global Ecology and Biogeography*. 22: 1217-1227.
- Salzer, M.W.; Hughes, M.K.; Bunn, A.G.; Kipfmüller, K.F. 2009. Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. *Proceedings of the National Academy of Sciences of the United States of America*. 106: 20,348-20,353.
- Saunders, M.R.; Arseneault, J.E. 2013. Potential yields and economic returns of natural disturbance-based silviculture: a case study from the Acadian Forest Ecosystem Research Program. *Journal of Forestry*. 111: 175-185.
- Savage, M.; Mast, J.N. 2005. How resilient are southwestern ponderosa pine forests after crown fires? *Canadian Journal of Forest Research*. 35: 967-977.
- Savage, M.; Mast, J.N.; Feddema, J.J. 2013. Double whammy: high-severity fire and drought in ponderosa pine forests of the Southwest. *Canadian Journal of Forest Research*. 43: 570-583.
- Savage, M.; Brown, P.M.; Feddema, J. 1996. The role of climate in a pine forest regeneration pulse in the Southwestern United States. *Ecoscience*. 3: 310-318.
- Scheller, R.M.; Mladenoff, D.J. 2007. An ecological classification of forest landscape simulation models: tools and strategies for understanding broad-scale forested ecosystems. *Landscape Ecology*. 22: 491-505.
- Scheller, R.M.; Mladenoff, D.J. 2008. Simulated effects of climate change, fragmentation, and inter-specific competition on tree species migration in northern Wisconsin, U.S.A. *Climate Research*. 36: 191-202.
- Scherstjanoi, M.; Poulter, B.; Kaplan, J.; Lischke, H. 2014. TreeM-LPJ: a computationally efficient plant physiological height-class-structured forest model. *Ecological Complexity*. 19: 96-110.
- Schumacher, F.X.; Day, B.B. 1939. The influence of precipitation upon the width of annual rings of certain timber trees. *Ecological Monographs*. 9: 387-429.
- Schuster, W.S.L.; Griffin, K.L.; Roth, H. [and others]. 2008. Changes in composition, structure and aboveground biomass over seventy-six years (1930-2006) in the Black Rock Forest, Hudson Highlands, southeastern New York State. *Tree Physiology*. 28: 537-549.
- Schwartz, M.W. 1993. Modelling effects of habitat fragmentation on the ability of trees to respond to climatic warming. *Biodiversity and Conservation*. 2: 51-61.
- Schwartz, M.W.; Hellmann, J.J.; Jason, M.M. [and others]. 2012. Managed relocation: integrating the scientific, regulatory, and ethical challenges. *Bioscience*. 62: 732-743.
- Shaw, J.D.; Steed, B.E.; DeBlander, L.T. 2005. Forest inventory and analysis (FIA) annual inventory answers the question: what is happening to pinyon juniper woodlands? *Journal of Forestry*. 103: 280-285.
- Sheppard, S.; Picard, P. 2006. Visual-quality impact of forest pest activity at the landscape level: a synthesis of published knowledge and research needs. *Landscape and Urban Planning*. 77: 321-342.
- Shinneman, D.J.; Baker, W.L.; Rogers, P.C.; Kulakowski, D. 2013. Fire regimes of quaking aspen in the Mountain West. *Forest Ecology and Management*. 299: 22-34.
- Shuman, B.; Henderson, A.K.; Plank, C. [and others]. 2009. Woodland-to-forest transition during prolonged drought in Minnesota after ca. AD 1300. *Ecology*. 90(10): 2792-2807.
- Shuman, J.K.; Shugart, H.H.; O'Halloran, T.H. 2011. Sensitivity of Siberian larch forests to climate change. *Global Change Biology*. 17: 2370-2384.
- Silvertown, J.W. 1987. Introduction to plant population ecology. White Plains, NY: Longman. 248 p.

- Sitch, S.; Smith, B.; Prentice, I.C. [and others]. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*. 9(2): 161-185.
- Skov, K.R.; Kolb, T.E.; Wallin, K.F. 2004. Tree size and drought affect ponderosa pine physiological response to thinning and burning treatments. *Forest Science*. 50: 81-91.
- Snell, R.S. 2014. Simulating long-distance seed dispersal in a dynamic vegetation model. *Global Ecology and Biogeography*. 23: 89-98.
- Song, X.; Zeng, X. 2014. Investigation of uncertainties of establishment schemes in dynamic global vegetation models. *Advances in Atmospheric Sciences*. 31: 85-94.
- Sork, V.L.; Davis, F.W.; Westfall, R. [and others]. 2010. Gene movement and genetic association with regional climate gradients in California valley oak (*Quercus lobata* Née) in the face of climate change. *Molecular Ecology*. 19(17): 3806-3823.
- St. George, S.; Ault, T.R. 2014. The imprint of climate within Northern Hemisphere trees. *Quaternary Science Reviews*. 89: 1-4.
- Stahle, D.W.; Cleaveland, M.K. 1992. Reconstruction and analysis of spring rainfall over the southeastern U.S. for the past 1,000 years. *Bulletin of the American Meteorological Society*. 73: 1947-1961.
- Stahle, D.W.; Cleaveland, M.K.; Hehr, J. 1988. North Carolina climate changes reconstructed from tree rings: AD 372 to 1985. *Science*. 240: 1517-1519.
- Stanosz, G.R.; Blodgett, J.T.; Smith, D.R.; Kruger, E.L. 2001. Water stress and *Sphaeropsis sapinea* as a latent pathogen of red pine seedlings. *New Phytologists*. 149: 531-538.
- Starkey, D.; Oak, S.; Ryan, G. [and others]. 1988. Evaluation of oak decline areas in the South. Protection Report R8 PR-17. Atlanta, GA: U.S. Department of Agriculture, Forest Service, Southern Region, State & Private Forestry, Forest Pest Management. 43 p.
- Stöcklin, J.; Bäumler, E. 1996. Seed rain, seedling establishment and clonal growth strategies on a glacier foreland. *Journal of Vegetation Science*. 7: 45-56.
- Stogsdili, W.R., Jr.; Wittwer, R.F.; Hennessey, T.C.; Dougherty, P.M. 1992. Water use in thinned loblolly pine plantations. *Forest Ecology and Management*. 50: 233-245.
- Swanston, C.; Janowiak, M.; Iverson, L. [and others]. 2011. Ecosystem vulnerability assessment and synthesis: a report from the Climate Change Response Framework Project in northern Wisconsin. Gen. Tech. Rep. NRS-82. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 142 p.
- Swetnam, T.W.; Betancourt, J.L. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *Journal of Climate*. 11: 3128-3147.
- Swinfield, T.; Lewis, O.T.; Bagchi, R.; Freckleton, R.P. 2012. Consequences of changing rainfall for fungal pathogen-induced mortality in tropical tree seedlings. *Ecology and Evolution*. 2: 1408-1413.
- Tardiff, J.C.; Conciatori, F.; Nantel, P.; Gagnon, D. 2006. Radial growth and climate responses of white oak (*Quercus alba*) and northern red oak (*Quercus rubra*) at the northern distribution limit of white oak in Quebec. *Canadian Journal of Biogeography*. 33(9): 1657-1669.
- Taylor, M.; Haase, D.L.; Rose, R.L. 2009. Fall planting and tree shelters for reforestation in the East Washington Cascades. *Western Journal of Applied Forestry*. 24: 173-179.
- Thomas, Z.; Waring, K.M. 2015. Enhancing resiliency and restoring ecological attributes in second-growth ponderosa pine stands in northern New Mexico, U.S.A. *Forest Science*. 60: 13-085. 12 p. doi: 10.5849/forsci.13-085. [Published online: May 8, 2014].
- Thuiller, W.; Lavorel, S.; Araujo, M.B. [and others]. 2005. Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences*. 102: 8245-8250.
- Trottier-Picard, A.; Thiffault, E.; DesRochers, A. [and others]. 2014. Amounts of logging residues affect planting microsites: a manipulative study across northern forest ecosystems. *Forest Ecology and Management*. 312: 203-215.
- Twidwell, D.; Wonkka, C.L.; Taylor, C.A., Jr. [and others]. 2014. Drought-induced woody plant mortality in an encroached semi-arid savanna depends on topoedaphic factors and land management. *Applied Vegetation Science*. 17(1): 42-52. doi: 10.1111/avsc.12044. [Published online: April 20, 2013].
- Uriarte, M.; Canham, C.D.; Thompson, J.; Zimmerman, J. K. 2009. Understanding natural disturbance and human land use as determinants of tree community dynamics in a subtropical wet forest: results from a forest simulator. *Ecological Monographs*. 79: 423-443.
- van Mantgem, P.J.; Stephenson, N.L. 2007. Apparent climatically-induced increase of tree mortality rates in a temperate forest. *Ecology Letters*. 10: 909-916.
- van Mantgem, P.J.; Stephenson, N.L.; Byrne, J.C. [and others]. 2009. Widespread increase of tree mortality rates in the Western United States. *Proceedings of the National Academy of Science*. 323: 521-524.
- Vanderwel, M.C.; Lyutsarev, V.S.; Purves, D.W. 2013. Climate-related variation in mortality and recruitment determine regional forest-type distributions. *Global Ecology and Biogeography*. 22: 1192-1203.
- Voelker, S.; Muzika, R.; Guyette, R. 2008. Individual tree and stand level influences on the growth, vigor, and decline of red oaks (*Quercus rubra*) in the Ozarks. *Forest Science*. 54: 8-20.
- Wackerman, A.E. 1929. Why prairies in Arkansas and Louisiana? *Journal of Forestry*. 27(6): 726-734.
- Wagner, R.G.; Robinson, A.P. 2006. Critical period of interspecific competition for four northern conifers: 10-year growth response and associated vegetation dynamics. *Canadian Journal of Forest Research*. 36: 2474-2485.
- Wagner, R.G.; Colombo, S.J., eds. 2001. Regenerating the Canadian Forest: principles and practices for Ontario. Markham, ON: Fitzhenry and Whiteside Limited. 650 p.
- Wang G.G.; Chhin, S.; Bauerle, W.L. 2006. Effect of natural atmospheric CO₂ fertilization suggested by open-grown white spruce in a dry environment. *Global Change Biology*. 12: 601-610.
- Weed, A.S.; Ayres, M.P.; Hicke, J.A. 2013. Consequences of climate change for biotic disturbances in North American forests. *Ecological Monographs*. 83: 441-470.
- Wehner, M.; Easterling, D.R.; Lawrimore, J.H. [and others]. 2011. Projections of future drought in the continental United States and Mexico. *Journal of Hydrometeorology*. 12(6): 1359-1377.
- Westerling, A.L.; Hidalgo, H.G.; Cayan, D.R.; Swetnam, T.W. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science*. 313: 940-943.
- Westerling, A.L.; Turner, M.G.; Smithwick, E.A.H. [and others]. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. *Proceedings of the National Academy of Sciences*. 108: 13,165-13,170.

- Wiens, J.A.; Stralberg, D.; Jongsomjit, D. [and others]. 2009. Niches, models, and climate change: assessing the assumptions and uncertainties. *Proceedings of the National Academy of Sciences*. 106: 19,729-19,736.
- Will, R.; Hennessey, T.; Lynch, T. [and others]. 2010. Effects of planting density and seed source on loblolly pine stands in southeastern Oklahoma. *Forest Science*. 56(5): 437-443.
- Williams, A.P.; Allen, C.D.; Macalady, A.K. [and others]. 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change*. 3: 292-297.
- Williams, A.P.; Michaelsen, J.; Leavitt, S.W.; Still, C.J. 2010. Using tree rings to predict the response of tree growth to climate change in the Continental United States during the Twenty-First Century. *Earth Interactions*. 14: 1–20.
- Williams, J.W.; Blois, J.L.; Shuman, B.N. 2011. Extrinsic and intrinsic forcing of abrupt ecological change: case studies from the late Quaternary. *Journal of Ecology*. 99: 664-677.
- Williams, M.I.; Dumroese, R.K. 2013. Preparing for climate change: forestry and assisted migration. *Journal of Forestry*. 111(4): 287-297.
- Woodall, C.W.; Zhu, K.; Westfall, J.A. [and others]. 2013a. Assessing the stability of tree ranges and influence of disturbance in Eastern U.S. forests. *Forest Ecology and Management*. 291: 172-180.
- Woodall, C.; Oswalt, C.M.; Westfall, J.A. [and others]. 2009. An indicator of tree migration in forests of the Eastern United States. *Forest Ecology and Management*. 257: 1434-1444.
- Woodall, C.W.; Domke, G.M.; Riley, K. [and others]. 2013b. A framework for assessing global change risks to forest carbon stocks. *PLOS One*. 8(9): e73222. 8 p. doi: 10.1371/journal.pone.0073222. [Published online: September 10, 2013].
- Worrall, J.J.; Rehfeldt, G.E.; Hamann, A. [and others]. 2013. Recent declines of *Populus tremuloides* in North America linked to climate. *Forest Ecology and Management*. 299: 35-51.
- Wyckoff, P.H.; Clark, J.S. 2002. The relationship between growth and mortality for seven co-occurring tree species in the southern Appalachian Mountains. *Journal of Ecology*. 90: 604-615.
- Yaussy, D.A.; Iverson, L.R.; Matthews, S.N. 2013. Competition and climate affects U.S. hardwood-forest tree mortality. *Forest Science*. 59: 416-430.
- Yeh, H.Y.; Wensel, L.C. 2000. The relationship between tree diameter growth and climate for coniferous species in northern California. *Canadian Journal of Forest Research*. 30: 1463-1471.
- Zahner, R. 1958. Hardwood understory depletes soil water in pine stands. *Forest Science*. 4(3): 178-184.
- Zahner, R. 1968. Water deficits and the growth of trees. In: Kozlowski, T.T. *Water deficits and plant growth*, volume II: plant water consumption and response. New York: Academic Press: 191-254.
- Zausen, G.L.; Kolb, T.E.; Bailey, J.D.; Wagner, M.R. 2005. Long-term impacts of stand management on ponderosa pine physiology and bark beetle abundance in northern Arizona: a replicated landscape study. *Forest Ecology and Management*. 218: 291-305.
- Zhang, J.; Webster, J.; Powers, R.F.; Mills, J. 2008. Reforestation after the Fountain Fire in northern California: an untold success story. *Journal of Forestry*. 106(8): 425-430.
- Zhu, K.; Woodall, C.W.; Clark, J.S. 2012. Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology*. 18: 1042-1052.
- Zhu, K.; Woodall, C.W.; Ghosh, S. [and others]. 2014. Dual impacts of climate change: forest migration and turnover through life history. *Global Change Biology*. 20: 251-264.
- Zimmermann, N.E.; Yoccoz, N.G.; Edwards, T.C. [and others]. 2009. Climatic extremes improve predictions of spatial patterns of tree species. *Proceedings of the National Academy of Sciences*. 106: 19,723-19,728.

Forest Biogeochemistry in Response to Drought

William H. Schlesinger

Michael C. Dietze

Robert B. Jackson

Richard P. Phillips

Charles C. Rhoades

Lindsey E. Rustad

James M. Vose

W.H. Schlesinger is a Biogeochemist and President Emeritus, Cary Institute of Ecosystem Studies, Millbrook, NY 12545.

M.C. Dietze is an Assistant Professor, Department of Earth and Environment, Boston University, Boston, MA 02215.

R.B. Jackson is a Professor and Senior Fellow, School of Earth, Energy and Environmental Science, Stanford University, Stanford, CA 94305.

R.P. Phillips is an Associate Professor, Department of Biology, Indiana University, Bloomington, IN 47405.

C.C. Rhoades is a Research Biogeochemist, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Fort Collins, CO 80526.

L.E. Rustad is a Research Ecologist, U.S. Department of Agriculture, Forest Service, Northern Research Station (NRS), Durham, NH 03824.

J.M. Vose is a Research Ecologist, U.S. Department of Agriculture, Forest Service, Southern Research Station (SRS), Center for Integrated Forest Synthesis (CIFS), North Carolina State University, Department of Forestry and Environmental Resources, Raleigh, NC 27695.

Introduction

Historical records of drought extend to Biblical times when lack of rainfall reduced crop yields, leading to famine and mass human migrations. Studies of tree rings also show periods of reduced forest growth that can be linked to historical records of low rainfall. In these examples, drought is taken to result from low rainfall, but in some cases, this linkage is too simple. Some trees may access deep sources of water that allow forests to avoid all but the most catastrophic periods of reduced rainfall. In other cases, extreme warmth can lead to drought-like symptoms even when rainfall is normal. In many cases, direct observations of plant responses to drought, as seen in lower leaf conductance to water loss or early leaf abscission, are better indications of drought than changes in meteorological or soil variables alone.

Changes in the forest canopy due to drought have impacts that extend throughout the ecosystem, affecting the input of organic materials to the soil and subsequent responses of the soil microbial community. The thresholds of physiological response may differ considerably between higher plants and soil microbes,

with altered biogeochemical cycling often continuing in the soil long after severe drought has caused a reduction in physiological activities in the aboveground plant tissues. Since most biogeochemical cycling occurs in soils, advances in our understanding of drought will come from studies that consider the response of entire ecosystems to limited water availability, which is likely to manifest first in plants (fig. 5.1).

Often, drought affects forest biogeochemical cycling through indirect pathways. Many drought-stressed trees are susceptible to insect attack (chapter 6), which can alter the movement of essential elements [e.g., nitrogen (N) and phosphorus (P)] from plants to the soil. Severe drought also makes fires more likely, and these fires release essential elements from live and dead organic matter in ecosystems to the atmosphere and to runoff waters (chapter 7). It may take many years to replace the nutrients that are lost from a single fire.

This chapter summarizes what we know about the effects of drought on forest biogeochemistry. Much of what we know derives from observations during prolonged droughts and from field experiments that have imposed artificial drought on ecosystems (Wu



Figure 5.1—Mortality of Ashe's juniper (*Juniperus ashei*) at Colorado Bend State Park, TX, after the 2011 drought. (photo by Rob Jackson, Stanford University)

and others 2010). These experiments offer a glimpse of what we should expect to occur more frequently in a warmer and drier World of the future and what climate change will mean for forest productivity and management.

Drought and Forest Biogeochemistry

The degree to which droughts impact nutrient cycling in vegetation depends on multiple factors: the severity and duration of the drought; the morphology, phenology, sensitivity, and physiology of the dominant trees; and the nutrients of interest. Prolonged droughts originating early in the growing season, for example, may induce some tree species to lose leaves (and possibly roots) prematurely—a process that would reduce nutrient uptake and accelerate nutrient losses from plants. Most nutrients are mobilized and transported in soil water, so water stress may lead to nutrient stress.

Nutrient Uptake

The acquisition of nutrients by plants requires the availability of water. Nutrients move toward the surface of an absorptive root by diffusion and mass flow and are taken up and transported through the plant as a result of water potential gradients between root, xylem, and leaf cells. Thus, as soils dry during prolonged drought, nutrient uptake is generally reduced, resulting in lower leaf nutrient concentrations and reduced photosynthetic activity (Rustad and others 2011). However, the impact of drought on nutrient uptake is species- and nutrient-dependent (Grabarova and Martinkova 2001). Hanson and others (2003) reported that after 6 years of experimentally induced drought (33-percent reduction in throughfall), foliar N was reduced in some tree species (relative to controls) but not in others. Some species respond to drought by reducing their leaf area but show little or no change in the nutrient content in their remaining leaves (Pilon and others 1996). In an experimental plantation of Norway spruce, Nilsson and Wiklund (1994) reported higher nutrient concentrations and greater nutrient uptake in drought treatments relative to controls.

A possible explanation for sustained nutrient uptake under drought conditions may be related to belowground responses of trees to water stress. Hanson and others (2003) reported that some species likely accessed water and nutrients from deep soil via tap roots or by preferentially allocating carbon (C) to subsurface roots (Joslin and others 2000).

Allocation of C to mycorrhizal fungi may also represent a viable rooting strategy for overcoming water/nutrient stress (Hawkes and others 2011, Lehto and Zwiazek 2011, Rapparini and Penuelas 2014). Mycorrhizal fungi can access water in soil micropores and hydraulically redistribute water to nutrient-rich surface soils (Neumann and Cardon 2012, Querejeta and others 2007). Moreover, deciduous hardwood forests may differ in their sensitivities to drought based on the abundance of trees associating with arbuscular mycorrhizal fungi (AM) relative to ectomycorrhizal fungi (ECM), as AM trees are generally less tolerant of water stress than ECM trees (Brzostek and others 2014).

In N-fixing trees, reduced nutrient uptake from the soil appears to be at least partially compensated by increased N-fixation in root-associated symbiotic bacteria. In experimental studies, drought increased nodule biomass in *Alnus* (Tobita and others 2010) and nitrogen fixation in black locust (*Robinia pseudoacacia*) (Wurtzburger and Miniati 2014), potentially increasing nitrogen inputs to forest ecosystems.

Aboveground Nutrient Cycling

While less quantitatively important than uptake by roots, some plant canopies acquire nutrients directly from precipitation and gases (Schlesinger and Bernhardt 2013). As such, drought may exacerbate nutrient stress by reducing foliar uptake of growth-limiting nutrients such as N. Drought-induced reductions in foliar uptake are likely to depend on the morphology of the crown (a function of the species, age, and stand structure), but may also depend on the availability of nutrients in soil relative to inputs in precipitation. In regions of the World where much of the N in soil is found in slow-degrading soil organic matter, for example, reductions in foliar N uptake owing to drought may be ecologically significant (Lockwood and others 2008, Sparks, 2009). Rain can also enhance nutrient losses from the canopy by leaching nutrients from leaves (throughfall) and stems (stemflow); as such, decreases in rain can reduce the cycling of mobile nutrients such as potassium (K) (Gundersen and others 1998).

Retranslocation

The reabsorption of nutrients from senescing leaves (i.e., retranslocation) plays a critical role in nutrient retention, as trees generally reabsorb approximately 50 percent of N and P from leaves prior to senescence (Aerts 1996, Vergutz and others 2012). While retranslocation rates are highly species- and site-dependent, there is some evidence that resorption

efficiencies are sensitive to changes in soil moisture (Boerner 1985, Killingbeck 1996, Minoletti and Boerner 1994). Drought may impact retranslocation in one of two ways: (1) by inducing early senescence of leaves, or (2) by altering the physiology of leaves in ways that impair nutrient resorption prior to senescence. Del Arco and others (1991) reported that N retranslocation depended on rates of leaf abscission, with trees that retained leaves longer resorbing less N.

Differences in the drought response of deciduous trees may also relate to the plant's overall strategy for dealing with water stress. Mesophytic tree species (e.g., *Acer*, *Liriodendron*, *Prunus*) may be more likely to drop leaves early during a drought than xerophytic tree species (e.g., *Quercus*, *Carya*), which often do not close stomates during drought and operate close to the margin of hydraulic failure (Choat and others 2012). In one of the few studies offering a direct examination of the effects of drought on leaf senescence and retranslocation, Marchin and others (2010) found that 4 of 18 tree species in the Southeastern United States dropped leaves early during drought. The early senescence of leaves resulted in greater reabsorption of N, P, and K (relative to species that retained their leaves), and enabled these trees to reabsorb nutrients before the leaf desiccated.

Susceptibility to Insect Attack

Forest ecologists have long recognized that when trees are stressed, such as by drought, they are more vulnerable to insect attack (chapter 6). Insect defoliation increases the rate of biogeochemical cycling in forests and may ultimately lead to the mortality of trees and increased susceptibility to forest fires, which have huge impacts on ecosystem biogeochemistry (Schlesinger and Bernhardt 2013). Some tree species are less able to allocate photosynthetic resources to the synthesis of protective compounds, such as terpenes, during droughts (Bonello and others 2006, McDowell and others 2013, Waring and Schlesinger 1985). Experimental drought, for example, stimulated insect attack on pinyon pine (Gaylord and others 2013). Mortality of oak in Arkansas and Missouri is related to drought and insect attack by oak borer (Fan and others 2008). Recent widespread bark beetle attack on western coniferous forests may be related to the drought stress encountered in recent warmer, drier conditions (Kurz and others 2008). Tree-ring records show that periods of spruce beetle attack have been correlated with drought in Colorado since 1650 C.E. (Hart and others 2014). When trees are defoliated,

there are major changes in the form and rate of nutrient return to the soil, especially by reducing the retranslocation of nutrients before leaf abscission (Lovett and others 2002).

Recent mountain pine beetle activity in the Rocky Mountain States was synchronized by regional-scale drought conditions that occurred around 2002 (Chapman and others 2012, Creeden and others 2014). In lodgepole pine (*Pinus contorta*), mountain pine beetles introduce blue-stain fungi to the tree's vascular system that blocks water uptake within weeks of a successful attack and causes drought-like symptoms and tree mortality (Hubbard and others 2013). Along with reduced water uptake, plant-available soil N pools increase soon after beetle attack (Clow and others 2011, Morehouse and others 2008). Deposition of relatively N-enriched litter is a common feature of beetle attacks in various forest types. Needle fall beneath beetle-infested ponderosa pine (*Pinus ponderosa*) contained 1.1 percent N compared to 0.6 percent in uninfested stands in Arizona (Morehouse and others 2008). Similar patterns occurred following infestation of lodgepole pine [0.75 percent versus 0.45 percent N for beetle-infested and healthy trees; Griffin and others (2011)] and Douglas-fir [1.4 percent versus 0.9 percent N; Griffin and Turner (2012)].

Drought-related insect outbreaks that reduce leaf area or kill trees can also have a substantial impact on ecosystem C cycling (Weed and others 2013). For example, Clark and others (2010) found that gypsy moth defoliation (75 percent canopy defoliation) reduced net ecosystem annual carbon dioxide (CO₂) exchange by 41–55 percent in upland forests, and severe bark beetle outbreaks (40 to >80 percent trees impacted) in the Western United States reduced aboveground woody C production by 20–60 percent (Hicke and others 2012). In severe cases, insect outbreaks can switch the forest from being a C sink to a source, at least over the short term (Amiro and others 2010).

Cycling of Elements in Soils

Drought and consequent reductions in soil water have a myriad of direct and indirect effects on the cycling of elements in soils. These include consequences for belowground microbial activity, nutrient availability, and solid- and solution-phases of soil chemistry. Changes in the timing and reductions of precipitation associated with drought also affect soil aeration and erosion by runoff, with effects on soil nutrient status.

For aerobic soil conditions, studies report a decline in rates of microbially driven processes such as N mineralization, nitrification, respiration, and litter decomposition with declining moisture, particularly as soil moisture falls below critical thresholds (Arnold and others 1999, Burton and others 1998, Emmett and others 2004, Pilbeam and others 1993, Rey and others 2002, Rustad and others 2000, Tate and others 1988). Stark and Firestone (1995) observed that ammonium oxidizers are sensitive to dry conditions, so during drought the rate of nitrification and nitrate (NO_3) losses in runoff decrease (Wetselaar 1968). Schimel and others (2007) estimated that osmolyte production by soil microbes during dry conditions immobilizes 10–40 percent of the N mineralization in grasslands, and perhaps a similar amount in forests. Nitrous oxide production is also lower in dry soils (Davidson and others 2008, Schlesinger 2013), and there is evidence that forest soils can even become net sinks for N_2O under drought (Goldberg and Gebauer 2009). Experimental drought treatments also show greater methane consumption by soils (Borken and others 2006, Castro and others 1995, Davidson and others 2008).

Declines in soil microbial processes during drought lead to reduced availability and leaching of C, N, P, and base cations [e.g., calcium (Ca^{2+}), magnesium (Mg^{2+}), potassium (K^+)]. Some of these effects are transient. For example, for red maple (*Acer rubrum*), O'Neill and others (2003) reported that lower rates of decomposition during a precipitation-exclusion in the spring were matched by higher rates under normal precipitation regimes later in the year, so that the annual rate of decomposition was similar in drought and control plots. These observations probably derive from the long-noted effect of wetting and drying on soil microbes, where microbial activity fluctuates with moisture availability (Sorensen 1974, Stevenson 1956).

In hydric soils such as wetlands, where soils are permanently or seasonally saturated by water, oxygen is limiting, and anaerobic processes dominate (Brady and Weil 2008), drought can actually induce more favorable conditions for aerobic microbial processes by increasing the oxygen status of the soils (Emmett and others 2004). Concurrently, rates of anaerobic processes, such as methanogenesis and denitrification, will decline.

Changes in the biomass, distribution, and physiology of plant roots have direct impacts on the cycling of elements in soils by altering plant nutrient uptake,

autotrophic root respiration, root-mycorrhizal interactions, and belowground detrital inputs via the turnover of roots (Borken and others 2002, Bryla and others 2001, Burton and others 1998, Rey and others 2002). Drought can decrease fine root biomass due to decreased root elongation and increased root cavitation and mortality (Jackson and others 2000, Joslin and others 2000). Field studies suggest that tree root systems respond to water stress by vertically and temporally shifting growth rates. This can result in less root growth in shallow soil layers (where moisture stress is greatest) and more root growth deeper in the soil (where moisture can be more available) or increases and decreases in root growth over time tracking changing soil moisture conditions (Jackson and others 2000, Joslin and others 2001). A decrease in fine roots during droughts is sometimes compensated by greater production during more favorable times of the year, as was shown at the Walker Branch Throughfall Displacement Experiment in Tennessee (Joslin and others 2000).

Over longer periods of time, trees adapt to dry climate regimes or longer term drought by increasing fine root biomass, increasing root-to-shoot ratios, and increasing rooting depth. Evidence for these responses to drought is apparent at the biome scale, where plants growing in xeric environments tend to have higher root-to-shoot ratios and deeper root systems compared to plants occupying more mesic environments (Schenk and Jackson 2005). In all cases, the redistribution of roots in response to water stress will directly affect the cycling of C, N, P, base cations, and trace elements in soils.

Soil water status directly affects solid- and solution-phase soil chemistry. In addition to changing the availability of elements through the biologic processes described above, changes in soil moisture also impact abiotic processes associated with ion-exchange reactions, leaching, diffusion, and weathering. Declines in soil water, for example, will increase ionic concentration in soils, resulting in intensified soil-surface exchange reactions (Sverdrup 1990). Decreased soil water also decreases rates of ion diffusion within soils, leaching loss of elements, and rates of mineral weathering (Schlesinger and Bernhardt 2013).

The rate of soil erosion by wind and water is typically low under closed-canopy forests, due to the moderating influence of the canopy on the energy of raindrops and threshold friction velocity of wind (Waring and

Schlesinger 1985). Erosion increases dramatically after forest harvest and forest fire, when soils are bare (Bormann and others 1974). These losses could be further exacerbated if a long period of drought is followed by intense rainfall. Globally, the greatest rates of erosion are typically when such events occur in semi-arid climates (Langbein and Schumm 1958).

Increased soil water stress and drought will also have significant impacts on the cycling of elements in soils via indirect pathways, including changes in forest composition, pests and pathogens, and fire. To the extent that drought reduces streamflow, a lower frequency of flooding will reduce nutrient inputs to floodplain forests, which are often subsidized by seasonal delivery of sediments (Mitsch and Rust 1984).

Fire

Prolonged droughts increase the likelihood of fires in many ecosystems (chapter 7). Drought-induced wildfires cause periodic C and nutrient losses from many ecosystems in gaseous and particulate forms released to the atmosphere (Raison and others 1985) and through leaching and erosion in runoff waters (Dunnette and others 2014). The biogeochemical consequences of wildfire are proportional to fire severity and depend on factors such as the amount of woody fuel and forest floor consumed, the duration of combustion, the depth of heat penetration into the soil, and the spatial extent of the fire. Nitrogen losses from wildfires in conifer forests can range from 300 to 855 kg N/ha (Johnson and others 1998), equivalent to 10–40 percent of the N in aboveground vegetation and forest floor layers (Schlesinger and Bernhardt 2013). In contrast, low-intensity fires cause relatively small N losses (i.e., 10–40 kg/ha from southeastern pine forests) (Richter and others 1982, Wells 1971). Low-severity surface fires (e.g., prescribed fires), which rarely cause mortality among canopy trees, may actually increase growth and C accumulation rates of the remaining trees due to reduced competition and temporarily increased nutrient availability (Anning and McCarthy 2013, Fiedler and others 2010, Hurteau and North 2010).

Recovery and regrowth of vegetation after fire restores carbon pools and the rate of nutrient cycling, such that long-term impacts on the ecosystem may be small (Kashian and others 2006, Ryan and others 2010, Wiedinmyer and Hurteau 2010). However, wildfires that cause high post-fire mortality (i.e., “stand replacing fires”), large fuel consumption, and slow post-fire

recovery can often result in large and long-lasting impacts on the magnitude and direction of carbon cycling processes (Amiro and others 2010, Kolb and others 2013). Carbon lost from wildfires in forests of the continental United States can be substantial, with recent estimates ranging from 13.4 Teragram (Tg) C/year for the period 1990–1999 to 25.6 Tg C/year for 1980–1989 (Goetz and others 2012). For comparison, the net primary productivity (NPP) of forests in the United States is about 3,500 Tg C/year (Xiao and others 2010) and total carbon sequestration is estimated at 100–200 Tg C/year (Zhang and others 2012).

Nutrient leaching usually increases after wildfire, though enhanced export to surface and groundwater is typically short-lived and small relative to losses to the atmosphere (Belillas and Feller 1998; Johnson and others 1998, 2007). Combustion of vegetation and forest floor litter exposes the mineral soil surface and increases erosion of C and nutrients. In areas that receive high-intensity rain storms, post-fire losses of forest floor C and nutrients by erosion can equal or exceed those from combustion. The consequences of these elemental losses are proportional to the extent of an area burned at high severity (Riggan and others 1994). For example, in the 2002 Hayman fire in Colorado, watersheds that sustained high severity wildfire on >45 percent of their area had streamwater NO₃ and turbidity roughly threefold higher than other watersheds that were subject to severe burns on only 10 percent of their area (Rhoades and others 2011).

Wildfires induce biogeochemical transformations that commonly increase nutrient availability in soils, despite losses of C and nutrients from vegetation and soils (Raison 1979, Wan and others 2001). Nutrients bound in vegetation and soil organic matter are released by combustion, adding inorganic forms of K, Ca, Mg, P, and N to the soil. Soil ammonium (NH₄) is increased by oxidation of organic matter, ash inputs, and release of N from interlayer clay exchange sites. Post-fire soil NH₄ typically remains elevated for about a year and is followed by an increase in soil NO₃ (Certini 2005). In addition to changes in the exchangeable forms of soil N, net N mineralization and nitrification can increase dramatically (DeLuca and Sala 2006, Grady and Hart 2006, Koyama and others 2010). Fires consume organic acids and release cations balanced by (bi)carbonates and hydroxides, reducing soil and stream acidity; these changes are often short-lived (Cerdà and Doerr 2008), though elevated soil pH may persist for years (Ulery and others 1993). Heating also affects the composition of

the organic matter remaining after a fire. Fires consume a greater proportion of the labile C and leave stable pyrogenic Ch (charcoal) that has implications for long-term C storage and N cycling (DeLuca and Aplet 2008, DeLuca and others 2006). Complex interactions between biotic and abiotic conditions in post-fire environments influence the duration and spatial scale of biogeochemical changes within and among ecosystem types.

The pace of biogeochemical recovery from wildfires depends on the magnitude and extent of elemental losses and transformations caused by the fire, coupled with the growth rate and composition of post-fire revegetation. Severe stand-replacing wildfires may reduce ecosystem N pools for decades to centuries (Certini 2005, Smithwick and others 2005). Post-fire recovery of plant and organic cover and nutrient demand relies on the persistence of soil microbes and vegetation capable of sprouting or germinating in burned soils or dispersing into burned areas. In Glacier National Park, rapid post-fire growth of residual vegetation was credited for the return of summertime stream NO_3 concentrations to pre-burn levels within 2 years (Mast and Clow 2008). Conversely, after the Hayman fire in Colorado, dry conditions inhibited recovery of vegetation in ponderosa pine (*Pinus ponderosa*) forests, and stream NO_3 remained elevated for more than 5 years (Rhoades and others 2011).

The abundance of nitrogen-fixing herbaceous plants and shrubs usually increases after wildfire. These species are known to add 10–100 kg N/ha/year and replace lost N within a few decades (Binkley and others 1982, Busse 2000). Nitrogen-fixing plants may contribute an order of magnitude more N than atmospheric deposition in regions not impacted by industry (Johnson and others 2005).

Tree mortality and large fires have increased significantly in the Western United States in recent years, likely in response to warmer and drier conditions (Dennison and others 2014, van Mantgem and others 2009); however, similar patterns are not yet apparent in the East (Dietze and Moorcroft 2011). Landscape-scale patterns of species composition, vegetation structure, ground cover, and litter layer conditions contribute to long-term wildfire effects (Giesen and others 2008, Turner and others 2003). Patterns of forest succession after fire are well known for many ecosystems, yet the biogeochemical responses and recovery from the more severe and higher frequency fires projected under warmer, drier climates remain poorly understood.

Drought and Carbon Balance in Forests

Large-scale droughts in recent decades have stimulated interest in field studies and modeling projections to assess the effects of future droughts on the carbon balance of forests. Most field experiments that impose drought show reduced net primary production and net carbon exchange (Wu and others 2010). Drought led to reduced gross primary productivity and carbon sequestration across Europe in 2003 (Ciais and others 2005) and the Amazon Basin in 2010 (Gatti and others 2014). Global estimates of the long-term trends in forest NPP show a 1-percent decline during 2000–2009, largely as a result of droughts in the Southern Hemisphere (Zhao and Running 2010). We can expect reductions in global NPP during the transient period of drought that is anticipated in most models of future global climate.

Severe drought in the Amazon Basin turned a system that is typically a carbon sink into carbon source. Tian and others (1998) reported losses of 0.2 Petagram (Pg) C from the Amazon Basin during hot, dry years associated with El Niño conditions in 1987 and 1992. In 2005 and 2010, Amazonian droughts extended across 2–3 million km^2 of tropical forests. Lewis and others (2011) estimated that the severe drought of 2010 reduced carbon uptake by ~2.2 Pg C, compared to a decrease of 1.6 Pg C during the 2005 drought. Gatti and others (2014) reported a net loss of 0.48 Pg C from the Amazon Basin during the 2010 drought, compared to a net uptake of 0.25 Pg C during normal conditions. This reduced carbon uptake during drought is large, equivalent to about 5 percent of total global carbon emissions from fossil fuel burning.

In other regions, including Central America and Southeast Asia, field experiments and modeling both suggest that the combination of increasing temperatures and drought could alter the balance of photosynthesis and respiration, leading to higher net CO_2 fluxes to the atmosphere and reducing carbon uptake (Cleveland and others 2010, Moser and others 2014, Wood and others 2012).

The effects of drought have been increasingly visible in boreal forests during the last decade. Boreal forests cover >10 million km^2 of the Earth's surface and contain >50 Pg of biomass C (Pan and others 2013). Tree mortality in Canada's boreal forests increased 4.7 percent per year from 1963 to 2008, with recent climate change and drought-induced water stress estimated to

be the dominant cause of this mortality (Ma and others 2012, Peng and others 2011). Drought stress decreased biomass accumulation particularly in western Canada, where moisture deficiency was greater, and increased annual tree mortality from <0.5 percent of biomass in the early 1970s to approximately 1.8 percent more recently (Pan and others 2013, Peng and others 2011). If the results apply to all of Canada's boreal forests, then the reduction in the carbon sink from mature forests would be 7.3 Tg C/year, equivalent to approximately 4 percent of Canada's fossil fuel emissions (Ma and others 2012).

In boreal forests, individual species show different vulnerabilities and potential for large-scale dieback as a result of drought. Michaelian and others (2011) used a combination of remotely-sensed, field, and modeling data to examine mortality of aspen (*Populus tremuloides*) across 115,000 km² (approximately 45,000 square miles) of Saskatchewan, Canada. The severe drought of 2001–2002 led to >50 percent aspen mortality across large areas of the region, reducing aboveground biomass by 20 percent and having consequences similar to those of a large-scale fire. In the southern part of the region where the drought was most severe, a third of the aspen trees died. Overall, the amount of dead biomass was estimated to contain approximately 45 meitnerium carbon (Mt C).

Each year, forests in the United States accumulate enough C (833 Tg C/year) to offset approximately 16 percent of U.S. fossil fuel emissions (Joyce and others 2014); however, the rate of C accumulation varies from year to year due to climatic variability, disturbances, and management practices (Xiao and others 2011), and drought can substantially decrease C accumulation rates (Schwalm and others 2012). Brzostek and others (2014) reported that droughts can reduce the C sink of deciduous forests in the United States by as much as 17 percent. In these forests, a 17-percent reduction in the C sink translates to an additional 1 to 3 days of global C emissions from fossil fuel burning each year. Further, the authors found that drought impacts can offset C gains of longer growing seasons as a result of warmer climate. For example, using decade-long records of climate and tree growth at the Morgan Monroe State Forest in Indiana, Brzostek and others (2014) found that despite 26 more days per year of C assimilation owing to milder temperatures, drought decreased the number of days of wood production by about 42 days over the same period, resulting in a 41-percent decrease in the amount of C stored in woody biomass. The impacts of

drought on forest carbon balance would be expected to vary considerably across the continental United States due to differences in the biophysical environment, species composition, and management intensity.

Ecosystem carbon models and long-term eddy covariance studies that include drought years provide an estimate of the net effects of drought on ecosystem carbon balance and suggest causal factors. Modeling studies suggest different carbon-cycling responses depending on the climate regime, where humid sites (such as in the Eastern United States) were generally less responsive to lower precipitation than drier sites (such as in the Western United States) (Gerten and others 2008). In the Southeast United States, Powell and others (2008) reported little change in the net ecosystem production (NEP)—NEP=gross ecosystem productivity minus ecosystem respiration—during drought in slash pine (*Pinus elliotti*) due to the counteracting effects of decreased canopy photosynthesis and soil respiration. Elsewhere in the Southeast, NEP in a loblolly pine (*Pinus taeda*) plantation was reduced by drought, primarily through decreased canopy and whole-tree leaf conductances (Noormets and others 2010), without a corresponding decrease in ecosystem respiration. In forests of the Western United States, net CO₂ uptake reported from eddy-flux towers during a prolonged drought indicated a reduction in NEP of 63 g/m²/year and a decline of 30 to 298 Tg C/year in the current carbon sink in that region (Schwalm and others 2012). For western coniferous forests, NEP declined primarily as a result of decreased gross ecosystem production, whereas ecosystem respiration declined only slightly (Schwalm and others 2012).

Management Implications

Forests will respond to existing and new disturbance regimes; however, the resulting forest structure and function may be inconsistent with the desired future conditions and associated ecosystem services. A key question is whether and how forest management can be used to maintain desired conditions and ecosystems services. Increased drought severity and frequency are likely to make forests more vulnerable to both direct (e.g., reduced growth and mortality) (chapter 4) and indirect (e.g., insect outbreaks, pathogens, wildfire) (chapters 6 and 7) impacts (Choat and others 2012, Dale and others 2001, Liu and others 2013, Weed and others 2013). Exactly how these impacts manifest will depend in large part on the nature of drought. For example, frequent low-severity drought may selectively

favor more drought-tolerant trees and create forests better adapted to future conditions without the need for management intervention. In contrast, severe drought (especially in combination with insect outbreaks or fire), may result in large-scale changes that warrant substantial management responses. These responses range from reducing vulnerability to drought, facilitating post-drought recovery, or facilitating a transition to a new forest condition (Millar and others 2007). Here, we focus primarily on management options that reduce vulnerability.

Forest management actions to minimize drought impacts on biogeochemical cycling will require altering forest structure and function in ways that increase adaptive capacity and/or reduce vulnerability to drought. Management options are highly site specific and constrained by a wide variety of factors; however, from the perspective of biogeochemical cycling, maintaining forest cover and minimizing forest floor loss and soil erosion are key objectives. Reducing stand density by thinning may decrease water demand and subsequent drought stress (D'Amato and others 2013, Dore and others 2012, McDowell and others 2006), with the potential added benefit of reducing fuel loading and wildfire risk (McIver and others 2009). Stand structure can also be altered and managed using multi-aged systems that may create stands with higher water-use efficiency (O'Hara and Nagel 2006). Some evidence suggests that younger (smaller) trees are more vulnerable to drought than larger trees (DeLucia and Schlesinger 1990, Hanson and others 2001) and older trees (Klos and others 2009), indicating that stand age and size class distributions could be managed to decrease vulnerability. Our current understanding of differences in functional attributes related to transpiration demands (Ford and others 2011) and rooting characteristics (Joslin and others 2000, Schenk and Jackson 2005) could be used to favor more drought-tolerant (or water-use efficient) tree species in existing stands and developing and planting more drought-resistant species for new stands. In some regions of the United States, planting or favoring more drought-tolerant species may conflict with management objectives that favor rapid accumulation of biomass, as fast-growing woody species often use more water and exacerbate drought impacts (King and others 2013). Drought impacts could also be reduced by designing road and drainage networks to keep more of the water in the forest (Grant and others 2013), instead of moving it rapidly to the streams or concentrating it in small

areas of the landscape as is typically the case (Kolka and Smidt 2004). Successful forest management in the face of drought will likely require a combination of many approaches. For example, Grant and others (2013) used simulation modeling to demonstrate the advantages of combining increased water availability, thinning, and mulching to reduce drought stress-related mortality in ponderosa pine (*Pinus ponderosa*) during an extreme drought.

Representation of Drought in Ecosystem and Global Models

To anticipate how forest biogeochemistry will respond to future drought, it is important to assess the representation of drought in ecosystem and biogeochemical models as these are our primary means of extrapolating the response of ecosystems into novel or rare conditions. Particularly useful in this assessment are the results of model inter-comparison projects (MIPs), where the performance of multiple models is judged against data from one or more sites or experiments. These give a better measure of the performance of the community of models, rather than assessing individual models tuned to individual sites. In a recent comparison of 22 ecosystem models against 44 eddy-covariance towers across North America, the biases and chi-squared error in the net ecosystem exchange (NEE) of carbon were only marginally higher under dry conditions, and this error was only apparent during the growing season (Schwalm and others 2010). This is encouraging since these errors were smaller than the errors across seasons or among biomes in the same models.

The same MIP found that model errors in gross primary productivity (GPP) were substantially higher under low-humidity conditions (Schaefer and others 2012). Furthermore, while all models captured the shape of the GPP response to moisture under high humidity conditions, for many models the shape of the GPP response curve was substantially different from observations, indicating underlying structural errors rather than simple miscalibration. Similarly, a MIP at the Duke and Oak Ridge FACE (Free Air CO₂ Enrichment) experiments showed substantial differences among 11 models that could be attributed to differences in moisture responses at the leaf level (stomatal closure), at the whole plant level (water uptake), and at the stand level (boundary layer exchange of water vapor) (De Kauwe and others 2013).

Likewise, a detailed analysis of the sources of uncertainty within a single model applied to 4 North American biomes and 17 vegetation types found that water uptake and stomatal closure responses were the second and third (respectively) largest sources of uncertainty in predicting NPP (Dietze and others 2014). Sims and others (2014) found that many deciduous forests don't lose their "greenness" in remote-sensing images taken during drought, despite large reductions in photosynthesis at the canopy scale (chapter 9). Given that satellite data products predicting GPP and NPP assume a relationship between greenness and photosynthesis, this implies that such global data products may underestimate the magnitude of droughts in terms of net ecosystem balance. As a whole, there is a pressing need to improve the ecophysiological responses of plants to drought in ecosystem and global models.

Few MIPs have focused on belowground biogeochemical responses. Traditionally, heterotrophic respiration has been modeled as proportional to soil carbon pool size and a temperature-varying turnover rate, with the effects of soil moisture entering as a scaling function (0–1) (Parton and others 1993). In such models, drought generally causes a substantial reduction in heterotrophic respiration. One recent MIP looking specifically at seven oak woodlands growing in Mediterranean climates found that across five models there was a tendency to overestimate ecosystem respiration during droughts (Vargas and others 2013).

In many cases models impose a tight stoichiometric coupling between soil carbon and nitrogen; thus, the reduction in respiration also results in a slowing of the nitrogen cycle. Recently, some models have considered microbial activity and soil enzymes more explicitly (Allison and others 2010, Davidson and others 2011, Lawrence and others 2009, Xu and others 2014). Such approaches improve predictions of transient fluxes that occur during post-drought rewetting (Lawrence and others 2009) and explain how drought can decouple the typical temperature-respiration responses (Davidson and others 2011). In contrast to soil CO₂, most models devote much less attention to the cycling of other nutrients in response to drought, largely because the other biogenic greenhouse gas (GHG) emissions considered by models are associated with wet conditions [nitrogen dioxide (NO₂), methane (CH₄)], while tree volatile organic compounds (VOCs) such as isoprene, which respond to heat stress, are seldom considered. Finally, many ecosystem models include a representation of fire, with fire probability explicitly

a function of either fuel moisture or soil moisture, and thus generate an interaction between fire and drought. By contrast, insects and pathogens are absent from most models, or are limited to case studies, as more general approaches to modeling their impacts have been lacking (Dietze and Matthes 2014, Hicke and others 2012). As such, models will, in general, miss the known interactions between drought and outbreak susceptibility.

Summary and Conclusions

Drought affects forest growth and carbon storage by lowering the rate of photosynthesis, while causing lesser effects on respiration, except in extreme conditions. Trees alter their use and allocation of nutrients in response to drought, and changes in soil nutrient cycling and trace gas flux (N₂O and CH₄) are observed when experimental drought is imposed on forests. In extreme droughts, trees are increasingly susceptible to attack by pests and pathogens, which can lead to major changes in nutrient flux to the soil. Extreme droughts often lead to more common and more intense forest fires, causing dramatic changes in the nutrient storage and loss from forest ecosystems. Changes in the future manifestation of drought will affect carbon uptake and storage in forests, leading to feedbacks to the Earth's climate system. We must improve the recognition of drought in nature, our ability to manage our forests in the face of drought, and the parameterization of drought in Earth system models for improved predictions of carbon uptake and storage in the World's forests.

Acknowledgments

This research was supported by the Cary Institute of Ecosystem Studies. R.B. Jackson acknowledges additional grant support from the U.S. Department of Agriculture–Agriculture and Food Research Initiative (USDA-AFRI) grant number 2012-00857, and M.C. Dietze acknowledges support from a National Science Foundation (NSF) Macrosystems grant number 1241894.

Literature Cited

- Aerts, R. 1996. Nutrient resorption from senescing leaves of perennials: Are there general patterns? *Journal of Ecology*. 84: 597–608.
- Allison, S.D.; Wallenstein, M.D.; Bradford, M.A. 2010. Soil-carbon response to warming dependent on microbial physiology. *Nature Geoscience*. 3: 336–340.

- Amiro, B.D.; Barr, A.G.; Barr, J.G. [and others]. 2010. Ecosystem carbon dioxide fluxes after disturbances in forests of North America. *Journal of Geophysical Research*. 115: 1-13.
- Anning, A.K.; McCarthy, B.C. 2013. Long-term effects of prescribed fire and thinning on residual tree growth in mixed oak forests of southern Ohio. *Ecosystems*. 16(8): 1473-1486. doi: 10.1007/s10021-013-9696-6. [Published online: August 1, 2013].
- Arnold, S.S.; Fernandez, I.J.; Rustad, L.E.; Zibilske, L.M. 1999. Microbial response of an acid forest soil to experimental soil warming. *Biology and Fertility of Soils*. 30: 239-244.
- Belillas, C.M.; Feller, M.C. 1998. Relationships between fire severity and atmospheric and leaching nutrient losses in British Columbia's coastal western hemlock zone forests. *International Journal of Wildland Fire*. 8: 87-101.
- Binkley, D.; Cromack, K.; Fredriksen, R.L. 1982. Nitrogen accretion and availability in some snowbrush ecosystems. *Forest Science*. 28: 720-724.
- Bonello, P.; Gordon, T.R.; Herms, D.A. [and others]. 2006. Nature and ecological implications of pathogen-induced systematic resistance in conifers: a novel hypothesis. *Physiological and Molecular Plant Pathology*. 68: 95-104.
- Boerner, R.E.J. 1985. Foliar nutrient dynamics, growth and nutrient-use efficiency of *Hamamelis virginiana* in three forest microsites. *Canadian Journal of Botany*. 63: 1476-1481.
- Borken, W.; Xu, Y.; Davidson, E.; Beese, F. 2002. Site and temporal variation of soil respiration in European Beech, Norway spruce, and Scots pine forests. *Global Change Biology*. 8: 1205-1216.
- Borken, W.; Davidson, E.A.; Savage, K. [and others]. 2006. Effect of summer throughfall exclusion, summer drought, and winter snow cover on methane fluxes in a temperate forest soil. *Soil Biology and Biochemistry*. 38: 1388-1395.
- Bormann, F.H.; Likens, G.E.; Siccama, T.G. [and others]. 1974. The export of nutrients and recovery of stable conditions following deforestation at Hubbard Brook. *Ecological Monographs*. 44: 25-277.
- Brady, N.; Weil, R. 2008. *The Nature and Properties of Soils*. 14th ed. Upper Saddle River, NJ: Prentice Hall/Pearson Education. 992 p.
- Bryla, D.R.; Bouma, T.J.; Hartmond, U.; Eissenstat, D.M. 2001. Influence of temperature and soil drying on respiration of individual roots in citrus: Integrating greenhouse observations into a predictive model for the field. *Plant, Cell & Environment*. 24: 781-790.
- Brzostek, E.R.; Dragoni, D.; Schmid, H.P. [and others]. 2014. Chronic water stress reduces tree growth and the carbon sink of deciduous hardwood forests. *Global Change Biology*. 20(8): 2531-2539. doi: 10.1111/gcb.12528. [Published online: February 21, 2014].
- Burton, A.J.; Pregitzer, K.S.; Zogg, G.P.; Zak, D.R. 1998. Drought reduces root respiration in sugar maple forests. *Ecological Applications*. 8: 771-778.
- Busse, M.D. 2000. Suitability and use of the ¹⁵N-isotope dilution method to estimate nitrogen fixation by actinorhizal shrubs. *Forest Ecology and Management*. 136: 85-95.
- Castro, M.S.; Melillo, J.M.; Steudler, P.A.; Chapman, J.W. 1995. Soil moisture as a predictor of methane uptake by temperate forest soils. *Canadian Journal of Forest Research*. 24: 1805-1810.
- Cerdà, A.; Doerr, S.H. 2008. The effect of ash and needle cover on surface runoff and erosion in the immediate post-fire period. *Catena*. 74: 256-263.
- Certini, G. 2005. Effects of fire on properties of forest soils: A review. *Oecologia*. 143: 1-10.
- Chapman, T.B.; Veblen, T.T.; Schoennagel, T. 2012. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. *Ecology*. 93: 2175-2185.
- Choat, B.; Jansen, S.; Brodrribb, T.J. [and others]. 2012. Global convergence in the vulnerability of forests to drought. *Nature*. 491: 752-756.
- Ciais, P.; Reichstein, M.; Viovy, N. [and others]. 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*. 437: 529-533.
- Clark, K.L.; Skowronski, N.; Hom, J. 2010. Invasive insects impact on forest carbon dynamics. *Global Change Biology*. 16: 88-101.
- Cleveland, C.C.; Wieder, W.R.; Reed, S.C.; Townsend, A.R. 2010. Experimental drought in a tropical rain forest increases soil carbon dioxide losses to the atmosphere. *Ecology*. 9: 2313-2323.
- Clow, D.W.; Rhoades, C.C.; Briggs, J. [and others]. 2011. Responses of soil and water chemistry to mountain pine beetle induced tree mortality in Grand County, Colorado, USA. *Applied Geochemistry*. 26: 174-178.
- Creeden, E.P.; Hicke, J.A.; Buotte, P.C. 2014. Climate, weather, and recent mountain pine beetle outbreaks in the Western United States. *Forest Ecology and Management*. 312: 239-251.
- Dale, V.H.; Joyce, L.A.; McNulty, S. [and others]. 2001. Climate change and forest disturbances. *BioScience*. 51: 723-734.
- D'Amato, A.W.; Bradford, J.B.; Fraver, S.; Palik, B.J. 2013. Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. *Ecological Applications*. 23: 1735-1742.
- Davidson, E.A.; Samanta, S.; Caramori, S.S.; Savage, K.E. 2011. The Dual Arrhenius and Michaelis-Menten (DAMM) kinetics model for decomposition of soil organic matter at hourly to seasonal time scales. *Global Change Biology*. 18: 371-384.
- Davidson, E.A.; Nepstad, D.C.; Yoko Ishida F.; Brando, P.A. 2008. Effects of an experimental drought and recovery on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest. *Global Change Biology*. 14: 2582-2590.
- De Kauwe, M.G.; Medlyn, B.E.; Zaehle, S. [and others]. 2013. Forest water use and water use efficiency at elevated CO₂: A model-data intercomparison at two contrasting temperate forest FACE sites. *Global Change Biology*. 19: 1759-1779.
- Del Arco, J.M.; Escudero, A.; Garrido, M.V. 1991. Effects of site characteristics on nitrogen retranslocation from senescing leaves. *Ecology*. 72: 701-708.
- DeLuca, T.H.; Sala, A. 2006. Frequent fire alters nitrogen transformations in ponderosa pine stands of the inland Northwest. *Ecology*. 87: 2511-2522.
- DeLuca, T.H.; Aplet, G.H. 2008. Charcoal and carbon storage in forest soils of the Rocky Mountain West. *Frontiers in Ecology and the Environment*. 6: 18-24.
- DeLuca, T.H.; MacKenzie, M.D.; Gundale, M.J.; Holben, V. 2006. Wildfire-produced charcoal directly influences nitrogen cycling in ponderosa pine forests. *Soil Science Society of America Journal*. 70: 448-453.
- DeLucia, E.H.; Schlesinger, W.H. 1990. Ecophysiology of Great Basin and Sierra Nevada vegetation on contrasting soils. In: Osmond, C.B.; Pitelka, L.F.; Hidy, G.M., eds. *Plant Biology of the Basin and Range*. New York: Springer-Verlag: 143-178.

- Dennison, P.E.; Brewer, S.C.; Arnold, J.D.; Moritz, M.A. 2014. Large wildfire trends in the Western United States, 1984–2011. *Geophysical Research Letters*. 41(8): 2928–2933. doi: 10.1002/2014GL059576. [Published online: April 25, 2014].
- Dietze, M.; Matthes, J.H. 2014. A general ecophysiological framework for modeling the impact of pests and pathogens on forest ecosystems. *Ecology Letters*. 17(11): 1418–1426.
- Dietze, M.; Moorcroft, P. 2011. Tree mortality in the eastern and central U.S.: patterns and drivers. *Global Change Biology*. 17: 3312–3326.
- Dietze, M.C.; Serbin, S.P.; Davidson, C. [and others]. 2014. A quantitative assessment of a terrestrial biosphere model's data needs across North American biomes. *Journal of Geophysical Research: Biogeosciences*. 119(3): 286–300. doi:10.1002/2013JG002392. [Published online: March 19, 2014].
- Dore, S.; Montes-Helu, M.; Hart, S.C. [and others]. 2012. Recovery of ponderosa ecosystem carbon and water fluxes from thinning and stand replacing fire. *Global Change Biology*. 18: 3171–3185.
- Dunnette, P.V.; Higuera, P.E.; McLauchlan, K.R. [and others]. 2014. Biogeochemical impacts of wildfires over four millennia in a Rocky Mountain subalpine watershed. *New Phytologist*. 203(3): 900–912. doi: 10.1111/nph.12828a. [Published online: May 6, 2014].
- Emmett, B.; Beier, C.; Estiarte, M. [and others]. 2004. The response of soil process to climate change: Results from manipulation studies of shrublands across and environmental gradient. *Ecosystems*. 7: 625–637.
- Fiedler, C.E.; Metlen, K.L.; Dodson, E.K. 2010. Restoration treatment effects on stand structure, tree growth, and fire hazard in a ponderosa pine/Douglas-fir forest in Montana. *Forest Science*. 56: 18–31.
- Fan, Z.F.; Kabrick, J.M.; Spetich, M.A. [and others]. 2008. Oak mortality associated with crown dieback and oak borer attack in the Ozark Highlands. *Forest Ecology and Management*. 255: 2297–2305.
- Ford, C.R.; Hubbard, R.M.; Vose, J.M. 2011. Quantifying structural and physiological controls on variation in canopy transpiration among planted pine and hardwood species in the Southern Appalachians. *Ecohydrology*. 4: 183–195.
- Gatti, L.V.; Gloor, M.; Miller, J.B. [and others]. 2014. Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements. *Nature*. 506: 76–80.
- Gaylord, M.L.; Kolb, T.E.; Pockman, W. [and others]. 2013. Drought predisposes pinyon-juniper woodlands to insect attacks and mortality. *New Phytologist*. 198: 567–578.
- Gerten, D.; Luo, Y.; LeMaire, G. [and others]. 2008. Modelled effects of precipitation on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biology*. 14: 2365–2379.
- Giesen, T.W.; Perakis, S.S.; Cromack, K. 2008. Four centuries of soil carbon and nitrogen change after stand-replacing fire in a forest landscape in the western Cascade Range of Oregon. *Canadian Journal of Forest Research*. 38: 2455–2464.
- Goetz, S.J.; Bond-Lamberty, B.; Law, B.E. [and others]. 2012. Observations and assessments of forest carbon dynamics following disturbance in North America. *Journal of Geophysical Research*. 117: 1–17.
- Goldberg, S.D.; Gebauer, G. 2009. Drought turns a central European Norway spruce forest soil from an N₂O source to a transient N₂O sink. *Global Change Biology*. 15: 850–860.
- Grabarova, S.; Martinkova, M. 2001. Changes in mineral nutrition of Norway spruce (*Picea abies* [L.] Karst.) under the impact of drought. *Ekológia (Bratislava) Suppl.* 1: 46–60.
- Grady, K.C.; Hart, S.C. 2006. Influences of thinning, prescribed burning, and wildfire on soil processes and properties in southwestern ponderosa pine forests: A retrospective study. *Forest Ecology and Management*. 234: 123–135.
- Grant, G.E.; Tague, C.L.; Allen, C.D. 2013. Watering the forest for the trees: an emerging priority for managing water in forest landscapes. *Frontiers in Ecology and Environment*. 11(6): 314–321. doi: 10.1890/120209. [Published online: May 30, 2013].
- Griffin, J.M.; Turner, M.G. 2012. Changes to the N cycle following bark beetle outbreaks in two contrasting conifer forest types. *Oecologia*. 170: 551–565.
- Griffin, J.M.; Turner, M.G.; Simard, M. 2011. Nitrogen cycling following mountain pine beetle disturbance in lodgepole pine forests of Greater Yellowstone. *Forest Ecology and Management*. 261: 1077–1089.
- Gundersen, P.; Boxman, A.W.; Lamersdorf, N. [and others]. 1998. Experimental manipulation of forest ecosystems: lessons from large roof experiments. *Forest Ecology and Management*. 101: 339–352.
- Hanson, P.J.; Todd, D.E.; Amthor, J.S. 2001. A six-year study of sapling and large-tree growth and mortality responses to natural and induced variability in precipitation and throughfall. *Tree Physiology*. 21: 345–358.
- Hanson, P.J.; Todd, D.E.; Joslin, J.D. 2003. Canopy production. In: Hanson, P.J.; Wullschlegel, S.D., eds. *North American temperate deciduous forest responses to changing precipitation regimes*. New York: Springer: 303–315.
- Hart, S.J.; Veblen, T.T.; Eisenhart, K.S. [and others]. 2014. Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. *Ecology*. 95: 930–939.
- Hawkes, C.V.; Kivlin, S.N.; Rocca, J.D. [and others]. 2011. Fungal community responses to precipitation. *Global Change Biology*. 17: 1637–1645.
- Hicke, J.A.; Allen, C.D.; Desai, A. [and others]. 2012. The effects of biotic disturbances on carbon budgets of North American forests. *Global Change Biology*. 18: 7–34.
- Hubbard, R.M.; Rhoades, C.C.; Elder, K.; Negron, J.F. 2013. Changes in transpiration and foliage growth in lodgepole pine trees following mountain pine beetle attack and mechanical girdling. *Forest Ecology and Management*. 289: 312–317.
- Hurteau, M.D.; North, M. 2010. Carbon recovery rates following different wildfire risk mitigation treatments. *Forest Ecology and Management*. 260: 930–937.
- Jackson, R.B.; Sperry, J.S.; Dawson, T.E. 2000. Root water uptake and transport: using physiological processes in global predictions. *Trends in Plant Science*. 5: 482–488.
- Johnson, D.; Murphy, J.D.; Walker, R.F. [and others]. 2007. Wildfire effects on forest carbon and nutrient budgets. *Ecological Engineering*. 31: 183–192.
- Johnson, D.W.; Murphy, J.F.; Susfalk, R.B. [and others]. 2005. The effects of wildfire, salvage logging, and post-fire N-fixation on the nutrient budgets of a Sierran forest. *Forest Ecology and Management*. 220: 155–165.
- Johnson, D.W.; Susfalk, R.B.; Dahlgren, R.A.; Klopatek, J.M. 1998. Fire is more important than water for nitrogen fluxes in semi-arid forests. *Environmental Science & Policy*. 1: 79–86.

- Joslin, J.D.; Wolfe, M.H.; Hanson, P.J. 2000. Effects of altered water regimes on forest root systems. *New Phytologist*. 147: 117-129.
- Joslin, J.D.; Wolfe, M.H.; Hanson, P.J. 2001. Factors controlling the timing of root elongation intensity in a mature upland oak stand. *Plant and Soil*. 228: 201-212.
- Joyce, L.A.; Running, S.W.; Breshears, D.D. [and others]. 2014. Forests. In: Melillo, J.M.; Richmond, T.; Yohe, G.W., eds. *Climate change impacts in the United States: the third national climate assessment*. U.S. Global Change Research Program: 175-194. Chapter 7. Available at: doi:10.7930/J0Z60KZC. [Published online: May 2014].
- Kashian, D.M.; Romme, W.H.; Tinker, D.B. [and others]. 2006. Carbon storage on landscapes with stand replacing fires. *Bioscience*. 56: 598-606.
- Killingbeck, K.T. 1996. Nutrients in senesced leaves: Keys to the search for potential resorption and resorption proficiency. *Ecology*. 77: 1716-1727.
- King, J.S.; Ceulemans, R.; Albaugh, J.M. [and others]. 2013. The challenge of lignocellulosic bioenergy in a water-limited World. *BioScience*. 63: 102-117.
- Klos, R.J.; Wang, G.G.; Bauerle, W.L.; Rieck, J.R. 2009. Drought impact on forest growth and mortality in the southeast USA: an analysis using Forest Health and Monitoring data. *Ecological Applications*. 19: 699-708.
- Kolb, T.; Dore, S.; Montes-Helu, M. 2013. Extreme late-summer drought causes neutral annual carbon balance in southwestern ponderosa pine forests and grasslands. *Environmental Research Letters*. 8: 015015. 8 p. doi:10.1088/1748-9326/8/1/015015. [Published online: February 12, 2013].
- Kolka, R.K.; Smidt, M.F. 2004. Effects of forest road amelioration techniques on soil bulk density, surface runoff, sediment transport, soil moisture, and seeding growth. *Forest Ecology and Management*. 202: 313-323.
- Koyama, A.; Kavanagh, K.; Stephan, K. 2010. Wildfire effects on soil gross nitrogen transformation rates in coniferous forests of Central Idaho, USA. *Ecosystems*. 13: 1112-1126.
- Kurz, W.A.; Dymond, C.C.; Stinson, G. [and others]. 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature*. 452: 987-990.
- Langbein, W.B.; Schumm, S.A. 1958. Yield of sediments in relation to mean annual precipitation. *Transactions of the American Geophysical Union*. 39: 1076-1084.
- Lawrence, C.R.; Neff, J.C.; Schimel, J.P. 2009. Does adding microbial mechanisms of decomposition improve soil organic matter models? A comparison of four models using data from a pulsed rewetting experiment. *Soil Biology and Biochemistry*. 41: 1923-1934.
- Lehto, T.; Zwiazek, J.J. 2011. Ectomycorrhizas and water relations of trees: a review. *Mycorrhiza*. 21: 71-90.
- Lewis, S.L.; Brando, P.M.; Phillips, P.L. [and others]. 2011. The 2010 Amazon drought. *Science*. 331(6017): 554.
- Liu, Y.; Goodrick, S.L.; Stanturf, J.A. 2013. Future U.S. wildfire potential trends projected using a dynamically downscaled climate change scenario. *Forest Ecology and Management*. 294: 120-135.
- Lockwood A.L.; Filley, T.R.; Rhodes, D.; Shepson, P.B. 2008. Foliar uptake of atmospheric organic nitrates. *Geophysical Research Letters*. 35(15): L15809. 5 p. doi:10.1029/2008GL034714. [Published online: August 9, 2008].
- Lovett, G.M.; Christenson, L.M.; Groffman, P.M. [and others]. 2002. Insect defoliation and nitrogen cycling in forests. *Bioscience*. 52: 335-341.
- Ma, Z.; Peng, C.; Zhub, Q. [and others]. 2012. Regional drought-induced reduction in the biomass carbon sink of Canada's boreal forests. *Proceedings of the National Academy of Sciences*. 109: 2423-2427.
- Marchin, R.; Zeng, H.N.; Hoffmann, W. 2010. Drought-deciduous behavior reduces nutrient losses from temperate deciduous trees under severe drought. *Oecologia*. 163: 845-854.
- Mast, M.A.; Clow, D.W. 2008. Effects of 2003 wildfires on stream chemistry in Glacier National Park, Montana. *Hydrological Processes*. 22: 5013-5023.
- McDowell, N.G.; Adams, H.D.; Bailey, J.D. [and others]. 2006. Homeostatic maintenance of ponderosa pine gas exchange in response to stand density changes. *Ecological Applications*. 16: 1164-1182.
- McDowell, N.G.; Fisher, R.A.; Xu, C. [and others]. 2013. Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework. *New Phytologist*. 200: 304-321.
- McIver, A.; Youngblood, A.; Stephens, S.L. 2009. The national fire and fire surrogate study: ecological consequences of fuel reduction methods in seasonally dry forests. *Ecological Applications*. 19: 283-284.
- Michaelian, M.; Hogg, E.H.; Hall, R.J.; Arsenault, E. 2011. Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Global Change Biology*. 17: 2084-2094.
- Millar, C.I.; Stephenson, N.L.; Stephens, S.L. 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecological Applications*. 17: 2145-2151.
- Minoletti, M.L.; Boerner, R.E.J. 1994. Drought and site fertility effects on foliar nitrogen and phosphorus dynamics and nutrient resorption by the forest understory shrub *Viburnum acerifolium* L. *American Midland Naturalist*. 131: 109-119.
- Mitsch, W.J.; Rust, W.G. 1984. Tree growth responses to flooding in a bottomland forest in northeastern Illinois. *Forest Science*. 30: 499-510.
- Morehouse, K.; Johns, T.; Kaye, J.; Kaye, M. 2008. Carbon and nitrogen cycling immediately following bark beetle outbreaks in southwestern ponderosa pine forests. *Forest Ecology and Management*. 255: 2698-2708.
- Moser, G.; Schuldt, B.; Hertel, D. [and others]. 2014. Replicated throughfall exclusion experiment in an Indonesian perhumid rainforest: wood production, litter fall and fine root growth under simulated drought. *Global Change Biology*. 20: 1481-1497.
- Neumann, R.B.; Cardon, Z.G. 2012. The magnitude of hydraulic redistribution by plant roots: a review and synthesis of empirical and modeling studies. *New Phytologist*. 194: 337-352.
- Nilsson, L.O.; Wiklund, K. 1994. Nitrogen uptake in a Norway spruce stand following ammonium-sulfate application, fertigation, irrigation, drought, and nitrogen-free fertilization. *Plant and Soil*. 164: 221-229.
- Noormets, A.; Gavazzi, M.J.; McNulty, S.G. [and others]. 2010. Response of carbon fluxes to drought in coastal plain loblolly pine forest. *Global Change Biology*. 16: 272-287.
- O'Hara, K.L.; Nagel, L.M. 2006. A functional comparison of productivity in even-aged and multiaged stands: a synthesis for *Pinus ponderosa*. *Forest Science*. 52: 290-303.

- O'Neill, E.G.; Johnson, D.W.; Ledford, J.; Todd, D.E. 2003. Acute seasonal drought does not permanently alter mass loss and nitrogen dynamics during the decomposition of red maple (*Acer rubrum* L.) litter. *Global Change Biology*. 9: 117-123.
- Pan, Y.; Birdsey, R.A.; Phillips, O.L.; Jackson, R.B. 2013. The structure, distribution, and biomass of the World's forests. *Annual Review of Ecology, Evolution, and Systematics*. 44: 593-622.
- Parton, W.J.; Scurlock, J.M.O.; Ojima, D.S. [and others]. 1993. Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochemical Cycles*. 7: 785-809.
- Peng, C.; Ma, Z.; Lei, X. [and others]. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change*. 1: 467-471.
- Pilbeam, C.J.; Mahapatra, B.S.; Wood, M. 1993. Soil matrix potential effects on gross rates of nitrogen mineralization in an Orthic Ferralsol from Kenya. *Soil Biology and Biochemistry*. 25: 1409-1413.
- Pilon, C.E.; Cote, B.; Fyles, J.W. 1996. Effect of an artificially induced drought on leaf peroxidase activity, mineral nutrition and growth of sugar maple. *Plant and Soil*. 179: 151-158.
- Powell, T.L.; Gholz, H.L.; Clark, K.L. [and others]. 2008. Carbon exchange of a mature, natural regenerated pine forest in north Florida. *Global Change Biology*. 14: 2523-2538.
- Querejeta, J.I.; Egerton-Warburton, L.M.; Allen, M.F. 2007. Hydraulic lift may buffer rhizosphere hyphae against the negative effects of severe soil drying in a California oak savanna. *Soil Biology and Biochemistry*. 39: 409-417.
- Raison, R.J. 1979. Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations—review. *Plant and Soil*. 51: 73-108.
- Raison, R.J.; Khanna, P.K.; Woods, P.V. 1985. Mechanisms of element transfer to the atmosphere during vegetation fires. *Canadian Journal of Forest Research*. 15: 132-140.
- Rapparini, F.; Penuelas, J. 2014. Mycorrhizal fungi to alleviate drought stress on plant growth. In: Miransari, M., ed. *Use of microbes for the alleviation of soil stress*. New York: Springer: 21-42.
- Rey, A.; Pegoraro, E.; Tedeschi, V. [and others]. 2002. Annual variation in soil respiration and its components in a coppice oak forest in central Italy. *Global Change Biology*. 8: 851-866.
- Rhoades, C.C.; Entwistle, D.; Butler, D. 2011. The influence of wildfire extent and severity on streamwater chemistry, sediment and temperature following the Hayman Fire, Colorado. *International Journal of Wildfire Science*. 20: 430-442.
- Richter, D.D.; Ralston, C.W.; Harms, W.R. 1982. Prescribed fire: effects on water quality and forest nutrient cycling. *Science*. 215: 661-663.
- Riggan, P.J.; Lockwood, R.N.; Jacks, P.M. [and others]. 1994. Effects of fire severity on nitrate mobilization in watersheds subject to chronic atmospheric deposition. *Environmental Science and Technology*. 28: 369-375.
- Rustad, L.E.; Huntington, T.G.; Boone, R.D. 2000. Controls on soil respiration: implications for climate change. *Biogeochemistry*. 48: 1-6.
- Rustad, L.; Lebrija-Trejos, E.; Beier, C. [and others]. 2011. The effects of changing precipitation on ecosystem carbon and nutrient cycling: a meta-analysis of global change experiments. Oral presentation 2011 annual meeting of the Soil Science Society of America. On file with: Lindsey Rustad, Research Ecologist, U.S. Department of Agriculture, Forest Service, Northern Research Station (NRS), Durham, NH 03824.
- Ryan, M.G.; Harmon, M.E.; Birdsey, R.A. [and others]. 2010. A synthesis of the science on forests and carbon for U.S. forests. *Issues in Ecology*. 13: 1-16.
- Schaefer, K.; Schwalm, C.R.; Williams, C. [and others]. 2012. A model-data comparison of gross primary productivity: results from the North American Carbon Program site synthesis. *Journal of Geophysical Research*. 117(G3): G03010. 15 p. doi:10.1029/2012JG001960. [Published online: July 19, 2012].
- Schenk, H.J.; Jackson, R.B. 2005. Mapping the global distribution of deep roots in relation to climate and soil characteristics. *Geoderma*. 126: 129-140.
- Schimel, J.; Balsler, T.C.; Wallenstein, M.D. 2007. Microbial stress-response physiology and its implications for ecosystem function. *Ecology*. 88: 1386-1394.
- Schlesinger, W.H. 2013. An estimate of the global sink for nitrous oxide in soils. *Global Change Biology*. 19: 2929-2931.
- Schlesinger, W.H.; Bernhardt, E.S. 2013. *Biogeochemistry: an analysis of global change*. 3d ed. San Diego: Elsevier/Academic Press. 688 p.
- Schwalm, C.R.; Williams, C.A.; Schaefer, K. [and others]. 2010. A model-data intercomparison of CO₂ exchange across North America: results from the North American Carbon Program site synthesis. *Journal of Geophysical Research*. 115(G3): G00H05. 22 p. doi:10.1029/2009JG001229. [Published online: December 9, 2010].
- Schwalm, C.R.; Williams, C.A.; Schaefer, K. [and others]. 2012. Reduction in carbon uptake during turn of the century drought in western North America. *Nature GeoScience*. 5: 551-556.
- Sims, D.A.; Brzostek, E.P.; Rahman, A.F. [and others]. 2014. An improved approach for remotely sensing water stress impacts on forest C uptake. *Global Change Biology*. 20(9): 2856-2866. doi:10.1111/gcb.12537. [Published online: April 12, 2014].
- Smithwick, E.H.; Turner, M.; Mack, M.; Chapin, III, F.S. 2005. Postfire soil N cycling in northern conifer forests affected by severe, stand-replacing wildfires. *Ecosystems*. 8: 163-181.
- Sorensen, L.H. 1974. Rate of decomposition of organic matter in soil as influenced by repeated air drying-rewetting and repeated additions of organic material. *Soil Biology and Biochemistry*. 6: 287-292.
- Sparks, J.P. 2009. Ecological ramifications of the direct foliar uptake of nitrogen. *Oecologia*. 159: 1-13.
- Stark, J.M.; Firestone, M.K. 1995. Mechanisms for soil moisture effects on activity of nitrifying bacteria. *Applied Environmental Microbiology*. 1: 218-221.
- Stevenson, I.L. 1956. Some observations on the microbial activity of remoistened air-dried soils. *Plant and Soil*. 8: 170-182.
- Sverdrup H. 1990. *The kinetics of base cation release due to chemical weathering*. Lund, Sweden: Lund University Press. 245 p.
- Tate, R.I.; Ross, D.J.; Feltham, C.W. 1988. A direct extraction method to estimate soil microbial C: effects of experimental variables and some different calibration procedures. *Soil Biology and Biochemistry*. 20: 329-335.
- Tian, H.J.; Melillo, M.; Kicklighter, D.W. [and others]. 1998. Effects of interannual variability on carbon storage in the Amazon Basin. *Nature*. 396: 664-667.
- Tobita, H.; Uemura, A.; Kitao, M. [and others]. 2010. Interactive effects of elevated CO₂, phosphorus deficiency, and soil drought on nodulation and nitrogenase activity in *Alnus hirsuta* and *Alnus maximowiczii*. *Symbiosis*. 50: 59-69.

- Turner, M.G.; Romme, W.H.; Tinker, D.B. 2003. Surprises and lessons from the 1988 Yellowstone fires. *Frontiers in Ecology and the Environment*. 1: 351-358.
- Ulery, A.L.; Graham, R.C.; Amrhein, C. 1993. Wood-ash composition and soil pH following intense burning. *Soil Science*. 156: 358-364.
- van Mantgem, P.J.; Stephenson, N.L.; Byrne, J.C. [and others]. 2009. Widespread increase of tree mortality rates in the Western United States. *Science*. 323: 521-524.
- Vargas, R.; Sonnentag, O.; Abramowitz, G. [and others]. 2013. Drought influences the accuracy of simulated ecosystem fluxes: a model-data meta-analysis for Mediterranean oak woodlands. *Ecosystems*. 16: 749-764.
- Vergutz L.; Manzoni, S.; Porporato, A. [and others]. 2012. Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. *Ecological Monographs*. 82: 205-220.
- Wan, S.; Hui, D.; Luo, Y. 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. *Ecological Applications*. 11: 1349-1365.
- Waring, R.H.; Schlesinger, W.H. 1985. *Forest Ecosystems: concepts and management*. Orlando, FL: Academic Press. 338 p.
- Weed, A.S.; Ayres, M.P.; Hicke, J.A. 2013. Consequences of climate change for biotic disturbances in North American forests. *Ecological Monographs*. 83: 441-470.
- Wells, C.G. 1971. Effects of prescribed burning on soil chemical properties and nutrient availability. In: *Prescribed Burning Symposium Proceedings*. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: 86-97. Available at: <http://www.treesearch.fs.fed.us/pubs/27646>. [Date accessed: September 14, 2015].
- Wetselaar, R. 1968. Soil organic nitrogen mineralization as affected by low soil water potentials. *Plant and Soil*. 29: 9-17.
- Wiedinmyer, C.; Hurteau, M.D. 2010. Prescribed fire as a means for reducing forest carbon emissions in the Western U.S. *Environmental Science and Technology*. 44: 1926-1932.
- Wood, T.E.; Cavaleri, M.A.; Reed, S.C. 2012. Tropical forest carbon balance in a warmer World: a critical review spanning microbial- to ecosystem-scale processes. *Biological Reviews*. 87: 912-927.
- Wu, Z.; Kijkstra, P.; Koch, G.W. [and others]. 2010. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biology*. 17: 927-942.
- Wurtzburger, N.; Miniati, C.F. 2014. Drought enhances symbiotic dinitrogen fixation and competitive ability of a temperate forest tree. *Oecologia*. 174: 1117-1126.
- Xiao, J.F.; Zhuang, Q.L.; Law, B.E. [and others]. 2010. A continuous measure of gross primary production for the conterminous United States derived from MODIS and AmeriFlux data. *Remote Sensing of Environment*. 114: 576-591.
- Xiao, J.; Zhuang, Q.; Law, B.E. [and others]. 2011. Assessing net ecosystem carbon exchange of U.S. terrestrial ecosystems by integrating eddy covariance flux measurements and satellite observations. *Agriculture and Forest Meteorology*. 151: 60-69.
- Xu, X.; Schimel, J.P.; Thornton, P.E. [and others]. 2014. Substrate and environmental controls on microbial assimilation of soil organic carbon: a framework for Earth system models. *Ecology Letters*. 17: 547-555.
- Zhang, F.; Chen, J.M.; Pan, V.D. [and others]. 2012. Attributing carbon changes in conterminous U.S. forests to disturbance and non-disturbance factors from 1901 to 2010. *Journal of Geophysical Research-Biogeosciences*. 117(G2): G02021. 18 p. doi:10.1029/2011JG001930. [Published online: June 7, 2012].
- Zhao, M.S.; Running, S.W. 2010. Drought-induced reduction in global terrestrial net primary production from 2000 to 2009. *Science*. 329: 940-943.

Forest Insect and Fungal Pathogen Responses to Drought

Thomas E. Kolb
Christopher J. Fettig
Barbara J. Bentz
Jane E. Stewart
Aaron S. Weed
Jeffery A. Hicke
Matthew P. Ayres

T.E. Kolb is a Professor, Northern Arizona University, School of Forestry, Flagstaff, AZ, 86001.

C.J. Fettig is a Research Entomologist, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station (PSW), Davis, CA 95618.

B.J. Bentz is a Research Entomologist, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Logan, UT 84321.

J.E. Stewart is an Assistant Professor, Colorado State University, Department of Bioagricultural Sciences and Pest Management, Fort Collins, CO 80521.

A.S. Weed is a Postdoctoral Research Associate, Dartmouth College, Department of Biological Sciences, Hanover, NH 03755.

J.A. Hicke is an Associate Professor, University of Idaho, Department of Geography, Moscow, ID 83844.

M.P. Ayres is a Professor, Dartmouth College, Department of Biological Sciences, Hanover, NH 03755.

Introduction

Recent changes in precipitation patterns and in the occurrence of extreme temperature and precipitation events have been documented in many forested regions of the United States (Ryan and Vose 2012). Changes in drought intensity and frequency have the potential to alter populations and impacts of tree-damaging forest insects and pathogens (Ayers and Lombardero 2000, Dale and others 2001, Weed and others 2013). Scientists, forest managers, and environmental policymakers need to better understand the role of drought in outbreaks of forest insects and diseases in order to anticipate the future condition of U.S. forests and to consider actions to mitigate undesirable changes.

Here we review evidence for a role of drought in outbreaks of, and tree damage by, herbivorous insects and fungal pathogens in forests of the United States. First, we describe our understanding of how drought affects host nutritional quality and susceptibility to attack, and how damage by insect herbivory and pathogens affect tree responses to drought. Second, we review the responses of herbivorous forest insects (bark beetles, defoliators, sapfeeders) and fungal pathogens to drought. Third, we highlight regional differences in the roles of drought on forest insects and diseases by contrasting the Western United States with the Eastern United States. Fourth, we discuss predictions of future drought-related insect and disease impacts to western and eastern forests. Finally, we summarize our findings and highlight important research needs.

Tree Responses to Drought

Host Tree Nutrition and Susceptibility to Attack

Drought affects many components of tree nutritional quality. Several reviews of hundreds of studies (Huberty and Denno 2004, Mattson and Haack 1987, Rouault and others 2006) have concluded that drought often increases plant tissue concentrations of nitrogen compounds such as amino acids and nitrate; osmolytes such as sugars and inorganic ions; and allelochemicals such as cyanogenic glycosides, terpenoids, and alkaloids. The responses of most of these compounds are hypothesized to be dome-shaped with increases in tissue concentration during mild or moderate drought, when water stress constrains growth more than photosynthesis and root uptake of nutrients, followed by decreases during long and severe drought when intense water stress constrains growth, photosynthesis, and root uptake (Mattson and Haack 1987).

Drought-induced changes in nitrogen content of tree tissues have been investigated in many studies because of the importance of nitrogen in insect metabolism and its influence on population growth (White 1984). Drought often increases nitrogen content of tree tissues. Positive effects of drought on tree damage by foliage-feeding insects are often attributed to increased nitrogen content of water-stressed leaves (Jactel and others 2012). For example, lepidopteran larval survival is positively associated with pine leaf nitrogen concentration (Hodar and others 2002).

Drought often causes early senescence of older leaves that remobilizes nitrogen into soluble forms through vascular tissues to younger tissues, where concentrations in water-stressed plants often exceed concentrations in non-stressed plants (White 1984). All forms of drought reduce tree tissue water content, which often interferes with insect utilization of nitrogen (Huberty and Denno 2004). Timing and duration of water stress are important controls over insect capacity to use concentrated zones of nitrogen in plants. For example, Huberty and Denno's (2004) pulsed stress hypothesis predicts that sapfeeding insects benefit by feeding on drought-stressed plants when drought is followed by wetter periods that increase plant turgor and hence allow insects to benefit from drought-induced increase in plant tissue nitrogen.

Drought often alters plant defenses. The growth-differentiation-balance hypothesis (GDBH) (Hermes and Mattson 1992) predicts that drought has nonlinear impacts on carbon-based plant defenses, such as terpenes, and defenses that ultimately require carbohydrates to support metabolic costs of synthesis. Specifically, mild or moderate water stress that does not cause closure of plant stomata is predicted to increase carbon-based defense due to surplus carbohydrates that result from a negative effect of stress on the use of carbohydrates for growth that is greater than the production of carbohydrates by photosynthesis (Lorio 1986, Reeve and others 1995). In contrast, intense water stress causes plants to close stomata to avoid excessive water loss, which consequently reduces photosynthesis (McDowell and others 2008, Pallardy 2008). Prolonged periods of low photosynthesis during intense water stress are predicted by the GDBH to reduce carbohydrate supply and metabolism of all plant processes, including defense. Intense drought likely causes defense failure due to a combination of tree carbon starvation and hydraulic failure (McDowell and others 2011, Tague and others 2013). The current

understanding of drought impacts on chemical composition of tree defenses is poor and largely based on experiments with seedlings that may not scale directly to mature trees (Lusebrink and others 2011, Turtola and others 2003). The few experimental studies of mature trees (Gilmore 1977, Hodges and Lorio 1975) have shown that drought can alter chemical composition of resin monoterpenes in pines, but effects of such alterations on tree defense and insect populations are not known. Drought-induced changes in tree defense compounds are rooted in alterations in transcription of genes associated with stress resistance (Arango-Velez and others 2014).

Drought often alters insect feeding by increasing leaf toughness. Physical characteristics of plant tissues, such as leaf toughness, are strongly associated with plant resistance against insects. A recent review reported stronger roles of physical traits than chemical and secondary metabolic traits in plant resistance to insect herbivory (Carmona and others 2011). During drought, leaf water content decreases and leaf toughness and dry matter content increases (McMillin and Wagner 1996, Pasquier-Barre and others 2001). These changes are associated with reduction in folivore feeding and reproduction (Awmack and Leather 2002, Pasquier-Barre and others 2001, Wagner and Zhang 1993).

Drought can increase plant attractiveness to insects by altering clues used to identify hosts (Mattson and Haack 1987, Rouault and others 2006). Leaf yellowing that often accompanies drought may be a spectral clue detected by insects, and warmer temperature of drought-stressed plant tissues may be detected by insect thermal sensors. Xylem cavitation in plants caused by drought results in ultrasonic acoustic emissions that likely are detectable by some insects (Haack and others 1988). Insect chemoreceptors may detect drought-induced changes in suites of plant compounds. For example, drought may induce plant production of volatile compounds and ethanol that are olfactory attractants for some insects, such as bark beetles (Kelsey and Joseph 2001, Kelsey and others 2014, Manter and Kelsey 2008, Miller and Rabaglia 2009).

Influence of Pathogens and Herbivory in Tree Drought Response

Few studies have addressed the impact of previous insect herbivory on tree response to drought. Insect defoliation of conifers during experimentally induced drought has been reported to reduce water stress (e.g., less negative xylem water potential) of isolated

potted trees (Kolb and others 1999), but to have little effect on water stress of trees sharing the same soil resources (Jacquet and others 2014). Feeding by the hemlock woolly adelgid (*Adelges tsugae*) on eastern and Carolina hemlocks (*Tsuga canadensis* and *Tsuga caroliniana*, respectively) increased tree water stress and predisposed trees to drought in a field observational study (Domec and others 2013, Gonda-King and others 2014). The few studies of the combined effects of previous herbivory and drought on tree growth and carbohydrate pools show largely additive effects. For example, an experimental study of 10-year-old maritime pine (*Pinus pinaster*) found additive effects with no interaction of artificial defoliation and water stress on tree growth and carbohydrate pools (Jacquet and others 2014). In this study, carbohydrate pools of whole trees, roots, and stems were lowest in water-stressed trees exposed to 100 percent defoliation. Defoliation also redistributed carbohydrates from roots to stems, a response which likely predisposes defoliated trees to future drought by reducing root growth. In another example, experimental defoliation of aspen (*Populus tremuloides*) reduced stem hydraulic conductance because of a decrease in xylem growth (Anderegg and Callaway 2012). This response likely predisposes aspen to water stress in future droughts. Moreover, defoliation of aspen reduced tree carbohydrate storage and increased occurrence of fungal cankers, stem borers, and bark beetle attacks (Anderegg and Callaway 2012). These findings show that previous herbivory that alters tree carbohydrate pools and defense metabolism can, in turn, influence tree response to future drought and insect and pathogen attacks. For example, whereas the associated mechanisms are not fully understood, previous tip moth (*Rhyacionia frustrana*) attacks predispose trees to higher levels of attack in subsequent generations (Coody and others 2000).

Fungal pathogens predispose trees to drought stress and drought-induced mortality. A recent framework (Oliva and others 2014) predicts that necrotrophs, which obtain nutrients from dead tree cells, accelerate drought-induced tree mortality by depleting tree resources as a result of repair and compartmentalization processes. Vascular wilts have been hypothesized to accelerate drought-induced tree mortality by reducing sapwood conductance of water and impairing phloem transport. Biotrophs, which obtain nutrients directly from living tree tissues, are expected to be negatively affected by drought because of the strong connection between their performance and tree nutritional status. However, if biotrophs are able to invade stressed

trees, they are expected to cause more severe drought impacts on trees because they deplete carbohydrate reserves important for tree drought tolerance (Oliva and others 2014).

Parasitic plants typically intensify negative impacts of drought on tree water stress and growth by obtaining water and nutrients from tree hosts (Sanguesa-Barreda and others 2012, Stanton 2007, Stewart and Press 1990). High transpiration rates by xylem-tapping parasites, such as the true mistletoes (*Phoradendron* spp.), often reduce xylem water potential, stomatal conductance, net photosynthetic rate, and water-use efficiency of host branches and leaves (Ehleringer and others 1986, Orozco and others 1990, Sanguesa-Barreda and others 2013, Zweifel and others 2012). Moreover, infection by xylem-tapping parasites can decrease xylem hydraulic conductivity of host branch portions distal to the infection (Tennakoon and Pate 1996). Xylem-tapping parasites often reduce ectomycorrhizae on tree roots (Gehring and Whitham 1992), which reduces host nutrient and water uptake. Phloem-tapping parasitic plants, such as the dwarf mistletoes (*Arceuthobium* spp.), predispose trees to drought by several processes including alteration of host hormones (Logan and others 2013) and hydraulic processes (Sala and others 2001), reduction of host net photosynthetic rate and water-use efficiency (Marias and others 2014, Meinzer and others 2004), and depletion of host carbohydrates transported in phloem (Knutson 1979, Stewart and Press 1990). These carbohydrate losses likely reduce tree capacity for metabolic processes of drought tolerance and reduce root uptake of water and nutrients because less carbohydrate is allocated to roots (Knutson and Toevs 1972, Stewart and Press 1990). Phloem-tapping parasitic plants, such as the dwarf mistletoes that occur on conifers, also predispose trees to lethal bark beetle attacks during drought (Kenaley and others 2008).

Insect and Pathogen Responses to Drought

Outbreaks of some herbivorous insects and fungal pathogens occur during or following drought (Koricheva and others 1998, Mattson and Hack 1987, Sturrock and others 2011). Performance and impacts of insects and pathogens during and following drought differ depending on the type of food substrate (i.e., woody or foliar), feeding guild, duration of stress, and the type and importance of host defenses. The intrinsic capacity for drought resistance, which can vary among individual

trees, species, and regions, will also influence tree response to water stress, insect herbivory, and fungal pathogens. Below we review impacts of drought and tree water stress on performance and impacts of major tree-feeding insect guilds (i.e., bark beetles, defoliators, sapfeeders) and tree fungal pathogens.

Bark Beetles

Bark beetles are chewing insects that feed on phloem and woody tissue beneath the bark of trees. A few notable species feed on live tissues causing death of the host tree, resulting in extensive economic and ecological impacts when widespread population outbreaks occur (Wood 1982) (fig. 6.1). Host trees have evolved defenses, however, that include chemical, physical, and histological components. A variety of chemical groups are involved in tree defense against bark beetle attack including terpenes, which are both a constituent and an inducible component of tree resin. Terpene concentrations can increase to levels that are repellent and toxic in a matter of days following beetle attack (Franceschi and others 2005). Structural aspects of trees, such as the number and size of resin ducts in the xylem and phloem, are also important as they are responsible for the production and storage of resin (Kane and Kolb 2010). Both terpene production and resin duct formation are dependent on carbon allocation within a tree, and carbon allocation can be nonlinearly influenced



Figure 6.1—Mountain pine beetle (*Dendroctonus ponderosae*) is one of several bark beetle species that has caused extensive tree mortality in pine forests of western North America. Tree mortality increased in multiple areas during the mid-2000s following a severe drought in the early 2000s. On the Helena National Forest, Montana, tree mortality exceeded 70 percent in some lodgepole (*Pinus contorta*) and ponderosa (*P. ponderosa*) pine stands. (photo by Barbara Bentz, U.S. Department of Agriculture, Forest Service)

,by drought (Herms and Mattson 1992). Intense drought reduces carbon assimilation, water transport, and cell turgor, thereby decreasing the synthesis and mobilization of secondary metabolites, such as terpenes, that are used in defense against bark beetle attack (Sala and others 2012). The level of water stress, however, may influence the allocation of assimilated carbon to defense and growth, as described above using the GDBH. Although at severe levels of water stress both growth and defense are most likely reduced, moderate water stress could lead to increased resistance if only growth is constrained, providing a surplus of carbon for resin synthesis and duct formation (Herms and Mattson 1992, Lieutier 2004, Rouault and others 2006). Although water stress can reduce overall emissions of volatile compounds due to stomatal closure, the relative concentrations of some terpenes can change (e.g., ethanol, α -pinene and β -pinene), often making trees more attractive to bark beetles (Cates and Alexander 1982, Hodges and Lorio 1975, Kelsey and Joseph 2001, Kelsey and others 2014, Kimmerer and Kozlowski 1982).

Bark beetles that feed in phloem can be either positively or negatively affected by drought, depending on drought intensity, duration, and tree water stress (Jactel and others 2012). Positive feedbacks between drought and bark beetle outbreaks have occurred in semi-arid forests of the Western United States during intense drought (fig. 6.2), whereas negative feedbacks are more



Figure 6.2—The aftermath of a western pine beetle (*Dendroctonus brevicomis*) outbreak. In the early 2000s, the mountain ranges of southern California experienced elevated levels of tree mortality due to western pine beetle, which many experts associated with severe drought (i.e., precipitation was the lowest in recorded history during 2001–2002) although other predisposing, inciting, and contributing factors were likely important. Despite continuing drought and an availability of suitable hosts, western pine beetle populations rapidly declined in 2004. This outbreak is considered by many to be among the largest recorded for this species of bark beetle. (photo by Christopher Fettig, U.S. Department of Agriculture, Forest Service)

,likely in the more mesic forests of the Eastern United States that experience milder drought than in the West. Although severely water-stressed trees may be more attractive to bark beetles and easier to overcome due to low defense capability, low levels of carbohydrates and nitrogen and reduced moisture content of phloem in such trees may negatively affect development of bark beetles and their associated fungi. This suggests that continuously stressed trees could result in poor bark beetle population performance as observed for other feeding guilds (Huberty and Denno 2004).

Few studies have experimentally investigated the effect of drought on bark beetle performance (Gaylord and others 2013); instead most studies have retrospectively analyzed the effect of either moisture- or temperature-induced drought on tree mortality due to bark beetles. Empirical associations have been found between reduced precipitation in the current year and years leading up to outbreaks of mountain pine beetle (*Dendroctonus ponderosae*) (Chapman and others 2012, Creeden and others 2014, Evangelista and others 2011, Thomson and Shrimpton 1984), spruce beetle (*Dendroctonus rufipennis*) (DeRose and Long 2012, Hart and others 2014, Hebertson and Jenkins 2008), and pinyon ips (*Ips confusus*) (Raffa and others 2008). The role of drought in predisposing pinyon pine to pinyon ips attacks has been confirmed by a recent experimental manipulation of precipitation (Gaylord and others 2013). The effect of drought on tree mortality from bark beetles can also vary depending on the lag time (Preisler and others 2012), and the duration of the outbreak event will depend on the species. For example, mountain pine beetle and spruce beetle are capable of causing widespread tree mortality for several years after drought has ceased when positive feedbacks on their populations, due to extensive host abundance, concentrated beetle density, optimal symbiotic associations, and escape from natural enemies, amplify over spatial and temporal scales (Raffa and others 2008). Conversely, pinyon ips depends more directly on stressed trees for successful reproduction, as illustrated by a rapid reduction in the population outbreak and tree mortality in the Southwestern United States during the early 2000s when wetter conditions returned (Raffa and others 2008) (fig. 6.3). The drought in the early 2000s that influenced outbreaks of mountain pine beetle, spruce beetle, and pinyon ips created conditions of severe water stress (Breshears and others 2009, Gaylord and others 2007), as it was one of the most severe droughts in the past 500 years in many parts of the Interior Western United States (Pielke and



Figure 6.3—Mortality of pinyon pine (*Pinus edulis*) due to pinyon ips (*Ips confusus*) associated with intense drought in the Southwestern United States. In some areas, tree mortality exceeded 90 percent. Populations of pinyon ips rapidly declined when wetter conditions returned to the region. (photo by Thomas Kolb, Northern Arizona University)

others 2005). This drought was also associated with warm temperatures that can have a direct positive effect on bark beetle population survival and growth (Breshears and others 2005). Warm winters can reduce cold-induced mortality (Bentz and Mullins 1999, Tr an and others 2007), and warm summers can reduce generation time (Bentz and others 2014, Thatcher and Pichard 1967). In general, warm summer temperatures positively influence bark beetle population success, and drought likely magnifies the effect. The effect of drought on bark beetle population growth is not straightforward, however, as increased precipitation can also have a positive effect on bark beetle population growth (Duehl and others 2011, Gumpertz and Pye 2000, Preisler and others 2012) by providing a more nutritious food resource for developing larvae, and by reducing tree defense because carbon is preferentially allocated to growth as predicted by the GDBH (Herms and Mattson 1992, McDowell and others 2011).

Defoliators

Forest defoliators consume, mine, and/or skeletonize the foliage of trees. A number of species may cause tree mortality depending on the timing, frequency, and severity of feeding, and a few are capable of causing extensive levels of tree mortality over large areas (e.g., eastern spruce budworm, *Choristoneura fumiferana*).

While outbreaks of forest defoliators have been linked to drought (Mattson and Haack 1987), much of the associated evidence supporting this relationship is largely circumstantial. There is considerable variation in the magnitude and direction of insect responses to drought, and this is perhaps best typified among defoliators. For example, several studies have shown drought increases the performance and impact of defoliators while others have shown the opposite (Jactel and others 2012). To that end, Jactel and others (2012) suggested that the type of trophic substrate impacted (e.g., foliage versus wood) may be a more appropriate criterion for evaluating the responses of forest insects to drought than feeding guild.

Research has focused on the indirect effects of drought on defoliators as mediated through changes in host tree physiology, primarily leaf chemistry and palatability. Due to the inherent difficulties of studying the responses of defoliators to drought-stressed mature trees in forest environments, much of what is known comes from laboratory studies on seedlings. These seedling data may or may not be indicative of responses to mature trees, and therefore a distinction should be made between them. Furthermore, it is important to emphasize that responses observed in laboratory studies are likely not indicative of responses that occur at the population level (Larsson 1989), and therefore such extrapolations should be viewed with some caution. Consequently, little is known about the direct effects of drought on populations and impacts of defoliators and their common associates, including predators, parasites, and competitors. Some insect fungal pathogens important in regulating defoliator populations are likely to be negatively impacted by drought. For example, *Entomophaga maimaiga*, which causes extensive epizootic outbreak in populations of the gypsy moth (*Lymantria dispar*) in the Eastern United States, requires high levels of moisture for conidial production and discharge (Hajek 1999). Interestingly, drought-stressed plants are consistently warmer than unstressed plants because reduced transpiration limits plant cooling, with differences as great as 15 °C being observed (Mattson and Haack 1987). This has obvious implications to populations and impacts of the insects colonizing them due to positive responses of many insects to increasing temperature.

Many defoliators preferentially feed on leaves with high protein and water content, low leaf toughness, and low concentrations of secondary metabolites (Dury and others 1998). As described earlier, drought often affects

the nutritional quality of foliage by causing changes in water, carbohydrate, and nitrogen concentrations. It has been well demonstrated that the magnitude and direction of responses to drought by defoliators are influenced by the severity and duration of drought stress (Jactel and others 2012). However, drought stress severity should be viewed in the context of the overall drought resistance of a given tree species. For example, trees that have narrow xylem conduits (gymnosperms) can generally maintain physiological function and recover from more severe drought than trees that have wide xylem conduits (most angiosperms) (Brodrribb and Cochard 2009). Overall, compromised physiological function and reduced productivity often leads to a higher vulnerability to insect attack (Bolton 2009).

Nitrogen concentrations often increase in foliage during drought stress (White 1969, 1984), which may increase the performance of defoliators as nitrogen is often a limiting growth factor (Mattson and Haack 1987). Rouault and others (2006) commented that some defoliators benefited from increased nitrogen in plant tissues associated with moderate water stress during the drought and heat waves that occurred in Europe during 2003. For some insects, nutrients in unstressed foliage are below levels optimal for development and even moderate stress has been reported to cause significant changes in the quality of foliage that affect defoliator performance (Herms and Mattson 1992, Larsson 1989, Larsson and Björkman 1993, Mattson and Haack 1987, Rouault and others 2006). Alternatively, Craig and others (1991) found no consistent evidence that drought stress led to increased performance of sawflies (*Neodiprion* spp.) in ponderosa pine (*Pinus ponderosa*) trees. Furthermore, they reported that performance was better on nonstressed trees during some years. In another study, sawfly performance was greatest on needles from ponderosa pine seedlings exposed to intermittent rather than continuous water stress (McMillin and Wagner 1995). Severe drought stress is generally recognized as causing a deterioration of host tissue quality; however, some defoliators may be attracted to chlorotic foliage as many insects are attracted to yellow hues (Prokopy and Owens 1983).

Drought may negatively impact the performance of defoliators through reduced leaf water content, which usually increases leaf toughness resulting in reduced palatability and lower leaf consumption. For example, leaf water content is thought to be one of the most important factors influencing the growth of

autumnal moth (*Epirrita autumnata*) and winter moth (*Operophtera brumata*) in Europe (Henriksson and others 2003, Tikkanen and Lyytikäinen-Saarenmaa 2002). Similarly, Scriber (1977) showed that cecropia moth (*Hyalophora cecropia*) larvae reared on water-stressed leaves of black cherry (*Prunus serotina*) in the laboratory grew more slowly and were less efficient at utilizing plant biomass than larvae that fed on leaves fully supplemented with water.

Concentrations of secondary metabolites often increase in foliage as a result of drought stress, which has been shown to negatively impact defoliators. Hale and others (2005) demonstrated that concentrations of total phenolic glycosides, important secondary defensive compounds (Hemming and Lindroth 1995), were lower in well-watered black poplar (*Populus nigra*) seedlings, and higher in drought-stressed seedlings despite the latter being constrained by a smaller carbon budget. In their study, continuous drought stress decreased the growth of gypsy moth larvae likely as a result of decreased foliar nitrogen and increased total phenolic glycoside concentrations, but had no effect on white-marked tussock moth (*Orgyia leucostigma*) larvae, which is thought to be less sensitive to increases in phenolic glycosides than gypsy moth (Kopper and others 2002). In another study, Roth and others (1997) investigated the effects of carbon dioxide and water availability on quaking aspen and sugar maple (*Acer saccharum*) seedlings. Foliar nitrogen levels declined and secondary metabolite concentrations increased under enriched carbon dioxide, but starch and sugar levels were unaffected. All phytochemicals, with the exception of simple sugars, declined or did not change in response to drought. Carbon dioxide and drought-mediated changes reduced performance of forest tent caterpillar (*Malacosoma disstria*) (Roth and others 1997).

In a recent meta-analysis, Jactel and others (2012) concluded that primary agents that feed on tree foliage inflicted greater damage on drought-stressed trees than unstressed trees, but the effect was largely attributed to gall-making insects and fungal pathogens. Their meta-analysis included 100 comparisons of forest insects and fungi on drought-stressed and unstressed trees (based on 40 publications, 1975–2010). Among foliage feeders, such notable forest pests as gypsy moth and forest tent caterpillar, as well as several sawflies, aphids (Aphididae), and leaf pathogens, were included. Results for chewing insects on foliage were highly variable among 20 studies included in the meta-analysis, and the overall effect of drought on foliage damage by chewing

insects was positive, but not significantly different from zero based on a 95-percent confidence interval.

Sapfeeders

Water stress is hypothesized to positively influence phloem sapfeeders, such as aphids and adelgids (*Adelgidae*), through an increase in host tissue nitrogen content. Meta-analyses, however, suggest that the response is highly variable among studies and dependent on the level of stress and resultant turgor pressure of the tree (Huberty and Denno 2004, Jactel and others 2012, Koricheva and others 1998). Similar to other phloem feeders, spruce aphid (*Elatobium abietinum*) performance and population growth was greatest when water stress was intermittent and was lowest when the stress was continuous (Major 1990). Under continuous water stress, leaf and phloem nitrogen are diminished due to reduced turgor, but moderate or periodic stress provides available nitrogen during periods of periodic turgor recovery. These results suggest that the optimum host would be a plant that has experienced long-term intermediate stress, and then temporarily released from the stress by abundant precipitation during insect feeding (Mopper and Whitham 1992). The response of sapfeeders, such as the Eastern spruce gall adelgid (*Adelges abietis*), which has both a sucking and galling life stage, can also vary with life stage. The sucking stage is often positively influenced by drought, while the galling life stage, which requires expanding plant tissues for successful gall formation, is negatively influenced (Björkman 2000).

Fungal Pathogens

Relatively few studies have directly addressed the effects of drought on fungal tree pathogens. However, it has been predicted that drought could alter the prevalence, severity, and geographic patterns of many forest pathogens because forest diseases are strongly influenced by environmental conditions, such as humidity and temperature (Sturrock and others 2011). On one hand, drought that increases tree water stress and reduces resources available for defense could make trees more susceptible to pathogens. On the other hand, drought may retard the development, survival, reproduction, and dispersal of fungal pathogens because many rely on moisture availability to cause infection (Klopfenstein and others 2009). Changes in moisture availability could directly influence fungal pathogen sporulation and infection of host species (Sturrock and others 2011). However, it is not clear how drought affects pathogen survival, as fungal pathogens are highly adaptable and have diverse reproductive

systems that are designed for coping with changing environmental conditions (Olatinwo and others 2013).

Several recent reviews have addressed impacts of drought on tree fungal pathogens and have highlighted sources of variation in drought response. Desprez-Loustau and others (2006) suggested that duration of drought is an important predictor of forest disease impact on trees as more infections are likely to develop during or after prolonged drought. Jactel and others (2012) reported that the most important factors for determining disease severity under drought conditions were pathogen status (primary or secondary), affected tree part (foliar versus woody organs), and water stress severity. Further, they reported that primary pathogens that infect wood and foliage of healthy trees inflict less damage on trees during drought (Jactel and others 2012). Moreover, pathogens whose reproduction, spread, infection, and survival are directly tied to the availability of moisture have been predicted to be negatively impacted by drought (Sturrock and others 2011). In contrast, drought is expected to increase host damage by secondary pathogens that colonize stressed trees and woody organs, such as root rot pathogens, stem wound colonizers, and latent colonizers of sapwood (Desprez-Loustau and others 2006, Jactel and others 2012, Sturrock and others 2011).

Needle diseases, which are caused by rust pathogens, and diseases caused by *Phytophthora* species are sensitive to precipitation and humidity, as rates of reproduction, spread, and infection are greater when conditions are moist (Harvell and others 2002). Therefore, drought may decrease the incidence and severity of these diseases (Thompson and others 2014). Rates of infection for many needle pathogens, such as *Dothistroma septosporum* and *D. pini* that cause Dothistroma needle blight of pine, spruce, larch, and Douglas fir (*Pseudotsuga menziesii*) (Barnes and others 2004), and *Phaeocryptopus gaeumannii* that causes Swiss needle cast of Douglas fir, are closely linked to temperature and moisture (Hansen and others 2000, Stone and others 2008). High levels of moisture were particularly critical for infection by *D. septosporum*. This pathogen required 10 or more consecutive hours of needle wetness at temperatures ranging from 16 °C to 20 °C for infection to occur (Bulman 1993). High levels of moisture have also been shown to be required for infection by *P. gaeumannii*. High levels of *P. gaeumannii* incidence have been positively correlated with winter rainfall accumulation and leaf wetness hours (Manter and others 2005). Similar to needle and foliar diseases,

drought conditions could also decrease the severity of stem rust diseases.

It has been suggested that the incidence of rust diseases will be affected not only by drought conditions, but also by the presence or absence of alternate hosts. Many stem rust pathogens, such as fusiform rust and white pine blister rust, are unusual as pathogens because in addition to the requirement of extended periods of free moisture to complete their lifecycles, they also require the presence of primary and secondary hosts. Drought conditions could alter the geographic range of primary and secondary hosts (Olatinwo and others 2013). Fusiform rust is a significant pathogen on pine, especially in southeastern species. The alternative host in the Southeast is primarily water oak (*Quercus nigra*). Fusiform rust would not complete its lifecycle if the geographic range of water oak changes during future drought and climate change. White pine blister rust, caused by *Cronartium ribicola*, was introduced to North America from Asia in the early 1900s. Infection causes branch dieback, productive failure, and tree mortality (Bega 1978). Environmental requirements for disease progression of *C. ribicola* are well documented. Needle infection requires 48 hours of 100 percent relative humidity and temperatures less than 20 °C (Van Arsdel and others 1956). Drought will likely result in less white pine blister rust infection in regions where moisture is or becomes a limiting factor to the rust (Kinloch 2003).

Phytophthora ramorum, the causal agent of sudden oak death, is a serious and devastating pathogen. Recently introduced, this pathogen has had a significant impact on tanoak (*Notholithocarpus densiflorus*) and live oak (*Quercus agrifolia*) in California and Oregon forests. *P. ramorum* has been demonstrated to be a high risk pathogen to many forests in North America because of its ability to infect a wide range of hosts (Dodd and others 2008). However, like all *Phytophthora* species, extended periods of rainfall in fall or spring are essential to the persistence of *P. ramorum*. Therefore infections by *Phytophthora* spp. would likely decrease during extended drought unless drought is followed by periods with extended rainfall (Venette 2009, Weed and others 2013).

Root rot pathogens of trees, such as *Armillaria* spp. and *Heterobasidion* spp., are predicted to become more severe and move into new geographic regions during drought because these pathogens most successfully colonize stressed trees (Olatinwo and others 2013,

Sturrock and others 2011). Armillaria root rot is a global disease caused by both primary and secondary pathogens that infect primarily pines and hardwoods (Kile and others 1991). Infections cause wood decay, overall growth reduction and tree mortality, and increase tree susceptibility to colonization by bark beetles or other insect pests (Sturrock and others 2011). On forested sites under drought conditions causing tree stress, Armillaria root rot severity could increase significantly and cause widespread tree mortality (Klopfenstein and others 2009, La Porta and others 2008, Shaw and Kile 1991). Similarly, Heterobasidion root rot caused by *Heterobasidion irregulare* and *H. occidentale*, could increase in geographic range and incidence during drought (Kliejunas and others 2009, Otrosina and Garbelotto 2010). Currently in the Southeastern United States, Heterobasidion root rot causes significant losses on conifers, and it has been suggested that with increased drought, growing numbers of trees will be impacted by this disease (Duerr and Mistretta 2013). In the central western coast of Italy, where environmental conditions are becoming increasingly hotter and drier, widespread mortality of Corsican pine (*Pinus nigra* var. *maritime*) was caused by Heterobasidion root rot (Gonthier and others 2007). In these drier conditions, the pathogen appears to be increasing its geographic range and incidence.

Several studies have reported increased severity of stem canker pathogens during drought because water-stressed trees are less effective at mechanisms of canker resistance, such as compartmentalization and callusing (Bevercombe and Rayner 1980, McIntyre and others 1996). Cankers caused by *Septoria musiva* on poplar (*Populus* spp.) stems were significantly larger on water-stressed trees compared to unstressed trees (Desprez-Loustau and others 2006, Maxwell and others 1997). Likewise, increased severity of Diplodia shoot blight caused by *Diplodia sapinea* has also been associated with water stress of trees in several studies (Blodgett and others 1997, Paoletti and others 2001).

Drought and forest pathogens often are implicated as causal factors in tree diseases of complex etiology or decline diseases (Manion 1981). Decline diseases are caused by a multitude of predisposing, inciting, and contributing factors including drought and fungal pathogens. In a review of aspen decline in North America, Worrall and others (2013) concluded that recent declines in many regions, including the Western United States, were primarily induced by drought, but biotic agents, including fungal pathogens, also played

a role. Primary pathogenic agents such as sooty-bark canker; multi-year defoliation by tent caterpillars (*Malacosoma* spp.); and secondary agents such as boring insects, fungal cankers, and *Armillaria* root disease have been associated with drought-induced aspen mortality in most studies (Worrall and others 2013). Previous defoliation likely increases aspen susceptibility to drought and secondary biotic agents via carbon limitation (Anderegg and Callaway 2012). Tree-ring studies in the Western United States show that chronically low growth rate predisposes aspens to die during severe drought (Hanna and Kulakowski 2012, Ireland and others 2014, Kane and Kolb 2014). Data from these studies strongly suggest that stresses leading to aspen death accrue over decades and that “sudden aspen death” is not due solely to recent severe drought. Overall, the role of drought and biotic agents in aspen mortality in the Western United States is consistent with Manion’s decline disease framework (Manion 1981) with drought acting as an inciting factor and biotic agents as contributing factors.

Regional and Sub-Regional Differences and Interactions

In the West

Bark beetles are the main biotic agent of tree mortality in the Western United States. Multiple large outbreaks have killed hundreds of millions of trees in recent decades (Meddens and others 2012). Aggressive bark beetle species such as mountain pine beetle and spruce beetle are able to kill healthy trees when beetle populations are large, and climate plays an important role in driving epidemics of these beetles through effects on the insects and on host trees (Bentz and others 2010, Raffa and others 2008). Drought provides an increased source of susceptible host trees, which allows beetle populations to build. Temperature-induced drought in the 1990s in Alaska and moisture-induced drought in the early 2000s in the Western conterminous United States have been linked to bark beetle outbreaks (Berg and others 2006, Chapman and others 2012, Creeden and others 2014, Hart and others 2014, Shaw and others 2005). Others have also found a relationship between drought and historic spruce beetle outbreaks (DeRose and Long 2012, Hebertson and Jenkins 2008, Sherriff and others 2011). However, when drought is relieved, epidemics of some species, including mountain pine beetle and spruce beetle, can continue due to positive feedbacks that allow high numbers of beetles to overwhelm the defenses of trees, despite their recovery from drought stress (Creeden and others

2014, Raffa and others 2008). The northward range expansion of mountain pine beetle into the Canadian boreal forest and the extensive outbreaks in high-elevation five-needle pines of the Western United States have been attributed to warming (Carroll and others 2004, Logan and others 2010). Drought may have played a role in initiating these outbreaks and facilitating population increase to levels that killed healthy trees, but warming was the primary reason for these epidemics occurring in historically unknown or rare locations.

In contrast to aggressive beetle species, successful attacks of less aggressive bark beetles in the Western United States are limited to stressed hosts, and as such outbreaks are closely tied to drought and associated warm temperatures. The pinyon pine (*Pinus edulis* and *P. monophylla*) mortality caused by severe drought and pinyon ips is an excellent example. In the early 2000s, a “global-change-type drought” occurred in the Southwest in which extremely dry conditions occurred during a period of time when conditions were already warmer than in the past (Breshears and others 2005). *Ips* populations increased in conjunction with the drought and warm temperatures, and together with extreme tree physiological stress, caused mortality in millions of hectares of pinyon pine stands (Breshears and others 2005, Meddens and others 2012, Raffa and others 2008). When wetter conditions returned after several years, *Ips* populations declined (Raffa and others 2008). *Ips* lack the positive feedback mechanisms that allow for increased population growth with increased beetle numbers. Outbreaks of other bark beetle species, such as Douglas-fir beetle (*Dendroctonus pseudotsugae*), western balsam bark beetle (*Dryocoetes confusus*), fir engraver (*Scolytus ventralis*), and pine engraver (*Ips pini*), also caused extensive tree mortality in the early 2000s (Meddens and others 2012), although the role of drought is less clear.

The role of drought in the Western United States in influencing outbreaks of another class of insects—defoliators—is less understood. The primary defoliating insect of the West is western spruce budworm, which attacks multiple conifer species and periodically erupts, causing widespread tree damage and death. Budworm outbreaks have been linked to drought conditions that cause tree stress or are related to the important synchrony of caterpillar development and foliage phenology (Campbell and others 2006, Thomson and others 1984, Williams and Liebhold 1995a), although other studies have found that outbreaks

were associated with wetter conditions at the end of droughts that increase food resources (Flower and others 2014, Ryerson and others 2003, Swetnam and Lynch 1993). Multiple drought influences may be important, and they may vary regionally (Lynch 2012). For many defoliators, either drought is not important or its influence is unknown (Jactel and others 2012).

Pathogens are also important forest disturbance agents in the Western United States. As described earlier, some forest pathogens important in the West, such as those causing *Phytophthora* root rot, sudden oak death, *Dothistroma* needle blight, Swiss needle cast, and white pine blister rust, prefer moist conditions, thereby suggesting that drought plays a limiting role in these outbreaks (Jactel and others 2012, Sturrock and others 2011). Other fungal pathogens, such as those causing *Armillaria* root disease or various cankers, are indirectly affected by drought through increasing stress of host trees, implying that drought leads to more favorable conditions for outbreaks (Jactel and others 2012, Klopfenstein and others 2009, Sturrock and others 2011).

In the East

The role of drought in insect and fungal pathogen outbreaks is less clear in mesic forests of the Eastern United States than in the more arid regions of the Western United States, where drought has been linked to outbreaks of certain insects and diseases. The generally mild droughts of the Eastern United States (i.e., compared to portions of the Western United States) can increase the concentration of plant secondary metabolites that are important for resisting pathogens and insects (Hale and others 2005, Herms and Mattson 1992, Lombardero and others 2000).

Hardwood forests—Water stress of broad-leaved hardwood trees generally decreases water content and increases concentrations of soluble nitrogen and secondary metabolites in plant tissues, but these physiological changes may have positive, negative, or neutral effects on insect growth and fitness depending on the species (Hale and others 2005, Huberty and Denno 2004, Mattson and Haack 1987, Scriber 1977). For example, experimental water stress of black poplar led to reduced concentrations of total phenolic glycosides and reduced feeding performance of gypsy moth, but not white-marked tussock moth (Hale and others 2005). Chakraborty and others (2013) found no effects of drought in either of two ash species on constitutive or induced phenolics in the phloem. Roth and others (1997) reported a rare case of

drought-induced reductions in defensive compounds in quaking aspen.

In the East, aspen and poplar, maple, oak, hickory, beech, ash, and birch are all widely distributed, important components of mixed-hardwood forests. These forests are periodically subjected to outbreaks from forest tent caterpillar, gypsy moth, winter moth, and other defoliators, and significant effects on forest composition and structure are expected with the arrivals of the nonnative emerald ash borer (*Agrilus planipennis*), thousand cankers disease, and laurel wilt into the region. The impacts of these hardwood pests seem largely unrelated to drought (Olatinwo and others 2013, Weed and others 2013). One exception could be the recent epidemic of red oak mortality in the Ozark Mountains (Jones and others 2014) that has been associated with drought and the wood-boring beetle, *Enaphalodes rufulus* (Haavik and Stephen 2010). However, even this case is not simple to interpret due to potentially confounding influences of forest age, structure, and *Armillaria* root rot (Wang and others 2007).

Conifer forests—Insects and pathogens are also continuous threats to the health of conifer forests in the Eastern United States. The southern pine beetle (*Dendroctonus frontalis*) is the most important disturbance agent of southern pine ecosystems; white pine blister rust is a perennial stress on eastern white pine (*Pinus strobus*); invasive adelgids threaten the persistence of mature hemlock and Fraser fir (*Abies fraseri*) stands across the mid-Atlantic; and eastern spruce budworm outbreaks periodically disturb the eastern boreal forest. Early hypotheses suggested that water stress would improve host quality to herbivores by favoring the balance of nutrients that are important for insect growth (Mattson and Haack 1987). However, oleoresin is the primary mechanism in conifers conferring resistance to herbivores and especially bark beetles (Raffa and Berryman 1983), and oleoresin flow and its chemical composition are key determinants of bark beetle success (Lombardero and others 2000, Lorio 1986, Raffa and others 2005). There is a pervasive suggestion in the scientific literature and among forest health managers that drought stress compromises tree defenses to a point where outbreaks of aggressive species such as southern pine beetle are permitted, but the growing, albeit small body of scientific evidence indicates that constitutive resin defenses actually increase at the moderate levels of drought stress that occur in the Eastern United States (Dunn and Lorio

1993, Lombardero and others 2000, Lorio and others 1995, Reeve and others 1995).

Resin flow in loblolly pine (*Pinus taeda*), the most abundant pine of the Southeastern United States, increases significantly under conditions of moderate water deficit (Dunn and Lorio 1993, Lombardero and others 2000, Reeve and others 1995), and does not decrease until drought is extreme (Lorio and others 1995). This matches expectations derived from the GDBH, which we describe in earlier sections (Lorio 1986, Lorio and others 1982). Resin flow of loblolly pine tends to be highest during seasonal periods of suboptimal growth, such as under moderate water stress (Lombardero and others 2000). Studies of conifers from other regions also show that moderate drought can increase some tree defensives. For example, foliar tannins, another class of important phenolic anti-herbivore defenses, had a nonlinear response to soil water deficits with greatest concentrations in Douglas-fir needles occurring at moderate water stress (Horner 1990). In Europe, drought stress generally increased the concentrations of several individual monoterpenes and resin acids in

the woody tissues and needles of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) (Turtola and others 2003).

The hypothesis that drought triggers outbreaks of southern pine beetle has been under investigation for nearly a century (Dunn and Lorio 1993, Hodges and Lorio 1975, Lorio 1986, Lorio and others 1995, McNulty and others 1997, Reeve and others 1995, St. George 1930, Turchin and others 1991). However, drought tends to increase defenses of southern pines rather than decrease them (above). Furthermore, analyses of time series data have failed to reveal the expected relations between drought and southern pine beetle fluctuations (McNulty and others 1997, Turchin and others 1991); if anything, southern pine beetle outbreaks have been positively correlated with rainfall (Duehl and others 2011, Gumpertz and Pye 2000). This correlation is consistent with a broad pattern in which the secondary colonizers of dying trees benefit from drought, rather than the aggressive tree-killing species such as southern pine beetle (Jactel and others 2012). Diverse evidence argues against the hypothesis that southern pine beetle outbreaks are promoted by drought (fig. 6.4).



Figure 6.4—A local infestation (“spot”) of southern pine beetle (*Dendroctonus frontalis*) in east Texas. In the Eastern United States, southern pine beetles are a dominant source of disturbance in pine forests from New Jersey to Texas. Epidemics are believed to be unrelated to drought, but instead are most prevalent in pine forests that are fast growing, unthinned, and overstocked. (photo by Ronald Billings, Texas A&M Forest Service)

Similar to hardwood species in the Eastern United States, we lack strong evidence that sustained population outbreaks of insects and pathogens on eastern conifers are triggered by water stress or drought. Whereas water stress and drought are often cited as a predisposing factor to pest and pathogen outbreaks (Edmonds and others 2000), evidence for a strong role of drought on insect and pathogen outbreaks in forests of the Eastern United States is not yet convincing. The few examples of positive correlations between spatial and temporal outbreak patterns of insects and pathogens in the Eastern United States (Haavik and Stephen 2010) may be spurious or associated with other mechanisms. One such mechanism could be the powerful effects of warming temperatures on developmental rates and fitness of insects and pathogens that together with reduced precipitation create drought-like conditions (Weed and others 2013).

Anticipating Impacts: Predictions of Future Drought-Related Insect and Disease Impacts

In the West

Future anthropogenic-induced changes to the Earth's climate are likely to include increases in temperature and significant changes in precipitation patterns. Across the Western United States, temperature increases are projected to exceed global mean increases and more frequent extreme weather events, such as droughts, are expected (Levinson and Fettig 2014). Winter precipitation is projected to increase in some areas, but to decrease by up to 20 percent in the Southwestern United States by the 2050s. Summer precipitation is projected to decrease by 10–30 percent throughout the West by the 2050s (Fettig and others 2013). Observed increases in temperature have been greater in winter and spring than in summer (IPCC 2007, Melillo and others 2014). Warming during winter will further exacerbate recent declines in snowpack. As such, many forests in the Western United States will experience further increases in drought stress whether associated with reductions in precipitation or increases in evaporative demand associated with elevated temperature. Williams and others (2013) reported that if the vapor-pressure deficit continues increasing in the Southwestern United States, as projected by climate models, by the 2050s mean forest drought stress will exceed that of the most severe droughts in the past 1,000 years.

As might be expected, an increase in the frequency and severity of some biotic disturbances is expected as a result of more intense drought stress and increasing temperature (Allen and others 2010, Bentz and others 2010, Fettig and others 2013, Sturrock and others 2011, Weed and others 2013). However, our understanding of these relationships in the Western United States is largely limited to select insects in conifer forests. Among insects, range expansions and increases in the frequency and severity of outbreaks by some bark beetle species have already been documented (Bentz and others 2009), and further changes are anticipated (Bentz and others 2010, Fettig and others 2013, Sambaraju and others 2012, Sturrock and others 2011, Williams and Liebhold 2002). It is thought that increasing temperatures and drought stress, exacerbated by high densities of suitable and susceptible hosts (Fettig and others 2007, Hicke and Jenkins 2008), have contributed to the positive feedbacks necessary for these range expansions and epidemic populations to occur (Raffa and others 2008). For example, Preisler and others (2012) reported that in addition to beetle pressure, climate variables with the largest effect on the odds of a mountain pine beetle outbreak exceeding a certain size in Oregon and Washington were minimum winter temperature and drought in the current and previous year. Precipitation levels the year prior to an outbreak had a positive effect on outbreak size, perhaps because of the positive influence of precipitation on the production of phloem, which is where larvae feed. While increases in the impact of several bark beetle species are expected with future climate change (Bentz and others 2010), it is important to note that significant areas of the Western United States have already suffered high levels of tree mortality due to bark beetles (Meddens and others 2012), and susceptible hosts may be currently depleted in these areas, which will dampen future outbreaks for decades.

Our understanding of the anticipated impacts of defoliators on drought-stressed forests in the Western United States is limited. This partially results from inconsistencies in the direction and magnitude of their responses to drought (see earlier), and because bark beetle outbreaks and wildfire have overshadowed the impacts of defoliators as primary disturbances associated with drought-stressed forests in the West, particularly in recent decades. Williams and Liebhold (1995a, 1995b) investigated potential changes in spatial distribution of outbreaks of western spruce budworm (fig. 6.5) in eastern Oregon under several climatic change scenarios. With an increase of 2 °C, the



Figure 6.5—Western spruce budworm (*Choristoneura occidentalis*) defoliation. Some experts suggest that defoliation due to western spruce budworm will decline in the future due to increasing drought. However, there is considerable uncertainty about the role of drought on the performance of defoliators and their influence on drought-stressed forests in the United States. (photo by Lia Spiegel, U.S. Department of Agriculture, Forest Service)

projected defoliated area decreased relative to ambient conditions, as was projected when temperature was increased and precipitation decreased. However, with an increase in temperature and precipitation, the defoliated area was projected to increase. Despite this, considerable uncertainty remains about the future impacts of defoliators to drought-stressed forests in the Western United States (Weed and others 2013).

Outbreaks of forest diseases caused by native and introduced pathogens are generally thought to become more frequent and severe as a result of climate change (Sturrock and others 2011). However, diseases caused by pathogens directly affected by climate (e.g., needle blights) are projected to have reduced impacts under warmer and drier conditions. These groups of pathogens may cause disease in healthy hosts if the pathogen's environmental requirements are met, many of which require moist conditions (Sturrock and others 2011).

In the East

In the Eastern United States, effects of drought on biotic disturbance in forests are anticipated to be modest relative to effects from warming and introductions of nonnative insects and pathogens (Duehl and others 2011, Olatinwo and others 2013, Weed and others 2013). In the Northeastern United States, droughts have been historically rare and are projected to remain

low in intensity through this century (Hayhoe and others 2007). Since projections of future changes in precipitation for the Eastern United States are generally flat (Ryan and Vose 2012), the eastern forests that are most likely to experience drought in the future are those already subject to occasional droughts (e.g., forests near the edge of the Great Plains). Forests with red oak may be at greater risk because drought can permit increased mortality from wood-boring beetles (Haavik and Stephen 2010) and *Armillaria* species (Clinton and others 1993). Impacts on ash from the emerald ash borer could be exacerbated by drought (Chakraborty and others 2013). There may be a tendency for drought to increase the susceptibility of hardwood trees to wood-boring beetles (Dunn and others 1990, Muilenburg and Herms 2012). Fortunately, the extensive and productive pine forests of the Southeastern United States do not seem dangerously vulnerable to drought-triggered outbreaks of tree-killing bark beetles (Duehl and others 2011, Duerr and Mistretta 2013, McNulty and others 1997, Weed and others 2013).

Summary and Research Needs for Insects and Pathogens

Bark Beetles

Our review of impacts of drought on bark beetle performance and tree mortality in U.S. forests is consistent with predictions of plant carbon allocation models (Herms and Mattson 1992, McDowell and others 2011) that suggest moderate drought/tree water stress can reduce bark beetle population performance and subsequent tree mortality, whereas intense drought increases bark beetle performance and tree mortality (fig. 6.6). Figure 6.6 provides a framework for understanding the apparent difference in the effect of drought on bark beetle performance and tree damage between eastern and western forests.

Most eastern forests have considerably higher precipitation and less severe drought than western forests, especially compared to forests east of the Sierra Nevada and Cascade Mountain crests and west of the Great Plains. Current evidence strongly suggests that the relatively moderate droughts that occur in eastern conifer forests do not increase performance and tree mortality from native bark beetles, but instead may reduce performance and impact. Because western arid forests are more water-limited than eastern mesic forests and at times experience more severe drought, insect-caused tree mortality has been more often

correlated with severe drought in the Western United States. The “global-change-type drought” that occurred in the Southwestern United States in the early 2000s (Breshears and others 2005) is an excellent example and provided an opportunity to examine the role of drought and temperature in bark beetle outbreak potential. We suggest that future research on the role of drought in bark beetle outbreaks should focus on:

- the relative role of temperature in drought-induced outbreaks of bark beetles;
- identification of species which are capable of self-perpetuating outbreaks after drought subsides;
- the level of drought-associated tree mortality that would occur without bark beetle attacks;
- the effectiveness of manipulating forest composition and structure to reduce drought stress and bark beetle attacks in semi-arid forests; and
- the level of drought intensity in pine forests of the Eastern United States that would shift the role of drought in beetle outbreaks from a negative to a positive driver (fig. 6.6).

Defoliators

In contrast to bark beetles, our review found inconsistent impacts of drought on defoliator performance and tree damage. Whereas individual studies have reported both positive and negative

impacts of drought on defoliator performance and damage, cumulative results over many studies are too variable to allow generalization of drought impacts on this insect guild. While substantial inconsistency and uncertainty exist in the response of defoliators to drought, it is clear from climate-change projections (Melillo and others 2014, Ryan and Vose 2012) that forest defoliators will increasingly interact with drought-stressed hosts. As such, we underscore the need for a greater understanding of the impacts of drought on defoliators.

Sapfeeders

The collective response of tree sapfeeders to drought is nonlinear based on available evidence (fig. 6.7). Sapfeeders typically have the highest performance and cause the most tree damage at moderate drought intensity, and when periods of intense drought are interrupted by precipitation, resulting in plant tissues enriched with nitrogen and with high turgor.

Fungal Pathogens

Our review highlights a complex response of tree fungal pathogens to drought (fig. 6.8). The overall consensus of our review and others is that some forest pathogens will become less severe during drought whereas some diseases will become more severe (Desprez-Loustau and others 2006, Jactel and others 2012, Klopfenstein and others 2009, Sturrock and others 2011). Specifically, available evidence suggests that drought reduces performance and damage by primary pathogens that infect healthy trees and foliage,

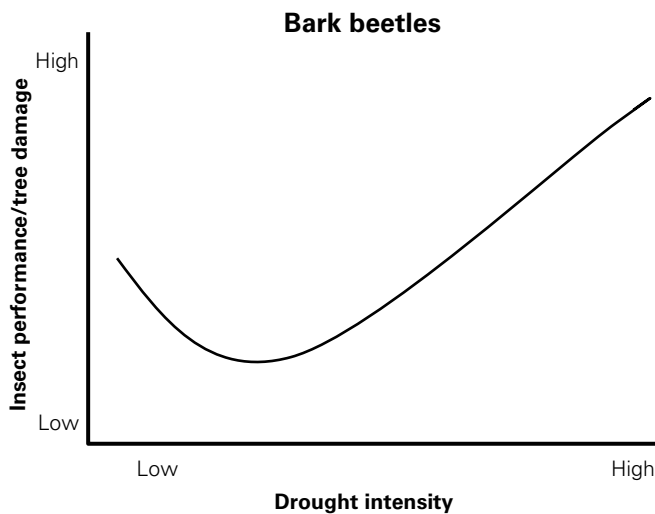


Figure 6.6—Nonlinear response trend of bark beetle performance and tree damage to drought intensity based on our literature review and tree carbon allocation frameworks.

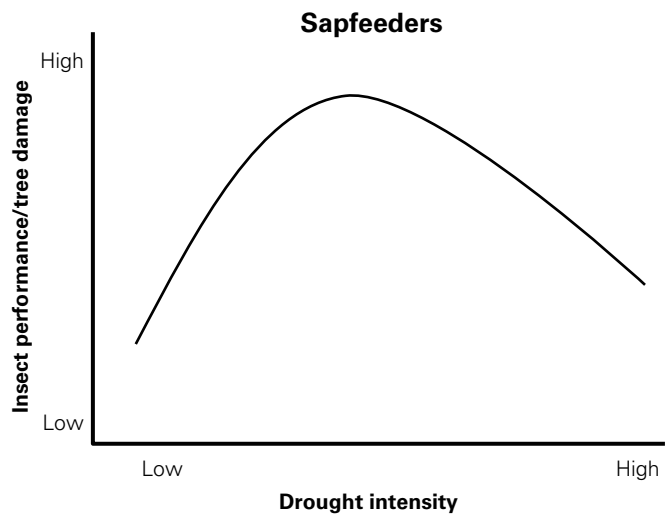


Figure 6.7—Nonlinear response trend of sapfeeder performance and tree damage to drought intensity for U.S. forests based on our literature review.

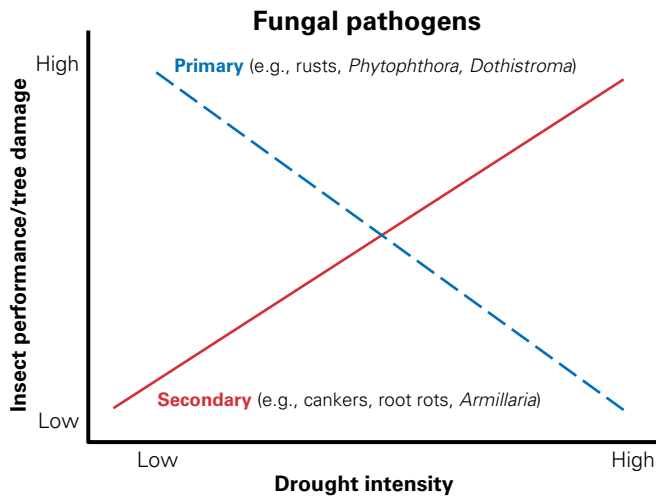


Figure 6.8—Response trends of performance and tree damage by primary (dashed blue line) and secondary (solid red line) fungal pathogens to drought intensity for U.S. forests based on our literature review.

such as rusts (*Phytophthora* and *Dothistroma*) and pathogens whose performance is directly tied to high availability of moisture. In contrast, drought typically increases performance and damage by secondary pathogens that colonize stressed trees and woody organs, such as stem cankers, root rots, and *Armillaria*. The response trends in figure 6.8, however, are based on knowledge about the role of available water on fungal performance and spread, and a few empirical studies of impacts of drought or tree water stress on pathogen performance and damage. There is a strong need for empirical data and predictive tools on how changes in drought frequency and severity will alter forest fungal pathogens. Future research using these data to model and predict forest disease incidents for forest ecosystems under different drought conditions would be useful for management (Klopfenstein and others 2009), as it will give forest managers additional foresight into potential outbreak conditions of the future.

Conclusions

It is clear that drought and associated temperature changes can significantly influence outbreaks of forest insects and pathogens, both positively and negatively, and that both drought and temperature are projected to increase in many parts of the United States in future years. In this review, we highlight specific research on insect and pathogens that is needed to better predict future climate-related impacts to forest ecosystems across the United States. Because eastern forests are

generally less limited by water availability than western forests, less is known about the potential for drought impacts on insects and their role in tree mortality in eastern forests. Climate-change projections, however, strongly suggest an increase in temperature in eastern forests, which will intensify drought even if precipitation does not change (Ryan and Vose 2012). Interactions between drought and biotic disturbances are crucial in determining continental-scale forest productivity, ecotones between forests and shrubland or grasslands, carbon balance, and many other forest ecosystem services. Emerging and new knowledge of the role of drought and associated temperature changes in forest insect and pathogen-caused tree mortality will be essential components of models and frameworks for future forest management planning.

Literature Cited

- Allen, C.D.; Macalady, A.K.; Chenchouni, H. [and others]. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*. 259: 660–684.
- Anderegg, W.R.L.; Callaway, E.S. 2012. Infestation and hydraulic consequences of induced carbon starvation. *Plant Physiology*. 159: 1866–1874.
- Arango-Velez, A.; González, L.M.G.; Meents, M.J. [and others]. 2014. Influence of water deficit on the molecular responses of *Pinus contorta* × *Pinus banksiana* mature trees to infection by the mountain pine beetle fungal associate, *Grosmannia clavigera*. *Tree Physiology*. 34(11): 1220–1239.
- Awmack, C.; Leather, S. 2002. Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology*. 47: 817–844.
- Ayres, M.P.; Lombardero, M.J. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Science of the Total Environment*. 262: 263–286.
- Barnes, I.; Crous, P.W.; Wingfield, B.D.; Wingfield, M.J. 2004. Multigene phylogenies reveal that red band needle blight of *Pinus* is caused by two distinct species of *Dothistroma*, *D. septosporum* and *D. pini*. *Studies in Mycology*. 50: 551–565.
- Bega, R.V. 1978. White pine blister rust. *Agric. Handb.* 521. In: Bega R.V., ed. *Diseases of Pacific Coast Conifers*. Washington, DC: U.S. Department of Agriculture, Forest Service: 94–98.
- Bentz, B.J.; Allen, C.D.; Ayres, M.P. [and others]. 2009. Bark beetle outbreaks in western North America: causes and consequences. Salt Lake City, UT: University of Utah Press. 42 p.
- Bentz, B.J.; Mullins, D.E. 1999. Ecology of mountain pine beetle (Coleoptera: Scolytidae) cold hardening in the Intermountain West. *Environmental Entomology*. 28: 577–587.
- Bentz, B.J.; Régnière, J.; Fettig, C.J. [and others]. 2010. Climate change and bark beetles of the Western United States and Canada: direct and indirect effects. *Bioscience*. 60: 602–613.
- Bentz, B.; Vandygriff, J.; Jensen, C. [and others]. 2014. Mountain pine beetle voltinism and life history characteristics across latitudinal and elevational gradients in the Western United States. *Forest Science*. 60: 434–449.

- Berg, E.E.; Henry, J.D.; Fastie, C.L. [and others]. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes. *Forest Ecology and Management*. 227: 219–232.
- Bevercombe, G.P.; Rayner A.D.M. 1980. Diamond-bark diseases of sycamore in Britain. *New Phytologist*. 86: 379–382.
- Björkman, C. 2000. Interactive effects of host resistance and drought stress on the performance of a gall-making aphid living on Norway spruce. *Oecologia*. 123: 223–231.
- Blodgett, J.T.; Kruger, E.L.; Stanosz, G.R. 1997. Effects of moderate water stress on disease development by *Sphaeropsis sapinea* on red pine. *Phytopathology*. 87: 422–428.
- Bolton, M.D. 2009. Primary metabolism and plant defense—fuel for the fire. *Molecular Plant-Microbe Interactions*. 22: 487–497.
- Breshears, D.D.; Cobb, N.S.; Rich, P.M. [and others]. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences*. 102: 15,144–15,148.
- Breshears, D.D.; Myers, O.B.; Meyer, C.W. [and others]. 2009. Tree die-off in response to global-change-type drought: mortality insights from a decade of plant water-potential measurements. *Frontiers in Ecology and the Environment*. 7: 185–189.
- Brodribb, T.J.; Cochard, H. 2009. Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant Physiology*. 149: 575–584.
- Bulman, L.S. 1993. *Cyclaneusma* needle-cast and *Dothistroma* needle blight in New Zealand pine plantations. *New Zealand Forestry*. 38: 21–24.
- Campbell, R.; Smith, D.J.; Arsénault, A. 2006. Multicentury history of western spruce budworm outbreaks in interior Douglas-fir forests near Kamloops, British Columbia. *Canadian Journal of Forest Research*. 36: 1758–1769.
- Carmona, D.; Lajeunesse, M.J.; Johnson, M.T.J. 2011. Plant traits that predict resistance to herbivores. *Functional Ecology*. 25: 358–367.
- Carroll, A.L.; Taylor, S.W.; Régnière, J.; Safranyik, L. 2004. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. In: Shore, T.L.; Brooks, J.E.; Stone, J.E., eds. Mountain pine beetle symposium: challenges and solutions. Kelowna, British Columbia: October 30–31, 2003. Information Report BC-X-399. Victoria, BC: Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre: 223–232.
- Cates, R.; Alexander, H. 1982. Host resistance and susceptibility. In: Mitton, J.; Sturgeon, K. eds. Bark beetles of North American conifers: a system for study of evolutionary biology. Austin, TX: University of Texas Press: 212–260.
- Chakraborty, S.; Whitehill, J.G.A.; Hill, A.L. [and others]. 2013. Effects of water availability on emerald ash borer larval performance and phloem phenolics of Manchurian and black ash. *Plant, Cell & Environment*. 37: 1009–1021.
- Chapman, T.B.; Veblen, T.T.; Schoennagel, T. 2012. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. *Ecology*. 93: 2175–2185.
- Clinton, B.; Boring, L.; Swank, W. 1993. Canopy gap characteristics and drought influences in oak forests of the Coweeta Basin. *Ecology*. 74: 1551–1558.
- Coody, A.R.; Fettig, C.J.; Nowak, J.T.; Berisford, C.W. 2000. Previous tip moth infestations predispose trees to heavier attacks in subsequent generations. *Journal of Entomological Science*. 35: 83–85.
- Craig, T.P.; Wagner, M.R.; McCullough, D.G.; Frantz, D.P. 1991. Effects of experimentally altered plant moisture stress on the performance of *Neodiprion* sawflies. *Forest Ecology and Management*. 39: 247–261.
- Creeden, E.P.; Hicke, J.A.; Buotte, P.C. 2014. Climate, weather, and recent mountain pine beetle outbreaks in the Western United States. *Forest Ecology and Management*. 312: 239–251.
- Dale, V.H.; Joyce, L.A.; McNulty, S. [and others]. 2001. Climate change and forest disturbances. *Bioscience*. 51: 723–734.
- DeRose, R.J.; Long, J.N. 2012. Drought-driven disturbance history characterizes a southern Rocky Mountain subalpine forest. *Canadian Journal of Forest Research*. 42: 1649–1660.
- Desprez Loustau, M.-L.; Marçais, B.; Nageleisen, L.-M. [and others]. 2006. Interactive effects of drought and pathogens in forest trees. *Annals of Forest Science*. 63: 597–612.
- Dodd, R.S.; Hüberli, D.; Mayer, W. [and others]. 2008. Evidence for the role of synchronicity between host phenology and pathogen activity in the distribution of sudden oak death canker disease. *New Phytologist*. 179: 505–514.
- Domec, J.-C.; Rivera, L.N.; King, J.S. [and others]. 2013. Hemlock woolly adelgid (*Adelges tsugae*) infestation affects water and carbon relations of eastern hemlock (*Tsuga canadensis*) and Carolina hemlock (*Tsuga caroliniana*). *New Phytologist*. 199: 452–463.
- Duehl, A.J.; Koch, F.H.; Hain, F.P. 2011. Southern pine beetle regional outbreaks modeled on landscape, climate and infestation history. *Forest Ecology and Management*. 261: 473–479.
- Duerr, D.A.; Mistretta, P.A. 2013. Invasive pests—insects and diseases. In: Wear, David N.; Greis, John G., eds. 2013. The Southern Forest Futures Project: technical report. Gen. Tech. Rep. SRS-178. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 457–508.
- Dunn, J.P.; Lorio, P.L. 1993. Modified water regimes affect photosynthesis, xylem water potential, cambial growth, and resistance of juvenile *Pinus taeda* L. to *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Environmental Entomology*. 22: 948–957.
- Dunn, J.P.; Potter D.A.; Kimmerer, T.W. 1990. Carbohydrate reserves, radial growth, and mechanisms of resistance of oak trees to phloem-boring insects. *Oecologia*. 83: 458–468.
- Dury, S.J.; Good, J.E.G.; Perrins, C.M. [and others]. 1998. The effects of increasing CO₂ and temperature on oak leaf palatability and the implications for herbivorous insects. *Global Change Biology*. 4: 55–61.
- Edmonds, R.L.; Agee, J.K.; Gara, R.I. 2000. Forest health and protection. Boston, MA: McGraw-Hill. 630 p.
- Ehleringer, J.R.; Cook, C.S.; Tieszen, L.L. 1986. Comparative water use and nitrogen relationships in a mistletoe and its host. *Oecologia*. 68: 279–284.
- Evangelista, P.H.; Kumar, S.; Stohlgren, T.J.; Young, N.E. 2011. Assessing forest vulnerability and the potential distribution of pine beetles under current and future climate scenarios in the Interior West of the US. *Forest Ecology and Management*. 262: 307–316.
- Fettig, C.J.; Klepzig, K.D.; Billings, R.F. [and others]. 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the Western and Southern United States. *Forest Ecology and Management*. 238: 24–53.

- Fettig, C.J.; Reid, M.L.; Bentz, B.J. [and others]. 2013. Changing climates, changing forests: a western North American perspective. *Journal of Forestry*. 111: 214–228.
- Flower, A.; Gavin, D.G.; Heyerdahl, E.K. [and others]. 2014. Drought predisposes pinyon-juniper woodlands to insect attacks in the interior Pacific Northwest: a multi-century dendrochronological record. *Forest Ecology and Management*. 324: 16–27.
- Franceschi, V.R.; Krokene, P.; Christiansen, E.; Krokling, T. 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytologist*. 167: 353–376.
- Gaylord, M.L.; Kolb, T.E.; Pockman, W.T. [and others]. 2013. Drought predisposes pinyon-juniper woodlands to insect attacks and mortality. *New Phytologist*. 198: 567–578.
- Gaylord, M.L.; Kolb, T.E.; Wallin, K.F.; Wagner, M.R. 2007. Seasonal dynamics of tree growth, physiology, and resin defenses in a northern Arizona ponderosa pine forest. *Canadian Journal of Forest Research*. 37: 1173–1183.
- Gehring, C.A.; Whitham, T.G. 1992. Reduced mycorrhizae on *Juniperus monosperma* with mistletoe: the influence of environmental stress and tree gender on a plant parasite and a plant-fungal mutualism. *Oecologia*. 89: 298–303.
- Gilmore, A.R. 1977. Effects of soil moisture stress on monoterpenes in loblolly pine. *Journal of Chemical Ecology*. 3: 667–676.
- Gonda-King, L.; Gomez, S.; Martin, J.L. [and others]. 2014. Tree responses to an invasive sap-feeding insect. *Plant Ecology*. 215: 297–304.
- Gonthier, P.; Nicoletti, G.; Linzer, R., [and others]. 2007. Invasion of European pine stands by a North American forest pathogen and its hybridization with a native interfertile taxon. *Molecular Ecology*. 16: 1389–1400.
- Gumpertz, L.; Pye, M. 2000. Logistic regression for southern pine beetle outbreaks with spatial and temporal autocorrelation. *Forest Science*. 46: 95–107.
- Haack, R.A.; Black, R.W.; Fink, F.T.; Mattson, W.J. 1988. Ultrasonic acoustic emissions from sapwood of eastern white pine, northern red oak, red maple, and paper birch: implications for bark- and wood-feeding insects. *Florida Entomologist*. 71: 427–440.
- Haavik, L.J.; Stephen, F.M. 2010. Historical dynamics of a native cerambycid, *Enaphalodes rufulus*, in relation to climate in the Ozark and Ouachita Mountains of Arkansas. *Ecological Entomology*. 35: 673–683.
- Hajek, A.E. 1999. Pathology and epizootiology of *Entomophaga maimaiga* infections in forest lepidoptera. *Microbiology and Molecular Biology Reviews*. 63: 814–835.
- Hale, B.K.; Herms, D.A.; Hansen, R.C. [and others]. 2005. Effects of drought stress and nutrient availability on dry matter allocation, phenolic glycosides, and rapid induced resistance of poplar to two lymantriid defoliators. *Journal of Chemical Ecology*. 31: 2601–2620.
- Hanna, P.; Kulakowski, D. 2012. The influences of climate on aspen dieback. *Forest Ecology and Management*. 274: 91–98.
- Hansen, E.M.; Stone, J.K.; Capitano, B.R. [and others]. 2000. Incidence and impact of Swiss needle cast in forest plantations of Douglas-fir in coastal Oregon. *Plant Disease*. 84: 773–778.
- Hart, S.J.; Veblen, T.T.; Eisenhart, K.S. [and others]. 2014. Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. *Ecology*. 95: 930–939.
- Harvell, C.J.; Mitchell, C.E.; Ward, J.R. [and others]. 2002. Climate warming and disease risks for terrestrial and marine biota. *Science*. 296: 2158–2162.
- Hayhoe, K.; Wake, C.P.; Huntington, T.G. [and others]. 2007. Past and future changes in climate and hydrological indicators in the U.S. Northeast. *Climate Dynamics*. 28: 381–407.
- Hebertson, E.G.; Jenkins, M.J. 2008. Climate factors associated with historic spruce beetle (Coleoptera: Curculionidae) outbreaks in Utah and Colorado. *Environmental Entomology*. 37: 281–292.
- Hemming, J.D.; Lindroth, R.L. 1995. Intraspecific variation in aspen phytochemistry: effects on performance of gypsy moths and forest tent caterpillars. *Oecologia*. 103: 79–88.
- Henriksson, J.; Haukioja, E.; Ossipov, V. [and others]. 2003. Effects of host shading on consumption and growth of the geometrid *Epirrita autumnata*: interactive roles of water, primary and secondary compounds. *Oikos*. 103: 3–16.
- Herms, D.; Mattson, W. 1992. The dilemma of plants: to grow or defend. *The Quarterly Review of Biology*. 67: 283–335.
- Hicke, J.A.; Jenkins, J.C. 2008. Mapping lodgepole pine stand structure susceptibility to mountain pine beetle attack across the Western United States. *Forest Ecology and Management*. 255: 1536–1547.
- Hodar, J.A.; Zamora, R.; Castro, J. 2002. Host utilization by moth and larval survival of pine processionary caterpillar *Thaumetopoea pityocampa* in relation to food quality in three *Pinus* species. *Ecological Entomology*. 27: 292–301.
- Hodges, J.D.; Lorio, P.L. 1975. Moisture stress and composition of xylem oleoresin in loblolly pine. *Forest Science*. 21: 283–290.
- Horner, J.D. 1990. Nonlinear effects of water deficits on foliar tannin concentration. *Biochemical Systematics and Ecology*. 18: 211–213.
- Huberty, A.F.; Denno, R.F. 2004. Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology*. 85: 1383–1398.
- Intergovernmental Panel on Climate Change (IPCC). 2007. Climate change 2007: the physical science basis. In: Solomon, S.; Qin, D.; Manning, M., eds. Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge, United Kingdom and New York: Cambridge University Press. Available at: <http://ipcc-wg2.org/>. [Date accessed: October 5, 2015].
- Ireland, K.B.; Moore, M.M.; Fulé, P.Z. [and others]. 2014. Slow lifelong growth predisposes *Populus tremuloides* trees to mortality. *Oecologia*. doi: 10.1007/s00442-014-2951-5. [Published online: May 10, 2014].
- Jacquet, J.; Bosc, A.; O'Grady, A.; Jactel, H. 2014. Combined effects of defoliation and water stress on pine growth and non-structural carbohydrates. *Tree Physiology*. 34: 367–376.
- Jactel, H.; Petit, J.; Desprez-Loustau, M.-L. [and others]. 2012. Drought effects on damage by forest insects and pathogens: a meta-analysis. *Global Change Biology*. 18: 267–276.
- Jones, J.S.; Tullis, J.A.; Haavik, L.J. [and others]. 2014. Monitoring oak-hickory forest change during an unprecedented red oak borer outbreak in the Ozark Mountains: 1990 to 2006. *Journal of Applied Remote Sensing*. 8(1): 1–13. doi:10.1117/1.JRS.8.083687. [Published online: January 23, 2014].
- Kane, J.M.; Kolb, T.E. 2010. Importance of resin ducts in reducing ponderosa pine mortality from bark beetle attack. *Oecologia*. 164: 601–609.
- Kane, J.M.; Kolb, T.E. 2014. Short- and long-term growth characteristics associated with tree mortality in southwestern mixed-conifer forests. *Canadian Journal of Forest Research*. 44: 1227–1235.

- Kelsey, R.G.; Joseph, G. 2001. Attraction of *Scolytus unispinosus* bark beetles to ethanol in water-stressed Douglas-fir branches. *Forest Ecology and Management*. 144: 229–238.
- Kelsey, R.G.; Gallego, D.; Sánchez-García, F.J.; Pajares, J.A. 2014. Ethanol accumulation during severe drought may signal tree vulnerability to detection and attack by bark beetles. *Canadian Journal of Forest Research*. 44: 554–561.
- Kenaley, S.; Mathiasen, R.; Harner, E.J. 2008. Mortality associated with a bark beetle outbreak in dwarf mistletoe-infested ponderosa pine stands in Arizona. *Western Journal of Applied Forestry*. 23: 113–120.
- Kile, G.A.; McDonald, G.I.; Byler, J.W. 1991. Ecology and disease in natural forests. In: Shaw, C.G., III.; Kile, G.A., eds. *Armillaria root disease*. Agricultural Handbook No. 691. Washington, DC: U.S. Department of Agriculture, Forest Service: 102–121. Chapter 8.
- Kimmerer, T.; Kozłowski, T. 1982. Ethylene, ethane, acetaldehyde, and ethanol production by plants under stress. *Plant Physiology*. 69: 840–847.
- Kinloch, B.B., Jr. 2003. White pine blister rust in North America: past and prognosis. *Phytopathology*. 93: 1044–1047.
- Kliejunas, J.T.; Geils, B.W.; Glaeser J.M. [and others]. 2009. Review of literature on climate change and forest diseases of western North America. Gen. Tech. Rep. PSW-GTR-225. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 54 p.
- Klopfenstein, N.B.; Kim, M.-S.; Hanna, J.W. [and others]. 2009. Approaches to predicting potential impacts of climate change on forest disease: an example with *Armillaria* root disease. Research Paper RMRS-RP-76. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 10 p.
- Knutson, D.M. 1979. How parasitic plants induce disease in other plants. In: Horsfall, J.G.; Cowling, E.B., eds. *Plant disease, an advanced treatise. How pathogens induce disease*. New York: Academic Press: 293–312. Vol. 4.
- Knutson, D.M.; Toevs, W.J. 1972. Dwarf mistletoe reduces root growth of ponderosa pine seedlings. *Forest Science*. 18: 323–324.
- Kolb, T.E.; Dodds, K.A.; Clancy, K.M. 1999. Effect of western spruce budworm defoliation on the physiology and growth of potted Douglas-fir seedlings. *Forest Science*. 45: 280–291.
- Kopper, B.J.; Jakobi, V.N.; Osier, T.L.; Lindroth, R.L. 2002. Effects of paper birch condensed tannin on white-marked tussock moth (Lepidoptera: Lymantriidae) performance. *Environmental Entomology*. 31: 10–14.
- Koricheva, J.; Larsson, S.; Haukioja, E. 1998. Insect performance on experimentally stressed woody plants: a meta-analysis. *Annual Review of Entomology*. 43: 195–216.
- La Porta, N.; Capretti, P.; Thomsen, I.M. [and others]. 2008. Forest pathogens with higher damage potential due to climate change in Europe. *Canadian Journal of Plant Pathology*. 30: 177–195.
- Larsson, S. 1989. Stressful times for the plant stress—insect performances hypothesis. *Oikos*. 56: 277–283.
- Larsson, S.; Björkman C. 1993. Performance of chewing and phloem-feeding insects on stressed trees. *Scandinavian Journal of Forest Research*. 8: 550–559.
- Levinson, D.H.; Fettig, C.J. 2014. Climate change: overview of data sources, observed and predicted temperature changes, and impacts on public and environmental health. In: Pinkerton, K.E.; Rom, W., eds. *Climate change and global public health*. New York: Springer-Verlag: 31–49.
- Lieutier, F. 2004. Mechanisms of resistance in conifers and bark beetle attack; In: Wagner M.R.; Clancy, K.M.; Lieutier, F.; Paine, T.D., eds. *Mechanisms and deployment of resistance in trees to insects*. Boston: Kluwer Academic: 31–78.
- Logan, B.A.; Reblin, J.S.; Zonana, D.M. [and others]. 2013. Impact of eastern dwarf mistletoe (*Arceuthobium pusillum*) on host white spruce (*Picea glauca*) development, growth and performance across multiple scales. *Physiologia Plantarum*. 147: 502–513.
- Logan, J.A.; Macfarlane, W.W.; Willcox, L. 2010. Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. *Ecological Applications*. 20: 895–902.
- Lombardero, M.; Ayres, M.P.; Lorio, P.L.; Ruel, J. 2000. Environmental effects on constitutive and inducible resin defences of *Pinus taeda*. *Ecology Letters*. 3: 329–339.
- Lorio, P.L. 1986. Growth-differentiation balance: a basis for understanding southern pine beetle-tree interactions. *Forest Ecology and Management*. 14: 259–273.
- Lorio, P.L.; Mason, G.N.; Autry, G.L. 1982. Stand risk rating for the southern pine beetle: integrating pest management with forest management. *Journal of Forestry*. 80: 212–214.
- Lorio, P.L.; Stephen, F.M.; Paine, T.D. 1995. Environment and ontogeny modify loblolly pine response to induced acute water deficits and bark beetle attack. *Forest Ecology and Management*. 73: 97–110.
- Lusebrink, I.; Evenden, M.L.; Blanchet, F.G. [and others]. 2011. Effect of water stress and fungal inoculation on monoterpene emission from an historical and a new pine host of the mountain pine beetle. *Journal of Chemical Ecology*. 37: 1013–1026.
- Lynch, A.M. 2012. What tree-ring reconstruction tells us about conifer defoliator outbreaks. In: Barbosa, P.; Letourneau, D.; Agrawal, A., eds. *Insect outbreaks revisited*. Chichester, UK: John Wiley & Sons: 126–155.
- Major, E. 1990. Water stress in Sitka spruce and its effect on the green spruce aphid *Elatobium abietinum*. In: Watt, A.; Leather, S.; Hunter, M.; Kidd, N., eds. *Population dynamics of forest insects*. Andover, UK: Intercept Ltd.: 85–93.
- Manion, P.D. 1981. *Tree disease concepts*. Englewood Cliffs, NJ: Prentice-Hall. 402 p.
- Manter, D.K.; Kelsey, R.G. 2008. Ethanol accumulation in drought-stressed conifer seedlings. *International Journal of Plant Science*. 169: 361–369.
- Manter, D.K.; Reeser, P.W.; Stone, K. 2005. A climate-based model for predicting geographic variation in Swiss needle cast severity in the Oregon coast range. *Phytopathology*. 95: 1256–1265.
- Marias, D.E.; Meinzer, F.C.; Woodruff, D.R. [and others]. 2014. Impacts of dwarf mistletoe on the physiology of host *Tsuga heterophylla* trees as recorded in tree-ring C and O stable isotopes. *Tree Physiology*. 34(6): 595–607. doi: 10.1093/treephys/tpu046. [Published online: June 27, 2014].
- Mattson, W.J.; Haack, R.A. 1987. The role of drought in outbreaks of plant-eating insects. *BioScience*. 37: 110–118.
- Maxwell, D.L.; Kruger, E.L.; Stanosz, G.R. 1997. Effects of water stress on colonization of poplar stems and excised leaf disks by *Septoria musiva*. *Phytopathology*. 87: 381–388.
- McDowell, N.G.; Beerling, D.J.; Breshears, D.D. [and others]. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology and Evolution*. 26: 523–532.

- McDowell, N.; Pockman, W.T.; Allen, C.D. [and others]. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist*. 178: 719–739.
- McIntyre, G.A.; Jacobi, W.R.; Ramaley, A.W. 1996. Factors affecting *Cytospora* canker occurrence on aspen. *Journal of Arboriculture*. 22: 229–233.
- McMillin, J.D.; Wagner, M.R. 1995. Season and intensity of water stress: host-plant effects on larval survival and fecundity of *Neodiprion gillettei* (Hymenoptera: Diprionidae). *Environmental Entomology*. 24: 1251–1257.
- McMillin, J.D.; Wagner, M.R. 1996. Season and intensity of water stress effects on needle toughness of ponderosa pine. *Canadian Journal of Forest Research*. 26: 1166–1173.
- McNulty, S.; Lorio, P., Jr; Ayres, M.P.; Reeve, D. 1997. Predictions of southern pine beetle populations under historic and projected climate using a forest ecosystem model. In: Mickler, R.A.; Fox, S., eds. *The productivity and sustainability of southern forest ecosystems in a changing environment*. New York: Springer-Verlag: 617–634.
- Meddens, A.J.H.; Hicke, J.A.; Ferguson, C.A. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the Western United States. *Ecological Applications*. 22: 1876–1891.
- Meinzer, F.C.; Woodruff, D.R.; Shaw, D.C. 2004. Integrated responses of hydraulic architecture, water and carbon relations of western hemlock to dwarf mistletoe infection. *Plant, Cell & Environment*. 27: 937–946.
- Melillo, J.M.; Terese, T.C.; Richmond, T.C.; Yohe, G.W., eds. 2014. Climate change impacts in the United States: the third national climate assessment. U.S. Global Change Research Program. 841 p. doi:10.7930/J0Z31WJ2. [Date accessed: October 5, 2015].
- Miller, D.R.; Rabaglia, R.J. 2009. Ethanol and (-)- α pinene: attractant kairomones for bark and ambrosia beetles in the southeastern US. *Journal of Chemical Ecology*. 35: 435–448.
- Mopper, S.; Whitham, T.G. 1992. The plant stress paradox: effects on pinyon sawfly sex ratios and fecundity. *Ecology*. 73: 515–525.
- Muilenburg, V.L.; Herms D.A. 2012. A review of bronze birch borer (Coleoptera: Buprestidae) life history, ecology, and management. *Environmental Entomology*. 41: 1372–1385.
- Olatinwo, R.O.; Guo, S.; Fei, W. [and others]. 2013. Climate-induced changes in vulnerability to biological threats in the Southern United States. In: Vose, J.M.; Klepzig, K.D., eds. *Climate change adaptation and mitigation management options: a guide for natural resource managers in southern forest ecosystems*. New York: CRC Press: 127–172.
- Oliva, J.; Stenlid, J.; Martinez-Vilalta, J. 2014. The effect of fungal pathogens on the water and carbon economy of trees: implications for drought-induced mortality. *New Phytologist*. 203(4): 1028–1035. doi:10.1111/nph.12857. [Published online: May 13, 2014].
- Orozco, A.; Rada, F.; Azocar, A.; Goldstein, G. 1990. How does a mistletoe affect the water, nitrogen and carbon balance of two mangrove ecosystem species? *Plant, Cell & Environment*. 13: 941–947.
- Otrosina, W.L.; Garbelotto, M. 2010. *Heterobasidion occidentale* sp. nov. and *Heterobasidion irregulare* nom. nov.: a disposition of North American *Heterobasidion* species. *Fungal Biology*. 114: 16–25.
- Pallardy, S.G. 2008. *Physiology of woody plants*. New York: Academic Press. 464 p.
- Paoletti, E.; Danti, R.; Strati, S. 2001. Pre- and post-inoculation water stress affects *Sphaeropsis sapinea* canker length in *Pinus halepensis*. *Forest Pathology*. 31: 209–218.
- Pasquier-Barre, F.; Palasse, C.; Goussard, F. [and others]. 2001. Relationship of Scots pine clone characteristics and water stress to hatching and larval performance of the sawfly *Diprion pini* (Hymenoptera: Diprionidae). *Environmental Entomology*. 30: 1–6.
- Pielke, R.A., Sr.; Doesken, N.; Bliss, O. [and others]. 2005. Drought 2002 in Colorado: an unprecedented drought or a routine drought? *Pure and Applied Geophysics*. 162: 1455–1479.
- Preisler, H.K.; Hicke, J.A.; Ager, A.A.; Hayes, J.L. 2012. Climate and weather influences on spatial temporal patterns of mountain pine beetle populations in Washington and Oregon. *Ecology*. 93: 2421–2434.
- Prokopy, J.R.; Owens, E.D. 1983. Visual detection of plants by herbivorous insects. *Annual Review of Entomology*. 28: 337–364.
- Raffa, K.F.; Aukema, B.H.; Bentz, B.J. [and others]. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: dynamics of biome-wide bark beetle eruptions. *Bioscience*. 58: 501–518.
- Raffa, K.F.; Aukema, B.H.; Erbilgin, N. [and others]. 2005. Interactions among conifer terpenoids and bark beetles across multiple levels of scale: an attempt to understand links between population patterns and physiological processes. In: Romeo, J.T., ed. *Recent advances in phytochemistry: chemical ecology and phytochemistry of forest ecosystems*. London, United Kingdom: Elsevier: 79–118.
- Raffa, K.F.; Berryman, A.A. 1983. The role of host plant-resistance in the colonization behavior and ecology of bark beetles (Coleoptera, Scolytidae). *Ecological Monographs*. 53: 27–49.
- Reeve, J.D.; Ayres, M.P.; Lorio, P.L., Jr. 1995. Host suitability, predation, and bark beetle population dynamics. In: Cappuccino, N.; Price, P.W., eds. *Population dynamics: new approaches and synthesis*. San Diego, CA: Academic Press: 339–357.
- Roth, S.; McDonald, E.P.; Lindroth, R.L. 1997. Atmospheric CO₂ and soil water availability: consequences for tree-insect interactions. *Canadian Journal of Forest Research*. 27: 1281–1290.
- Rouault, G.; Candau, J.-N.; Lieutier, F. [and others]. 2006. Effects of drought and heat on forest insect populations in relation to the 2003 drought in western Europe. *Annals of Forest Science*. 63: 613–624.
- Ryan, M.G.; Vose, J.M. 2012. Effects of climatic variability and change. In: Vose, J.M.; Peterson, D.L.; Patel-Weyand, T. eds. *Effects of climatic variability and change on forest ecosystems: a comprehensive science synthesis for the U.S. forest sector*. Gen. Tech. Rep. PNW-GTR-870. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 7–95.
- Ryerson, D.E.; Swetnam, T.W.; Lynch, A.M. 2003. A tree-ring reconstruction of western spruce budworm outbreaks in the San Juan Mountains, Colorado, USA. *Canadian Journal of Forest Research*. 33: 1010–1028.
- Sala, A.; Carey, E.V.; Callaway, R.M. 2001. Dwarf mistletoe affects whole-tree water relations of Douglas fir and western larch primarily through changes in leaf to sapwood ratios. *Oecologia*. 126: 42–52.
- Sala, A.; Woodruff, D.; Meinzer, F. 2012. Carbon dynamics in trees: feast or famine? *Tree Physiology*. 32: 764–775.
- Sambaraju, K.R.; Carroll, A.L.; Zhu, J. [and others]. 2012. Climate change could alter the distribution of mountain pine beetle outbreaks in western Canada. *Ecography*. 35: 211–223.

- Sanguesa-Barreda, G.; Linares, J.C.; Camarero, J.J. 2012. Mistletoe effects on Scots pine decline following drought events: insights from within-tree spatial patterns, growth and carbohydrates. *Tree Physiology*. 32: 585–598.
- Sanguesa-Barreda, G.; Linares, J.C.; Camarero, J.J. 2013. Drought and mistletoe reduce growth and water-use efficiency of Scots pine. *Forest Ecology and Management*. 296: 64–73.
- Scriber, J.M. 1977. Limiting effects of low leaf-water content on the nitrogen utilization, energy budget, and larval growth of *Hyalophora cecropia* (Lepidoptera: Saturniidae). *Oecologia*. 28: 261–287.
- Shaw, C.G.; Kile, G.A. 1991. Armillaria root disease. *Agric. Handb.* 691. Washington, DC: U.S. Department of Agriculture, Forest Service. 233 p.
- Shaw, J.D.; Steed, B.S.; DeBlander, L.T. 2005. Forest Inventory and Analysis (FIA) annual inventory answers the question: what is happening to pinyon-juniper woodlands? *Journal of Forestry*. 103: 280–285.
- Sherriff, R.L.; Berg, E.E.; Miller, A.E. 2011. Climate variability and spruce beetle (*Dendroctonus rufipennis*) outbreaks in south-central and southwest Alaska. *Ecology*. 92: 1459–1470.
- St. George, R.A. 1930. Drought-affected and injured trees attractive to bark beetles. *Journal of Economic Entomology*. 23: 825–828.
- Stanton, S. 2007. Effects of dwarf mistletoe on climate response of mature ponderosa pine trees. *Tree-Ring Research*. 63: 69–80.
- Stewart, G.R.; Press, M.C. 1990. The physiology and biochemistry of parasitic angiosperms. *Annual Review of Plant Physiology and Molecular Biology*. 41: 127–151.
- Stone, J.K.; Coop, L.B.; Manter, D.K. 2008. Predicting effects of climate change on Swiss needle cast disease severity in Pacific Northwest forests. *Canadian Journal of Plant Pathology*. 30: 169–176.
- Sturrock, R.N.; Frankel, S.J.; Brown, A.V. [and others]. 2011. Climate change and forest diseases. *Plant Pathology*. 60: 133–149.
- Swetnam, T.W.; Lynch, A.M. 1993. Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecological Monographs*. 63: 399–424.
- Tague, C.L.; McDowell, N.G.; Allen, C.D. 2013. An integrated model of environmental effects on growth, carbohydrate balance, and mortality of *Pinus ponderosa* forests in the southern Rocky Mountains. *PLOS One*. 8(11): e80286. doi: 10.1371/journal.pone.0080286. [Published online: November 25, 2013].
- Tennakoon, K.U.; Pate, J.S. 1996. Effects of parasitism by a mistletoe on the structure and functioning of branches of its host. *Plant, Cell & Environment*. 19: 517–528.
- Thatcher, R.; Pichard, L. 1967. Seasonal development of the southern pine beetle in east Texas. *Journal of Economic Entomology*. 60: 656–658.
- Thomson, A.J.; Shepherd, R.F.; Harris, J.W.E.; Silversides, R.H. 1984. Relating weather to outbreaks of western spruce budworm, *Choristoneura occidentalis* (Lepidoptera, Tortricidae), in British Columbia. *Canadian Entomologist*. 116: 375–381.
- Thomson, A.J.; Shrimpton, D.M. 1984. Weather associated with the start of mountain pine beetle outbreaks. *Canadian Journal of Forest Research*. 14: 255–258.
- Thompson, S.E.; Levin, S.; Rodriguez-Iturbe, I. 2014. Rainfall and temperatures changes have confounding impacts on *Phytophthora cinnamomi* occurrence risk in the southwestern USA under climate change scenarios. *Global Change Biology*. 20: 1299–1312.
- Tikkanen, O.-P.; Lyytikäinen-Saarenmaa, P. 2002. Adaptation of a generalist moth, *Operophtera brumata*, to variable budburst of host plants. *Entomologia Experimentalis et Applicata*. 103: 123–133.
- Trần, J.K.; Ylioja, T.; Billings, R.F. [and others]. 2007. Impact of minimum winter temperatures on the population dynamics of *Dendroctonus frontalis*. *Ecological Applications*. 17: 882–899.
- Turchin, P.; Lorio, P.L.; Taylor, A.D.; Billings, R.F. 1991. Why do populations of southern pine beetles (Coleoptera, Scolytidae) fluctuate? *Environmental Entomology*. 20: 401–409.
- Turtola, S.; Manninen, A.-M.; Rikala, R.; Kainulainen, P. 2003. Drought stress alters the concentration of wood terpenoids in Scots pine and Norway spruce seedlings. *Journal of Chemical Ecology*. 29: 1981–1995.
- Van Arsdel, E.P.; Riker, A.J.; Patton, R.F. 1956. The effects of temperature and moisture on the spread of white pine blister rust. *Phytopathology*. 46: 307–318.
- Venette, R.C. 2009. Implication of global climate change on the destruction and activity of *Phytophthora ramorum*. In: McManus, K.A.; Gottschalk K.W., eds. *Proceedings of the 20th U.S. Department of Agriculture interagency research forum of invasive species*. Gen. Tech. Rep. NRS-P-51. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station: 58–59.
- Wagner, M.R.; Zhang, Z. 1993. Host plant traits associated with resistance of ponderosa pine to the sawfly, *Neodiprion fulviceps*. *Canadian Journal of Forest Research*. 23: 839–845.
- Wang, C.; Lu, Z.; Haithcoat, T.L. 2007. Using Landsat images to detect oak decline in the Mark Twain National Forest, Ozark Highlands. *Forest Ecology and Management*. 240: 70–78.
- Weed, A.S.; Ayres, M.P.; Hicke, J.A. 2013. Consequences of climate change for biotic disturbances in North American forests. *Ecological Monographs*. 83: 441–470.
- White, T.C.R. 1969. An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. *Ecology*. 50: 905–909.
- White, T.C.R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia*. 63: 90–105.
- Williams, A.P.; Allen, C.D.; Macalady, A.K. [and others]. 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change*. 3: 292–297.
- Williams, D.W.; Liebhold, A.M. 1995a. Forest defoliators and climatic change: potential changes in spatial distribution of outbreaks of western spruce budworm (Lepidoptera: Tortricidae) and gypsy moth (Lepidoptera: Lymantriidae). *Environmental Entomology*. 24: 1–9.
- Williams, D.W.; Liebhold, A.M. 1995b. Herbivorous insects and global change: potential changes in the spatial distribution of forest defoliator outbreaks. *Journal of Biogeography*. 22: 665–671.
- Williams, D.W.; Liebhold, A.M. 2002. Climate change and the outbreak ranges of two North American bark beetles. *Agricultural and Forest Entomology*. 4: 87–99.
- Worrall, J.J.; Rehfeldt, G.E.; Hamann, A. [and others]. 2013. Recent declines of *Populus tremuloides* in North America linked to climate. *Forest Ecology and Management*. 299: 35–51.
- Wood, S.L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. *Great Basin Naturalist Memoirs*. 6: 1-1356.
- Zweifel, R.; Bangerter, S.; Rigling, A.; Sterck, F.J. 2012. Pine and mistletoes: how to live with a leak in the water flow and storage system? *Journal of Experimental Botany*. 63(7): 2565–2578.

Fire and Drought

Jeremy S. Littell
David L. Peterson
Karen L. Riley
Yongqiang Liu
Charles H. Luce

J.S. Littell is a Research Ecologist, U.S. Geological Survey (USGS), U.S. Department of the Interior, Alaska Climate Science Center, Anchorage, AK 99508.

D.L. Peterson is a Research Biologist, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station (PNW), Pacific Wildland Fire Sciences Lab, Seattle, WA 98103.

K.L. Riley is a Research Geoscientist, University of Montana, Numerical Terradynamic Simulation Group, Missoula, MT 59808.

Y.-Q. Liu is a Research Meteorologist, U.S. Department of Agriculture, Forest Service, Southern Research Station (SRS), Center for Forest Disturbance Science, Athens, GA 30602.

C.H. Luce is a Research Hydrologist, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Boise, ID 83702.

Introduction and Historical Perspective

Historical and presettlement relationships between drought and wildfire have been well documented in much of North America, with forest fire occurrence and area burned clearly increasing in response to drought. Drought interacts with other controls (forest productivity, topography, and fire weather) to affect fire intensity and severity. Fire regime characteristics (area, frequency, severity) are the product of many individual fires, so both weather and climate—including short- and long-term droughts—are important. It is worth noting, however, that the factors controlling fire events and fire regimes are complex and extend beyond drought and climate alone, and so fire regimes and wildfires are affected by other variables from local-to-global scales. Fire history evidence from diverse climate regimes and forest ecosystems suggests that North American forest fire regimes were moderately to strongly controlled by climate prior to Euro-American settlement and subsequent fire exclusion and fire suppression (Flatley and others 2013, Hessl and others 2004, Heyerdahl and others 2002, Heyerdahl and others 2008, Swetnam 1990, Swetnam and Betancourt 1998, Weisberg and Swanson 2003). These presettlement fire histories indicate a relationship between low precipitation anomalies and widespread fire activity, especially in the Western United States. This is consistent with a regional depletion of soil and atmospheric moisture, which leads to low moisture in foliage and surface fuels and ultimately to the potential for widespread fire (Swetnam and Betancourt 1998). Some fire histories in the American Southwest also demonstrate a lagged relationship with above-average antecedent precipitation (Swetnam and Betancourt 1998) and/or cooler temperatures (Veblen and others 2000) in the year(s) prior to years of widespread fire. Most of these records are derived from fire-scarred trees that survived fire events and thus are primarily indicative of low- or mixed-severity fire regimes, although some work has focused also on evidence from high-severity fire regimes (Heyerdahl and others 2002).

In the mid- to late-20th century, relationships between area burned and climate parallel those in the fire history record. From 1980 forward, area burned on Federal lands was related to monthly Palmer Drought Severity Index (PDSI), and the sign and magnitude of the relationships were consistent with reconstructed fire histories (Westerling and others 2003). Littell and others (2009) documented ecologically and geographically

variable responses of area burned to year-of-fire climate, with area burned increasing with increased temperature, decreased precipitation, or anomalously low (negative) PDSI in most forests and in some nonforest vegetation. Area burned in nonforested systems is associated with drought, but in some fuel conditions and regions, stronger relationships exist between anomalously *high* antecedent precipitation (or positive PDSI) and area burned (Littell and others 2009). This body of evidence indicates that the role of drought in historical, and likely future, fire regimes is an important contingency that creates anomalously high potential for ignition, fire spread, and large fire events. However, drought is only one aspect of a broader set of controls on fire regimes, and by itself is insufficient to predict fire dynamics or effects. Whereas the relationships between fire occurrence or area burned and drought are well documented, the relationship between drought and fire severity is still emerging. Clear relationships between years with extensive fires and the proportion of area with high severity do not exist (Dillon and others 2011, Holden and others 2012); however, the years with more widespread fires show substantially less landscape and topographic controls on severity (Dillon and others 2011). For example, north-facing slopes might offer some degree of local protection during mild droughts, but even they become dry under extreme conditions, reducing fine-scale heterogeneity in vegetation consequences.

The conditions that affect fires after ignition, from initial spread to eventual extinguishment, exert the strongest control over fire behavior (Rothermel 1972) and thus the ultimate outcomes in terms of area burned and severity. Drought influences the likelihood of ignition and availability of fuels at multiple time scales, and shorter-term weather affects fuel moisture and propagation, but intensity and severity are also determined by other more local factors that interact with drought.

At long time scales (seasons to centuries or longer), moisture availability and drought affect fuel availability via controls on ecosystem characteristics and productivity, and at short time scales (seasons to years) via controls on fuel structure and flammability (Loehman and others 2014). Climate, therefore, acts to facilitate fire by both producing fuels through vegetation growth and making those fuels flammable. The paleoecological record indicates that on time scales of centuries to millennia, the tension between climatic controls on fuel availability and fuel flammability manifests as the fire regime, with fire responding to the limits of available fuels (vegetation) and vegetation responding to the

frequency, severity, and extent of fire resulting from changes in flammability (Prichard and others 2009, Whitlock and others 2010).

Climate exerts a strong control over fire, but other factors that affect fuel abundance, frequency of flammability, and propensity for ignition can affect fire regimes. Human management of landscapes and fuels, suppression of fire, and use of fire all exert control in tandem with the effects of climate (Moritz and others 2005). Collectively, the fire regime and how it changes through time are a function of fuels and how other factors affect their availability and flammability. Climate, management, and land use affect availability, flammability, continuity of fuels, and probability of ignition differently in different parts of the World. At the scale of seasons to decades, drought directly affects flammability and thus the frequency of conditions conducive to large fires and possibly the severity of those fires. At the scale of years to millennia, drought directly affects the distribution and abundance of vegetation and indirectly affects disturbances including fire.

Characterizing Drought: Metrics of Fire Risk

Which Drought Metrics Relate to Fire Risk?

Drought is not a necessary or sufficient condition for fire, because fires burn during conditions of normal seasonal aridity (e.g., dry summers that occur annually in California), and drought occurs without wildfires in the absence of ignitions. However, when drought occurs, both live and dead fuels can dry out and become more flammable, and probability of ignition increases along with rate of fire spread (Andrews and others 2003, Scott and Burgan 2005). If drought continues for a long period, the number of days with elevated probability of ignition and fire spread increases, raising the risk of widespread burning. Long droughts are not necessary to increase risk of large wildfires; anomalous aridity of 30 days or more is sufficient to dry fuels substantially in all size classes (Cohen and Deeming 1985, Riley and others 2013) as well as live fuels. Drought can therefore be defined in meteorological terms, or in relative terms with respect to hydrology or ecosystems (chapter 2).

Because drought influences fire both directly via fuel moisture and indirectly through biological and ecological effects on vegetation, fire risk can be quantified by both drought indices and fire behavior metrics. Interpretation of these metrics is complicated by the fact that not all vegetation types respond the same to meteorological

drought in terms of fuel availability and flammability, but the probability of ignition increases in most fuels when fuel moisture is low. Although fuels are capable of burning under different conditions in different ecosystems, even short-term drought generally increases wildfire risk through its effects on fuel moisture, and thus on probability of ignition and spread rate.

Palmer Drought Severity Index—Palmer Drought Severity Index (PDSI) (Palmer 1965) is commonly used in fire occurrence research in the United States (Balling and others 1992, Collins and others 2006, Littell and others 2009, Miller and others 2012, Westerling and others 2003). PDSI was designed to capture agricultural drought, using a water-balance method to add precipitation to the top two layers of soil, and a temperature-driven evapotranspiration algorithm to remove moisture (Thornthwaite 1948). PDSI assumes all precipitation falls as rain rather than snow, making its application less reliable where snow comprises a significant proportion of annual precipitation. Because the algorithm does not include some of the important drivers of evapotranspiration (relative humidity, solar radiation, wind speed), its correlation with soil moisture is weak ($r = 0.5\text{--}0.7$; Dai and others 2004). Correlation between PDSI and soil moisture peaks during late summer and autumn, corresponding with fire season in much of the Western United States. PDSI does not have an inherent time scale, but its “memory” varies from 2 to 9 months depending on location (Guttman 1998).

During the past century, PDSI is weakly to moderately associated with fire occurrence in many parts of the Western United States. In Yellowstone National Park (Wyoming, MT), year-of-fire summer PDSI calculated for two adjacent climate divisions had a Spearman’s rank correlation of -0.55 to -0.60 (1895–1990), with the correlation decreasing to -0.23 to -0.27 during the previous winter and -0.2 for the previous year (Balling and others 1992). Regional PDSIs for groups of Western States using the average of the PDSI value for each State were $r^2 = 0.27\text{--}0.43$ (1926–2002) for current year PDSI and area burned (Collins and others 2006). Including the PDSI from the two antecedent years increased correlations with area burned to $r^2 = 0.44\text{--}0.67$, indicating that multi-year droughts may increase fire occurrence.

PDSI was a significant predictor, along with precipitation and sometimes temperature, in modeling area burned in 12 of 16 ecoregions in the Western United States for the period 1916–2003 (Littell and others 2009). During

the period 1910–1959, summer PDSI explained 37 percent of area burned and number of fires in national forests of northwestern California. However, during the later period of 1987–2008, total summer precipitation was a significant predictor, not PDSI (Miller and others 2012). Among an array of possible drought indices, PDSI values from the previous October showed the strongest correlation with nonforested area burned in the western Great Basin ($r^2=0.54$ for 1984–2010), indicating that wet conditions during the previous autumn predicted area burned during the next fire season. The index did not perform well in other regions (Abatzoglou and Kolden 2013).

Precipitation totals (monthly, seasonal)—

Precipitation totals and anomalies are a measure of meteorological drought. In addition to the study by Miller and others (2012) referenced earlier, monthly and seasonal precipitation anomalies have been used in several studies relating drought to fire occurrence (Balling and others 1992, Littell and others 2009, Morgan and others 2008). Littell and others (2009) further demonstrated that seasonal precipitation was a significant factor in multivariate models predicting area burned in most ecoregions in the Western United States. However, the magnitude and sign of the precipitation term varied; in mountain and forest ecoregions, summer precipitation was generally negatively correlated with area, but in nonforested ecoregions, antecedent (usually winter) precipitation was positively correlated with area burned.

In Yellowstone National Park, total annual precipitation had a Spearman's rank correlation of -0.52 to -0.54 with area burned, which was a stronger correlation than was demonstrated in the same study using PDSI (Balling and others 1992). Summer precipitation had the strongest relationship among drought indices with area burned in nonforested areas of the Pacific Northwest ($r^2=0.48$) and eastern Great Basin ($r^2=0.31$; Abatzoglou and Kolden 2013).

Standardized Precipitation Index—The Standardized Precipitation Index (SPI) is a measure of meteorological drought, calculated as the difference of precipitation from the mean for a specified time period divided by the standard deviation (McKee and others 1993). Because the distribution of precipitation amounts is generally right-skewed (Riley and others 2013), it must be normalized before this equation is applied (Lloyd-Hughes and Saunders 2002). One can calculate SPI for any time period, typically ranging from 1 to 24 months.

Because SPI is normalized, one can use it to estimate probability of a drought of a certain severity, and the index has a similar meaning across ecosystems (e.g., a value of -1 means that precipitation is one standard deviation below normal). Riley and others (2013) found that 3-month SPI explained 70 percent of the variability in area burned and 83 percent of variability in number of large fires in the Western United States. With increasing time intervals for calculating SPI, correlations decreased until 24-month SPI explained essentially none of the variability. Fernandes and others (2011) also found strong correlations between 3-month SPI and anomalies in fire incidence in the western Amazon.

Energy Release Component—Energy Release Component (ERC) is a fire danger metric used in the National Fire Danger Rating System for the United States and a proxy for fuel moisture or amount of fuel available to burn. The calculation of ERC is based on recent weather (temperature, solar radiation, precipitation duration, and relative humidity). ERC can be calculated for different fuel conditions, but is most commonly used to estimate fire occurrence for larger fuels (>7.5–20 cm diameter) (Andrews and others 2003, Bradshaw and others 1983). ERC approximates dryness (a proxy for amount of fuel available to burn) based on weather during the previous 1.5 months, the amount of time required for fuels 7.5–20 cm diameter (i.e., 1,000-hour fuels) to equilibrate to atmospheric conditions (Fosberg and others 1981). Because ERC varies across different ecosystems, the raw values are commonly converted to percentiles to indicate departure from average conditions (Riley and others 2013).

Over the population of individual wildfires, ERC percentile during the first week of burning is highly correlated with fire occurrence at the scale of the Western United States, explaining over 90 percent of the variability in area burned and number of large fires for the period 1984–2008 (Riley and others 2013). Probability of a large fire ignition can be predicted from ERC (Andrews and Bevins 2003, Andrews and others 2003), although the prediction parameters vary with location because fires are likely to ignite at different ERCs, depending on local fuels and climate. Because of its strong association with fire occurrence, ERC is used operationally as an indicator of heightened fire risk (Calkin and others 2011). It was shown to be correlated with area burned in southern Oregon and northern California (Trouet and others 2009) and the U.S. Northern Rockies (Abatzoglou and Kolden 2013).

Keetch-Byram Drought Index—The Keetch-Byram Drought Index (KBDI) is an indicator of soil moisture deficit and is based on a number of physical assumptions (Keetch and Byram 1968). Soil water transfer to the atmosphere through evapotranspiration is determined by temperature and annual precipitation, which is used as a surrogate for vegetation cover (areas with higher annual rainfall are assumed to support more vegetation). KBDI was developed and evaluated for the Southeastern United States, and has been used for guidelines on expected fire conditions and potential suppression problems for this region (Melton 1989). KBDI has been useful beyond the Southeastern United States, with possible limitations in some cases (Liu and others 2010, Xanthopoulos and others 2006).

Wildfire potential is divided into four levels based on KBDI values (National Interagency Fire Center 1995):

- **Low (KBDI=0–200)**—soil moisture and fuel moistures for large fuels are high and do not contribute much to fire intensity;
- **Moderate (200–400)**—lower litter and duff layers are drying and beginning to contribute to fire intensity;
- **High (400–600)**—lower litter and duff layers contribute to fire intensity and will actively burn; and
- **Extreme (600–800)**—intense, deep burning fires with significant downwind spotting can be expected.

The four KBDI levels are typical of spring dormant season following winter precipitation, late spring and early in the growing season, late summer and early autumn, and severe drought and increased wildfire occurrence, respectively.

The fire hazard measured by KBDI shows large spatial, seasonal, and interannual variability across the continental United States (Liu and others 2013b). In winter, there are high values in the intermountain region, which decrease rapidly towards the east and become <200 (low fire potential) in the Great Plains. This spatial pattern remains during other seasons but with some changes. In summer, KBDI values >300 (moderate fire potential) are observed in the Southern United States. In autumn, KBDI values are higher in both the Western and Southern United States, with values >400 in the latter (high fire potential). Multiple-year trends of seasonal fire hazard measured by the slope of a linear line fitting the normalized KBDI time series show a positive sign in all

seasons and regions except three seasons in the Pacific Northwest and two seasons in the Southeast.

Fosberg Fire Weather Index—The Fosberg Fire Weather Index (FFWI) measures fire potential and hazard (Fosberg 1978). It is dependent on temperature, relative humidity, and wind speed, assuming constant grass fuel and equilibrium moisture content (Preisler and others 2008). In order to gauge fire-weather conditions, FFWI combines the equilibrium moisture content (Simard 1968) with Rothermel's (1972) rate of spread calculation (Crimmins 2006). FFWI demonstrated significant skill in explaining monthly fire occurrence in the Western United States (Preisler and others 2008). To further include the effect of precipitation, a modified version of FFWI (mFFWI) was developed by adding KBDI as a factor (Goodrick 2002). One can use the mFFWI as a refinement of KBDI by adding the effects of relative humidity and winds.

Evapotranspiration—Evapotranspiration (ET), the combined evaporation from the surface and transpiration from plant tissues, is affected by meteorological conditions near the surface, plant physiology, and soil characteristics. Summer evapotranspiration had the highest correlations among drought indices with forested area burned in the Southwest and southern California, and with nonforested area burned in the U.S. Northern Rockies and Southwest ($r^2=0.44-0.83$) (Abatzoglou and Kolden 2013). June through September values of potential evapotranspiration, the evapotranspiration that could occur if plants did not limit water loss through stomata, was a significant predictor ($r^2=0.19-0.61$) of area burned in forested Pacific Northwest ecoregions during recent decades (1980–2009) (Littell and Gwozdz 2011, Littell and others 2010).

Ecological water deficits: water balance deficit and climatic water deficit—Various algorithms are used to define water deficit, but all approach deficit as the evaporative demand not met by available water. It is estimated as the difference between atmospheric demand for water from plants and the land surface and how much water is available to meet that demand. Like PDSI, water deficit attempts to integrate energy and water balance of some area to describe water availability. Some calculations of water deficit attempt to account for more of the factors in the soil-plant-atmosphere continuum than PDSI (e.g., storage in snow, effects of plant canopy energy balance, albedo, and wind).

Stephenson (1990, 1998) defined water balance deficit (WBD) as the difference between potential evapotranspiration (PET) and actual evapotranspiration (AET), and related it to the coarse distribution of biomes. Littell and Gwozdz (2011) showed that PET, AET, and WBD are related (i.e., $WBD = PET - AET$) with a range of $R^2=0.25-0.78$ to area burned in ecosystems of the Pacific Northwest. Summer WBD had the highest correlation of several indices with area burned in forested areas of the Pacific Northwest ($r^2=0.66$) (Abatzoglou and Kolden 2013). Others have used a version closer to Thornthwaite's (1948) approximation and defined deficit as $PET - \text{precipitation}$.

Relationship to Hydrologic Drought

Many of the same factors affecting moisture in vegetation also affect moisture available for streamflow (chapter 2), and both fire and hydrologic drought occur with some lag after meteorological drought begins. Understanding such relationships could be useful for operational fire forecasts based on the same mechanisms that could be built from the substantial infrastructure and capacity for forecasting hydrologic drought. Broad changes and trends in snowpack, streamflow timing, and streamflow volume have been noted in various parts of the Western United States (Luce and Holden 2009, Luce and others 2012, Mote and others 2005, Regonda and others 2005, Stewart 2009), as have recent trends in fire occurrence related to climatic forcings (Dennison and others 2014).

Analysis of wildfire occurrence across the Western United States with streamflow records noted a moderately strong interannual correlation between the first principal component of streamflow center of timing and burned area in forests (Westerling and others 2006). Other work contrasting the correlation with total streamflow volume and center of timing in the Northwestern United States found similar relationship strength between burned area and annual streamflow volumes and between burned area and streamflow timing (Holden and others 2012). In the Pacific Northwest, a decline in streamflow and precipitation, particularly during drought years, suggested that much of the trend in fire in the historic record may be related to precipitation trends (Luce and Holden 2009, Luce and others 2013).

Synthesis of Index Relationships

The time window, over which the drought indices discussed earlier are computed, determines both the mechanistic relationships with fire they capture and their

skill in predicting different aspects of fire regimes (fig. 7.1). For example, for fire occurrence at the spatial scale of the Western United States, ERC (calculated based on fuel moistures during the previous 1.5 months) is strongly correlated with both number of large fires and the burned area (Riley and others 2013). Monthly precipitation anomalies were comparably correlated. As the time window for the index increases to longer lags, the correlation with fire occurrence decreases. At finer scales, however, the relationships differ significantly across ecosystems. For example, above-normal precipitation in the year(s) prior to fire is associated with higher area burned in the Southwestern United States (Littell and others 2009, Swetnam and Betancourt 1998, Westerling and others 2003) and Great Basin (Littell and others 2009, Westerling and others 2003). Long-term drought (>4 months) is not necessarily a prerequisite for extensive area burned, and seasonal climate can override the effect of antecedent climate (Abatzoglou and Kolden 2013).

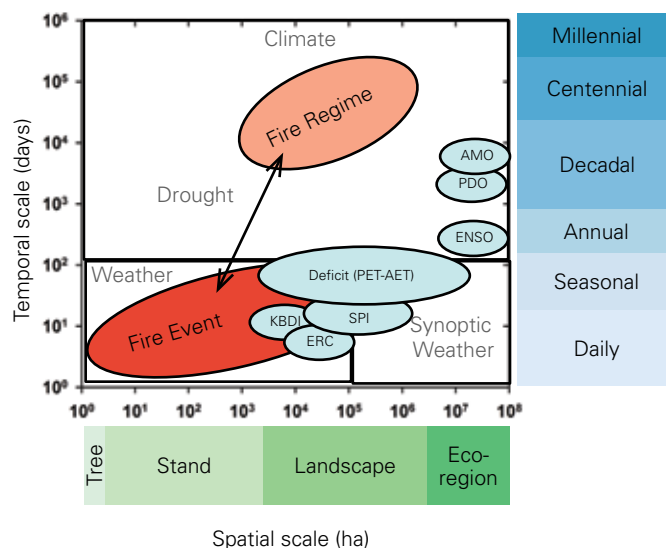


Figure 7.1—Scaling of controls on fire events, fire regimes (top, after climatic scaling of Clark [1985]), drought metrics, and climatic drivers related to their variation. In general, drought metrics are temporally coincident with fire events. The correlation between drought metrics and components of the fire regime in a location varies with time and space. Climatic factors that affect probability of ignitions, spread, area burned, and severity in a location in a given year is the product of multiscale influences of the climate system (top down) on fuel flammability and historical controls on fuel availability. Atlantic Multidecadal Oscillation (AMO), El Niño Southern Oscillation (ENSO), and Pacific Decadal Oscillation (PDO) refer to modes of climatic variability. AET=actual evapotranspiration; PET=potential evapotranspiration; ERC=Energy Release Component; KBDI=Keetch-Byram Drought Index; and SPI=Standardized Precipitation Index.

Regional Differences in Fire and Interactions With Other Stressors

Drought clearly increases probability of fire occurrence in forest ecosystems, but other disturbances and stressors, both biotic and abiotic, interact with drought and fire in stress complexes that affect the vigor and sustainability of forest ecosystems (McKenzie and others 2009). Although some of these interactions are predictable, they are poorly quantified and complicated by the fact that most ecosystems are rarely in dynamic equilibrium with biophysical processes. In addition, equilibrium rarely occurs even in relatively constant climate, and it is typically punctuated by disturbance episodes that may or may not be associated with climatic variability; these disturbance episodes allow succession to proceed along multiple pathways (Frelich and Reich 1995) and create forest dynamics that are difficult to project accurately. These dynamics and their consequences reflect natural processes in many forest ecosystems. However, the role of climate change in increasing the probability of drought and the simultaneous effects of climate on forest processes that feed back to disturbance bears consideration of interactions that may result in more rapid change than drought alone.

Increasing air temperatures are expected to change the frequency, severity, and extent of wildfires (Littell 2006, McKenzie and others 2004, Moritz and others 2012). Large wildfires that have occurred during a warmer climatic period during the past two decades portend a future in which wildfire is an increasingly dominant feature of western landscapes. Similarly, bark beetles, whose life cycles are accelerated by increased temperatures, are causing extensive mortality across the West (Logan and Powell 2001, Swetnam and Betancourt 1998, Veblen and others 1991).

Tropospheric ozone, a stressor of forest ecosystems, is an indirect product of fossil fuel emissions and is exacerbated by sunlight and high temperature, although most other air pollutants are the direct result of human-caused emissions. Fire and insect disturbance clearly interact, often synergistically, thus compounding rates of change in forest ecosystems (Veblen and others 1994). For example, mountain pine beetles (*Dendroctonus ponderosae*)—which have caused high mortality, mostly in lodgepole pine (*Pinus contorta* subsp. *latifolia*) forests across 20 million ha in western North America—may significantly increase fine fuels and fire hazard for years following outbreaks (see review by Hicke and

others 2012), though there is some uncertainty as to whether the probability of severe fires is affected positively or negatively by bark beetle mortality after dead needles have fallen (Lundquist 2007, Pollet and Omi 2002). In addition, fire severity in subalpine forests can be altered by a combination of bark beetles and annual-scale drought (Bigler and others 2005).

To explore the consequences of these interactions for different ecosystems, we extend a pathological model of cumulative stress in trees (Manion 1991, 2003) to forest ecosystems by describing interacting disturbances and stresses as stress complexes that have potentially far-reaching effects. Temperature increases are a predisposing factor causing often lethal stresses on forest ecosystems, acting both directly through increasingly negative water balances (Littell 2006, Milne and others 2002, Stephenson 1998) and indirectly through increased frequency, severity, and extent of disturbances (chiefly fire and insect outbreaks) (Logan and Powell 2001, 2009; McKenzie and others 2004; Skinner and others 2006). Increased disturbances can in turn cause rapid changes in forest structure and function and will be more important than temperature increase alone in altering the distribution and abundance of plant and animal species. We use examples from several forest ecosystems to document the existence of stress complexes and how they may be affected by a warmer climate.

Pinyon-Juniper Woodlands of the American Southwest

Pinyon pine (*Pinus edulis*) and various juniper species (*Juniperus* spp.) are among the most drought-tolerant trees in western North America, and characterize lower treelines across much of the West. Although pinyon-juniper woodlands appear to be expanding in some areas, possibly due to fire suppression or cessation of Native American fuelwood harvesting (Samuels and Betancourt 1982), they are clearly water-limited systems. At fine scales, pinyon-juniper ecotones are affected by local topography and existing canopy structure that may buffer trees against drought to some degree (Milne and others 1996), although severe multi-year droughts periodically cause massive dieback of pinyon pines, overwhelming any local buffering. Dieback of pine species—both ponderosa pine (*Pinus ponderosa*) and pinyon pine—occurred during and before the 20th century (Allen and Breshears 1998, Breshears and others 2005), and the recent (since the early 2000s) dieback is clearly associated with low precipitation and higher temperatures (Breshears and others 2005).

In the stress complex for pinyon-juniper woodlands (fig. 7.2), climate change is a predisposing factor; pinyon pine mortality and fuel accumulations result from warming and can lead to other impacts. Ecosystem change, possibly irreversible, comes from large-scale, severe fires that lead to colonization of invasive species, which further compromise the ability of pines to regenerate. However, it is worth noting that severe fires were historically characteristic of some pinyon pine systems (Floyd and others 2004).

Mixed-Conifer Forests of the Sierra Nevada and Southern California

Dominated by various combinations of ponderosa pine, Jeffrey pine (*Pinus jeffreyi*), sugar pine (*P. lambertiana*), Douglas-fir (*Pseudotsuga menziesii*), incense cedar (*Libocedrus decurrens*), and white fir (*Abies concolor*), these forests experience a Mediterranean climate in which summers are dry and long. Despite increasing temperatures since the early 20th century, fire frequency and extent did not increase in the mid- to late-20th century (McKelvey and others 1996). Rather, 20th century fire frequency and likely area were at lower levels than those present over the rest of the

last 2,000 years (Swetnam 1993, Swetnam and Baisan 2003). Stine (1996) attributes this to decreased fuel loads from sheep grazing, decreased Native American fire management, and fire exclusion. Fire exclusion has led to increased fuel loadings and competitive stresses on individual trees as stand densities have increased (Ferrell 1996, van Mantgem and others 2004).

Elevated levels of ambient ozone, derived from vehicular and industrial sources in urban environments upwind, are phytotoxic and reduce net photosynthesis and growth of ponderosa pine, Jeffrey pine, and possibly other species in the Sierra Nevada and the mountains of southern California (Bytnerowicz and Grulke 1992, Miller 1992, Peterson and Arbaugh 1988, Peterson and others 1991). Sierra Nevada forests support endemic levels of a diverse group of insect defoliators and bark beetles (typically *Dendroctonus* spp.), but bark beetles in particular have reached outbreak levels in recent years, facilitated by protracted droughts. Ferrell (1996) refers to biotic complexes in which bark beetles interact with root diseases and mistletoes. Dense stands, fire suppression, and nonnative pathogens such as white pine blister rust (*Cronartium ribicola*) can exacerbate

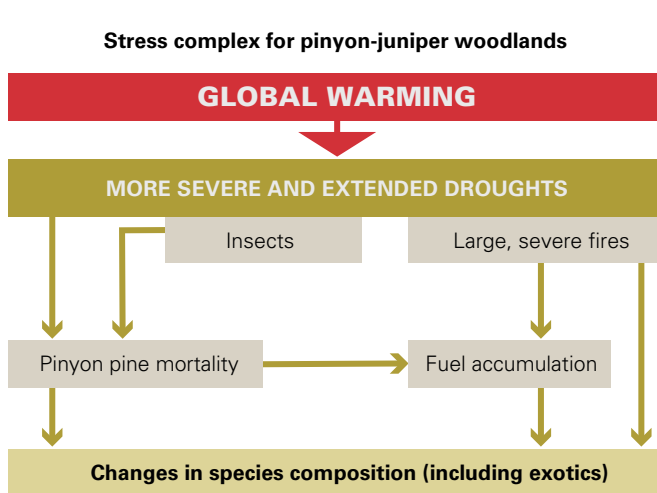


Figure 7.2—Stress complex in pinyon-juniper woodlands of the American Southwest. The effects of disturbance regimes (insects and fire) will be exacerbated by global warming. Stand-replacing fires and drought-induced mortality both contribute to species changes and exotic invasions. (Adapted from McKenzie and others 2009).

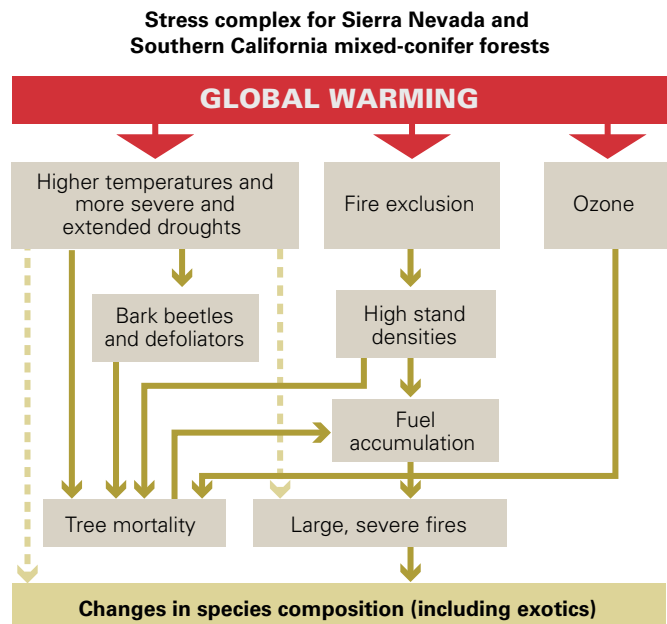


Figure 7.3—Stress complex in Sierra Nevada and southern Californian mixed-conifer forests. The effects of disturbance regimes (insects and fire) and fire exclusion will be exacerbated by global warming. Stand-replacing fires and drought-induced mortality both contribute to species changes and exotic invasions. Dashed lines indicate potential direct effects of higher temperature and drought. (Adapted from McKenzie and others 2009).

both biotic interactions (van Mantgem and others 2004) and drought stress. The stress complex associated with Sierra Nevada forest ecosystems (fig. 7.3) is likely applicable to the mountain ranges east and north of the Los Angeles basin as well.

Interior Lodgepole Pine Forests

Lodgepole pine is widely distributed across western North America and is the dominant species over much of its range, forming nearly monospecific stands that are maintained either because poor soils preclude other species or through adapting to stand-replacing fires via cone serotiny (Burns and Honkala 1990). Lodgepole pine is the principal host of the mountain pine beetle, and older, low-vigor stands are vulnerable to massive mortality during beetle outbreaks. Recent beetle outbreaks have caused extensive mortality across western North America, with large mature cohorts (age 70–80 years) contributing to widespread vulnerability. Warmer temperatures facilitate insect outbreaks by drought stress, making trees more vulnerable to attack and speeding up the reproductive cycles of some insect species (Logan and Bentz 1999, Logan and Powell 2001). Scientists accept that warming temperatures will

exacerbate these outbreaks northward and into higher elevations (Hicke and others 2006, Logan and Powell 2009), but lodgepole pine ecosystems are poised for significant changes even at current levels of mortality.

In the stress complex for lodgepole pine forests (fig. 7.4), warmer temperatures combine with the highly flammable dead biomass (associated with beetle-induced mortality), and this combination exacerbates the natural potential for severe crown fires for roughly 5 years. Then, after fine fuels decompose and become compressed, the fire hazard may be lessened considerably.

Interior Alaskan Forests

A combination of large crown fires and outbreaks of spruce bark beetle (*Dendroctonus rufipennis*) in south-central Alaska has affected millions of hectares of boreal forest during the past 20 years (Berg and others 2006). Although periodic beetle outbreaks have occurred in southern Alaska and the southwestern Yukon throughout the historical record, the recent outbreaks are unprecedented in extent and percentage mortality (over 90 percent in many places) (Berg and others 2006, Ross and others 2001). Summer temperatures in the Arctic have risen 0.3–0.4 °C per decade since 1961 (Chapin and others 2005), and wildfire and beetle outbreaks are both likely associated with this temperature increase (Berg and others 2006, Duffy and others 2005, Werner and others 2006). Although fire-season length in interior Alaska is associated with the timing of onset of the late-summer precipitation, the principal driver of annual area burned is early summer temperature (Duffy and others 2005).

White spruce (*Picea glauca*) and black spruce (*P. mariana*) are more flammable than co-occurring deciduous species [chiefly paper birch (*Betula papyrifera*)]. Similarly, conifers are a target of bark beetles, so spruce in south-central Alaska will be disadvantaged compared to deciduous species, most of which respond to fire by sprouting. The stress complex for Alaskan boreal forests (fig. 7.5) projects a significant transition to deciduous species via more frequent and extensive disturbance associated with warmer temperatures. Scientists contend that this transition is unlikely without changes in disturbance regimes, because both empirical data and modeling suggest that warmer temperatures alone will not favor a life-form transition (Bachelet and others 2005, Boucher and Mead 2006, Johnstone and others 2004).

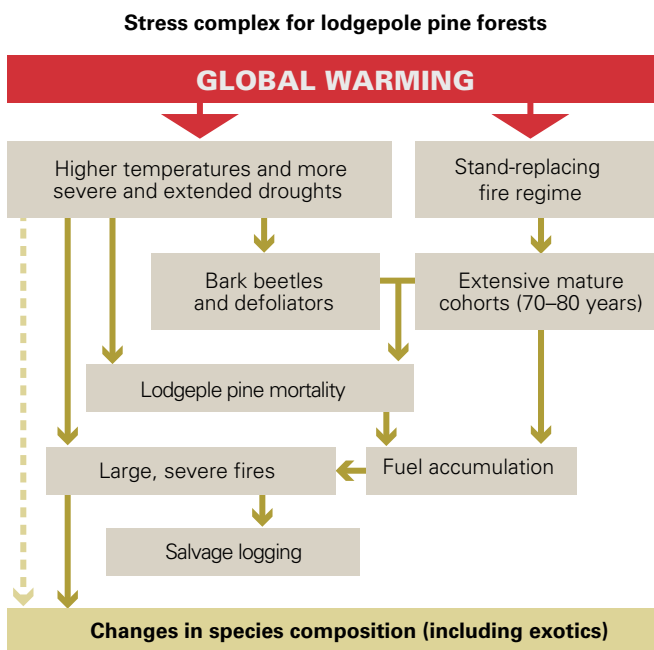


Figure 7.4—Stress complex in interior lodgepole pine forests. The effects of disturbance regimes (insects and fire) will be exacerbated by global warming. Stand-replacing fires, beetle mortality, and other stressors contribute to species changes. Dashed lines indicate potential direct effects of higher temperature and drought. (Adapted from McKenzie and others 2009).

Southern Pine Forests

Much of the forested landscape in the Southeastern United States is adapted to frequent fire, and unlike most of the rest of the country, prescribed fire is a mainstay of ecosystem management. Fire-adapted inland forests overlap geographically with coastal areas affected by hurricanes and potentially by sea-level rise (Ross and others 2009); therefore, interactions between wildfires and hurricanes are synergistic (fig. 7.6). For example, dry-season (prescribed) fires may have actually been more severe than wet-season (lightning) fires in some areas, causing structural damage via cambium kill and subsequent increased vulnerability to hurricane damage (Platt and others 2002). The stress complex for Southern pine forests is represented conceptually in figure 7.6, where different disturbances “meet” in the outcomes for forest ecosystems.

Increasing frequency and magnitude of drought is expected to increase the flammability of both live and

dead fine fuels in upland forests and pine plantations (Mitchell and others 2014). This may increase the frequency and intensity of some wildfires, and it may also reduce opportunities for safe implementation of prescribed burning. Both drought and increased fire may lead to greater dominance by invasive species [e.g., cogongrass (*Imperata cylindrical*)], which can in turn alter the flammability of fuels (Mitchell and others 2014). Proactive fuel reduction through prescribed burning, a common practice in Southern pine forests, will be even more important in a warmer climate.

Discussion

Rapid climate change and qualitative changes in disturbance regimes may send ecosystems across thresholds into dominance by different life forms and cause significant changes in productivity and capacity for carbon storage. For example, in the Southwest, stand-replacing fires are becoming common in what were historically low-severity fire regimes (Allen and

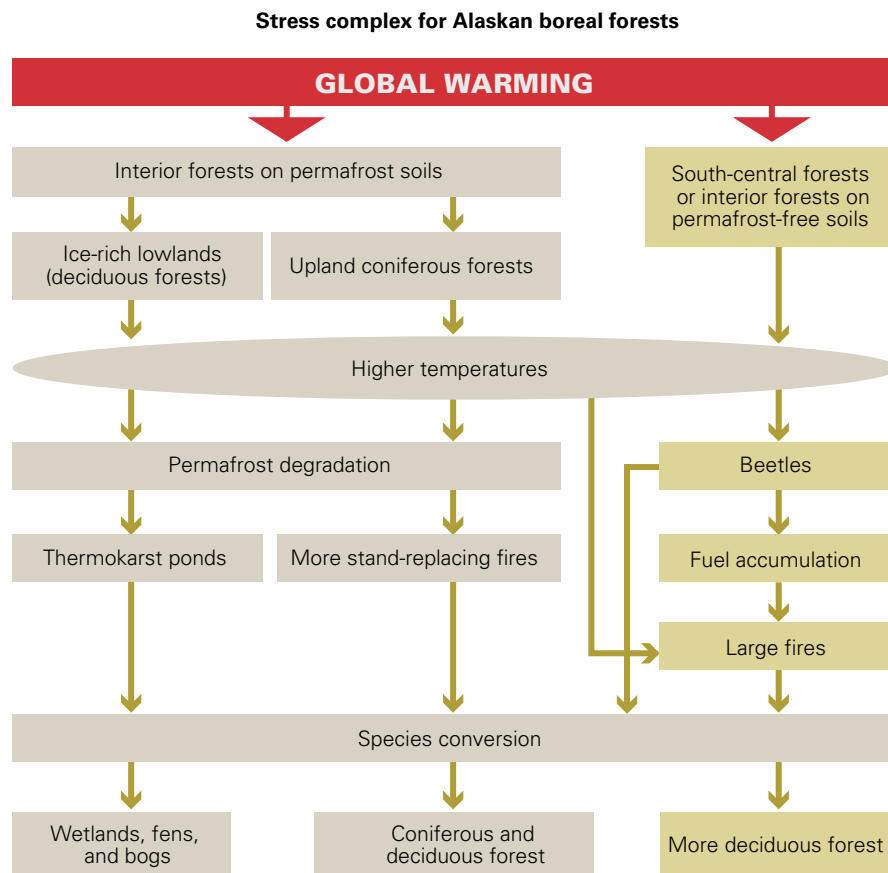


Figure 7.5—Stress complex in interior and coastal forests of Alaska. Rapid increases in the severity of disturbance regimes (insects and fire) will likely be triggered by global warming. Stand-replacing fires, mortality from insects, and stress-induced dieback contribute to species changes and conversion to deciduous species. (Adapted from McKenzie and others 2009).

others 2002), and protracted drought is killing species (ponderosa pine) that are adapted to low-severity fire (Allen and Breshears 1998). If these trends continue, ponderosa pine may be lost from some of its current range in the Southwest, and productivity of these systems will decline. In contrast, if warming temperatures accelerate mountain pine beetle reproductive cycles (Logan and Powell 2001) such that outbreaks are more frequent and more prolonged, lodgepole pine might be replaced by a more productive species such as Douglas-fir, at least on mesic sites where conditions for establishment are favorable.

As the climate warms, we expect that more ecosystems will become water limited (Albright and Peterson 2013, Littell 2006, Milne and others 2002), more sensitive to variability in temperature (due to its controls on both phenological and ecophysiological processes), and prone to more frequent disturbance. Consequently, productivity may decline across much

of the West (Hicke and others 2002), and long-term carbon sequestration may be limited by a continuous mosaic of disturbances of various severities. Species and ecosystems will be affected in various ways and not all undesirable changes will be preventable by management intervention (McKenzie and others 2004).

There is no historical or current analog for the combination of climate, disturbance regimes, and land-use changes expected by the end of the 21st century. For example, tempering the idea of “desired future conditions” with “achievable future conditions” will facilitate more effective adaptive management and more efficient allocation of resources to maintain forest resilience. Conceptual models of stress complexes improve our understanding of disturbance interactions in forest ecosystems affected by climate change. Quantitative models of stress complexes are now needed to characterize alternative future states for a broad range of forest ecosystems across North America.

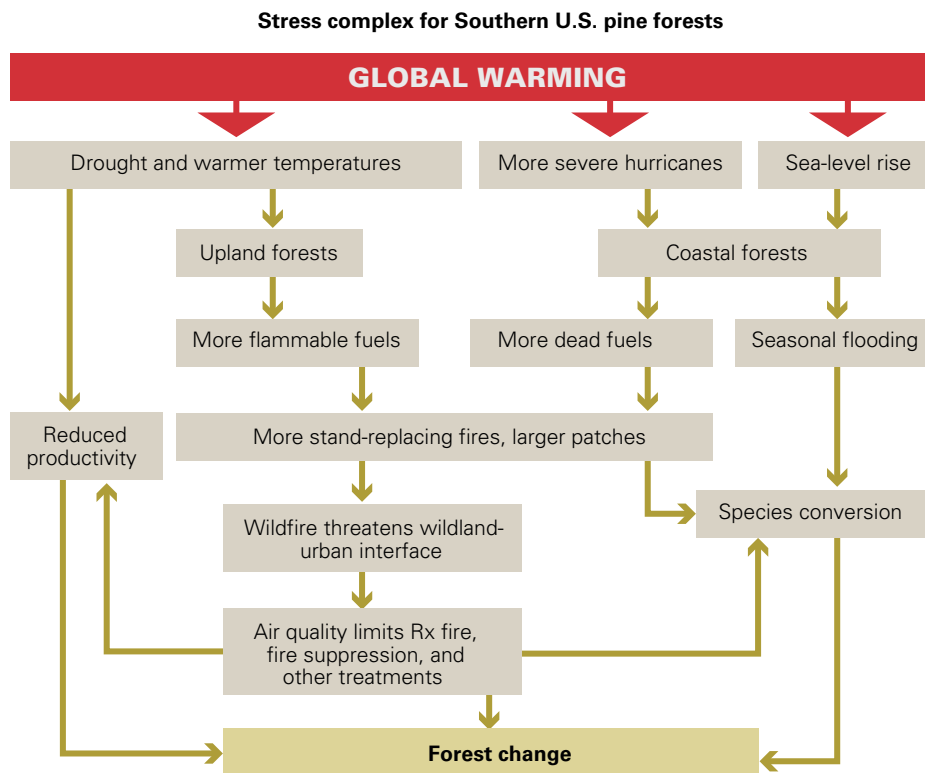


Figure 7.6—Stress complex in interior and coastal forests of the southeastern United States. Increases in the severity of hurricanes are triggered by global warming. Warmer and drier climate in uplands leads to longer periods with flammable fuels. Changes in fire and hydrologic regimes, and responses to them, lead to species change and altered carbon dynamics.

Quantifying and Projecting Drought Effects on Wildfire: Biological and Physical Factors

In chapter 2 of this publication, drought is defined as an area-specific anomalous lack of water. Here, we expand this definition to an uncharacteristic lack of water, specific to an ecosystem and a time scale. Risk is often defined as the product of the probability of an event and its consequences. Wildland fire researchers calculate fire risk as the probability of fire of a certain intensity times the effect on resource values (Bratten 1982, Calkin and others 2011, Mills and Bratten 1982). Wildfire probability increases as the moisture stored in fuels (live and dead vegetation) declines. Wildfire risk therefore responds to meteorological drought, and fire occurrence and area are correlated with metrics that measure precipitation delivery, relative humidity, and/or fuel moisture, reflecting both supply of water and demand for it (Abatzoglou and Kolden 2013, Littell and others 2009, Littell and Gwozdz 2011, Riley and others 2013). Drought is related to fire risk because it increases fuel dryness (in both live and dead fuels), which is correlated with probability of ignition and increases rate of spread. Drought may also increase the number of days with heightened probability of ignition.

Wildfire risk differs across the continental United States (Finney and others 2011, Preisler and Westerling 2007, Radeloff and others 2005) as a function of probability of burning and values at risk (buildings, municipal watersheds, endangered species habitat, etc.). Fire probability is generally related to the inverse of fire return interval, with longer fire return intervals having a lower annual probability of burning; for example, annual probability of burning in forests that burn infrequently is lower than that of chaparral which burns frequently (Agee 1993, Frost 1998). Probability of burning is also affected by quantity and distribution of fuels, land management, fire suppression, and invasive plants. Because many ecosystems in the United States were structured by fire until effective suppression, some consider wildfire to be a regulating ecosystem service through periodic reduction of fuels, which would otherwise require costly treatment. Cessation of Native American burning combined with fire suppression may have reduced area burned annually in the United States by an order of magnitude (Leenhouts 1998, Marlon and others 2012). If that burning takes place preferentially under extreme drought conditions when it cannot be suppressed, it is more likely to be of uncharacteristically high severity than if it took place under more moderate conditions.

Tree-ring evidence of North American “megadroughts” indicates that droughts of severity and duration not yet encountered by modern societies occurred on a widespread basis in the past (Cook and others 2007). Currently, only thin consensus exists regarding the effect of climate change on drought occurrence (Maloney and others 2014; chapter 2). High confidence exists for projected temperature increases across most of the planet in future decades, whereas altered precipitation and relative humidity are uncertain (Blöschl and Montanari 2010, Walsh and others 2014), and that uncertainty varies geographically. As temperatures continue to warm, all else being equal, droughts of given magnitude and low fuel moistures may become more likely in summer-dry climates even if precipitation increases, because potential evapotranspiration will also increase.

Seasonal timing of increases or decreases in precipitation would have important effects on risk, leading to geographic heterogeneity driven by historical fire regimes, ecological responses to climate change, and management. Regardless of specific climatic mechanisms, fire risk may increase or decrease depending on temporal scale and factors influencing probability and consequences of fires. Fire occurrence probabilities could be affected both through fuel production (frequency or severity of drought, affecting species assemblages and thus fire regime through fuels) or through flammability (fire frequency responds to flammability and drives changes in species assemblages). As noted in chapter 2, leaf area of some forests may decrease in response to prolonged drought, which could increase the water available for understory plants. In this case, understory plants could contribute to the intensity of surface fires.

Expected Changes in Drought and Consequences for Wildfire

It is important to account for physical, hydrological, ecological, and human dimensions in translating projected climate into future fire risk. However, in the near term (e.g., the first half of the 21st century) it can be argued that changes in fire risk will occur on landscapes and within management strategies that already exist. Given that expected physical and hydrologic changes can be quantified, we present projections of two fire-related drought indicators discussed earlier: an ecohydrological indicator (define as PET – AET) (fig. 7.7) and the hydrologic indicator 7Q10 (the lowest 7-day average flow that occurs on average once every 10 years) (fig. 7.8). A composite of 10 General Circulation Models shows that summer

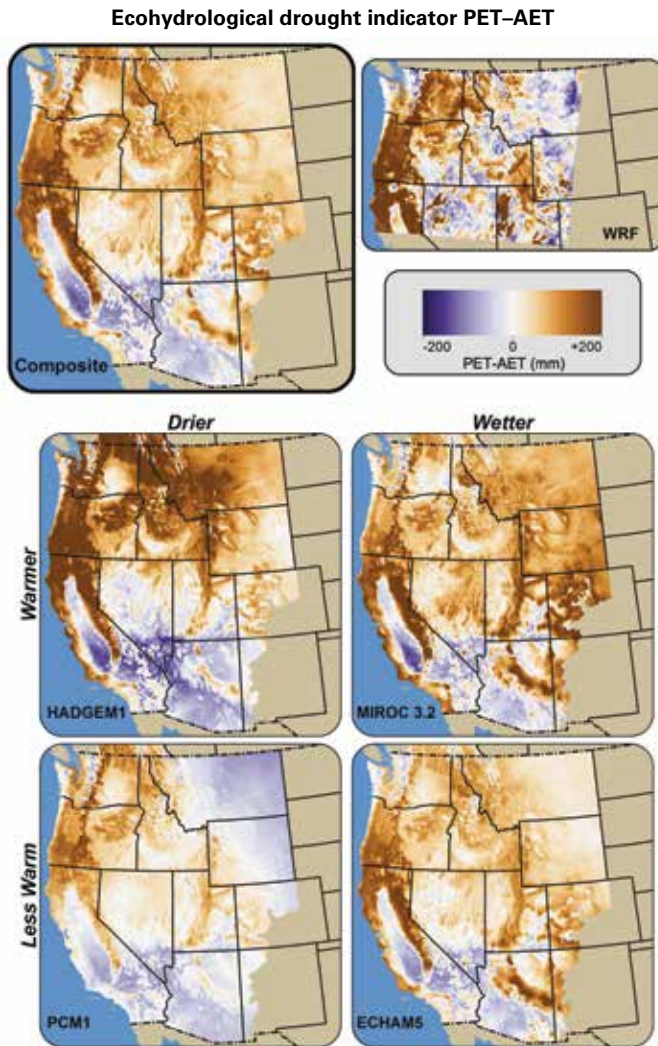


Figure 7.7—Downscaled change (2030–2059) in summer (June through August) water-balance deficit from historical (1916–2006): potential evapotranspiration (PET) – actual evapotranspiration (AET), measured in total mm water. Water-balance deficit (WBD) is well correlated with many climate effects on vegetation. In this representation, positive responses reflect an increase in deficit (less water availability and brown shaded), while negative responses reflect a decrease (more water availability and blue shaded). Ten-model composite (upper left) and output from the Weather Research and Forecasting (WRF) model (upper right) is followed by four bracketing General Circulation Model (GCM) scenarios [Coupled Model Inter-comparison Program (CMIP3)/AR4, after Littell and others 2011 and Elsner and others 2010] (Figure: Robert Norheim. Data source: U.S. Geological Survey, Western U.S. Hydroclimate Scenarios Project Datasets.)

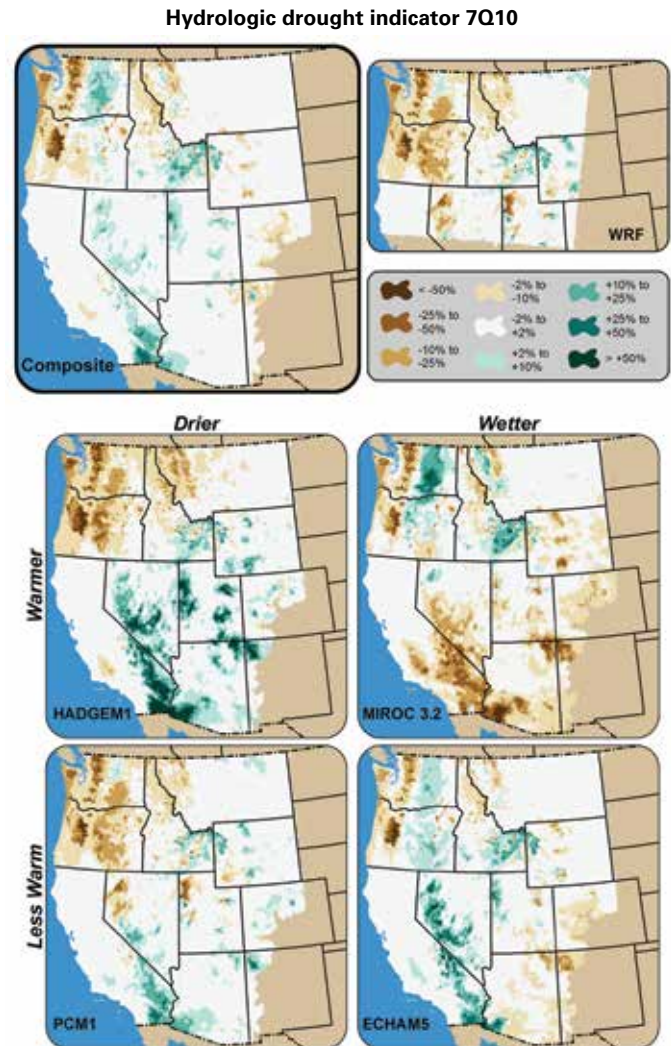


Figure 7.8—Changes (2030–2059) from historical (1916–2006) in 7Q10 (the lowest weekly average flow that occurs on average once every 10 years)—a measure of extreme low-flow periods in streams. The climate-change driven variation in low flows depends on characteristics unique to watersheds, regions, and future climate. Upper left: composite of statistically downscaled changes from 10 climate models. Upper right: dynamically downscaled changes from a single climate model (ECHAM5). Lower four panels illustrate bracketing General Circulation Models (warmer drier, warmer wetter, less warming drier, less warming wetter). (Figure: Robert Norheim. Data source: U.S. Geological Survey, Western U.S. Hydroclimate Scenarios Project Datasets.)

(June through August) water-balance deficit is projected to increase in much of the West except in portions of the Southwest that have significant monsoon precipitation and in some mountainous areas in the Pacific Northwest. The geographic distribution and magnitude of projected changes differ among climate models. Four climate models that bracket the range of projected changes in temperature and precipitation suggest that extreme low streamflows would be more frequently exceeded in the Cascades than in other areas of the West. Model output suggests that the Columbia Basin, upper Snake River, and southeastern California/southwestern Oregon may exceed extreme low flows less frequently than they did historically. Given the historical relationships between fire occurrence and drought indicators such as water-balance deficit and streamflow, climate change can be expected to have significant effects on fire risk.

Similarly, future fire hazards as measured by KBDI are projected to increase in most seasons and regions of the continental United States in the 21st century (Liu and others 2013b). The largest increases in fire hazard are in the Southwest, Rocky Mountains, northern Great Plains, and Southeast and Pacific Coasts, mainly caused by future temperature increase. The most pronounced increases occur in summer and autumn, including an extended fire season in several regions.

Fire Feedbacks to Drought

Drought is caused by changes in one or more of three atmospheric properties: thermal instability, water vapor supply, and dynamic systems creating upward motion. Wildfires can contribute to these properties from local to global scales by emitting particles and gases that affect atmospheric dynamics and by modifying land cover, feedbacks that were not systematically investigated until recently (Liu and others 2013a).

Smoke Particles

Fires emit particles including organic carbon (OC), which is bound in various compounds derived from plant tissue, and black carbon (BC), which is a pure carbon component of fine particulate matter [$<2.5 \mu\text{m}$ (micrometers)] formed through incomplete combustion as soot. BC emissions from biomass (forest and savanna) burning account for 5–10 percent of fire smoke particles and about 40 percent of total global BC emissions (Bond and others 2004). These smoke particles can affect atmospheric radiative budgets by scattering and absorbing solar radiation (direct radiative forcing). This can further affect cloud

cover and precipitation at regional scales. Koren and others (2004) analyzed Moderate Resolution Imaging Spectroradiometer (MODIS) satellite measurements during biomass burning in the Amazon region and found that cloud cover was reduced from 38 percent in clean conditions to nearly 0 percent for heavy smoke.

The radiative forcing of smoke can affect regional precipitation in many ways (fig. 7.9), but especially by modifying atmospheric thermal stability. The land surface and the atmosphere below the smoke layer are cooled by scattering and absorption of solar radiation by smoke particles. During a wildfire near Boulder, CO, in 2010, the surface under the smoke plume was cooled 2–5 °C (Stone and others 2011). Meanwhile, the upper air with smoke particles was warmed by solar radiation absorption. These changes in the vertical temperature profile stabilize the atmosphere and suppress cloud development.

Air relative humidity of the smoke layer is reduced from the warming effect of solar radiation absorption by BC, and cloud formation is inhibited. Relatively low cloud cover over the ocean has been documented due to the large concentration of soot aerosols, which leads to higher air temperature and lower relative humidity that help to “burn out” clouds (Ackerman and others 2000). Clouds and precipitation are reduced during the burning season over the Amazon because water vapor transport from the ground is low, and the planetary boundary layer to clouds is weakened from lower turbulent activity (Liu 2005a).

Atmospheric horizontal airflow convergence and vertical ascending in the lower troposphere favor cloud and precipitation formation. The radiative forcing of smoke particles leads to cooling on the ground and in the lower troposphere, despite possible warming at some elevations due to solar radiation absorption by BC. In a simulation study of the 1988 Yellowstone National Park wildfires that occurred during a drought (Liu 2005b), absorption of solar radiation by smoke particles over the fire area released heat in the upper smoke layer. This phenomenon altered westerly airflows, transporting warmer air downwind and converging in the trough area over the Midwest. The trough weakened, reducing clouds and rainfall, which suggests that feedbacks from wildfires may enhance drought.

Greenhouse Gases

Carbon dioxide is the largest fire emission component, accounting for 87–92 percent of total carbon burned

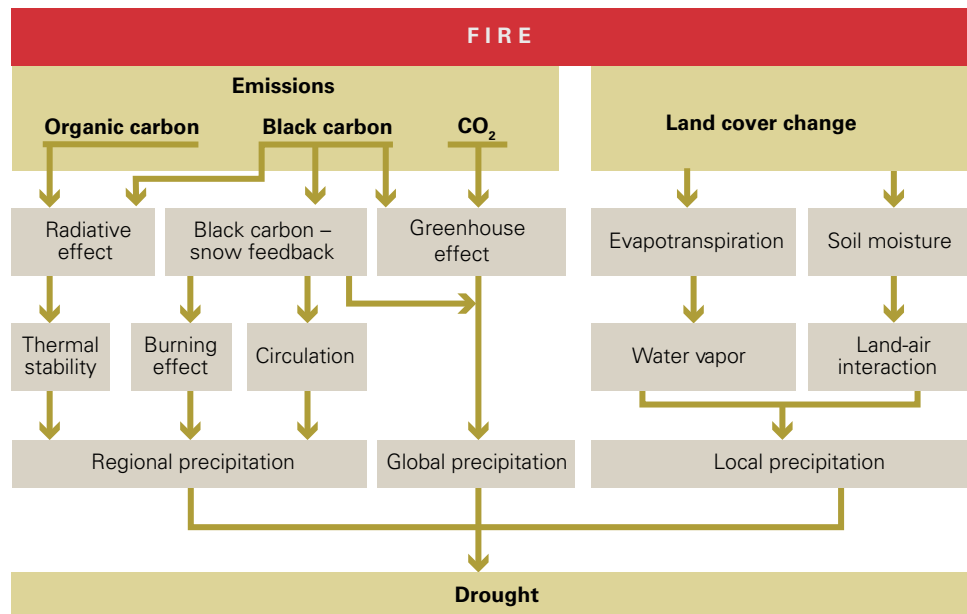


Figure 7.9—Physical processes for feedbacks of wildfires to drought.

(Urbanski and others 2008). Average annual global fire carbon emissions were about 2 picograms (Pg) in the recent decade, about one-third of total carbon emissions. BC emissions enhance the greenhouse effect in the atmosphere, and deposition of BC emissions on snow and ice at high latitudes reduces albedo and increases solar radiation absorbed by the surface, which in turn accelerates snow melting (Hansen and Nazarenko 2004). Boreal fires contribute more BC to the Arctic than human sources in summer based on multi-year averages (Stohl and others 2006). As a major source of atmospheric carbon dioxide and BC, wildfire emissions contribute significantly to atmospheric carbon dynamics and radiation absorption. Analyses of the Coupled Model Inter-comparison Program phase 3 (CMIP3) and phase 5 (CMIP5) indicate that future drought occurrence, duration, and severity will likely increase in response to the greenhouse effect globally and in many mid-latitude areas including the United States (Maloney and others 2014). Increasing drought amplifies the warming effect over decades to centuries.

Land Cover Change

Water transfer from the land surface, a local water vapor source for precipitation, is much higher on vegetated lands through evapotranspiration than unvegetated lands through evaporation. Leaf area after stand-replacing fires decreases greatly from pre-fire conditions, and evapotranspiration is temporarily

reduced, leading to reduced water transfer through transpiration. The Bowen ratio (a ratio of sensible to latent heat flux) increases after burning, meaning that more solar energy absorbed on the surface is converted to sensible heat instead of being used as latent energy for water-phase change. After fire, the capacity of soil to store water is reduced, canopy and understory interception is decreased, and evapotranspiration from live vegetation is decreased, with a net effect of increased runoff and reduced soil water available for transfer to the atmosphere despite the reduction in evapotranspiration. As a result, the atmosphere will receive more heat energy and more intense convective activities, but less water from the ground for a long post-fire period.

During the 2004 Alaska fire season, wildfires altered land cover over large areas, leading to changes in dynamic, radiative, vegetative, thermal, and hydrological surface characteristics (Möldersa and Kramma 2007). A simulation to quantify the effects of fire-caused land cover changes indicated that sensible heat fluxes into the atmosphere increased by up to 225 Watts per square meter (W/m^2) over burned areas. There was enough enhanced lifting in the areas with large burns to produce areas of increased clouds followed by an area of decreased clouds downwind of them. Precipitation increased significantly in the lee of burned areas, but decreased slightly a few days after large fires.

Management and Social Implications

To the extent that drought affects fire directly, management implications mirror those associated with changes in fire regimes stemming from climate change (Littell and others 2009). In regions where area burned has historically been higher with high temperature and low precipitation anomalies (most of the Western United States), area burned will likely increase with temperature and possibly the frequency of drought (Committee on Stabilization Targets for Atmospheric Greenhouse Gas Concentrations, National Research Council 2011). Fire severity and frequency may also increase, but blanket statements about these phenomena are strongly affected by local conditions and therefore differ considerably. However, larger fires and higher area burned will continue to challenge fire suppression efforts and budgets, and may require rethinking historical approaches to fire management on landscapes. If annual area burned increases >200 percent in most of the Western United States as projected for the mid-21st century (Peterson and Littell 2014), the proportion of landscapes recently burned would also increase. Combined with the effects of increasing temperature on climatic suitability for regeneration, ecosystem function and structure may change rapidly (Littell and others 2010), thus altering the landscapes for which land management agencies have responsibility.

In some regions of the United States, a longer season during which fuels are highly flammable may affect management activities intended to reduce the quantity of those fuels. Even if there is minimal change in probability of historically extreme droughts, effective or “ecological” drought due to increased water demand may decrease favorable conditions for prescribed fire. However, the duration of time when burning can be conducted (relative to fuel conditions, regulatory compliance, and social acceptance) could simply move to earlier in spring and later in autumn. If drought-caused wildfire activity increases, wildland-urban interface areas will face increased fire risk, thus increasing suppression costs and potentially altering social perceptions of management and risk in fire-prone human communities.

Literature Cited

- Abatzoglou, J.T.; Kolden, C.A. 2013. Relationships between climate and macroscale area burned in the Western United States. *International Journal of Wildland Fire*. 22: 1003–1020.
- Ackerman, A.S.; Toon, O.B.; Stevens, D.E. [and others]. 2000. Reduction of tropical cloudiness by soot. *Science*. 288: 1042–1047.
- Agee, J.K. 1993. *Fire ecology of Pacific Northwest forests*. Covelo, CA: Island Press. 493 p.
- Albright, W.L.; Peterson, D.L. 2013. Tree growth and climate in the Pacific Northwest, U.S.A.: a broad-scale analysis of changing growth environments. *Journal of Biogeography*. 40: 2119–2133.
- Allen, C.D.; Breshears, D.D. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences, U.S.A.* 95: 14,839–14,842.
- Allen, C.D.; Savage, M.; Falk, D.A. [and others]. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecological Applications*. 12: 1418–1433.
- Andrews, P.L.; Bevins, C.D. 2003. BehavePlus Fire modeling system, version 2: overview. In: *Second International Wildland Fire Ecology and Fire Management Congress*, 16–20 November 2003, Orlando, FL. Boston, MA: American Meteorological Society: P5.11. https://ams.confex.com/ams/FIRE2003/techprogram/paper_65993.htm. [Date accessed: December 2013].
- Andrews, P.L.; Loftsgaarden, D.O.; Bradshaw, L.S. 2003. Evaluation of fire danger rating indexes using logistic regression and percentile analysis. *International Journal of Wildland Fire*. 12: 213–226.
- Bachelet, D.; Lenihan, J.; Neilson, R. [and others]. 2005. Simulating the response of natural ecosystems and their fire regimes to climatic variability in Alaska. *Canadian Journal of Forest Research*. 35: 2244–2257.
- Balling, R.C.; Meyer, G.A.; Wells, S.G. 1992. Relation of surface climate and burned area in Yellowstone National Park. *Agricultural and Forest Meteorology*. 60: 285–293.
- Berg, E.E.; Henry, J.D.; Fastie, C.L. [and others]. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes. *Forest Ecology and Management*. 227: 219–232.
- Bigler, C.; Kulakowski, D.; Veblen, T.T. 2005. Multiple disturbance interactions and drought influence fire severity in Rocky Mountain subalpine forests. *Ecology*. 86: 3018–3029.
- Blöschl, G.; Montanari, A. 2010. Climate change impacts—throwing the dice? *Hydrological Processes*. 24: 374–381.
- Bond, T.C.; Streets, D.; Yarber, K.F. [and others]. 2004. A technology-based global inventory of black and organic carbon emissions from combustion. *Journal of Geophysical Research*. 109(D14): D14203. 43 p. doi: 10.1029/2003JD003697. [Published online: July 24, 2004].
- Boucher, T.V.; Mead, B.R. 2006. Vegetation change and forest regeneration on the Kenai Peninsula, Alaska, following a spruce beetle outbreak, 1987–2000. *Forest Ecology and Management*. 227: 233–246.

- Bradshaw, L.S.; Deeming, J.E.; Burgan, R.E.; Cohen, J.D., comps. 1983. The 1978 National Fire-Danger Rating System: technical documentation. Gen. Tech. Rep. INT-169. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 44 p.
- Bratten, F.W. 1982. Probability model for analyzing fire management alternatives: theory and structure. Gen. Tech. Rep. PSW-66. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 11 p.
- Breshears, D.D.; Cobb, N.S.; Rich, P.M. [and others]. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences, U.S.A.* 102: 15,144–15,148.
- Burns, R.M.; Honkala, B.H., tech coords. 1990. *Silvics of North America: Volume 1. Conifers*. Agric. Handb. 654. Washington, DC: U.S. Department of Agriculture Forest Service. 675 p.
- Bytnerowicz, A.; Grulke, N.E. 1992. Physiological effects of air pollutants on western trees. In: Olson, R.K.; Binkley, D.; Böhm, M., eds. *Response of western forests to air pollution*. New York: Springer-Verlag: 183-233.
- Calkin, D.E.; Thompson, M.P.; Finney, M.A.; Hyde, K.D. 2011. A real-time risk assessment tool supporting wildland fire decisionmaking. *Journal of Forestry*. 109: 274–280.
- Chapin, F.S.; Sturm, M.; Serreze, M.C. 2005. Role of land-surface changes in Arctic summer warming. *Science*. 28: 657–660.
- Clark, W.C. 1985. Scales of climate impacts. *Climatic Change*. 7: 5-27.
- Cohen, J.D.; Deeming, J.E. 1985. The National Fire Danger Rating System: basic equations. Gen. Tech. Rep. PSW-82. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 16 p.
- Collins, B.M.; Omi, P.N.; Chapman, P.L. 2006. Regional relationships between climate and wildfire-burned area in the Interior West, U.S.A. *Canadian Journal of Forest Research*. 36: 699–709.
- Committee on Stabilization Targets for Atmospheric Greenhouse Gas Concentrations, National Research Council. 2011. Impacts in the next few decades and the next century. In: *Climate stabilization targets: emissions, concentrations, and impacts over decades to millennia*. Washington, DC: National Research Council: 159-216.
- Cook, E.R.; Seager, R.; Cane, M.S.; Stahle, D.W. 2007. North American drought: reconstructions, causes, and consequences. *Earth-Science Reviews*. 81: 93–134.
- Crimmins, M.A. 2006. Synoptic climatology of extreme fire-weather conditions across the Southwest United States. *International Journal of Climatology*. 26: 1001–1016.
- Dai, A.; Trenberth, K.E.; Qian, T. 2004. A global dataset of Palmer Drought Severity Index for 1870–2002: relationship with soil moisture and effects of surface warming. *Journal of Hydrometeorology*. 5: 1117–1130.
- Dennison, P.E.; Brewer, S.C.; Arnold, J.D.; Moritz, M.A. 2014. Large wildfire trends in the Western United States, 1984–2011. *Geophysical Research Letters*. 41: 2928–2933.
- Dillon, G.K.; Holden, Z.A.; Morgan, P. [and others]. 2011. Both topography and climate affected forest and woodland burn severity in two regions of the Western U.S., 1984 to 2006. *Ecosphere*. 2(12): article 130. 33 p. doi:10.1890/ES11-00271.1. [Published online: December 12, 2011].
- Duffy, P.A.; Walsh, J.E.; Graham, J.M. [and others]. 2005. Impacts of large-scale atmospheric-ocean variability on Alaskan fire season severity. *Ecological Applications*. 15: 1317–1330.
- Elsner, M.M.; Cuo, L.; Voisin, N. [and others]. 2010. Implications of 21st century climate change for the hydrology of Washington State. *Climatic Change*. 102: 225–260.
- Fernandes, K.; Baethgen, W.; Bernardes, S. [and others]. 2011. North Tropical Atlantic influence on western Amazon fire season variability. *Geophysical Research Letters*. 38: L12701. 5 p. doi:10.1029/2011GL047392. [Published online: June 17, 2011].
- Ferrell, G.T. 1996. The influence of insect pests and pathogens on Sierra forests. In: *Sierra Nevada Ecosystem Project: final report to Congress, v. II, Assessments and scientific basis for management options*. Davis, CA: University of California, Centers for Water and Wildland Resources: 1177–1192. <http://pubs.usgs.gov/dds/dds-43/TOC.PDF>. [Date accessed: September 15, 2015].
- Finney, M.A.; McHugh, C.W.; Grenfell, I.C. [and others]. 2011. A simulation of probabilistic wildfire risk components for the continental United States. *Stochastic Environmental Research and Risk Assessment*. 25: 973–1000.
- Flatley, W.T.; Lafon, C.W.; Grissino-Mayer, H.D.; LaForest, L.B. 2013. Fire history, related to climate and land use in three southern Appalachian landscapes in the Eastern United States. *Ecological Applications*. 23: 1250–1266.
- Floyd, M.L.; Hanna, D.D.; Romme, W.H. 2004. Historical and recent fire regimes in pinyon-juniper woodlands on Mesa Verde, Colorado, U.S.A. *Forest Ecology and Management* 198: 269-289.
- Fosberg, M.A. 1978. Weather in wildland fire management: the fire weather index. Conference on Sierra Nevada Meteorology, June 19-21. Lake Tahoe, CA. Boston, MA: American Meteorological Society: 1–4.
- Fosberg, M.A.; Rothermel, R.C.; Andrews, P.L. 1981. Moisture content calculations for 1000-hour timelag fuels. *Forest Science*. 27: 19–26.
- Frelich, L.E.; Reich, P.B. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. *Ecological Monographs*. 65: 325–346.
- Frost, C.C. 1998. Presettlement fire frequency regimes of the United States: a first approximation. In: Pruden, T.L.; Brennan, L.A., eds. *Fire in ecosystem management: shifting the paradigm from suppression to prescription*. Tall Timbers Fire Ecology Conference Proceedings No. 20. Tallahassee, FL: Tall Timbers Research, Inc.: 70–81.
- Goodrick, S.L. 2002. Modification of the Fosberg Fire Weather Index to include drought. *International Journal of Wildland Fire*. 11: 205–211.
- Guttman, N.B. 1998. Comparing the Palmer Drought Index and the Standardized Precipitation Index. *Journal of the American Water Resources Association*. 34: 113–121.
- Hansen, J.; Nazarenko, L. 2004. Soot climate forcing via snow and ice albedos. *Proceedings of the National Academy of Sciences, U.S.A.* 101: 423–428.
- Hicke, J.A.; Asner, G.P.; Randerson, J.T. 2002. Trends in North American net primary productivity derived from satellite observations, 1982–1998. *Global Biogeochemical Cycles*. 16(2): 1018. 22 p. doi:10.1029/2001GB001550. [Published online: May 14, 2002].
- Hicke, J.S.; Johnson, M.C.; Hayes, J.L.; Preisler, H.K. 2012. Effects of bark beetle-caused tree mortality on wildfire. *Forest Ecology and Management*. 271: 81–90.

- Hicke, J.A.; Logan, J.A.; Powell, J.A.; Ojima, D.S. 2006. Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the Western United States. *Journal of Geophysical Research-Biogeosciences*. 111(G2): G02019. 12 p. doi: 10.1029/2005JG000101. [Published online: June 16, 2006].
- Holden, Z.A.; Luce, C.H.; Crimmins, M.A.; Morgan, P. 2012. Wildfire extent and severity correlated with annual streamflow distribution and timing in the Pacific Northwest, USA (1984–2005). *Ecohydrology*. 5: 677–684.
- Johnstone, J.F.; Chapin, F.S.; Foote, J. 2004. Decadal observations of tree regeneration following fire in boreal forests. *Canadian Journal of Forest Research*. 34: 267–273.
- Keetch, J.J.; Byram, G.M. 1968. A drought index for forest fire control. Res. Pap. SE-38. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeast Forest Experiment Station. 35 p.
- Koren, I.; Kaufman, Y.J.; Remer, L.; Martins, J.V. 2004. Measurement of the effect of Amazon smoke on inhibition of cloud formation. *Science*. 303: 1342–1345.
- Leenhouts, B. 1998. Assessment of biomass burning in the conterminous United States. *Conservation Ecology*. 2(1): 1. <http://www.consecol.org/vol2/iss1/art1>. [Date accessed: December 2013].
- Littell, J.S. 2006. Climate impacts to forest ecosystem processes: Douglas-fir growth in north-western U.S. mountain landscapes and area burned by wildfire in western U.S. eco-provinces. Seattle, WA: University of Washington. 171 p. Ph.D. dissertation.
- Littell, J.S.; Elsner, M.M.; Mauger, G.S. [and others]. 2011. Regional climate and hydrologic change in the northern U.S. Rockies and Pacific Northwest: internally consistent projections of future climate for resource management. Project report, USFS JVA 09-JV-11015600-039. Seattle: University of Washington, Climate Impacts Group. http://cses.washington.edu/picea/USFS/pub/Littell_etal_2010/Littell_etal_2011_Regional_Climatic_And_Hydrologic_Change_USFS_USFWS_JVA_17Apr11.pdf. [Date accessed: September 2013].
- Littell, J.S.; Gwozdz, R. 2011. Climatic water balance and regional fire years in the Pacific Northwest, U.S.A.: linking regional climate and fire at landscape scales. In: McKenzie, D.; Miller, C.M.; Falk, D.A., eds. *The landscape ecology of fire*. New York: Springer: 117–139.
- Littell, J.S.; McKenzie, D.; Peterson, D.L.; Westerling, A.L. 2009. Climate and wildfire area burned in western U.S. ecoprovinces, 1916–2003. *Ecological Applications*. 19: 1003–1021.
- Littell, J.S.; Oneil, E.E.; McKenzie, D. [and others]. 2010. Forest ecosystems, disturbance, and climatic change in Washington State, USA. *Climatic Change*. 102: 129–158.
- Liu, Y.-Q. 2005a. Atmospheric response and feedback to radiative forcing from biomass burning in tropical South America. *Agricultural and Forest Meteorology*. 133: 40–53.
- Liu, Y.-Q. 2005b. Enhancement of the 1988 northern U.S. drought due to wildfires. *Geophysical Research Letters*. 32: L10806. 4 p. doi:10.1029/2005GL022411. [Published online: May 20, 2005].
- Liu, Y.-Q.; Stanturf, J.; Goodrick, S. 2010. Trends in global wildfire potential in a changing climate. *Forest Ecology and Management*. 259: 378–1127.
- Liu Y.-Q.; Goodrick S.A.; Heilman W.E. 2013a. Wildland fire emissions, carbon, and climate: wildfire-climate interactions. *Forest Ecology and Management*. 317: 80–96.
- Liu Y.-Q.; Goodrick, S.L.; Stanturf, J.A. 2013b. Future U.S. wildfire potential trends projected using a dynamically downscaled climate change scenario. *Forest Ecology and Management*. 294: 120–135.
- Lloyd-Hughes, B.; Saunders, M.A. 2002. A drought climatology for Europe. *International Journal of Climatology*. 22: 1571–1592.
- Loehman, R.A.; Reinhardt, E.; Riley, K.L. 2014. Wildland fire emissions, carbon, and climate: seeing the forest and the trees—a cross-scale assessment of wildfire and carbon dynamics in fire-prone, forested ecosystems. *Forest Ecology and Management*. 317: 9–19.
- Logan, J.A.; Powell, J.A. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist*. 47: 160–172.
- Logan, J.A.; Powell, J.A. 2009. Ecological consequences of climate change altered forest insect disturbance regimes. In: Wagner, F.H., ed. *Climate change in western North America: evidence and environmental effects*. Salt Lake City: University of Utah Press: 98–109.
- Luce, C.H.; Abatzoglou, J.T.; Holden, Z.A. 2013. The missing mountain water: slower westerlies decrease orographic enhancement in the Pacific Northwest, U.S.A. *Science*. 342: 1360–1364.
- Luce, C.H.; Holden, Z.A. 2009. Declining annual streamflow distributions in the Pacific Northwest United States, 1948–2006. *Geophysical Research Letters*. 36(16): L16401. 6 p. doi: 10.1029/2009GL039407. [Published online: August 22, 2009].
- Luce, C.; Morgan, P.; Dwire, K. [and others]. 2012. Climate change, forests, fire, water, and fish: building resilient landscapes, streams, and managers. Gen. Tech. Rep. RMRS-GTR-290. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 209 p.
- Lundquist, J.E. 2007. The relative influence of diseases and other small-scale disturbances on fuel loading in the Black Hills. *Plant Disease*. 91: 147–152.
- Maloney, E.D.; Camargo, S.J.; Chang, E. [and others]. 2014. North American climate in CMIP5 experiments: part III: assessment of twenty-first-century projections. *Journal of Climate*. 27: 2230–2270.
- Manion, P.D. 1991. *Tree disease concepts*. 2d ed. Englewood Cliffs, NJ: Prentice Hall. 399 p.
- Manion, P.D. 2003. Evolution of concepts in forest pathology. *Phytopathology*. 93: 1052–1055.
- Marlon, J.R.; Bartlein, P.J.; Long, C. [and others]. 2012. Long-term perspective on wildfires in the Western U.S. *Proceedings of the National Academy of Sciences, U.S.A.* 109: E535–E543.
- McKee, T.B.; Doesken, N.J.; Kleist, J. 1993. The relationship of drought frequency and duration to time scales. In: Preprints, 8th Conference on Applied Climatology, 17–22 January 1993, Anaheim, CA. Boston, MA: American Meteorological Society: 179–184.
- McKelvey, K.S.; Skinner, C.N.; Chang, C. [and others]. 1996. An overview of fire in the Sierra Nevada. In: *Sierra Nevada Ecosystem Project: final report to Congress, v. II, Assessments and scientific basis for management options*. Davis, CA: University of California, Centers for Water and Wildland Resources: 1033–1040. <http://pubs.usgs.gov/dds/dds-43/TOC.PDF>. [Date accessed: September 15, 2015].
- McKenzie, D.; Gedalof, Z.M.; Peterson, D.L.; Mote, P. 2004. Climatic change, wildfire, and conservation. *Conservation Biology*. 18: 890–902.

- McKenzie, D.; Peterson, D.L.; Littell, J. 2009. Global warming and stress complexes in forests of western North America. In: Bytnerowicz, A.; Arbaugh, M.J.; Riebau, A.R.; Andersen, C., eds. Wildland fires and air pollution. The Hague, Netherlands: Elsevier Publishers: 317–337.
- Melton, M. 1989. Keetch-Byram Drought Index: a guide to fire conditions and suppression problems. *Fire Management Notes*. 50(4): 30–34.
- Miller, J.D.; Skinner, C.N.; Safford, H.D. [and others]. 2012. Trends and causes of severity, size, and number of fires in northwestern California, U.S.A. *Ecological Applications*. 22: 184–203.
- Miller, P.R. 1992. Mixed conifer forests of the San Bernardino Mountains, California. In: Olson, R.K.; Binkley, D.; Böhm, M., eds. Response of western forests to air pollution. New York: Springer-Verlag: 461–497.
- Mills, T.J.; Bratten, F.W. 1982. FEES: design of a Fire Economics Evaluation System. Gen. Tech. Rep. PSW-065. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 26 p.
- Milne, B.T.; Gupta, V.K.; Restrepo, C. 2002. A scale-invariant coupling of plants, water, energy, and terrain. *EcoScience*. 9: 191–199.
- Milne, B.T.; Johnson, A.R.; Keitt, T.H. [and others]. 1996. Detection of critical densities associated with pinyon-juniper woodland ecotones. *Ecology*. 77: 805–821.
- Mitchell, R.J.; Liu, Y.-Q.; O'Brien, J.J. [and others]. 2014. Future climate and fire interactions in the southeastern region of the United States. *Forest Ecology and Management*. 327: 316–326. doi:10.1016/j.foreco.2013.12.003. [Published online: January 7, 2014].
- Möldersa, N.; Kramma G. 2007. Influence of wildfire induced land-cover changes on clouds and precipitation in interior Alaska—a case study. *Atmospheric Research*. 84: 142–168.
- Morgan, P.; Heyerdahl, E.K.; Gibson, C.E. 2008. Multi-season climate synchronized forest fires throughout the 20th century, Northern Rockies, U.S.A. *Ecology*. 89: 717–728.
- Moritz, M.A.; Morais, M.E.; Summerell, L.A. [and others]. 2005. Wildfires, complexity, and highly optimized tolerance. *Proceedings of the National Academy of Sciences, U.S.A.* 102: 17,912–17,917.
- Moritz, M.A.; Parisien, M.; Batillori, E. [and others]. 2012. Climate change and disruptions in global fire activity. *Ecosphere* 3: 49.
- Mote, P.W.; Hamlet, A.F.; Clark, M.P.; Lettenmaier, D.P. 2005. Declining mountain snowpack in western North America. *Bulletin of the American Meteorological Society*. 86: 39–49.
- National Interagency Fire Center. 1995. Keetch-Byram drought index [Homepage]. Wildland Fire Assessment System. Boise, ID: U.S. Department of Agriculture, Forest Service, Fire and Aviation Management, National Information Systems Team. <http://www.wfas.net/index.php/keetch-byram-index-moisture--drought-49>. [Date accessed: September, 24, 2014].
- Palmer W.C. 1965. Meteorological drought. Res. Pap. 45. Washington, DC: U.S. Department of Commerce. 58 p.
- Peterson, D.L.; Arbaugh, M.J. 1988. Growth patterns of ozone-injured ponderosa pine (*Pinus ponderosa*) in the southern Sierra Nevada. *Journal of the Air Pollution Control Association*. 38: 921–927.
- Peterson, D.L.; Arbaugh, M.J.; Robinson, L.J. 1991. Growth trends of ozone-stressed ponderosa pine (*Pinus ponderosa*) in the Sierra Nevada of California, U.S.A. *The Holocene*. 1: 50–61.
- Peterson, D.L.; Littell, J.S. 2014. Risk assessment for wildfire in the Western United States. In: Peterson, D.L.; Vose, J.M.; Patel-Weyand, T., eds. Climate change and United States forests. Dordrecht, The Netherlands: Springer: 232–235.
- Platt, W.J.; Beckage, B.; Doren, R.F.; Slater, H.H. 2002. Interactions of large-scale disturbances: prior fire regimes and hurricane mortality of savanna fires. *Ecology*. 83: 1566–1572.
- Pollet, J.; Omi, P.N. 2002. Effect of thinning and prescribed burning on crown fire severity in ponderosa pine forests. *International Journal of Wildland Fire*. 11: 1–10.
- Preisler, H.K.; Chen, S.-C.; Fujioka, F. [and others]. 2008. Wildland fire probabilities estimated from weather model-deduced monthly mean fire danger indices. *International Journal of Wildland Fire*. 17: 305–316.
- Preisler, H.K.; Westerling, A.L. 2007. Statistical model for forecasting monthly large wildfire events in Western United States. *Journal of Applied Meteorology and Climatology*. 46: 1020–1030.
- Prichard, S.J.; Oswald, W.W.; Gedalof, Z.; Peterson, D.L. 2009. Holocene fire and vegetation dynamics in a montane forest, North Cascade Range, Washington, U.S.A. *Quaternary Research*. 72: 57–67.
- Radeloff, V.C.; Hammer, R.B.; Steward, S.I. 2005. The wildland-urban interface in the United States. *Ecological Applications*. 15: 799–805.
- Regonda, S.; Rajagopalan, B.; Clark, M.; Pitlick, J. 2005. Seasonal cycle shifts in hydroclimatology over the Western United States. *Journal of Climate*. 18: 372–384.
- Riley, K.L.; Abatzoglou, J.T.; Grenfell, I.C. [and others]. 2013. The relationship of large fire occurrence with drought and fire danger indices in the western U.S.A, 1984–2008: the role of temporal scale. *International Journal of Wildland Fire*. 22: 894–909.
- Ross, D.W.; Daterman, G.E.; Boughton, J.L.; Quigley, T.M. 2001. Forest health restoration in south-central Alaska: a problem analysis. Gen. Tech. Rep. PNW-GTR-523. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 38 p.
- Ross, M.S.; O'Brien, J.J.; Ford, R.G. [and others]. 2009. Disturbance and the rising tide: the challenge of biodiversity management on low-island ecosystems. *Frontiers in Ecology and the Environment*. 7: 471–478.
- Rothermel, R.C. 1972. A mathematical model for predicting fire spread in wildland fuels. Res. Pap. INT-115. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Experiment Station. 40 p.
- Samuels, M.L.; Betancourt, J.L. 1982. Modeling the long-term effects of fuelwood harvest on pinyon-juniper woodlands. *Environmental Management*. 6: 505–515.
- Scott, J.H.; Burgan, R.E. 2005. Standard fire behavior fuel models: a comprehensive set for use with Rothermel's surface fire spread model. Gen. Tech. Rep. RMRS-GTR-153. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 72 p.
- Simard, A.J. 1968. The moisture content of forest fuels: a review of the basic concepts. Information Report FF-X-14. Ottawa, Ontario: Forest Fire Research Institute. 47 p.
- Skinner, W.R.; Shabbar, E.; Flannigan, M.D.; Logan, K. 2006. Large forest fires in Canada and the relationship to global sea surface temperatures. *Journal of Geophysical Research*, 111(D14): D14106. doi:10.1029/2005JD006738. [Published online: July 26, 2006].

- Stephenson, N.L. 1990.** Climatic control of vegetation distribution: the role of the water balance. *American Naturalist*. 135: 649–670.
- Stephenson, N.L. 1998.** Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *Journal of Biogeography*. 25: 855–870.
- Stewart, I.T. 2009.** Changes in snowpack and snowmelt runoff for key mountain ranges. *Hydrological Processes*. 23: 78–94.
- Stine, S. 1996.** *Climate, 1650-1850*. In: Sierra Nevada Ecosystem Project: final report to Congress, v. II, Assessments and scientific basis for management options. Davis, CA: University of California, Centers for Water and Wildland Resources: 25–30. <http://pubs.usgs.gov/dds/dds-43/TOC.PDF>. [Date accessed: September 15, 2015].
- Stohl, A.; Andrews, E.; Burkhardt, J.F. [and others]. 2006.** Pan-Arctic enhancements of light absorbing aerosol concentrations due to North American boreal forest fires during summer 2004. *Journal of Geophysical Research*. 111(D22): D22214. 20 p. doi: 10.1029/2006JD007216. [Published online: November 23, 2006].
- Stone, R.S.; Augustine, J.A.; Dutton, E.G. [and others]. 2011.** Empirical determinations of the longwave and shortwave radiative forcing efficiencies of wildfire smoke. *Journal of Geophysical Research*. 116(D12): D12207. 9 p. doi:10.1029/2010JD015471. [Published online: June 25, 2011].
- Swetnam, T.W. 1993.** Fire history and climate change in giant sequoia groves. *Science*. 262: 885–889.
- Swetnam, T.W.; Betancourt, J.L. 1998.** Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *Journal of Climate*. 11: 3128–3147.
- Swetnam, T.W.; Baisan, C.H. 2003.** Tree-ring reconstructions of fire and climate history in the Sierra Nevada and Southwestern United States. In: Veblen, T.T.; Baker, W.L.; Montenegro, G.; Swetnam, T.W., eds. *Fire and climatic change in temperate ecosystems of the western Americas*. New York: Springer-Verlag: 158-195.
- Thorntwaite, C.W. 1948.** An approach toward a rational classification of climate. *Geographical Review*. 38: 55–94.
- Trouet, V.; Taylor, A.H.; Carleton, A.M.; Skinner, C.N. 2009.** Interannual variations in fire weather, fire extent, and synoptic-scale circulation patterns in northern California and Oregon. *Theoretical and Applied Climatology*. 95: 349–360.
- Urbanski, S.P.; Hao, W.M.; Baker, S. 2008.** Chemical composition of wildland fire emissions. In: Bytnerowicz, A.; Arbaugh, M.J.; Riebau, A.R.; Andersen, C., eds. *Wildland Fires and Air Pollution*. The Hague, Netherlands: Elsevier: 79–107.
- van Mantgem, P.J.; Stephenson, N.L.; Keifer, M.; Kelley, J. 2004.** Effects of an introduced pathogen and fire exclusion on the demography of sugar pine. *Ecological Applications*. 14: 1590–1602.
- Veblen, T.T.; Hadley, K.S.; Nel, E.M. [and others]. 1994.** Disturbance regimes and disturbance interactions in a Rocky Mountain subalpine forest. *Journal of Ecology*. 82: 125–135.
- Veblen, T.T.; Hadley, K.S.; Reid, M.S.; Rebertus, A.J. 1991.** The response of subalpine forests to spruce beetle outbreak in Colorado. *Ecology*. 72: 213–231.
- Veblen, T.T.; Kitzberger, T.; Donnegan, J. 2000.** Climatic and human influences on fire. In: regimes in ponderosa pine forests in the Colorado Front Range. *Ecological Applications*. 10: 1178–1195.
- Walsh, J.; Wuebbles, D.; Hayhoe, K. [and others]. 2014.** Appendix 3: Climate science supplement. In: Melillo, J.M.; Richmond, T.C.; Yohe, G.W., eds. *Climate change impacts in the United States: the third National Climate Assessment*. Washington, DC: United States Global Change Research Program: 735–789. doi:10.7930/J0Z31WJ2. [Published online: May 2014].
- Werner, R.A.; Holsten, E.H.; Matsuoka, S.M.; Burnside, R.E. 2006.** Spruce beetles and forest ecosystems in south-central Alaska: a review of 30 years of research. *Forest Ecology and Management*. 227: 195–206.
- Westerling, A.L.; Gershunov, A.; Brown, T.J. [and others]. 2003.** Climate and wildfire in the Western United States. *Bulletin of the American Meteorological Society*. 84: 595–604.
- Westerling, A.L.; Hidalgo, H.G.; Cayan, D.R.; Swetnam, T.W. 2006.** Warming and earlier spring increases western U.S. forest wildfire activity. *Science*. 313: 940–943.
- Whitlock, C.; Higuera, P.E.; McWethy, D.B.; Briles, C.E. 2010.** Paleocological perspectives on fire ecology: revisiting the fire-regime concept. *The Open Ecology Journal*. 3: 6–23.
- Xanthopoulos, G.; Maheras, G.; Gouma, V.; Gouvas, M. 2006.** Is the Keetch-Byram drought index (KBDI) directly related to plant water stress? *Forest Ecology and Management*. 234: (supplement 1), S27.

Rangeland Drought: Effects, Restoration, and Adaptation

Deborah M. Finch

Rosemary L. Pendleton

Matt C. Reeves

Jeffrey E. Ott

Francis F. Kilkenny

Jack L. Butler

Jacqueline P. Ott

Jeremy R. Pinto

Paulette L. Ford

Justin B. Runyon

Mark A. Rumble

Stanley G. Kitchen

D.M. Finch is a Biologist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Albuquerque, NM 87102.

R.L. Pendleton is a Research Plant Ecologist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Albuquerque, NM 87102.

M.C. Reeves is a Research Ecologist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Missoula, MT 59807.

J.E. Ott is a Research Geneticist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Boise, ID 83702.

F.F. Kilkenny is a Research Biologist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Boise, ID 83702.

J.L. Butler is a Research Ecologist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Rapid City, SD 57702.

J.P. Ott is a Post-Doctoral Research Botanist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Rapid City, SD 57702.

J.R. Pinto is a Research Plant Physiologist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Moscow, ID 83843.

P.L. Ford is a Research Ecologist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Albuquerque, NM 87102.

J.B. Runyon is a Research Entomologist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Bozeman, MT 59717.

M.A. Rumble is a Research Wildlife Biologist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Rapid City, SD 57702.

S.G. Kitchen is a Research Botanist with U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Provo, UT 84606.

Introduction

Drought can have severe impacts on rangeland ecosystems in North America. For the purposes of this chapter, rangelands include natural grasslands, savannas, shrublands, many deserts, tundras, alpine communities, marshes, meadows, and woodlands. Drought impacts vary depending on the severity, frequency, duration, and aerial extent of the drought(s); how the land is managed; and whether plans are in place and implemented to respond to drought. Drought can be simply defined as “a lack of water” characteristic of time, not of place; or it can be defined in a climatic context, as “precipitation levels that are much lower than the annual average” (chapter 2). Chapter 2 identifies four drought classifications: (1) meteorological drought which focuses on water in the atmosphere, (2) hydrologic drought which focuses on available surface water, (3) agricultural or soil moisture drought which emphasizes crop response to declining moisture in soils, and (4) socioeconomic drought which emphasizes the social and economic impacts of drought. These classifications emphasize the harmful impacts of drought, particularly on managed systems and people.

One of the most harmful droughts impacting American rangelands and farmlands was the drought of the 1930s known as the Dust Bowl. Direct effects of the drought were both agricultural and socioeconomic; the drought caused damage to crops, livestock, and ultimately humans. The 1930s drought was several distinct events occurring in such rapid succession that affected regions were unable to recover adequately before another drought began. These severe, sequential droughts and the vast aerial extent the droughts covered, in combination with poor agricultural practices, overexpansion, and poverty associated with the Great Depression, made the 1930s drought period the most widely accepted “drought of record” for the United States (Hurt 1981, Warrick 1980). Reduced plant cover and increased bare ground led to dust storms (during high winds) and loss of topsoil. The resulting agricultural depression contributed to the Great Depression’s bank closures, business losses, increased unemployment, and other physical and emotional hardships.

Many lessons in resiliency and adaptation were learned in response to the calamitous effects of the Dust Bowl. Proactive measures following the 1930s drought included increased conservation practices and irrigation, improved farming and ranching practices, and diversified regional economy. Other actions included

new or enlarged reservoirs, improved domestic water systems, new insurance and aid programs, and removal of some of the most sensitive agricultural lands from production (Riebsame and others 1991). These learned strategies helped to reduce the region’s vulnerability to the negative impacts associated with drought.

With these adaptations, the likelihood of having a rangeland drought as catastrophic as the Dust Bowl has lessened substantially. Nevertheless, given the recent history, paleo-record, and recurring nature of drought and its relationship to climate change, it remains critical to understand the full range of its effects on natural and managed lands; to know techniques to reduce species and ecosystem vulnerability to drought; and to have information available that will assist in recovering natural and managed systems from the impacts of drought. High temperatures and lack of precipitation associated with the Dust Bowl would not only have affected crops, livestock, and people, they would also have affected native plants and animals, and they would have created water shortages—yet these ecological effects were not well-understood or reported at the time. Thus, while agricultural and socioeconomic classifications of drought have sharp bearing on rangelands and farmlands, they do not adequately encompass the ecological impacts of drought on native rangeland species, plant communities, and wildlife habitat. The direct and indirect consequences of severe and extended drought are complex, interactive, and numerous. There are a number of early ecological indicators that signal the impending possibility of serious agricultural and socioeconomic drought on rangelands, and they are important to understand and monitor. Listed sequentially, these early ecological indicators include:

- Water shortages stress plants and animals
- Vegetation production is reduced
- Plant mortality increases
- Plant cover is reduced
- Amount of bare ground increases
- Soil erosion become more prevalent
- Habitat and food resources for wildlife are reduced
- Wildlife mortality increases

- Rangeland fires may increase
- Some insect pests and invasive weeds may increase
- Forage value and livestock carrying capacity decreases
- Economic depression in the agricultural sector sets in

To convey the full importance of drought impacts on rangelands in both natural and managed settings, our goals in this chapter are to describe: (1) the ecological history of rangeland drought, (2) the ecological consequences of drought to native rangeland species and ecosystems, (3) the effects of drought on natural disturbances, (4) the effects of drought on land management practices, and (5) the adaptive responses of ecosystems to drought.

Types and Patterns of Rangeland Drought

Droughts are of grave concern to policymakers, livestock producers, and the agricultural sector because droughts are among the most costly of disasters (Andreadis and others 2005), and they significantly impact numerous goods and services. Large-scale, persistent droughts have periodically occurred across North American rangelands and are not unusual (Andreadis and others 2005, Cook and others 2007, Weakley 1965). Dai and others (1998) suggest that trends in drought intensity over the past two to three decades derive from global warming. While severe, these conditions have not yet clearly exceeded drought severity in the 20th century (e.g., the Dust Bowl era) (Cook and others 2010). Similarly, a review of drought trends by Cook and others (2010) suggests that the Western United States has recently entered a period of protracted aridity; a perspective accentuated by the particularly troublesome, ongoing situations in Texas and California. The year 2011 was the single worst year on record for Texas with drought continuing into a third year. That year, wildfires in Texas burned 2.7 million acres along with 2,725 residential homes (National Interagency Fire Center; http://www.predictiveservices.nifc.gov/intelligence/2011_statsum/fires_acres.pdf, date accessed: October 15, 2015). Cattle sector losses were reported at \$3.23 billion just for a single year (Amico and others 2011).

The 2011 drought conditions in Texas are an example of “flash drought” when soils dry very rapidly. These

events coincide with high temperatures, low cloud cover, low rainfall, and high winds. Because they generally occur during the growing season, flash droughts can be particularly devastating for agriculture and livestock grazing (Otkin and others 2013).

Drought Trends and Regional Effects

To understand long-term trends and impacts of drought over rangelands of the coterminous United States, we present trends from three sources including Parameter-elevation Relationships on Independent Slopes Model (PRISM) project data (1982–2012), weekly drought maps from the U.S. Drought Monitor (2000–2013), and Normalized Difference Vegetation Index (NDVI) from the Moderate Resolution Imaging Spectroradiometer (MODIS) at 250-m² spatial resolution (2000–2013). We wanted to illustrate the number of seasonal periods indicative of a drying landscape where seasonal or annual temperatures have been increasing while precipitation has been decreasing. Such an index is a practical way to assimilate large amounts of data for understanding impacts of changing climates on vegetation and other resources (Zargar and others 2011).

In figure 8.1, warmer tones indicate increasingly restrictive growth conditions. Since 1982, the southern part of the United States has been exhibiting unfavorable trends in growing conditions resulting from warmer temperatures and decreasing precipitation. Relative to other western regions, much of Arizona, Texas, New Mexico, and the Oklahoma Panhandle exhibit the most notable decreasing trends in growing conditions. The reddish regions in north central New Mexico correspond with the massive dieoff (90 percent) of pinyon pine (*Pinus edulis*) and illustrate the scale of vegetation change these conditions can induce (Breshears and others 2005). A loss of this magnitude of a long-lived, arid-adapted tree is attributed to persistent drought accompanied by warmer temperatures, resulting in greatly reduced soil moisture and water stress (Breshears and others 2005). Conversely, much of the upper Midwest and northern Great Plains have become wetter and slightly warmer, indicating improved growing conditions. It is worth noting that this type of climatic trend assessment will not usually capture the episodic or ephemeral droughts; those events are more appropriately captured in shorter timeframes, such as the weekly spatially explicit data from the U.S. Drought Monitor.

Since 2000, there have been several significant events in which intense drought has enveloped western

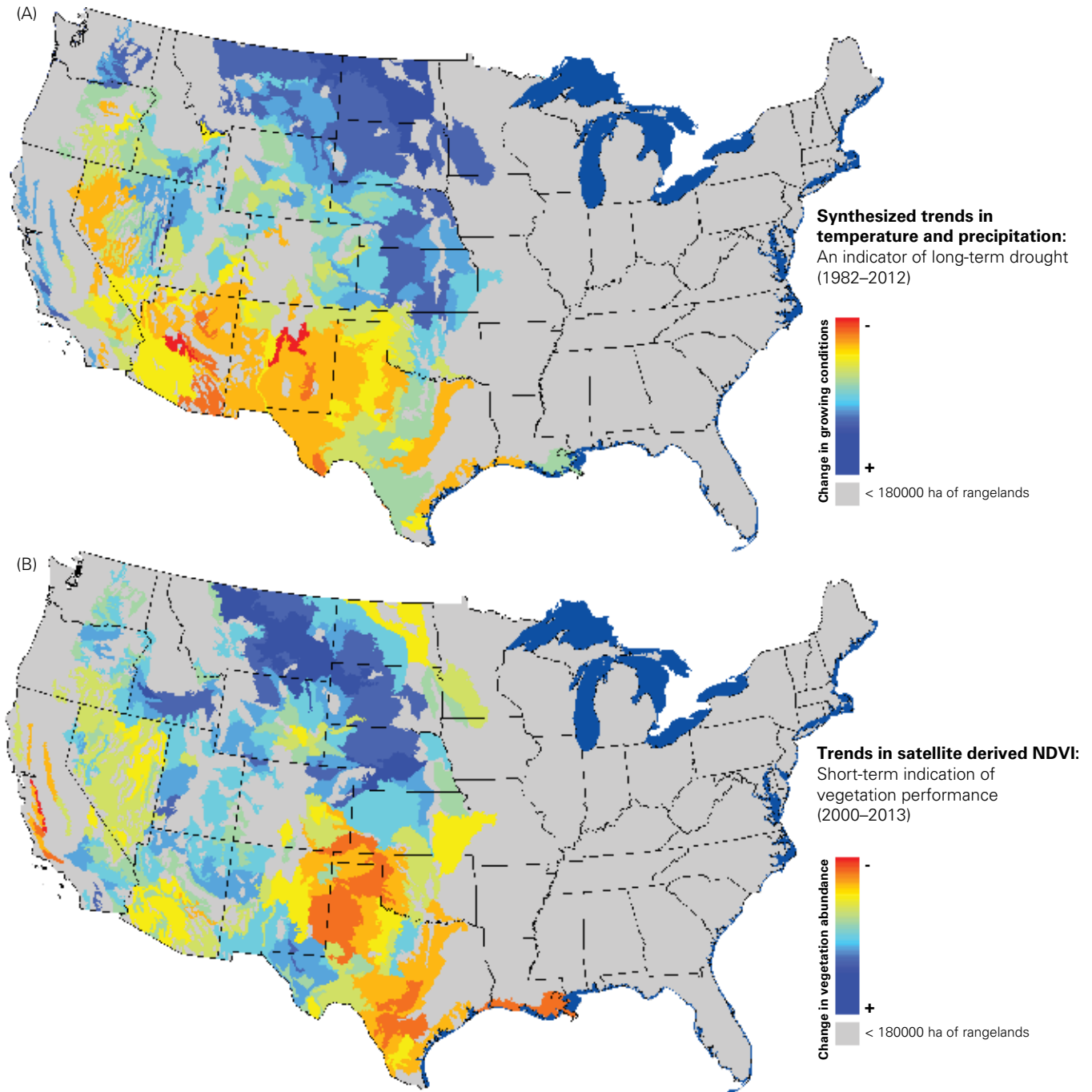


Figure 8.1—Drought intensity and effects on vegetation. Top panel (A) represents trends in gridded surface climatology from the Parameter-elevation Relationships on Independent Slopes Model (PRISM) project, 1982–2012. Warmer tones indicate areas where temperature has been increasing while precipitation has been decreasing; cooler tones represent improved growing conditions. Bottom panel (B) represents the trend of Normalized Difference Vegetation Index (NDVI) from Moderate Resolution Imaging Spectroradiometer (MODIS) at 250-m² spatial resolution averaged over ecological subsections (Bailey and Hogg 1986), 2000–2013. Warmer tones indicate where vegetation abundance has been decreasing through time (i.e., a “browning” of the landscape), while cooler tones represent greater vegetation (i.e., a “greening”) of the landscape. (Maps created by Matt Reeves).

rangelands (fig. 8. 2). Since 2011, the average area occupied by the most significant drought category (D4 in fig. 8.2) has more than doubled compared with 2000–2010 records. The information in figure 8.3 was developed from weekly estimates of drought categories very similar to that represented in figure 8.2. Figure 8.2 depicts the ongoing drought conditions over much of Texas and California. These drought episodes combined with longer term deterioration of growing conditions seen in other regions (fig. 8.1) have negatively affected the growth and abundance of rangeland vegetation. Because rangeland vegetation responds relatively quickly to changing meteorological conditions, it can be efficiently monitored using satellite remote sensing.

Reeves and Baggett (2014) developed an algorithm for quantifying trends in MODIS 250-m² NDVI for the United States. For this report, we evaluated vegetation types or U.S. Ecological Systems (Comer and others 2003) associated with negative vegetation trends since 2000. Table 8.1 indicates that many vegetation types have experienced declining trends

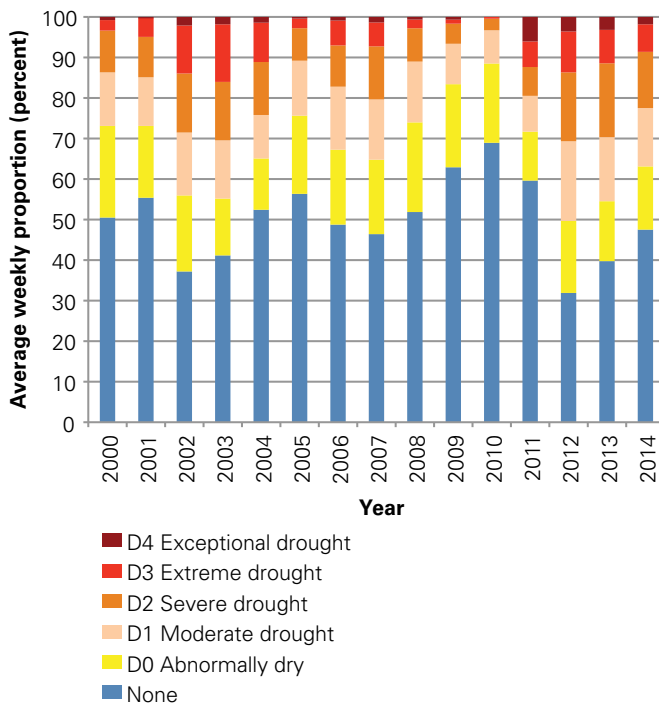


Figure 8.2—Drought categories derived from annualized U.S. Drought Monitor maps (weekly), 2000–2014 in the coterminous United States. Data courtesy of the U.S. Department of Agriculture (USDA) and the National Oceanic and Atmospheric Administration (NOAA). The y-axis represents the annual average of weekly proportion of land in each drought category. So, for the year 2000, averaged over 52 data points (weeks), about 50 percent of lands experienced “none”, i.e., no drought.

on over 30 percent of the total area they occupy in the coterminous United States. Over 41 million ha of vegetation (~15 percent of all rangeland vegetation in the coterminous United States) (Reeves and Mitchell 2011) has exhibited declining trends in abundance since 2000. From a regional perspective, vegetation has responded in a similar pattern as indicated by the PRISM climatology. Note the decline of rangeland vegetation abundance on the southern Great Plains area in addition to the marked declines in the central California region (fig. 8.1). Although drought events in California in the 20th century were less frequent than previous patterns, there have been a number of recent drought episodes of significance to natural systems and socioeconomic well-being (Hughes and Brown 1992). At least three drought years (2000, 2002, 2008) occurred in the Southwestern United States during the 2000s, making the early 21st century the driest period in several centuries (Cayan and others 2010). Even more recently, California has been in drought since 2012, with record dry years reported and the majority of the State in extreme or exceptional drought as of the spring of 2014 (see fig. 8.2) (U.S. Drought Monitor report http://www1.ncdc.noaa.gov/pub/data/cmb/sotc/drought/2014/04/20140429_usdm.jpg. Date accessed: April 29, 2014). The climatological index derived here using PRISM data does not reflect the recent drought episodes in California, due to the relatively longer time period of the climate data compared with the recentness of the drought period. This illustrates the need to include a variety of data sources over multiple time periods to more completely understand drought effects on vegetation and other resources.

Variability in North American Drought Over Time: The Paleo-Record

Recurrent drought is to be expected with frequencies in sync with the phenomena that drive fluctuations in climate across broad spatial and temporal scales (Herweijer and others 2007). Droughts vary across time (frequency and duration), space, and severity in rangelands and other ecosystems. An understanding of the full range of natural variability in each dimension is needed to provide context for assessing the “normality” of historic drought in rangelands relative to past events and for projecting the novelty of future climatic conditions.

Consistent characterization of a drought or series of droughts is dependent upon selection of appropriate metrics that remain consistent across time and space. Instrumental meteorological data are sufficiently

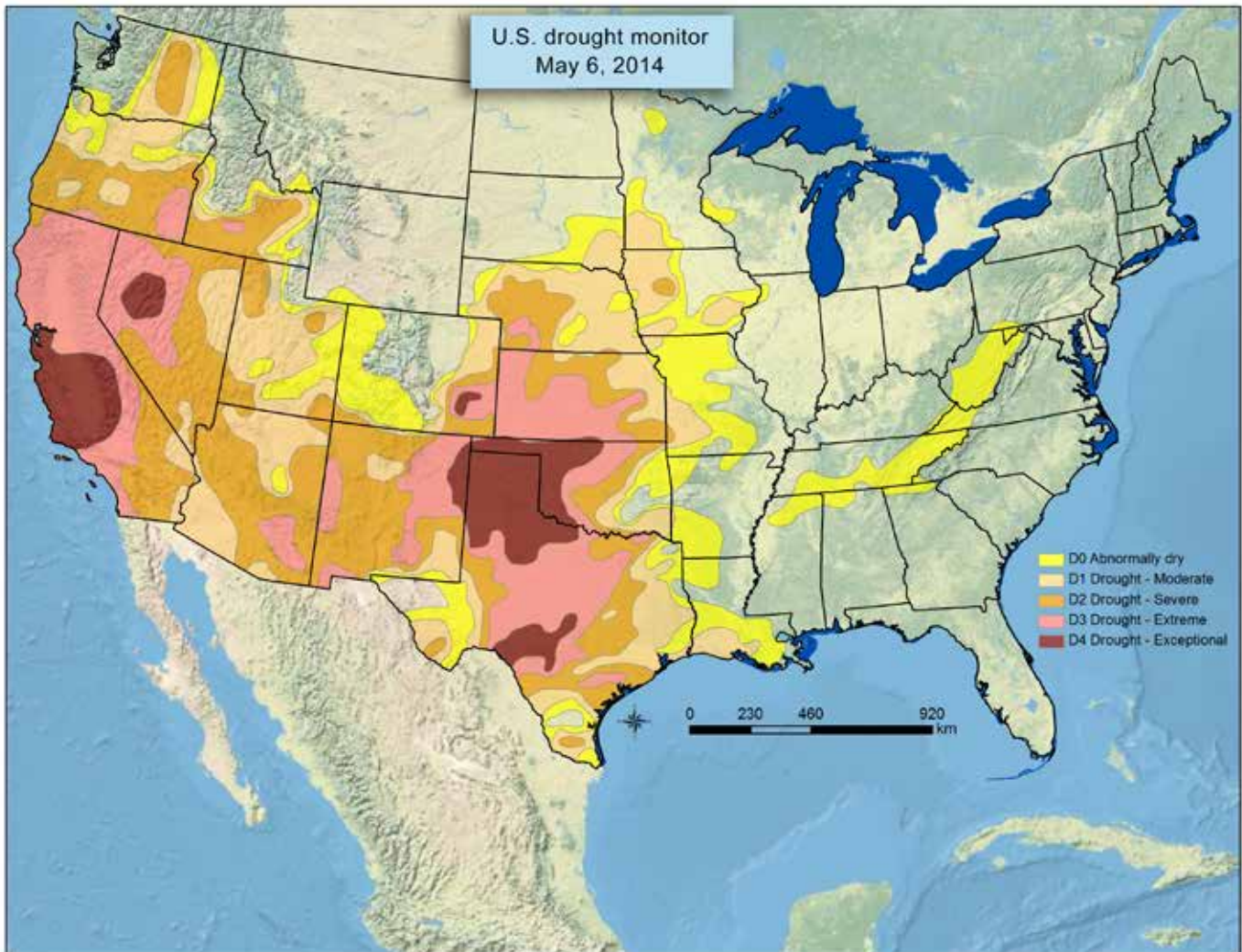


Figure 8.3—These data represent drought categories for the week of May 6, 2014. Notice the exceptional drought category in central California and northern Texas. Data courtesy of the U.S. Department of Agriculture (USDA) and the National Oceanic and Atmospheric Administration (NOAA).

Table 8.1—Breakdown of the top 20 U.S. Ecological Systems exhibiting negative trends in vegetation performance since 2000

Ecological System	Negative NDVI area (ha)	Area in declining trend (percent)
Tamaulipan Mixed Deciduous Thornscrub	225,588	56
California Annual Grassland	1,942,520	43
Tamaulipan Calcareous Thornscrub	604,070	41
South Texas Sand Sheet Grassland	434,402	40
Tamaulipan Mesquite Upland Scrub	3,460,482	37
Western Great Plains Mesquite Woodland and Shrubland	7,058,207	35
Edwards Plateau Limestone Shrubland	4,141,955	35
Southern California Coastal Scrub	938,878	33
Tamaulipan Savanna Grassland	634,618	33
Central Mixedgrass Prairie	8,473,944	32
Central and Southern California Mixed Evergreen Woodland	646,718	32
Sonora-Mojave Semi-Desert Chaparral	425,250	32
Western Great Plains Sandhill Steppe	3,782,085	30
Southern California Oak Woodland and Savanna	253,198	29
Chihuahuan-Sonoran Desert Bottomland and Swale Grassland	174,880	29
Western Great Plains Shortgrass Prairie	16,499,262	28
California Mesic Chaparral	1,220,700	27
Western Great Plains Foothill and Piedmont Grassland	256,282	26
Southern California Dry-Mesic Chaparral	837,099	25
Sonora-Mojave Mixed Salt Desert Scrub	352,823	24

NDVI = Normalized Difference Vegetation Index.

consistent but lack temporal depth for long-term analysis. Historic documents extend the record for North American drought by a few centuries, but have major spatial and temporal gaps. In addition, these records are largely subjective and difficult to quantify, rendering them of limited value by themselves for analyzing large-scale patterns of variability. During the Holocene (last 10,000+ years), western North America experienced multi-century episodes when conditions were consistently drier than the present. Examples include the mid-Holocene warm period lasting from 7,500–6,000 years before present (YBP) (Benson and others 2002, Grayson 2011) and a late-Holocene period of persistent drought that occurred in the central Great Basin (but not further north) from about 2800 to 1850 YBP (Mensing and others 2013). The later dry period was characterized by drops in lake levels, shifts to more xeric-adapted vegetation, an upward shift in upper tree line, and increased alluvial fan aggradation; collectively, those changes have been attributed to conditions that were warmer and drier than present.

Numerous studies have used tree-ring-based reconstructions of the Palmer Drought Severity Index (PDSI) (Cook and others 1999, 2004; Herweijer and others 2007) and other supportive data to compare the severity, duration, and spatial patterns of historical drought to those that occurred during the last 2,000 years. Long-term reconstructed streamflow for the Potomac (Maxwell and others 2011) and the Colorado Rivers (Meko and others 2007) reveal more severe and longer lasting droughts prehistorically than those known from 20th century instrumented records. Analyses of paleo-drought from the Central United States using multiple proxies (Woodhouse and Overpeck 1998) and continental-scale studies (Herweijer and others 2007) using tree-ring reconstructions of PDSI suggest that megadroughts during the Medieval Climate Anomaly (MCA), also known as Medieval Warm Period, were of similar severity but longer duration (20–40 years) and possibly greater spatial extent than those of the 20th century. Temporal analyses identified climate cycles at interannual to centennial scales (Herweijer and others 2007, Meko and others 2007, Stambaugh and others 2011). Herweijer and others (2007) determined that the central and western regions of the continent had the highest climate variability, and the Central and Southwestern United States were drought centers with highest drought activity over time. Drought spatial patterns supported a strong linkage of drought to the El Niño Southern Oscillation (ENSO) of Pacific sea surface temperature (SST), and this and other studies (Cole and

Overpeck 2002, Cook and others 2004, Stahle and others 2000) suggest a persistent La Niña-like phase, unlike any observed in recent centuries, may have been responsible for prolonged drought events in the past.

Collectively, these studies indicate that 20th century measures of climate, including drought, represent only a subset of the full range of conditions experienced in the past as a result of natural variation. Although drivers and feedback mechanisms are not fully understood, there is sufficient indication from past climate records and future projections to prioritize development of effective strategies for coping with the consequences of more frequent, more severe, and longer drought, especially in central and western regions of North America where water resources are already scarce.

The Future of Drought on Rangelands

Although it is difficult to model a detailed picture predicting the occurrence and extent of future drought, it is clear that higher temperatures will increase severity of drought episodes when they occur. Drought in North America appears to be strongly related to Pacific Ocean SSTs and is sensitive to even small temperature changes (Cayan and others 2010). Change in SSTs induced the recent severe drought in California, 2013–2014, and the associated circulation patterns were intensified—perhaps even created—by global warming (Wang and others 2014). Higher temperatures will reduce soil moisture critical to plant productivity, species composition, and erosion potential (Polley and others 2013). Models of net primary productivity predict overall better growing conditions for the northern Great Plains, while the opposite is true of the southern Great Plains (Polley and others 2013, Reeves and others 2014). Trends indicated by PRISM and NDVI data may continue with persistent and increasing aridity for the southern Great Plains and central California (figs. 8.1 and 8.2). Cayan and others (2010) predict droughts in this century will extend for periods of time of ≥ 12 years in the Southwest, which will severely tax already limited water supplies (Foti and others 2012). More frequent drought episodes interspersed with fewer episodes of higher-than-average rainfall indicate vegetation in the Southwest may not recover to what is currently considered a typical or average state (Seager and others 2007).

Although the future of SST patterns is uncertain, warmer temperatures will exacerbate any deficit in soil moisture, and several studies point towards more frequent and severe drought along with large-scale

ecological change for the future (Breshears and others 2005, Cayan and others 2010, Cook and others 2007). Drying may be particularly pervasive in the Southwestern United States, northern Mexico, and the interior West (Andreadis and Letterman 2006, Seager and others 2007). California can expect continued intensification of drought episodes (Wang and others 2014).

Drought severity has not increased recently in other regions of the United States, including the northern Great Plains; this indicates that although these regions will still be subject to periodic drought, they may be better able to recover after drought episodes under current management practices (Andreadis and Letterman 2006, Clark and others 2002). Of particular interest to the sustainability of ecosystem services are megadroughts—spanning decades rather than years, they are unprecedented for our recorded history, and thus not integrated into disaster preparedness or resource contingency plans (Cook and others 2010). It is unclear if global change will induce megadroughts or not, but predicted warmer temperatures and unchanged or declining precipitation across rangelands could induce negative, persistent impacts.

Effects of Drought on Rangelands

This section reviews how drought influences water availability, soil moisture, and plant physiology, as well as plant growth, abundance, and productivity, vegetation changes, and wildlife habitat.

Water Availability, Soil Moisture, and Plant Productivity

Soil moisture is affected by a number of factors in addition to the amount of annual precipitation. Soil recharge is heavily influenced by the season, timing, and amount of precipitation events. Event size, number of events, and length of time between events influence vegetation in different ways (Lauenroth and Sala 1992). In hot summer months, moisture is quickly lost through evaporation from the soil surface and vegetative transpiration. In winter, evaporation and transpiration are reduced, allowing moisture to accumulate and infiltrate to deeper soil levels (Weltzin and others 2003). Cooler summer temperatures may explain the observation of decreased interannual variability in grass production in northern regions as compared with hotter southern regions (Sala and others 1988). Infiltration from gentle rains of long duration is most effective at recharging

soil profiles. Infrequent, small precipitation events may wet only the soil surface, where moisture is quickly lost through evaporation. Lauenroth and Sala (1992) reported that a precipitation event of at least 15–30 mm was necessary in order to wet those soil layers that have largest effect on production. High-intensity summer storms may result in sheet runoff, with most infiltration occurring in lower lying areas. Dry, bare ground can take nearly three times longer to rewet than vegetated areas (Weaver and Albertson 1943).

Vegetative growth and reproduction is ultimately and directly linked to soil moisture. Multiple studies have reported a direct correlation between aboveground net primary production (ANPP) and mean annual precipitation (Briggs and Knapp 1995, Haddad and others 2002). Variability in annual rainfall may affect productivity more in grasslands than in all other biomes of North America (Knapp and Smith 2001). An analysis of 9,500 sites across the Central United States confirmed the tremendous importance of water availability to plant productivity (Sala and others 1988). Regional patterns in ANPP were correlated with an east-to-west gradient in annual precipitation. Production levels during years of drought were observed to shift eastward, with high production levels restricted to the more mesic eastern plains. Vicente-Serrano and colleagues (2013), using satellite imagery for the continental United States, also found a direct correlation between precipitation and ANPP.

Plant Physiological Responses to Drought

The consequences of drought on plant physiological functioning can vary depending on the duration and severity of the drought. When droughts occur, critical edaphic variables such as soil moisture, temperature, and vapor pressure deficit (VPD) are affected and have impacts on plant physiological functioning. Of largest consequence for grassland plants is the reduction in soil water content, which leads to plant moisture stress and possibly mortality (Poirier and others 2012). This is because the critical link between desiccation and carbon gain (or starvation) is regulated through plant stomata, where fluxes of carbon dioxide (CO₂) and water vapor share the same pathway. The longer plants can withstand desiccation, the better their prospects for drought survival and recovery (Larcher 2003).

Drought, to varying degrees, will impact plant available moisture in the soil profile (James and others 2003). For periods of short drought duration, large deficits in plant available water may occur at the soil surface;

conversely, deeper in the soil profile, plant available water may be higher. As droughts lengthen in duration and become more severe, deeper soil moisture reserves will also decrease. These spatial and temporal differences are critical for short- versus long-rooted species as well as their strategies for avoiding or tolerating drought effects (Kozlowski and Pallardy 1997, Larcher 2003).

As drought severity increases and water availability decreases for perennial grassland species, a number of ecophysiological strategies can be employed to prevent mortality (fig. 8.4) (Volaire and others 2014). Growth maintenance, dehydration delay, dehydration tolerance, and dormancy strategies work on a continuum from no drought to severe drought, respectively. From a whole plant perspective, low-to-moderate drought stress may

still allow some leaf and root growth, albeit reduced. These low soil moisture conditions are often linked to reduced stomatal conductance and photosynthesis (Milbau and others 2005). From this, corresponding shifts in carbon allocation patterns emerge: leaf growth is reduced, followed later by reduced root growth, while carbon reserves may increase. As drought conditions increase, leaf senescence is employed to reduce transpirational surface area. Eventually, extreme drought stress will cause irreversible damage to the protoplasm, leading to leaf and tiller mortality.

Shrub species in grasslands employ similar strategies to endure drought conditions. Dehydration delay and the control of transpiration during drought are critical for maintaining water balance in woody species. Kozlowski and Pallardy (1997) list five adaptations to reduce

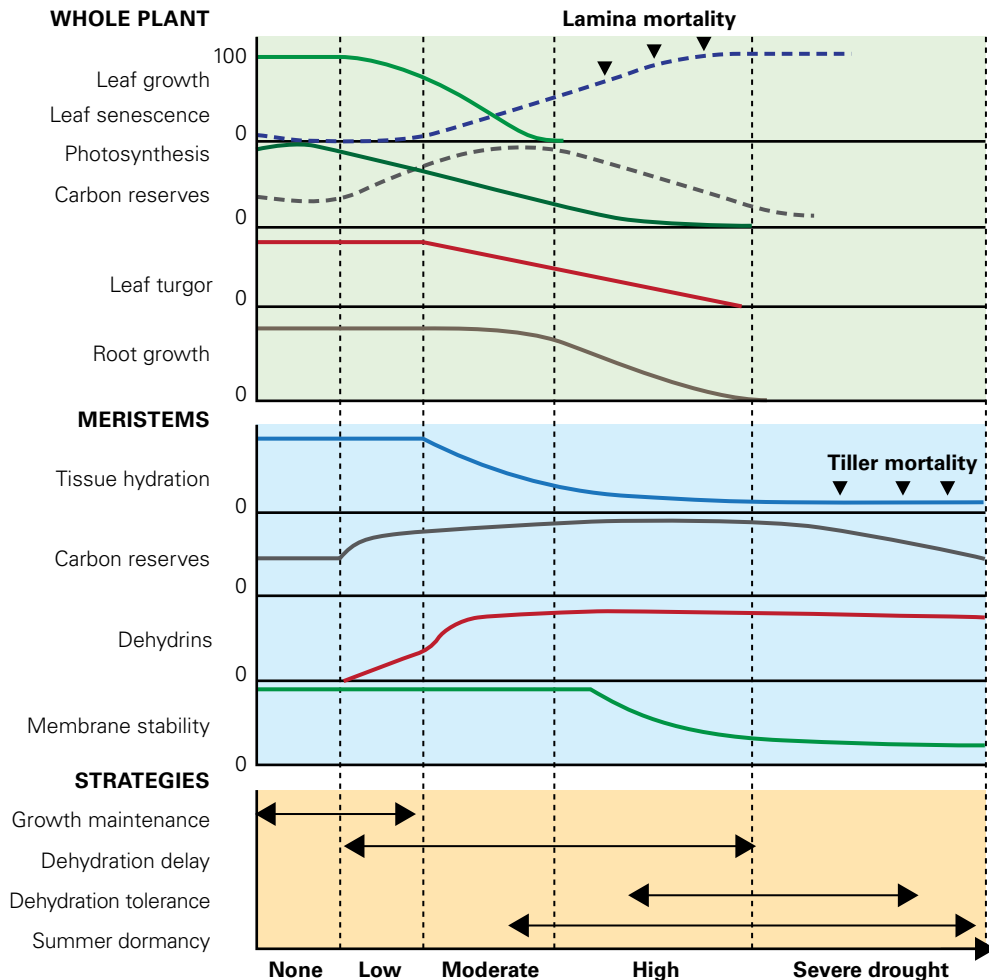


Figure 8.4—Perennial grass whole plant and meristem responses and ecophysiological strategies to increasing drought. Volaire and others (2014).

transpiration: (1) reduced capacity for growth, (2) reduced leaf size and altered morphology, (3) leaf abscission, (4) cuticular effectiveness, and (5) stomatal control. Kolb and Sperry (1999) found that these adaptations are similarly employed by different subspecies of big sagebrush (*Artemisia tridentata*) across elevation and precipitation gradients of the Great Basin of North America. However, their ability to withstand dry conditions and preserve hydraulic functioning varied. The subspecies from an arid locale showed greater resistance to xylem cavitation (50-percent loss) than subspecies from mesic conditions.

In some cases, plants are known to acclimate to drought conditions through repeated exposure (Bruce and others 2007). In Mediterranean shrubs, two species showed differences in photosynthesis and water-use efficiency from repeated drought and re-watering cycles, with one species showing much better photosynthesis recovery and improved water-use efficiency (Galle and others 2011). Grass has also shown acclimation to drought repetition with improved photoprotection, yet plants still experience an overall reduction in photosynthesis (Walter and others 2011). The mechanisms by which “stress imprints” occur are still largely under investigation. Drought-stress recovery will no doubt vary by species and degree, but the critical question is whether grassland species have the capacity and resiliency for the potentially repeated and worsened events caused by climate change (Scheffer and others 2001).

Effects of Drought on Vegetation

Climate instability and recurrence of extreme events can have a more profound effect on vegetation than do changes in average conditions (Weltzin and others 2003). Climate of the 20th century and early 21st century has been highly variable, exhibiting fairly rapid shifts between wet and dry periods that vary geographically (Grissino-Mayer and others 2002). This period has been marked by several large-scale droughts as well as several more local short-term droughts. The Great Plains experienced the unprecedented Dust Bowl drought of the 1930s. New Mexico experienced its worst multiyear drought between 1945 and 1963 (Betancourt and others 1993, Swetnam and Betancourt 1998), known as the 1950s drought. This drought extended from southern Arizona north to the Colorado River Basin, and east to western Texas and some parts of the Southeast. In 1985, there was a large-scale drought throughout much of the West, whereas the central and eastern portions of the United States experienced large-scale drought in 1988 (Kogan 1995). The effects of drought are cumulative. The longer a

drought persists without water recharge, the greater the severity. Using a standardized precipitation index, McKee and others (1993) reported that the single worst drought of the 20th century was that of the 1950s, whereas four consecutive droughts of shorter duration combined to produce the exceptional water deficits of the 1930s.

Vegetation response to historic drought—The great drought of the 1930s resulted from the combined effects of widespread cultivation of the soil and overgrazing brought on by the post-war demand for meat, and it was exacerbated by 6 preceding years of below average precipitation and high temperatures (Albertson and Weaver 1942). Average precipitation was 33–39 percent below normal, with most of the deficit occurring during the growing season. High winds whipped the dry, friable soil particles, creating enormous dust storms and smothering vegetation with thin blankets or deep drifts of silt.

Albertson and Weaver (1942, 1944) documented vegetation response and recovery from the drought over an 11-year period from 1933 to 1943 at locations near Hays, KS. Grasses and forbs died as deeper soil layers were depleted (Weaver and Albertson 1943). Basal area of little bluestem (*Andropogon scoparius*) declined 78 percent between 1932 and 1939, disappearing entirely from many areas, with little recovery exhibited by 1944 (Albertson and Weaver 1944). Hillsides dominated by little bluestem converted to more drought-tolerant sideoats grama (*Bouteloua curtipendula*) and shortgrass species. Uplands dominated by buffalograss (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*) declined in cover, but recovered with only slight shifts in dominance. Big bluestem (*A. gerardii*), decreased 79 percent in cover between 1932 and 1939, but did survive and later reestablished. Bare areas gradually recovered to shortgrass prairie dominated by buffalograss and blue grama. Species that reproduce vegetatively or those having deeper root systems were more resilient to drought. The overall result was a long-lasting shift in species composition: loss of little bluestem and an increase in grama grasses, buffalograss, and wheatgrass (*Agropyron smithii*).

The 1930s drought extended far beyond the southern plains. Sagebrush steppe of the upper Snake River Plain experienced several periods of severe drought. The summer of 1934 was the driest on record, accompanied by high temperatures and strong winds. The preceding years had also been drier than normal (Pechanec and others 1937). Shrub density, mostly of

sagebrush (*Artemisia* spp.), decreased to 46.8 percent of that present in 1932; the decrease was caused by dieback or death of whole plants. Basal area of perennial grasses declined 60 percent. The disintegration and death of grass clumps continued well into 1935 despite favorable conditions. Anderson and Inouye (2001) monitored vegetation at a similar location in the Snake River Plain between 1950 and 1975. Perennial grass cover increased from 0.5 percent in 1950 to 6.2 percent in 1975. Shrub cover, dominated by big sagebrush (*Artemisia tridentata*), increased from 17 percent in 1950 to 25 percent in 1975, although a subsequent drought during the late 1970s resulted in substantial mortality of big sagebrush. The authors postulated that high rainfall years can set up species for death when followed by sudden drought. They further noted that a lag time can occur between the resumption of normal rainfall and the response of vegetation. The presence of a lag time before vegetative recovery has also been noted by others (Ji and Peters 2003).

Ellison and Woolfolk (1937) documented the effects of a sustained drought near Miles City, MT, that peaked in 1934; this drought was aggravated by above-average temperatures and preceding years of below-normal precipitation. They documented substantial death of pine, juniper, and cottonwood, but also noted declines in sagebrush and other species. All shrubs experienced considerable dieback. Grass cover was reduced by up to 79 percent depending on the species. Effects of the drought were multiyear despite a favorable season in 1935. Needle-and-thread grass (*Stipa comata*) and Sandburg bluegrass (*Poa secunda*) were able to recover relatively quickly, despite mortality, through the establishment of new seedlings. Stands of big sagebrush experienced considerable mortality and did not regenerate, whereas silver sagebrush (*A. cana*) was able to resprout from the base.

Reports from other droughts also document large reductions in perennial grass cover, as well as shifts in plant community composition. Lauenroth and Sala (1992) found that 39–45 percent of the interannual variation in forage production over a 52-year period in north-central Colorado was explained by precipitation. Tilman and El Haddi (1992) reported an initial 47-percent decrease in plant biomass due to the 1980s drought. While biomass did recover within 2 years, species richness did not. Hobbs and others (2007) observed considerable changes in individual species' abundance over a 20-year study

in response to variation in rainfall amounts. Species richness also varied with precipitation. Morecroft and others (2004) recorded an approximate 50-percent reduction in vegetative cover in response to a drought occurring from 1995 to 1997. The relative proportion of vegetation also changed from one dominated by perennial grasses to one dominated by ruderal forbs. In a drought manipulation experiment, Evans and others (2011) found that 11 years of drought resulted in large reductions in total cover and cover of the dominant species, but significant differences did not emerge until the fourth and seventh year of drought.

Mechanisms of vegetation change—Ecosystems differ in their response to drought (Knapp and Smith 2001). On a biome scale, vulnerability to drought is thought to be greater in more humid regions, such as tallgrass prairie, where drought has historically occurred less frequently. Vegetation of arid and semiarid regions is more resilient to drought, as many species are adapted to water shortage. The response of the dominant vegetation may depend on the average time-scale at which drought typically occurs (Vicente-Serrano and others 2013). Seasonality of precipitation also affects ecosystems differently. In the southern Great Plains, precipitation during the summer growing season had the greatest effect on productivity (Albertson and Weaver 1942, 1944; Pechanec and others 1937). In the Great Basin and regions northward, accumulation of winter snow recharges soil moisture, resulting in a flush of spring growth.

Individual plant species also differ in their ability to tolerate and recover from drought. Deep-rooted species, such as big bluestem, can persist through longer periods of drought provided the deeper soil layers were moist to begin with (Albertson and Weaver 1942, Fay and others 2003, Morecroft and others 2004). An ability to reproduce vegetatively through resprouting, tillering, or the production of rhizomes or stolons, may also increase a plant's ability to recover from drought (Albertson and Weaver 1942, Pechanec and others 1937). Dominant species in wet areas may not tolerate drought well (Swemmer and others 2007). Plants of more arid regions have many adaptations for coping with moisture deficits. Small leaves, thick cuticles, sunken stomates, trichomes, or photosynthetic stems limit the amount of water vapor lost through evapotranspiration. Avoidance adaptations, such as drought-deciduous leaves or an annual habit, limit periods of photosynthesis to the most favorable times of year (Rundel and Gibson 1996).

Plants differ in their depth of rooting as well as in root morphology, both of which affect their ability to take up water from different soil layers (Ehleringer and others 1991, Schwinning and Ehleringer 2001, Walter 1971 as cited in Schwinning and others 2005). Grasses with shallow fibrous roots can extract water rapidly after a pulse event, but they are also the first to run out of water as soils dry (Schwinning and others 2005). Species with taproots can take up water from deeper levels and, consequently, are able to take up water during longer periods of drought. Many dominant shrubs, including juniper, have an extensive shallow root system in addition to roots that can penetrate to several meters in depth (Krämer and others 1996, Lin and others 1996). This allows them to exploit moisture from multiple soil depths, giving them an advantage over herbaceous root systems during drought. Reynolds and others (2000) postulated that such water resource partitioning can only occur when annual precipitation exceeded a certain threshold. Otherwise, soil recharge was not sufficiently deep to allow extraction from deeper soil layers.

Variability in species responses to drought can help to buffer productivity. Although species richness often declines during periods of drought (Cleland and others 2013, Hobbs and others 2007, Tilman and El Haddi 1992), plots with greater diversity have been reported to be more stable over time (Hobbs and others 2007). Cleland and others (2013) suggest that a large regional species pool can buffer site-level diversity from variation in climate. Known as the insurance hypothesis, this hypothesis states that differential species' responses to environmental change allow for functional compensation, as individual species come and go. Overall plant cover can then be maintained despite variations in species makeup (Yachi and Loreau 1999). Rates of species turnover are higher in dry areas, largely as a function of rare or annual species (Cleland and others 2013, Morecroft and others 2004, Tilman and El Haddi 1992).

A lag in plant recovery response after drought, even when precipitation is good, has been noted by a number of researchers (Ellison and Woolfolk 1937, Ji and Peters 2003, Lauenroth and Sala 1992, Pechanec and others 1937) and may result from a number of reasons. Plants may need to build up reserves before expending energy on renewed growth. A 2-year lag may result as seed is matured during the first good year followed by a year of recruitment. Many arid land species have inherently low growth rates, requiring substantial amounts of time before cover is restored to pre-drought levels.

Plant productivity and nutrient cycling—Another potential reason for reduced productivity in years following drought is due to changes in nutrient cycling. Haddad and others (2002), working in tallgrass prairie, followed plant production and diversity over an extended period that included a 2-year drought. Production was stable for 5 years preceding the drought, then oscillated on a 2-year cycle for 9 years after the drought. They concluded that the drought-induced oscillation was related to nutrient resources. In mesic systems, carbon and nitrogen cycling are coupled through production and decomposition of organic matter because water is available for plant and decomposer metabolism. In more arid systems and under drought conditions, these cycles become decoupled and nutrients accumulate until moisture is sufficient to reactivate biogeochemical processes (Asner and others 1997, Austin and others 2004, Evans and Burke 2013).

The loss of herbaceous cover due to drought can result in a substantial increase in soil erosion by both water and wind, with an accompanying loss of soil nutrients (Li and others 2007, Okin and others 2001, Schlesinger and others 2000). Grasses, in particular, help to bind together soil particles of the upper horizon (Worster 1982). The more sparsely distributed woody species are generally ineffective in reducing wind erosion compared with grasses (Li and others 2007). Erosion by wind differentially removes finer soil particles that contain more of the soil nutrients, resulting in a coarser, less fertile soil (Hennessy and others 1986, Leys and McTainsh 1994). Blowing dust redistributes soil, denuding some areas while killing plants by burial or abrasion (Okin and others 2001).

Biological soil crusts—Where vegetation is sparse, interspaces in rangelands are often colonized by biological soil crusts (BSCs), a group of organisms consisting of algal filaments, lichens, and mosses that bind surface soil particles together, reducing wind erosion (Belnap and Gillette 1997, Williams and others 1995). BSCs occur from the Columbia River Basin, south through the Great Basin and Colorado Plateau to the southern Mojave, Sonoran, and Chihuahuan Deserts, and from California chaparral east to the Great Plains. Smooth crusts composed of cyanobacteria and green algae dominate in hot desert sites, with lichen and moss cover increasing northward to the less arid conditions of the Great Basin and Columbia River Basin (Rosentreter and Belnap 2003). Crusts of those areas with colder winters are pinnacled or gently rolling in topography. In the Great Plains, BSCs

are most abundant in short-grass steppe and consist mostly of green algae and cyanobacteria, along with vagrant lichens that roll about, unattached to the soil. The highly pinnacled crusts of the Colorado Plateau are composed of cyanobacteria, with up to 40-percent cover of lichens and mosses. Many crust species are ubiquitous and can be found throughout the Western United States. Others are adapted to a specific range of temperatures or to certain substrates, such as calcium carbonate or gypsum (Rosentreter and Belnap 2003).

Biological soil crusts fix both carbon and nitrogen, adding to fertility of the soils. They also increase soil surface roughness, thereby increasing the capture of nutrient-rich soil fines (dust) and water-holding capacity of the soil (Belnap 2003). The organisms comprising soil crusts are only metabolically active when wet and are highly responsive to temperature (Belnap 2003, Stradling and others 2002). Most are adapted to withstand extended periods of high heat with little or no water by suspending all metabolic processes. However, prolonged periods of drought can effectively starve soil crust organisms, increasing the incidence of mortality. Lichens and mosses are particularly vulnerable, and the resulting crust composition is simplified, mimicking an earlier successional state (Belnap 2003). The timing of precipitation events also has an impact on crust function. Small, frequent events during periods of high temperature means that crusts dry quickly, resulting in less carbon available to produce or repair protective pigments and a loss of lichen cover and richness (Housman and others 2006). Conversion of soil crusts back to early successional stages results in large reductions of carbon and nitrogen inputs into the ecosystem (Housman and others 2006), which can affect plant growth and competitive interactions. Recovery rates from early to later successional stages is thought to be on the order of decades or centuries, depending on the amount of effective precipitation (Belnap 2003). Recovery, if it occurs, would be significantly slowed under extensive drought conditions. Loss of soil crusts would result in increased rates of wind erosion, blowing dust, and soil deposition similar to that described earlier.

Effects of Drought on Wildlife and Wildlife Habitat

Wildlife habitat occupancy is typically associated with structural characteristics of rangeland vegetation communities (Rotenberry and Wiens 1980, Wiens and Rotenberry 1985). Precipitation is the primary

cause of variability in grasslands (Wiens 1974), and structure and production of herbaceous vegetation is reduced during drought and can lag behind recovery of the precipitation (Laurenroth and Sala 1992). Height and density of herbaceous vegetation (structure) is strongly related to biomass (Benkobi and others 2000). Drought and grazing alter plant community composition and habitat structure. These vegetation changes influence positive and negative responses of wildlife (Benkobi and others 2007, Knowles 1986, Uresk 1990). For example, black-tailed prairie dog towns expand when vegetation cover and biomass decrease (Cincotta and others 1988, Uresk 1987), whether influenced by grazing or drought. Severe drought in North Dakota resulted in significant declines of a number of grassland-nesting bird species owing to nest abandonment, reduced nesting success, and a truncation of the nesting season in mid-June (George and others 1992). In early seral communities, small mammals and birds that prefer low vegetation structure and bare ground are more abundant, whereas those that prefer taller vegetation and litter are more abundant in higher seral vegetation communities (Agnew and others 1986, Fritcher and others 2004). Thus, sustained drought would shift bird and small mammal communities to favor those associated with early seral habitats. In prairie woodlands, drought and grazing reduce regeneration of trees and shrubs (Uresk and Boldt 1986), which in turn alters the bird and small mammal communities (Rumble and Gobeille 1998, 2001, 2004) toward species associated with early seral vegetation. Shrub-nesting bird populations may lag in response to loss of herbaceous understory vegetation if the shrub structure remains (Wiens and Rotenberry 1985).

Most, if not all, birds feed on or consume insects when the physiological needs of reproduction or early growth of young are high. Insect abundance is highly related to biomass of herbaceous vegetation (Healy 1985, Ramobo and Faeth 1999, Rumble and Anderson 1997, Wenninger and Inouye 2008). The amino acids that occur in birds reflect those of the insects they consume (Hurst and Poe 1985)—they are what they eat. Birds that are not able to consume enough insect protein do not develop properly or die (Johnson and Boyce 1990). Abundance and biomass of insects in south-central Wyoming exhibited significant correlations with grass and forb cover.¹ Drought in 2012 affected nest

¹ Personal communication. Mark Rumble, Research Wildlife Biologist, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Rapid City, SD 57702.

productivity and chick survival of greater sage-grouse (*Centrocercus urophasianus*) (Schreiber 2013) and insect abundance was significantly lower than in 2011 when nest productivity and chick survival was greater.

Lek counts in south-central Wyoming made each year from 2011 through 2013, showed approximately a 15-percent decline in the maximum male attendance the year following the drought of 2012 (see footnote 1). Low precipitation and high temperatures had negative effects on recruitment, survival, and population growth of sage-grouse populations in Nevada (Blomberg and others 2012), and precipitation the preceding spring influenced sage-grouse nesting success (Holloran and others 2005). Vegetation responses to precipitation (e.g., taller grass) is associated with greater nest success of sage-grouse (Herman-Brunson and others 2009, Holloran and others 2005, Kaczor and others 2011a) and is selected for by sage-grouse broods (Kaczor and others 2011b). Brood success of sage-grouse is associated with greater insect abundance and vegetation communities with high cover of herbaceous vegetation (Harju and others 2013).

Increased prevalence of severe drought increases the chances that local sage-grouse populations are extirpated (Aldridge and others 2008). Drought also tends to concentrate sage-grouse around water where they may be susceptible to West Nile Virus (Naugle and others 2004). Sage-grouse are not unique in their response to drought. Gambel's quail (*Lophortyx gambellii*) populations fluctuate considerably in direct response to increases and decreases in precipitation and in response to food availability from forb seeds (Gullion 1960). Pheasant populations in South Dakota demonstrate a quadratic relation to precipitation; low populations are associated with drought and extremely wet conditions (Runia 2013). Regions of South Dakota where the 2012 drought was considered exceptional or extreme showed population declines of 12–13 percent, whereas populations in regions where drought was moderate to severe only declined 2 percent (Runia 2013). Plains sharp-tailed grouse (*Tympanuchus phasianellus jamesi*) populations also decline in association with heat stress and low precipitation during June (Flanders-Wanner and others 2004), and it has long been known that nesting success by sharp-tailed grouse increases when height-density of grassland vegetation increases from 5 to 20 cm (Prose 1987).

Drought Interactions With Other Disturbances and Stressors

Grasshopper Outbreaks

Rangeland and grassland ecosystems worldwide are prone to periodic outbreaks of native insect herbivores. The most common and noticeable insect outbreaks in western North America involve grasshoppers (Orthoptera), which contribute significantly to the structure and function of grasslands and other rangelands (Branson and others 2006). Grasshopper outbreaks can have severe economic impacts on the grazing industry, especially during periods of drought when available forage is already scarce (Hewitt and Onsager 1983). Climate, especially drought, is thought to play a key role in outbreaks of grasshoppers and other insect species on rangelands, but the underlying mechanisms are poorly understood (Capinera and Horton 1989, Gage and Mukerji 1977, Kemp and Cigliano 1994, White 1976). Drought can have both direct effects on the growth and survival of insects and also indirect effects via changes in food quality and susceptibility to disease.

Non-severe drought and warm temperatures generally have a positive effect on grasshopper populations. Warm, dry weather in winter and early spring can lead to increased survival, early egg hatch, and faster population growth; warm, dry weather in the fall can extend the life of females and allow them to produce and lay more eggs (Joern and Gaines 1990, Kemp and Sanchez 1987). Moreover, grasshoppers often prefer to feed on drought-stressed plants, partly due to drought-induced changes in plant chemistry (Bernays and Lewis 1986, Haglund 1980, Lewis 1982). Drought could further promote grasshopper populations by reducing incidence of disease, especially due to fungi as many fungi require moisture (Hajek and St. Leger 1994, Streett and McGuire 1990). However, extreme or prolonged drought can negatively affect grasshoppers through desiccation (especially eggs) or by killing their food plants (Farrow 1979, Joern and Gaines 1990, Mukerji and Gage 1978). Therefore, short-term, less-severe droughts can increase grasshopper outbreaks, but longer term, severe droughts will likely have a strong negative effect on grasshoppers and rangeland/grassland biodiversity in general (Kemp and Cigliano 1994, Tilman and El Haddi 1992).

Invasive Species

Droughts are predicted to accelerate the pace of invasion by some nonnative plant species into rangelands and grasslands (Abatzoglou and Kolden 2011, Everard and others 2010, Ford and others 2012, Runyon and others 2012). One route by which drought promotes plant invasions is through increased movement of hay across State lines to feed livestock in drought-affected areas (Conn and others 2010). Drought conditions can also exacerbate invasions by favoring invasive species over native species. For example, invasive saltcedar (*Tamarix ramosissima*) is more drought tolerant than co-occurring native species, and its capacity to invade is predicted to increase with drought (Cleverly and others 1997). In California, it has been argued that invasive grassland species tolerate drought-like conditions better than native species and that drought was a contributor to the invasion of annual species into California grasslands (Corbin and D'Antonio 2004, D'Antonio and Vitousek 1992, Everard and others 2010, Jackson 1985). However, Funk and Zachary (2010) found no differences in physiological responses to drought of three native versus three invasive species in southern California, suggesting that not all invasive species will be favored. Conversely, invasive species could be negatively affected by drought; for example, some have attributed drought to a recent decline in spotted knapweed (*Centaurea stoebe*) in western Montana grasslands [but biological control could have played a role, see discussion in Ortega and others (2012)].

Drought can also promote plant invasion indirectly by modifying the environment to favor nonnative species. For example, opportunities for invasion are created when drought kills native plants leaving open niches and bare ground (Breshears and others 2005). This was apparently the case following the Dust Bowl of the 1930s which resulted in increases in nonnative plant abundance (Weaver and Albertson 1936, 1939).

Drought is also an important contributor to the invasive annual grass–wildfire loop that threatens ecosystems not adapted to fire [e.g., cheatgrass (*Bromus tectorum*) forms a positive feedback with fire in parts of western North America's sagebrush biome] (Abatzoglou and Kolden 2011, D'Antonio and Vitousek 1992). In this self-perpetuating cheatgrass–fire loop, drought increases the frequency of wildfires (Abatzoglou and Kolden 2011), and burned sites are more likely to be invaded by nonnative plants, especially annual grasses (Balch and

others 2013). Drought-induced fire also threatens to convert Sonoran Desert ecosystems to monocultures of nonnative plants such as buffelgrass (*Pennisetum ciliare*) and Lehmann lovegrass (*Eragrostis lehmanniana*) (Finch and others 2012).

Not only can drought affect invasions by nonnative plants, but it can also affect the tools used to manage them. The effectiveness of both herbicides and biological control can be altered by drought. To be effective, herbicides must be taken up through the leaves and stems of actively growing, green plants (Ashton and Crafts 1981). Herbicides applied to the foliage during periods of drought are usually much less effective than those applied when moisture is adequate (Bussan and Dyer 1999, Kogan and Bayer 1996). This is because many plant responses to drought—including reduced growth, closed stomata, thickened waxy cuticle, and increased pubescence—can reduce the uptake or translocation of herbicides (Kogan and Bayer 1996). For example, Morrison and others (1995) found that drought stress reduced translocation of herbicides and control of Russian knapweed (*Acroptilon repens*), a problematic rangeland weed in the Western United States. Therefore, our ability to manage invasive plants using herbicides could be reduced during periods of drought.

There is also some evidence that drought can alter the effectiveness of biological control of invasive plants. Historically, drought stress in plants was thought to benefit plant-feeding insects (Mattson and Haack 1987), which suggested that drought could benefit biocontrol using insects. However, a meta-analysis by Huberty and Denno (2004) found that continuous drought stress in plants negatively affected many insect herbivores, suggesting that biocontrol efficacy could generally be reduced by drought. Few studies have explicitly examined the effect of drought on biocontrol. Corn and others (2007) report that drought had little effect on the impact of the root weevil *Cyphocleonus achates* on spotted knapweed (*Centaurea stoebe*). However, Ortega and others (2012) found that the impact of *C. achates* on spotted knapweed was negated by drought conditions. Shishkoff and Bruckart (1996) found that drought stress has no effect on damage to yellow star-thistle (*Centaurea solstitialis*) caused by the rust fungus *Puccinia jaceae* in the laboratory. More research is needed to better understand how drought will affect biological control, an important management tool of rangeland invasive plants.

Wildfire and Drought

In the United States, more than 80 percent of all wildfires are started by humans. Lightning strikes are another common cause for natural wildfires (National Wildfire Coordinating Group Fire Investigation Working Team 2005). Recent increases in fire activity in some parts of the World have been attributed to climate change (Gillett and others 2004, Kasischke and Turetsky 2006, Pinol and others 1998, Westerling and others 2006). U.S. ecoregions with increasing trends in the number of large fires and total fire area also displayed increasing trends in drought severity (Dennison and others 2014). The incidence of large fires and extent of area burned have increased across the Western United States. Fire activity trends were most significant in southern and mountain ecoregions. Increased fire in these ecoregions coincided with increased drought severity (Moritz and others 2012). Under extended drought condition, wildfires are getting bigger, and more fires are starting earlier in the year. Since 1984, the area burned by the West's largest wildfires—those of more than 1,000 acres—increased by about 87,700 acres per year, and the areas where fire has been increasing the most are areas where drought has been worsening (Dennison and others 2014).

Climate change can indirectly affect rangeland vegetation by altering fire regimes. Increasing fire frequency leads to a replacement of fire-sensitive plant species with those that are more fire-tolerant (Nelson and Hu 2008). Most wildfires in the Western United States occur during the hottest, driest portion of the year (Westerling and others 2006), and the size of the area burned during any single year is correlated with the current drought condition (i.e., PDSI) and with wetter-than-normal conditions in May and August of the previous year (Polley and others 2013). In grass- and shrub-dominated ecosystems, fires are largest when unusually wet summers (during which fine fuels accumulate) are followed by dry conditions that enhance fuel flammability and ignition (Littell and others 2009). Fire activity is projected to increase considerably in the Western United States as the climate becomes both warmer and drier (Pechony and Shindell 2010, Polley and others 2013).

The largest U.S. grassland region is the Great Plains, a vast area of prairie, agriculture, and rangelands extending from the Dakotas through Iowa, Nebraska, Kansas, Oklahoma, and parts of Texas, and including the eastern parts of Montana, Wyoming, Colorado, and New Mexico (Bagne and others 2012). Fire is an

important feature of many Great Plains rangelands, and its frequency, intensity, and seasonality are likely to be affected by changes in climate, productivity, and species composition. Fire was an important factor in maintaining grass dominance in the more productive rangelands of the eastern Great Plains. In more recent times, the removal of fire and/or changes in its seasonality, along with rising CO₂, have encouraged woody plant encroachment in many of these productive rangelands (Morgan and others 2008).

Indeed, woody encroachment has emerged as the dominant threat to grassland ecosystem services in the Great Plains (Engle and others 2008). In areas of long-term juniper encroachment, fires have shifted from frequent, grass-driven surface fires that vary in flame length (range ≤ 0.1 m to well over 3.4 m) (Finney and others 2011) to infrequent, juniper-driven crown fires that consistently exhibit extremely long flames (>14 m) and are of increasing societal concern (Twidwell and others 2013). Such alterations to the fire regime and fire suppression potential are important contributors to the recent rise in housing losses, suppression costs, and human injuries and deaths resulting from wildfires in the Great Plains (Twidwell and others 2013). Predicted changes in precipitation patterns are likely to encourage more frequent and intense fires in the future, with increased winter precipitation driving early-season plant growth, and warmer, drier summers desiccating vegetation, thus increasing the probability of fire (Morgan and others 2008).

A chief concern in the arid and semiarid rangelands of the Western United States is the rapid conversion of shrublands and desert into annual grassland through the spread of invasive annual grass species and the negative impacts this conversion will have on wildfire regimes, surface hydrology, and loss of critical habitat for threatened and endangered species (Abatzoglou and Kolden 2011, Bradley and Mustard 2005, Brooks and Esque 2002, Brooks and others 2004, Mack 1981, Wilcox and Thurow 2006). Over the past three decades, there has been a significant increase in the abundance and extent of invasive annual grass species in the Southwest, including cheatgrass across the Great Basin Desert, red brome (*Bromus rubens*) across the Mojave Desert, and buffelgrass across the Sonoran Desert (Betancourt 2007, Bradley and Mustard 2005, Brooks and Esque 2002). This change, along with a change in climate, has coincided with an increase in the number of large fires and area burned across the arid and semiarid Western United States (Brooks and

others 2004, Westerling and others 2006, Whisenant 1990). For example, in the Great Basin, fires were found to be more likely to start in cheatgrass than in other vegetation types, and cheatgrass is associated with increased fire frequency, size, and duration. As sites burn, more and more of the sites are likely to become cheatgrass grasslands, thus increasing their future probability of burning (Balch and others 2013). Also, elevated cheatgrass biomass following El Niño events is strongly linked to increased risk of fire during the following years' summer (Balch and others 2013). Future projections of climate change suggest that the Western United States is likely to become warmer and have greater precipitation variability, which could increase or decrease cheatgrass fire probability depending on how much warmer temperatures influence moisture availability. In general, evidence suggests that observed changes in climate have assisted in the spread of invasive annual grasses across western U.S. deserts both directly through changes in temperature and precipitation and indirectly through their influence on wildfire (Abatzoglou and Kolden 2011). For example, increased temperature and reduced humidity during spring and summer associated with recent protracted drought conditions since 2000 have doubled the frequency of extreme fire danger in the Sonoran Desert, resulting in an earlier start and lengthening of the fire season (Abatzoglou and Kolden 2011, Weiss and others 2009).

Pinyon-juniper woodlands—the third largest vegetation type in the West—characterize many Rocky Mountain and Intermountain rangelands and are vitally important for biodiversity, aesthetics, and commodity production (Mitchell and Roberts 1999, West 1999). Extreme drought conditions have characterized the American Southwest during the past decade, causing widespread mortality in pinyon-juniper woodlands. While comparably low precipitation levels have occurred at other times in the past century, rising temperatures have accompanied the latest drought, increasing water stress on vegetation and triggering increases in bark beetle-caused mortality. Drought-related outbreaks in bark beetles have killed pinyon pines on over 12,000 km² in the Southwest (Breshears and others 2005, Floyd and others 2009, Shaw and others 2005). The current severe, regional drought is providing the dry conditions necessary for extensive wildfire activity.

Historical fire rotation for pinyon-juniper woodlands has been estimated across the United States. Studies report very long fire rotations—for example, 410 years

in Barrett Canyon of central Nevada (Bauer 2006), 480 years in southern California (Wangler and Minnich 1996), 400–600+ years on the Uncompahgre Plateau in western Colorado (Shinneman and Baker 2009), and 400+ years on Mesa Verde in southwestern Colorado and on the Kaiparowits Plateau of southern Utah (Floyd and others 2004, 2008; Romme and others 2009). An upsurge of large fires (>400 ha) in forested landscapes throughout much of the Western United States began in the mid-1980s (Westerling and others 2006). Increasing trends in large fire frequency and total area burned are particularly noticeable in regions having extensive pinyon-juniper woodlands (e.g., the Southwest and the northern Great Basin). For example, a greater proportion of the pinyon-juniper woodland on Mesa Verde, Colorado, burned in the decade between 1995 and 2005 than had burned throughout the previous 200 years (Floyd and others 2004, Romme and others 2009). A combination of canopy fuel build-up during two wet decades before 1995 and the current drought conditions resulted in unprecedented fire activity (six large wildfires between 1996 and 2003) when compared with the reference period 1700–1900 (Floyd and others 2004).

Given the very long fire rotations that naturally characterize pinyon-juniper woodlands, it has not yet been determined whether the recent increase in frequency of large fires occurring in this vegetation type represents genuine directional change related to changing climate or fuel conditions, or whether it is simply a temporary episode of increased fire activity, comparable to similar episodes in the past. Ultimately, the suite of current and upcoming broad-scale environmental changes including warming temperatures, increasing tree densities in some areas, and expansion of fire-promoting species, such as cheatgrass, may all interact to dramatically increase the amount of burning in pinyon-juniper and other vegetation types over the next century (Romme and others 2009).

In the near term, the most consistent increases in fire activity occur in biomes with already somewhat warm climates (Moritz and others 2012). However, as the Arctic warms, wildfire may become increasingly important even within the coldest of all terrestrial ecosystems: tundra (Joly and others 2012). Tundra covers over 5,000,000 km² of the Arctic (Walker and others 2005), including a large portion of Alaska. Warmer and drier summers are associated with greater area burned in Alaska (Duffy and others 2005). The effects

of climate change are already apparent in the Arctic (Callaghan and others 2004, IPCC 2007). Mean annual temperatures have increased by 2–3 °C in the region in recent decades, with larger increases apparent during the winter months (Hinzman and others 2005, Joly and others 2012, Stafford and others 2000).

Climate change impacts on the habitats of Arctic land mammals are predicted to be severe (Lawler and others 2009) and have already been implicated in the decline of caribou (*Rangifer tarandus*) populations there (Vors and Boyce 2009). Mechanisms by which climate change may negatively impact caribou include increased frequency of wildland fire on winter ranges (Joly and others 2012). Although wildfires occur during the summer, they negatively impact caribou winter range. Migratory caribou rely heavily on tundra plants to sustain them through the winter months, and these plants can take 50 or more years to recover after wildland fires consume them (Joly and others 2012). Tundra has the potential to re-burn much more quickly than boreal forests, so warmer summer conditions could lead to additional fires (Joly and others 2009).

Effects of Drought on, or in Combination With, Human Uses and Practices

Drought Impacts on Livestock, and Forage Yield and Availability

Drought and livestock grazing are two major drivers of rangeland structure and productivity within the Great Plains. No geographic location is immune to the wide-ranging social and economic impacts of drought (Riebsame and others 1991). The Great Plains were historically grazed by bison until settlement in the 19th century when cattle were introduced as the major livestock. Ungulate grazing often leads to an increase in spatial heterogeneity and species diversity (Adler and others 2001, Bakker and others 2003a). However, grazing severity and timing largely determine the effect of ungulate grazers on rangelands.

Rangeland drought management is influenced by both historical perceptions and the drought class framework of the manager. Vegetation reports of the early explorers in the 19th century depended on the year observations were made (Coupland 1958). Early settlers expected productive lands and were accustomed to the more predictable and dependable precipitation patterns of the Eastern United States. Therefore, initial farming and ranching practices failed to accommodate the abiotic

and biotic changes associated with a highly variable climate and the combined effects of periodic drought and livestock grazing. Although current land managers have gained more experiential knowledge in these arid environments, management decisions in response to drought are still affected by the first perceptions of the early settlers. In recent years, unsustainable rangeland use has exacerbated the effect of drought, causing more land managers to experience financial hardship and perceive that meteorological drought is increasing in frequency (Thurow and Taylor 1999). Land managers are encouraged to plan proactively for drought and maintain flexibility in rangeland management by diversifying livestock operations and types of land use (Coppock 2011, Kachergis and others 2014, Thurow and Taylor 1999).

Depending on intensity and frequency, grazing and drought independently can adversely impact the ecology and management of rangeland ecosystems by reducing plant cover and forage availability, reducing root growth, shortening the season of forage production, and exposing the soil to erosion (Vallentine 1989). However, because grazing and drought often occur at the same time, identifying the relative contribution of grazing and drought to these impacts is a difficult task requiring long-term monitoring (Fuhlendorf and others 2001). While the effects of grazing can occur relatively quickly to produce obvious contrasts, droughts often emerge slowly with cumulative effects that merge gradually into a catastrophic event (Riebsame and others 1991).

The separate and interactive effects of drought and grazing on rangeland vegetation can also be amplified by a variety of direct and indirect factors. For example, the broad-scale effects of drought are locally modified by variation in soil and topography (slope and aspect, which interact to influence water infiltration and runoff) and soil moisture retention. Often, the effects of drought are first observed on hilltops and ridges, followed by side slopes, and then depressions and valleys. South-facing slopes are impacted more than north-facing slopes, especially at higher latitudes (Coupland 1958, Weaver and others 1935). Concentrated and continuous grazing causes soil compaction that reduces water infiltration and increases surface erosion, thus exacerbating the effects of drought (Vallentine 1989). Droughts are also frequently accompanied by high populations of grasshoppers and accumulations of wind-blown soil particles, which can develop into drifts up to 3 feet deep (Coupland 1958, Weaver and Albertson 1940).

Grazing effects can produce a significant and somewhat predictable directional change in vegetation composition and productivity, which is primarily augmented directly by water stress and secondarily by additional factors that accompany drought. Water stress and grazing have been considered convergent selection pressures that involve the periodic reduction of biomass (Koerner and Collins 2014, Milchunas and others 1988). Consequently, plant traits selected due to a reduction in biomass by one driver, such as grazing, can enhance plant survival when exposed to other drivers, such as drought. Semiarid grassland communities with a long evolutionary history of grazing are dominated by relatively short-statured, grazing-tolerant, rhizomatous or stoloniferous grasses that compete primarily for soil resources (Milchunas and others 1988). In semi-arid grasslands, grazing before and during drought has little impact on community composition and structure (Heitschmidt and others 1999.)

By contrast, in sub-humid grasslands where mid- and tall-grasses must compete for light, grasses are not as tolerant of grazing because growth of the aboveground canopy is primarily vertical. Therefore, depending on the grazing evolutionary history, grazing in more mesic grasslands would have moderate to large effects on composition and canopy structure (Milchunas and others 1988). However, during droughts prior to settlement, free-ranging grazers (e.g., bison) would have either died and/or migrated out of the impacted area (Heitschmidt and others 1999). Consequently, grazing and severe drought may have not occurred together historically in some rangeland ecosystems, except possibly for short periods of time.

Relative contributions of drought and grazing to biomass reduction and shifts in vegetation composition within a rangeland may shift between mesic and more arid rangelands. In mesic tallgrass prairies, grazing and fire had a greater effect on community structure than precipitation (Koerner and Collins 2014). However, in the semi-arid northern Great Plains, climatic variation had a greater effect on vegetation composition and production than grazing intensity (Biondini and others 1998, Olson and others 1985). Semi-arid and arid grasslands of the Western United States are noted for their small (<5 mm) rainfall events and intervening dry periods (Loik and others 2004). Although small rainfall events may not contribute measurable increments in biomass, they are able to increase leaf water potential and help sustain physiological activity between larger rainfall events (Sala and Lauenroth 1982). Reduction in the

occurrence of small rainfall events during drought may explain the greater sensitivity of more arid grasslands to precipitation than grazing. In sagebrush steppe, both drought and grazing independently reduce perennial grass and forb cover (Anderson and Inouye 2001; West 1983, 1988). Although dominant shrubs such as big sagebrush can be affected by drought, they are affected to a lesser degree than grasses and increase in relative abundance within the shrubland community (Pechanec and others 1937, West 1983).

Rangeland response to the effects of drought and/or grazing was exemplified by observational studies conducted before, during, and following the 1930s extreme drought in the Great Plains (i.e., the Dust Bowl) [see Weaver (1954) and references there-in, Pechanec and others (1937)]. Severe drought substantially reduced plant cover and forage availability. Continuous grazing at almost any level during severe drought can adversely impact rangeland structure and function. Heavy grazing can have the greatest impact and substantially increase the length of the recovery period (Albertson and others 1957). With low vegetative cover and high winds that usually accompany drought, the potential for soil erosion is high. Despite the negative long-term impacts, grazing during drought was a common practice used to maintain livestock herds until favorable conditions returned (Weaver 1954).

The directional, selective influence of grazing on vegetation is especially prominent in heavily grazed, mixed-grass prairies. Prolonged heavy grazing can simultaneously decrease grass basal area and increase plant density (Briske 1991 and references there-in). Grazed sites with a high density of plants with small basal areas may be subject to higher drought-induced mortality compared to a lower density of plants with larger basal areas in lightly and moderately grazed grasslands (Albertson and others 1957, Fuhlendorf and others 2001). A high density of plants with small basal areas may serve as a valuable indicator of pending compositional changes during drought conditions (Fuhlendorf and others 2001). During the drought of the 1930s, drought-induced plant mortality under heavy grazing increased the amount of bare soil, which was often quickly colonized by Russian thistle (*Salsola kali*) (Albertson and others 1957).

Moderate grazing also influences the long-term directional change of vegetation that is magnified by drought, but to a lesser degree than heavy grazing (Coupland 1958). Actually, reductions in basal area

during periodic droughts were sometimes less in moderately grazed grasslands compared to ungrazed grasslands (Coupland 1958, Weaver and Albertson 1936). Weaver and Albertson (1936) attributed the higher basal area observed in moderately grazed pastures compared to lightly and ungrazed pastures to grazing-induced increases in drought-resistant species such as blue grama and buffalograss. However, buffalograss is more sensitive to drought than blue grama, which often becomes the dominant species during periodic droughts. On the other hand, buffalograss has the ability to rapidly produce new stolons once favorable conditions return. If the drought is not severe or prolonged, then moderate grazing also allows the less drought-resistant species to persist. However, during prolonged, severe drought, the drought-sensitive mid-grasses will suffer high mortality (Coupland 1958). Post-drought vegetation recovery was always slower on sites dominated exclusively by blue grama compared to sites with a combination of blue grama and buffalograss (Albertson and Weaver 1944). Consequently, blue grama was important for protecting the soil during drought, while buffalograss was important for recovery following the drought.

Vegetation recovery following drought is generally proportional to the intensity of grazing before, during, and after the drought (Albertson and Weaver 1944). Weaver (1954) described several cases where livestock were sold during the drought of the 1930s because of severe shortages of forage. Because of economic hardships (including The Great Depression), producers were unable to re-stock their pastures with livestock for several years. Therefore, many rangelands damaged by combinations of grazing and drought were rested, especially heavily grazed pastures where forage was reduced very early in the drought cycle. In this context, rangeland recovery during a severe drought was more rapid than recovery during a short-term drought event where herds of cattle were maintained during and immediately following the drought (Weaver 1954).

In general, moderately grazed, mixed-grass prairie can recover fairly quickly from moderate (Coupland 1958) and severe drought (Albertson and Weaver 1944). Vegetation recovery on heavily grazed grasslands with few remnants of the pre-drought vegetation remaining and considerable bare soil will include several years of an annual weed stage, which will substantially delay recovery of native perennial grasses. If dry conditions return during the post-drought recovery, the annual

weed stages could persist for several years (Albertson and Weaver 1944). In contrast, sagebrush shrublands that have transitioned from a sagebrush-native perennial grass mixture to a heavily shrub-dominated community remain in this stable state even after grazers are excluded for multiple years (West and others 1984).

Few perennial grass seeds persist in the soil for more than 5 years, with the seeds of some species living <1 year (Baskin and Baskin 1998). Consequently, recovery of perennial grasses from drought and/or grazing is dependent upon stem recruitment from belowground meristematic tissue (the bud bank sensu Harper 1977; Benson and Hartnett 2006). Weaver and Albertson (1936) reported that with the return of normal precipitation following the 1930s drought, western wheatgrass (*Pascopyrum smithii*) rapidly expanded into areas of bare soil created by the drought. Because the drought had significantly reduced (eliminated) opportunities for sexual reproduction, the rapid expansion of western wheatgrass most likely occurred through vegetative growth via the bud bank. A few small precipitation events during drought may play a significant role in maintaining the viability of bud banks through extreme dry conditions (Sala and Lauenroth 1982).

As individual drivers, drought and grazing can have a similar effect on rangelands. In combination, the relative contributions of drought and grazing to the response and recovery of a rangeland strongly depend on the severity of each driver and the climate and dominant vegetation of the rangeland. Although effects of drought and grazing on rangeland community structure and function continue to be documented, a more mechanistic understanding of the impact of drought and grazing should be sought. Understanding how drought and grazing alter factors such as nutrient availability or the bud bank will provide land managers with more tools to respond to joint drought and grazing issues.

Effects of Drought on Restoration Success

Ecological restoration encompasses a variety of management actions intended to restore or repair degraded ecosystems. Degradation can range from minor deviations of vegetation structure and community composition from a desired state, to complete denudation of vegetation, soil loss, and associated disruption of ecosystem function (Allen 1995, Bainbridge 2007, SER 2004). Many U.S. rangelands have been dramatically altered by intensive uses such as agriculture, mining, military operations, and

vehicular traffic (Bainbridge 2007). Other grasslands and shrublands remain intact but have been degraded to various degrees by overgrazing or mismanagement, often resulting in depletion of forage and encroachment by woody plants (Archer and others 2011). Invasive exotic species are also a serious problem in many areas (Brown and others 2008, Sheley and others 2011).

Different types of restoration are applicable to different circumstances. Grazing management, prescribed fire, herbicides, and mechanical treatments such as mowing and chaining may be used to selectively reduce undesirable species (Archer and others 2011, Briske and others 2011, Fuhlendorf and others 2011, Vallentine 1989). If desirable species are not present in sufficient quantity to recover on their own, active planting (seeding or transplanting) may be necessary (Bainbridge 2007, Hardegree and others 2011). On severely degraded sites, soil remediation or topsoil replacement may be required (Pinchak and others 1985, Schuman and others 1985).

The ultimate goal of full-scale ecological restoration is to reestablish functioning ecological communities resembling those that existed prior to intensive human disturbance (SER 2004), as illustrated by longstanding efforts to restore native prairies in agricultural regions of the U.S. Midwest (Rowe 2010). In other settings, site integrity and productivity are the primary goals, and the terms rehabilitation or reclamation are applicable (SER 2004); for example, reclamation of surface mine disturbances (OSM 1997), rehabilitation following wildfire on Federal lands (Beyers 2004), and rehabilitation of agricultural lands in the Conservation Reserve System (Baer and others 2009). Although nonnative plants have a long history of use for rehabilitation and reclamation in the United States, current policies encourage use of native species on Federal lands (Johnson and others 2010a, Richards and others 1998) and some sites previously planted with nonnatives have been targeted recently for restoration with natives (Bakker and others 2003b, Hulet and others 2010, Wilson and Gerry 1995).

Because of the critical role of water in plant establishment, growth, and survival, restoration plantings are directly impacted by drought conditions. Insufficient precipitation has been invoked to explain suboptimal plant establishment for many restoration plantings in grassland and shrubland systems (Bakker and others 2003b, Bleak and others 1965, Fehmi and others 2014, Glenn and others 2001, Hulet and

others 2010, Ratzlaff and Anderson 1995). If low plant establishment is accompanied by intensive soil disturbance (e.g., seeding using rangeland drills), there may be a risk of increased erosion by wind (Miller and others 2012) or water (Pierson and others 2007), as well as impacts to preexisting plants (Ratzlaff and Anderson 1995). Even in cases where plant establishment is initially successful, plantings may later die back during drought years (Bleak and others 1965, Currie and White 1982).

Although drought conditions are a disadvantage for plantings, they can be advantageous for plant control to the extent that water deficits make undesirable plants more susceptible to mechanical treatments, herbicides, or fire. For example, control of crested wheatgrass (*Agropyrum cristatum*) by clipping or herbicides has been shown to work better under drier conditions (Bakker and others 2003b, Hansen and Wilson 2006). The effectiveness of foliar herbicides may be reduced under drought conditions because of poor translocation following application (Vallentine 1989), although this differs by herbicide and plant species (Abbott and Sterling 2006, Lauridson and others 1983, Morrison and others 1995, Roche and others 2002). Soil herbicides require water for dissolution and soil penetration and are thus likely to be less effective during drought (Vallentine 1989).

The use of prescribed fire as a restoration tool during drought requires special considerations. In desert grasslands encroached by mesquite, drought conditions may make prescribed fire difficult to implement because of insufficient fine herbaceous fuel (Britton and Wright 1971, Teague and others 2010, White and Loftin 2000). In other settings where fuel is more abundant, it may be especially dry during drought, and this combined with low air humidity can make fires explosive and difficult to control (Ralphs and Busby 1979).

Narratives of escaped prescribed fires frequently include drought as a contributing factor, leading to loss of control and ensuing damage (Brunson and Evans 2005, Earles and others 2004). Furthermore, the effects of prescribed fires may be different during drought compared to wetter years. Increases in light, higher temperatures, and nutrient inputs to soils that represent positive effects of fire under high moisture conditions could become detrimental when soil moisture is low (Augustine and others 2010, Bremer and Ham 1999, Teague and others 2008, Whisenant and others 1984).

Depending on the seasonal incidence of drought conditions, optimal dates for prescribed burning might also differ compared to normal years. Burns intended to control certain species or groups (e.g., annual weeds, cool-season grasses) by burning during their active stage (Adkins and Barnes 2013, Anderson and others 1970, DiTomaso and others 2006) might be constrained by smaller windows of opportunity due to early onset of dormancy. On the other hand, if the purpose of burning can be met during the dormant stages (Brockway and others 2002, Ford and Johnson 2006), then the window of time for burning may be longer during drought. Benefits of prescribed fire ultimately depend on vegetation regrowth, which may be diminished if drought occurs during the post-fire period. Ladwig and others (2014) found that drought conditions delayed expected grass recovery following prescribed fire in a Chihuahuan Desert grassland, and that effects of burn timing (spring, summer, and fall) were short-lived due to the overriding influence of the drought.

Increasing Rangeland Ecosystem Resilience to Drought

Adaptive Strategies for Managing Livestock

Land managers and livestock producers must periodically cope with and adapt to drought, both in the short term and in the long term. Adaptive strategies can vary regionally, but appropriate measures must be taken to provide adequate recovery of vegetation to ensure proper ecological function and economic returns. Greatest success will be achieved with careful planning of strategies to employ before, during, and after droughts. Some adaptive responses to drought include:

- Reducing stocking rate to allow plant recovery
- Using fencing and other developments to manage livestock distribution
- Using drought-resistant feed crops
- Using drought-adapted stock
- Adjusting season of use
- Diversifying ways for economic gain
- Implementing deferred grazing system
- Developing, restoring, or reclaiming water

- Providing shade structures for livestock
- Reducing the time livestock graze a specific pasture/unit/paddock
- Increasing the time or rest between periods of grazing
- Testing new techniques for responding to drought

The most obvious and arguably the single most important strategy for adapting to drought is reduction in stocking rate because plants that have been overgrazed or cropped too frequently are less able to recover after drought (Hart and Carpenter 2005). Conservative and flexible stocking rates enable maintenance of proper amounts of residual forage. Where droughts are relatively common, breeding stock should only represent 50–70 percent of the total carrying capacity (Hart and Carpenter 2005). Grazing time in pastures can also be reduced, as an action or in combination with other actions, such as supplemental feeding and reducing number of livestock. In addition, ranchers can first sell stocker cattle as a means of herd reduction during drought to protect the breeding herd so that restocking after recovery is easily accomplished. Another technique for coping with drought is use of fencing, salt, water development, and strategic herding to increase uniformity of use. Likewise, some animals inherently make more uniform use of the landscape than others, suggesting that selective breeding can preemptively aid drought adaptation (Howery and others 1998).

As a last measure, supplemental forage can be used to augment the sparse forage that drought conditions induce; however, use of supplemental forage can potentially exacerbate the problem by maintaining an unsustainable number of animals. In addition, animals will likely continue to use greener, more-palatable rangeland vegetation even if ample supplemental feed is supplied. From a herd-management or economic perspective, consideration should be given to selling animals before they have lost excessive weight and weaning calves earlier than normal which reduces forage demand (Howery 1999). Additionally, nonproductive animals or animals with low fertility rates should be culled first during drought periods.

Since economic returns and ecological integrity are linked to vegetative resources, careful consideration of vegetation conditions is required, during and after droughts in concert with herd management adaptations.

In this vein, extra monitoring is prudent to ensure that forage yields and ecological integrity can be maintained in the future. Extra rest periods can aid recovery while ranges are recovering after a drought. The timing of grazing also becomes a critical factor in determining recovery after a drought. For example, use of ranges when nondesirable species are green and palatable and deferring grazing until perennial species have produced seed can aid recovery. However, this generalization does not always apply as it may be more advantageous to utilize perennial grasses during the early vegetative stages but prior to the booting phase, emphasizing the importance of planning and monitoring before, during, and after drought.

Regardless of the strategies used, adaptation to and recovering from drought requires careful planning before, during, and after for maximum effectiveness. Moreover, the single most important outcome that can be controlled by management is selecting an appropriate and flexible stocking rate.

Adjusting Restoration Practices Under Drought Conditions

Drought conditions generally pose constraints for restoration practices such as planting or prescribed burning (see previous section). Such practices might best be deferred during periods following extended drought or preceding predicted drought conditions. However, postponing a restoration project may not be satisfactory in situations where policy, funding, logistics, or other concerns favor immediate action. In such cases, restoration practices can be implemented but modified in ways that compensate for limited soil moisture (e.g., irrigation, water catchments) or use alternative techniques to achieve the desired outcome (e.g., mechanical treatment instead of prescribed fire).

If a decision is made to use prescribed fire during a drought, it should be done with careful planning and precautions. As reported by Guse (2009), The Nature Conservancy successfully carried out a ca. 730-ha prescribed burn during extreme drought conditions in southern Texas, noting that the drought provided an unprecedented opportunity to restore shrub-invaded grasslands. The success of the operation was attributed to extensive commitments of resources (reportedly 2-3 times the minimum required number of firefighters and water delivery systems), by assuring that firefighters were well trained and equipped, and implementing burns in incremental, manageable stages over a period of 9 days (Guse 2009).

During periods of drought, it may be best to focus restoration efforts on removal of undesirable plants as opposed to planting treatments. In reference to native grassland restoration in the northern Great Plains, Bakker and others (2003b) recommended that crested wheatgrass control measures be undertaken during drier years while seeding of native species take place in wetter years. In the Great Basin, juniper removal by mastication (shredding) can be beneficial for herbaceous species by both releasing competitive water use of the woody overstory and enhancing soil moisture beneath shredded debris (Young and others 2013).

If planting is deemed necessary during a drought year, a variety of strategies and techniques can be employed to increase the probability of successful plant establishment in the short term and species persistence in the long term. Plant materials should be carefully selected to ensure that the species and ecotypes are adapted to drought conditions, especially during the establishment phase, and are resilient if drought is episodic or long-term climate change is projected. The ability to rapidly extend roots downward into the soil is an important trait for seedlings facing a soil drying front (Abbott and Roundy 2003). Equally important is the capacity of seeds to remain dormant until soil moisture is sufficient to sustain seedling growth (Biedenbender and others 1995, Frasier and others 1987). Larger seeds will likely have greater capacity to endure water limitations during the critical establishment phase compared to smaller seeds (Hallett and others 2011, Leishman and Westoby 1994). In addition, larger seeds are better able to emerge when buried beneath soil, and can thus be planted at depths where they are buffered from surface soil moisture fluctuations (Carren and others 1987, Monsen and Stevens 2004, Montalvo and others 2002).

As seedlings become larger, they tend to become less sensitive to moisture fluctuations, hence, it may be advantageous to transplant seedlings (or even fully grown plants) rather than attempting to establish plants from seed. Transplanting has been found to be effective for establishing shrubs and forbs in water-limited environments, especially if transplants are hardened off prior to planting and provided with supplementary water afterwards (Anderson and Ostler 2002, Bainbridge 2007, Glenn and others 2001, Grantz and others 1998a, Holden and Miller 1995, Watson and others 1995). The use of water-holding materials such as sepiolite clay and hydrogels in root plugs of transplants may enhance their survival in dry soils (Chirino and others 2011, Minnick and Alward 2012).

Irrigation can be helpful for restoration plantings, although it may be untenable for large restoration projects or remote sites where transport is an issue and water sources are distant (Anderson and Ostler 2002). Its feasibility is perhaps highest when restoring abandoned agricultural sites with an existing irrigation infrastructure. Roundy and others (2001), Chambers and others (2014), and Porensky and others (2014) demonstrated benefits of sprinkler irrigation for restoring abandoned agricultural fields in western deserts, although Banerjee and others (2006) noted problems with this approach due to weed proliferation and accumulation of salinity in the soil from low-quality irrigation water. Alternative irrigation techniques such as drip-lines, wicks, and clay pots can be used to direct water toward specific plants and/or deeper horizons (Bainbridge 2007). Precipitation data from weather stations near restoration sites have reportedly been used to determine how much irrigation water to supply (i.e., to ensure that total monthly water matches amounts recorded during years with average to above-average moisture) (Anderson and Ostler 2002, Bashan and others 2012, Belnap and Sharpe 1995, Hall and Anderson 1999). The importance of watering during the appropriate season was highlighted by Allen (1995), who found that summer irrigation did not compensate for lack of springtime moisture when seeding purple needlegrass (*Stipa pulchra*), a cool-season grass, at a summer-drought environment in California.

Beyond direct irrigation, a variety of measures can be implemented to enhance or conserve existing water supplies at restoration sites. By placing seed at the bottom of furrows, drill seeding enhances precipitation capture for seedling establishment, and the effect can be amplified by deepening the furrows (Monsen and Stevens 2004). In a similar manner, pitters and imprinters can be used to create micro-catchments that capture and concentrate water (Bainbridge 2007, Dixon 1995, Holden and Miller 1995). Edwards and others (2000) found that catchments of 4–25 m² improved establishment for many, but not all, shrub species tested at a Mojave Desert site. Because ponded water appeared to adversely affect some species planted in catchment bottoms, they recommended planting on the berm in cases where the soil has low infiltration (Edwards and others 2000).

Other treatments aim to improve soil infiltration or water-holding capacity. Deep ripping reportedly improves water-holding properties of the soil, as well as making soil more accessible to plant roots (Brown

and others 2008, Montalvo and others 2002, Schmidt and Belford 1994). Short-term intensive trampling by livestock has reportedly increased infiltration on crusted sandy loam soils (Roundy and others 1992). On recently burned sites, soil water repellency is a common problem that could potentially be mitigated through tillage or the application of wetting agents (Madsen and others 2012a, 2012b). Mulches made from materials such as straw, gravel, wood chips, and shredded brush may be helpful for moderating soil temperatures and reducing evaporative water loss from the soil surface (Bainbridge 2007, Eldridge and others 2012, Nyamai and others 2011, Winkel and others 1995, Young and others 2013). However, Belnap and Sharpe (1995) concluded that dry straw mulch was not helpful for plant establishment in a cold desert environment with sandy soils having poor water-holding capacity. They hypothesized that the mulch absorbed water that would otherwise have been available to plants, and that by concentrating water near the soil surface, plants were triggered to germinate at times when deeper water supplies were not actually present to sustain them. Fehmi and Kong (2012) drew similar conclusions upon finding that mulching led to lower seeded plant establishment on very coarse-textured soils (very gravelly sands). Mulches may also be problematic if they are applied too thickly and thereby have an inhibitory effect on seedling emergence (Dodson and Peterson 2010, Winkel and others 1995).

In areas receiving snow, snow fences can be placed upwind of plantings to increase soil moisture through the accumulation of snowdrifts (Greb 1980). David (2013) described snow fences constructed and arranged so as to maximize snow capture for sagebrush establishment on abandoned natural gas pads in Wyoming. Stubble from winter-sown annual crops has been used to capture snow on agricultural land in the northern Great Plains (Greb 1980), although its effects may be negligible in areas with low snowfall and shifting wind patterns (Hart and Dean 1986).

Because of water limitations during droughts, it may not be possible to establish plants at desired densities even when applying the strategies described earlier. Resources might thus best be focused on the most favorable sites, such as drainages or areas of naturally occurring snowdrifts (Meyer 1994), which could later serve as centers for vegetation spread. In situations where rapid plant establishment is desired for soil stabilization, as in post-fire rehabilitation on public lands (Beyers 2004), greater emphasis could be placed on physical erosion control measures as opposed

to revegetation treatments. Runoff and sediment loads from recently burned slopes can be reduced independent of vegetation by applying straw, bark, or wood shred mulch (Fernandez and Vega 2014; Groen and Woods 2008; Robichaud and others 2013a, 2013b) or constructing erosion barriers such as contour trenches (Robichaud and others 2008). Wind erosion and dust emissions from burned areas have been reduced using wind fences, dispersed barriers (e.g., plastic cones), and mechanical soil furrowing applied perpendicular to prevailing winds (Grantz and others 1998a, 1998b). Recently developed soil aggregating agents (He and others 2008, Liu and others 2012, Orts and others 2007, Stabnikov and others 2013) might also prove useful for erosion control in certain settings.

Given the cyclical nature of drought, some years will likely be much better for restoration plantings than others (Holmgren and Scheffer 2001), and to the degree that favorable years can be predicted, they should be utilized to initiate plant communities that will be able to withstand subsequent periods of drought. Plant materials selected for restoration plantings should ideally be adapted, collectively if not individually, to the full range of conditions expected over time at the planting sites. If some species are better adapted for higher moisture and others for drier conditions, shifts from one group to the other may help protect communities from extreme fluctuations in biomass during drought cycles (Richardson and others 2010, Seabloom 2007, Tilman 1996, Tilman and Downing 1994). Accordingly, over-reliance on one or few species in restoration plantings can increase their susceptibility to drought perturbations in comparison to more diverse plantings, although diversity in and of itself may not be advantageous if the species do not complement or compensate for each other in some way (Carter and Blair 2012, Seabloom 2007). Complementary/compensatory traits relevant to restoration of grasslands and shrublands include functional type (e.g., grass versus shrub versus forb), leaf phenology (e.g., evergreen versus drought-deciduous; cool- versus warm-season), drought dormancy strategy (e.g., seeds versus buds), rooting depth, water-use efficiency, and responsiveness to changes in water availability within the soil profile (Carter and others 2012; Munson 2013; Schwinning and others 2002, 2005; Volaire and others 2014; Weaver and others 1935). Mariotte and others (2013) found that competitiveness of dominant grassland species declined during drought, allowing drought-resistant subordinate species to assert greater dominance. The subordinates in turn reduced the degree to which the dominants

declined, apparently through facilitative interactions in the soil environment (Mariotte and others 2013).

Techniques for restoring species diversity in grasslands and shrublands are continually being evaluated and improved. Seeding equipment such as the rangeland drill, originally designed for seeding a limited class of large-seeded grasses, has been modified over time to handle a greater diversity of seed types that can be planted at different depths (Monsen and Stevens 2004, Vallentine 1989). The difficulty of establishing subordinate forbs in the presence of competitive dominant prairie grasses has prompted strategies involving seeding rate adjustments and allowing forbs to establish prior to interseeding with grasses (Kindscher and Fraser 2000) or seeding subordinate and dominant species in separate patches (Dickson and Busby 2009).

Genetics-Based Strategies To Manage for Drought Resilience

Strategies to manage for drought resilience in grassland, shrubland, and desert ecosystems need to incorporate an understanding of the genetics of drought tolerance in plants (Khasanova and others 2013), how adaptive responses to drought vary within and between plant species (Cory 1995), and how natural selection operates on drought tolerance traits both before and after management practices are put into effect (Kulpa and Leger 2013). In this section, we explore the ecological genetics of drought tolerance in arid-land plants and discuss current management strategies that incorporate genetic information in drought resilience and how these practices might evolve in the face of rapid global change.

Ecological genetics of drought tolerance—Drought tolerance in plants can be defined as persistence through periods of low water availability (Passioura 1996). A suite of traits that increase water-use efficiency by decreasing water loss and/or water use through morphological and physiological means, or shift phenology and dormancy to avoid water stress can contribute to drought tolerance (Chaves and others 2003, Reich and others 2003). Underlying these traits is an array of genetic and developmental pathways that control the timing of seed germination, plant growth, and reproduction; the development of morphological structures, such as leaf shape and lignification; and physiological processes, including protein synthesis and recycling, carbon uptake, and osmotic adjustment (Chaves and others 2003, Ingram and Bartels 1996, Peñuelas and others 2013).

Traits that have positive effects on plant survival and reproduction under drought stress are considered adaptive and will be favored by natural selection in drought-prone environments (Ackerly and others 2000). Because the climatic factors leading to drought stress vary substantially through both time and space (Cook and others 2004, McKee and others 1993) and interact with physiological processes and life history in complex ways, plant species will generally exhibit a combination of traits that contribute to drought tolerance (Reich and others 2003). Also, because species often persist in a variety of climatic conditions, populations are likely to be adapted to local water availability conditions (Heschel and others 2002), which will lead to intraspecific variation in drought tolerance across the species range.

Climate change is likely to increase the severity and frequency of droughts (Cook and others 2004); therefore, plant populations that currently persist in arid and semi-arid ecosystems are likely to face increasing selective pressure to evolve more robust drought-tolerance traits or face local extirpation (Aitken and others 2008). With recent climate change, some plant species have undergone rapid evolution due to increased drought stress (Franks and others 2007). However, as rates of change increase, conditions may shift too rapidly for most species to evolve rapidly enough (Aitken and others 2008). The rate of evolutionary response of plant populations to increased drought severity and frequency will also depend on a number of species and population-specific constraints (Ackerly and others 2000), including: (1) available genetic variation—populations with low genetic variation in important drought-tolerance traits will be less likely to keep pace with changing conditions; (2) life history traits—species with complex mating systems, such as those that depend on specific pollinators, or species with longer generation times, such as trees and shrubs, may be more vulnerable to environmental shifts; and (3) genetic correlations between selected traits—when selection acts in different directions on multiple traits that are linked through developmental, physiological, or genetic pathways, populations will be less likely to evolve.

Ecological genetics and management strategies—

An understanding of the ecological genetics of drought tolerance can help managers practice “evolutionarily enlightened management” in drought-prone ecosystems (Ashley and others 2003). In particular, efforts to conserve plant communities *in situ* will benefit from genetic vulnerability assessments that take into account a population’s adaptive match to its

current environment, its rate of evolutionary response as climates shift, and possible constraints on its further evolution as conditions continue to change. Plant populations that demonstrate adaptive mismatches, slow evolutionary rates, or numerous evolutionary constraints will require more attention and resources than populations that do not face these challenges.

Restoration efforts will also benefit from a genetic approach. The use of seed sources that are adapted to environmental conditions at a restoration site is widely recommended, because these plants are more likely to establish and reproduce (Lesica and Allendorf 1999). Plants from nearby sources are more likely to have adaptive advantages than more distant sources because they are likely to have evolved in similar environments and be related to local ecotypes. In addition, nearby seed sources may be less likely to cause genetic swamping, where genotypes of local remnants are replaced by introduced genotypes, or outbreeding depression, where hybridization with local remnants leads to a loss of fitness through the disruption of locally adapted gene complexes (Hufford and Mazer 2003).

Artificial selection for drought tolerance—One way to use genetic information in wildland drought management strategies is through artificial selection for drought tolerance. Indeed, since the later part of the 20th century, greater attention has been directed at selecting for drought tolerance in wildland restoration species (Johnson and Asay 1993). Delayed stress onset, a type of drought resistance in agricultural crops developed through genetic engineering, has not yet been developed or applied in rangeland or forest ecosystems (Lawlor 2013). Assessment of drought tolerance in wildland species is often more challenging than in agricultural species because plants are rarely grown in conditions that approximate their source environments, and often little is known about their molecular genetics. Therefore, a suite of measurable phenotypic traits, such as rapid seedling emergence, root development, specific leaf area, and water-use efficiency, have generally been used to assess potential drought tolerance in wildland plant breeding programs (Johnson and Asay 1993).

It is important for managers to understand the selection criteria of a germplasm release before using it in restoration projects, particularly in drought-prone plant communities. In the Western United States, artificial selection for drought tolerance has primarily been performed on nonnative grasses that are common

components of post-fire stabilization seedings (Asay and others 2003), though some programs have used drought tolerance as a selection criterion in the development of native plant releases (Jensen and others 2012, Mukherjee and others 2011). Most native plant releases have been selected for high growth rates and seed production (Asay and others 2003), which can lead to high fitness at some wildland sites, but may be counter-productive to success in drought-prone environments (Kulpa 2010). For example, Kulpa and Leger (2013) studied the squirreltail (*Elymus elymoides* ssp. *Californicus*) Toe Jam Creek accession (Jones and others 2003, 2004) in two post-fire seedings with very low establishment success; they found that the surviving populations had undergone extreme directional selection for smaller plant and seed size, as well as earlier flowering phenology. These traits have been associated with drought tolerance in many plant species, but ran counter to the initial traits of the Toe Jam Creek accession, which was selected for release because of its high biomass and seed size. This mismatch may have contributed to the low success rate of the plantings.

Seed transfer guidelines, drought tolerance, and assisted migration—Seed transfer guidelines are useful in identifying seed sources that are likely to be well adapted to a given transplant location (Campbell 1991, Ying and Yanchuk 2006). The use of seed transfer guidelines dates back to the 1920s in North American forestry, when foresters recognized large differences in hardiness and growth of trees with different geographic origins (Bates 1928, Thrupp 1927). Tree seed transfer guidelines were initially based on variation in climatic zones within a species range (Haddock 1962), and they have been updated as genetic information from common garden studies has become more available (Campbell 1986, St. Clair and others 2005). In the past decade, managers and researchers have recognized the usefulness of seed transfer guidelines in the restoration of nonforest communities, particularly in arid and fire-prone environments (Erickson 2008; Johnson and others 2004, 2010a), and seed transfer guidelines have been developed for grass (Erickson and others 2004, Johnson and others 2010b, St. Clair and others 2013), forb (Johnson and others 2013), and shrub (Horning and others 2010) species in the intermountain west.

While seed transfer guidelines do not focus on drought tolerance per se, they do delineate climatic zones where populations of a given species are likely to be adapted, which can be useful in finding seed sources that can

persist in arid conditions (Ying and Yanchuk 2006). In addition, species-specific guidelines are developed using multivariate analyses of common garden data on climatically based adaptive traits (Campbell 1991), and these data allow researchers to find traits that correlate with specific environmental conditions. For example, St. Clair and others (2013) found that in bluebunch wheatgrass (*Pseudoroegneria spicata*), leaf length-to-width ratio (measure of length adjusted leaf narrowness) was highly correlated with annual heat moisture index (a measure of aridity). This makes sense because narrower leaves are less likely to suffer from water loss in stressful conditions due a lower number of exposed stomata. To help refine seed source selection decisions, research is needed to identify populations with traits that contribute to drought tolerance.

Assisted migration, a management strategy where organisms are translocated from sites with suboptimal environmental conditions to sites with more optimal conditions, may become integral to conservation strategies as the rate of climate change increases (Peters and Darling 1985). Assisted migration can encompass a broad range of goals, from minimizing loss of biodiversity to preventing extinction, and operate at a range of spatial scales, from local to continental (Williams and Dumroese 2013). Seed transfer guidelines, because they determine transfer distances that avoid maladaptation (Johnson and others 2004) and can be re-projected using models of expected future environmental conditions (Thomson and others 2010), will play an integral role in the planning of assisted migration efforts under global change.

Conclusions

To conclude, drought has significant ecological impacts—both direct and indirect—on native rangeland plant species, including effects on their physiology, growth, reproduction, physiognomy, and abundance. Drought also impacts rangeland ecosystem functioning and resilience through impacts on water availability, soil integrity, habitat, wildlife populations, livestock, and humans. Drought influences the likelihood and dynamics of other stressors and disturbances such as insect outbreaks, invasive species, wildfire, and human land uses. Drought often requires adjustments in methods for managing livestock and restoring plant communities. Managing and restoring native plant communities resilient to drought and climate change involves matching seed sources and adaptive traits to appropriate environmental and climatic conditions. Seed transfer

guidelines and assisted migration techniques are being developed to aid managers in need of restoration tools in the face of drought and climate change.

Acknowledgments

We thank anonymous reviewers for their helpful comments, Karen Bagne for assistance in literature review, and Nancy Shaw for review of sections of the chapter.

Literature Cited

- Abatzoglou, J.T.; Kolden, C.A. 2011. Climate change in western U.S. deserts: potential for increased wildfire and invasive annual grasses. *Rangeland Ecology & Management* 64: 471-478.
- Abbott, L.B.; Roundy, B.A. 2003. Available water influences field germination and recruitment of seeded grasses. *Journal of Range Management*. 56: 56-64.
- Abbott, L.B.; Sterling, T.M. 2006. African rue (*Peganum harmala*) seedling response to herbicides applied under water-deficit stress. *Weed Science*. 54: 198-204.
- Ackerly, D.D.; Dudley, S.A.; Sultan, S.E. [and others]. 2000. The evolution of plant ecophysiological traits: recent advances and future directions. *BioScience*. 50: 979-995.
- Adkins, J.K.; Barnes, T.G. 2013. Herbicide treatment and timing for controlling Kentucky bluegrass (*Poa pratensis*) and tall fescue (*Festuca arundinacea*) in cool season grasslands of central Kentucky, U.S.A. *Natural Areas Journal*. 33: 31-38.
- Adler, P.B.; Raff, D.A.; Lauenroth, W.K. 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia*. 128: 465-479.
- Agnew, W.M.; Uresk, D.W.; Hansen, R.M. 1986. Flora and fauna associated with prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. *Journal of Range Management*. 39: 135-139.
- Aitken, S.N.; Yeaman, S.; Holliday, J.A. [and others]. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*. 1: 95-111.
- Albertson, F.W.; Tomanek, G.W.; Riegel, A. 1957. Ecology of drought cycles and grazing intensity of grasslands of central great plains. *Ecological Monographs*. 27: 27-44.
- Albertson, F.W.; Weaver, J.E. 1942. History of the native vegetation of western Kansas during seven years of continuous drought. *Ecological Monographs*. 12: 23-51.
- Albertson, F.W.; Weaver, J.E. 1944. Nature and degree of recovery of grassland from the Great Drought of 1933 to 1940. *Ecological Monographs*. 14: 393-479.
- Aldridge, C.L.; Nielsen, S.E.; Beyer, H.L. [and others]. 2008. Range-wide patterns of greater sage-grouse. *Diversity and Distributions*. 14: 983-994.
- Allen, E.B. 1995. Restoration ecology: limits and possibilities in arid and semiarid lands. Gen. Tech. Rep. INT-GTR-315. In: Roundy, B.A.; McArthur, E.D.; Haley, J.S.; Mann, D.K., eds. Proceedings: Wildland Shrub and Arid Land Restoration Symposium. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 7-15.
- Amico, C.; DeBelius, D.; Henry, T.; Stiles, M. 2011. Dried out: confronting the Texas drought. *State Impact: Texas*. [A reporting project of local public media and NPR®]. <http://stateimpact.npr.org/texas/drought/>. [Date accessed: May 2014].
- Anderson, D.C.; Ostler, W.K. 2002. Revegetation of degraded lands at U.S. Department of Energy and U.S. Department of Defense installations: Strategies and successes. *Arid Land Research and Management*. 16: 197-212.
- Anderson, J.E.; Inouye, R.S. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steep over 45 years. *Ecological Monographs*. 71: 531-556.
- Anderson, K.L.; Smith, E.F.; Owensby, C.E. 1970. Burning bluestem range. *Journal of Range Management*. 23: 81-92.
- Andreadis, K.M.; Clark, E.A.; Wood, A.W. [and others]. 2005. Twentieth-century drought in the conterminous United States. *Journal of Hydrometeorology*. 6: 985-1001.
- Andreadis, K.M.; Lettenmaier, D.P. 2006. Trends in 20th century drought over the continental United States. *Geophysical Research Letters*. 33(10): L10403. 4 p. doi:10.1029/2006GL025711. [Published online: May 25, 2006].
- Archer, S.R.; Davies, K.W.; Fulbright, T.E. [and others]. 2011. Brush management as a rangeland conservation strategy: a critical evaluation. In: Briske, D.D., ed. Conservation benefits of rangeland practices: assessment, recommendations, and knowledge gaps. U.S. Department of Agriculture, Natural Resources Conservation Service. Lawrence, KS: Allen Press: 105-170.
- Asay, K.H.; Chatterton, N.J.; Jensen, K.B. [and others]. 2003. Breeding improved grasses for semiarid rangelands. *Arid Land Research and Management*. 17: 469-478.
- Ashley, M.V.; Willson, M.F.; Pergams, O.R.W. [and others]. 2003. Evolutionarily enlightened management. *Biological Conservation*. 111: 115-123.
- Ashton, F.M.; Crafts, A.S. 1981. Mode of action of herbicides. 2d ed. New York: Wiley. 525 p.
- Asner, G.P.; Seasted, T.R.; Townsend, A.R. 1997. The decoupling of terrestrial carbon and nitrogen cycles. *Bioscience*. 47: 226-234.
- Augustine, D.J.; Derner, J.D.; Milchunas, D.G. 2010. Prescribed fire, grazing, and herbaceous plant production in shortgrass steppe. *Rangeland Ecology & Management*. 63: 317-323.
- Austin, A.T.; Yahdjian, L.; Stark, J.M. [and others]. 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia*. 141: 221-235.
- Baer, S.G.; Engle, D.M.; Knops, J.M.H. [and others]. 2009. Vulnerability of rehabilitated agricultural production systems to invasion by nontarget plant species. *Environmental Management*. 43: 189-196.
- Bagne, K.; Ford, P.; Reeves, M. 2012. Grasslands and climate change. U.S. Department of Agriculture, Forest Service, Climate Change Resource Center. <http://www.fs.fed.us/ccrc/topics/grasslands/index.shtml>. [Date accessed: November 2012].
- Bailey, R.G.; Hogg, H.C. 1986. A World ecoregions map for resource reporting. *Environmental Conservation*. 13: 195-202.
- Bainbridge, D.A. 2007. A guide for desert and dryland restoration. Washington DC: Island Press and Society for Ecological Restoration International. 391 p.
- Bakker, C.; Blair, J.M.; Knapp, A.K. 2003a. Does resource availability, resource heterogeneity or species turnover mediate changes in plant species richness in grazed grasslands? *Oecologia*. 137: 385-391.

- Bakker, J.D.; Wilson, S.D.; Christian, J.M. [and others]. 2003b. Contingency of grassland restoration on year, site, and competition from introduced grasses. *Ecological Applications*. 13: 137-153.
- Balch, J.K.; Bradley, B.A.; D'Antonio, C.M.; Gómez-Dans, J. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). *Global Change Biology*. 19: 173–183.
- Banerjee, M.J.; Gerhart, V.J.; Glenn, E.P. 2006. Native plant regeneration on abandoned desert farmland: effects of irrigation, soil preparation, and amendments on seedling establishment. *Restoration Ecology*. 14: 339-348.
- Bashan, Y.; Salazar, B. G.; Moreno, M. [and others]. 2012. Restoration of eroded soil in the Sonoran Desert with native leguminous trees using plant growth-promoting microorganisms and limited amounts of compost and water. *Journal of Environmental Management*. 102: 26-36.
- Baskin, C.C.; Baskin, J.M. 1998. Ecology of seed dormancy and germination. In: Chepwick, G.P., ed. *Population biology of grasses*. Cambridge: Cambridge University Press: 30-83.
- Bates, C.G. 1928. Some problems of seed production, collection and distribution. *Forestry Chronicles*. 5: 17-29.
- Bauer, J. 2006. Fire history and stand structure of a central Nevada piñon-juniper woodland. Reno, NV: University of Nevada, Reno. 143 p. M.S. thesis.
- Belnap, J. 2003. The World at your feet: desert biological soil crusts. *Frontiers in Ecology and the Environment*. 1: 181-189.
- Belnap, J.; Gillette, D.A. 1997. Disturbance of biological soil crusts: impacts on potential wind erodibility of sandy desert soils in southeastern Utah. *Land Degradation and Development*. 8: 355-362.
- Belnap, J.; Sharpe, S. 1995. Reestablishing cold-desert grasslands: a seeding experiment in Canyonlands National Park, Utah. Gen. Tech. Rep. INT-GTR-315. In: Roundy, B.A.; McArthur, E.D.; Haley, J.S.; Mann, D.K., eds. *Proceedings: Wildland Shrub and Arid Land Restoration Symposium*. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 46-51.
- Benkobi, L.; Uresk, D.W.; Child, R.D. 2007. Ecological classification and monitoring model for the Wyoming big sagebrush steppe habitat type of northeastern Wyoming. *Western North American Naturalist*. 67(3): 347-358.
- Benkobi, L.; Uresk, D.W.; Schenbeck, G.; King R.M. 2000. Protocol for monitoring standing crop in grasslands using visual obstruction. *Journal of Range Management*. 53: 627-633.
- Benson, E.J.; Hartnett, D.C. 2006. The role of seed and vegetative reproduction in plant recruitment and demography in tallgrass prairie. *Plant Ecology*. 187: 163-177.
- Benson, L.; Kashgarian, M.; Rye, R. [and others]. 2002. Holocene multi-decadal and multi-centennial droughts affecting northern California and Nevada. *Quaternary Science Review*. 21: 659-682.
- Bernays, E.A.; Lewis, A.C. 1986. The effect of wilting on palatability of plants to *Schistocerca gregaria*, the desert locust. *Oecologia*. 70: 132-135.
- Betancourt, J.L. 2007. From fireproof desert to flammable grassland: buffelgrass invasion in the Sonoran desert. *Eos Transactions AGU*. 88(52), Fall Meeting Supplement, Abstract B34A-02. <http://adsabs.harvard.edu/abs/2007AGUFM.B34A..02B>. [Date accessed: October 13, 2015].
- Betancourt, J.L.; Pierson, E.A.; Rylander, K.A. [and others]. 1993. Influence of history and climate on New Mexico piñon-juniper woodlands. In: Aldan, E.F.; Shaw, D.W., eds. *Managing piñon-juniper ecosystems for sustainability and social needs*. Gen. Tech. Rep. RM-236. Ft. Collins, CO: U.S. Department of Agriculture, Rocky Mountain Forest and Range Experiment Station: 42-62.
- Beyers, J.L. 2004. Postfire seeding for erosion control: effectiveness and impacts on native plant communities. *Conservation Biology*. 18: 947-956.
- Biedenbender, S.H.; Roundy, B.A.; Abbott, L. 1995. Replacing Lehmann lovegrass with native grasses. Gen. Tech. Rep. INT-GTR-315. In: Roundy, B.A.; McArthur, E.D.; Haley, J.S.; Mann, D.K., eds. *Proceedings: Wildland Shrub and Arid Land Restoration Symposium*. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 52-56.
- Biondini, M.E.; Patton, B.D.; Nyren, P.E. 1998. Grazing intensity and ecosystem processes in a northern mixed-grass prairie. *Ecological Applications*. 8: 469-479.
- Bleak, A.T.; Frischknecht, N.C.; Plummer, A.P.; Eckert, R.E.J. 1965. Problems in artificial and natural revegetation of the arid shadscale vegetation zone of Utah and Nevada. *Journal of Range Management*. 18: 59-65.
- Blomberg, E.J.; Sedinger, J.S.; Atamian, M.T.; Nonne, D.V. 2012. Characteristics of climate and landscape disturbance influence the dynamics of greater sage-grouse populations. *Ecosphere*. 3(6):55. <http://dx.doi.org/10.1890/ES11-00304.1>. [Published online: June 27, 2012].
- Bradley, B.A.; Mustard, J.F. 2005. Identifying land cover variability distinct from land cover change: cheatgrass in the Great Basin. *Remote Sensing of Environment*. 94: 204-213.
- Branson, D.H.; Joern, A.; Sword, G.A. 2006. Sustainable management of insect herbivores in grassland ecosystems: new perspectives in grasshopper control. *BioScience*. 56: 743-755.
- Bremer, D.J.; Ham, J.M. 1999. Effect of spring burning on the surface energy balance in a tallgrass prairie. *Agricultural and Forest Meteorology*. 97: 43-54.
- Breshears, D.D.; Cobb, N.S.; Rich, P.M. [and others]. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences*. 102: 15,144-15,148.
- Briggs, J.M.; Knapp, A.K. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. *American Journal of Botany*. 82: 1024-1030.
- Briske, D.D. 1991. Developmental morphology and physiology of grasses. In: Heitschmidt, R.K.; Stuth, J.W., eds. *Grazing management: an ecological perspective*. Portland, OR: Timber Press: 85-108.
- Briske, D.D.; Derner, J.D.; Milchunas, D.G.; Tate, K.W. 2011. An evidence-based assessment of prescribed grazing practices. In: Briske, D.D., ed. *Conservation benefits of rangeland practices: assessment, recommendations, and knowledge gaps*. U.S. Department of Agriculture, Natural Resources Conservation Service. Lawrence, KS: Allen Press: 21-74.
- Britton, C.M.; Wright, H.A. 1971. Correlation of weather and fuel variables to mesquite damage by fire. *Journal of Range Management*. 24: 136-141.
- Brockway, D.G.; Gatewood, R.G.; Paris, R.B. 2002. Restoring fire as an ecological process in shortgrass prairie ecosystems: initial effects of prescribed burning during the dormant and growing seasons. *Journal of Environmental Management*. 65: 135-152.
- Brooks, M.L.; D'antonio, C.M.; Richardson, D. M. [and others]. 2004. Effects of invasive alien plants on fire regimes. *BioScience*. 54(7): 677–688.
- Brooks, M.L.; Esque, T.C. 2002. Alien grasses in the Mojave and Sonoran Deserts. In: Kelly, M.; Howe, M.; Neill, B., eds. *Proceedings California Exotic Plant Pest Council Symposium 15–16 October 1999*; Sacramento, CA. San Diego, CA: California Exotic Plant Pest Council: 39-44.

- Brown, C.S.; Anderson, V.J.; Claassen, V.P. [and others]. 2008. Restoration ecology and invasive plants in the semiarid West. *Invasive Plant Science and Management*. 1: 399-413.
- Bruce, T.J.A.; Matthes, M.C.; Napier, J.A.; Pickett, J.A. 2007. Stressful “memories” of plants: evidence and possible mechanisms. *Plant Science*. 173: 603-608.
- Brunson, M.W.; Evans, J. 2005. Badly burned? Effects of an escaped prescribed burn on social acceptability of wildland fuels treatments. *Journal of Forestry*. 103: 134-138.
- Bussan, A.J.; Dyer, W.E. 1999. Herbicides and rangeland. In: Sheley, R.; Petroff, J. eds. *Biology and management of noxious rangeland weeds*. Corvallis, OR: Oregon State University Press: 116-132.
- Callaghan, T.V.; Björn, L.O.; Chernov, Y. [and others]. 2004. Key findings and extended summaries. *AMBIO: A Journal of the Human Environment*. 33(7): 386-392.
- Campbell, R.K. 1986. Mapped genetic variation of Douglas fir to guide seed transfer in southwest Oregon. *Silvae Genetica*. 35: 85-96.
- Campbell, R.K. 1991. Soils, seed-zone maps, and physiography: guidelines for seed transfer of Douglas-fir in southwestern Oregon. *Forest Science*. 37: 973-986.
- Capinera, J.L.; Horton, D.R. 1989. Geographic variation in effects of weather on grasshopper infestation. *Environmental Entomology*. 18: 8-14.
- Carren, C.J.; Wilson, A.M.; Cuany R.L. 1987. Caryopsis weight and planting depth of blue grama II. Emergence in marginal soil-moisture. *Journal of Range Management*. 40: 212-216.
- Carter, D.L.; Blair, J.M. 2012. High richness and dense seeding enhance grassland restoration establishment but have little effect on drought response. *Ecological Applications*. 22: 1308-1319.
- Carter, D.L.; VanderWeide, B.L.; Blair, J.M. 2012. Drought-mediated stem and below-ground bud dynamics in restored grasslands. *Applied Vegetation Science*. 15: 470-478.
- Cayan, D.R.; Das, T.; Pierce, D.W. [and others]. 2010. Future dryness in the southwest U.S. and the hydrology of the early 21st century drought. *Proceedings of the National Academy of Sciences*. 107: 21,271-21,276.
- Chambers, J.C.; Eldredge, E.P.; Snyder, K.A. [and others]. 2014. Restoring abandoned agricultural lands in cold desert shrublands: tradeoffs between water availability and invasive species. *Invasive Plant Science and Management*. 7: 176-189.
- Chaves, M.M.; Maroco, J.P.; Pereira, J.S. 2003. Understanding plant responses to drought—from genes to the whole plant. *Functional Plant Biology*. 30: 239-264.
- Chirino, E.; Vilagrosa, A.; Ramon Vallejo, V. 2011. Using hydrogel and clay to improve the water status of seedlings for dryland restoration. *Plant and Soil*. 344: 99-110.
- Cincotta, R.P.; Uresk, D.W.; Hansen, R.M. 1988. A statistical model of expansion in a colony of black-tailed prairie dogs. *Gen. Tech. Rep. RM-154*. In: Uresk, D.W.; Schenbeck, G.L.; Cefkin, R., tech. coords. *Eighth Great Plains Wildlife Damage Control Workshop Proceedings*: April 28-30, 1987, Rapid City, SD. Fort Collins, CO: Rocky Mountain Forest and Range Experiment Station: 30-33.
- Clark, J.S.; Grimm, E.C.; Donovan, J.J. [and others]. 2002. Drought cycles and landscape responses to past aridity on prairies of the northern Great Plains, USA. *Ecology*. 83: 595-601.
- Cleland, E.E.; Collins, S.L.; Dickson, T.L. [and others]. 2013. Sensitivity of grassland plant community composition to spatial vs. temporal variation in precipitation. *Ecology*. 94: 1687-1696.
- Cleverly, J.R.; Smith, S.D.; Sala, A.; Devitt, D.A. 1997. Invasive capacity of *Tamarix ramosissima* in a Mojave Desert floodplain: the role of drought. *Oecologia*. 111: 12-18.
- Cole, J.E.; Overpeck, J.T. 2002. Multiyear La Niña events and persistent drought in the contiguous United States. *Geophysical Research Letters*. 29(13): 1647. 4 p. doi:10.1029/2001GL013561. [July 12, 2002].
- Comer, P.; Faber-Langendoen, D.; Evans, R. [and others]. 2003. *Ecological systems of the United States: a working classification of U.S. terrestrial systems*. Arlington, VA: NatureServe. <http://www.natureserve.org/library/usEcologicalsystems.pdf>. [Date accessed: November 2015].
- Conn, J.S.; Casie, A.; Stockdale, A. [and others]. 2010. Characterizing pathways of invasive plant spread to Alaska: II. Propagules from imported hay and straw. *Invasive Plant Science and Management*. 3: 276-285.
- Cony, M.A. 1995. Rational afforestation of arid and semiarid lands with multipurpose trees. *Interciencia*. 20: 249-253.
- Cook, E.R.; Meko, D.M.; Stahle, D.W.; Cleaveland, M.K. 1999. Drought reconstructions for the continental United States. *Journal of Climate*. 12: 1145-1162.
- Cook, E.R.; Seager, R.; Cane, M.A.; Stahle, D.W. 2007. North American drought: reconstructions, causes, and consequences. *Earth-Science Reviews*. 81: 93-134.
- Cook, E.R.; Seager, R.; Heim, R.R. [and others]. 2010. Megadroughts in North America: placing IPCC projections of hydroclimatic change in a long-term palaeoclimate context. *Journal of Quaternary Science*. 25: 48-61.
- Cook, E.R.; Woodhouse, C.A.; Eakin, C.M. [and others]. 2004. Long-term aridity changes in the Western United States. *Science*. 306: 1015-1018.
- Coppock, D.L. 2011. Ranching and multiyear droughts in Utah: production impacts, risk perceptions, and changes in preparedness. *Rangeland Ecology and Management*. 64: 607-618.
- Corbin, J.D.; D’Antonio, C.M. 2004. Competition between native and exotic annual grasses: implications for an historical invasion. *Ecology*. 85: 1273-1283.
- Corn, J.G.; Story J.M.; White L.J. 2007. Effect of summer drought relief on the impact of the root weevil *Cyphocleonus achates* on spotted knapweed. *Environmental Entomology*. 36: 858-863.
- Coupland, R.T. 1958. The effects of fluctuations in weather upon the grasslands of the Great Plains. *Botanical Review*. 24: 274-317.
- Currie, P.O.; White, R.S. 1982. Drought survival of selected forage grasses commonly seeded in the northern Great Plains. *Canadian Journal of Plant Science*. 62: 949-955.
- D’Antonio, C.M.; Vitousek, P.M. 1992. Biological invasions by exotic grasses, the grass-fire cycle, and global change. *Annual Review of Ecology and Systematics*. 23: 63-87.
- Dai, A.; Trenberth, K.E.; Karl, T.R. 1998. Global variations in droughts and wet spells: 1900-1995. *Geophysical Research Letters*. 25(17): 3367-3370.
- David, E. 2013. Innovative snow harvesting technology increases vegetation establishment success in native sagebrush ecosystem restoration. *Plant and Soil*. 373: 843-856.
- Dennison, P.E.; Brewer, S.C.; Arnold, J.D.; Moritz, M.A. 2014. Large wildfire trends in the Western United States, 1984-2011. *Geophysical Research Letters*. 41(8): 2928-2933.
- Dickson, T.L.; Busby, W.H. 2009. Forb species establishment increases with decreased grass seeding density and with increased forb seeding density in a northeast Kansas, USA, experimental prairie restoration. *Restoration Ecology*. 17: 597-605.

- DiTomaso, J.M.; Brooks, M.L.; Allen, E.B. [and others]. 2006. Control of invasive weeds with prescribed burning. *Weed Technology*. 20: 535-548.
- Dixon, R.M. 1995. Water infiltration control at the soil surface— theory and practice. *Journal of Soil and Water Conservation*. 50: 450-453.
- Dodson, E.K.; Peterson, D.W. 2010. Mulching effects on vegetation recovery following high severity wildfire in north-central Washington State, USA. *Forest Ecology and Management*. 260: 1816-1823.
- Duffy, P.A.; Walsh, J.E.; Graham, J.M. [and others]. 2005. Impacts of large-scale atmospheric-ocean variability on Alaskan fire season severity. *Ecological Applications*. 15: 1317-1330.
- Earles, T.A.; Wright, K.R.; Brown, C.; Langan, T.E. 2004. Los Alamos forest fire impact modeling. *Journal of the American Water Resources Association*. 40: 371-384.
- Edwards, F.S.; Bainbridge, D.A.; Zink, T.A.; Allen, M.F. 2000. Rainfall catchments improve survival of container transplants at Mojave Desert site. *Ecological Restoration*. 18: 100-103.
- Ehleringer, J.R.; Phillips, S.L.; Schuster, W.S.F.; Sandquist, D.R. 1991. Differential utilization of summer rains by desert plants. *Oecologia*. 88: 430-434.
- Eldridge, J.D.; Redente, E.F.; Paschke, M. 2012. The use of seedbed modifications and wood chips to accelerate restoration of well pad sites in western Colorado, USA. *Restoration Ecology*. 20: 524-531.
- Ellison, L.; Woolfolk, E.J. 1937. Effects of drought on vegetation near Miles City, Montana. *Ecology*. 1: 329-336.
- Engle, D.M.; Coppedge, B.R.; Fuhlendorf, S.D. 2008. From the Dust Bowl to the green glacier: human activity and environmental change in Great Plains grasslands. In: *Western North American Juniperus Communities*. New York: Springer: 253-271.
- Erickson, V.J. 2008. Developing native plant germplasm for national forests and grasslands in the Pacific Northwest. *Native Plants Journal*. 9: 255-266.
- Erickson, V.J.; Mandel, N.L.; Sorenson, F.C. 2004. Landscape patterns of phenotypic variation and population structuring in a selfing grass, *Elymus glaucus* (blue wildrye). *Canadian Journal of Botany*. 82: 1776-1789.
- Evans, S.E.; Byrne, K.M.; Lauenroth, W.L.; Burke, I.C. 2011. Defining the limit to resistance in a drought-tolerant grassland: long-term severe drought significantly reduces the dominant species and increases ruderals. *Journal of Ecology*. 6: 1500-1507.
- Evans, S.E.; Burke, I.C. 2013. Carbon and nitrogen decoupling under an 11-year drought in the shortgrass steppe. *Ecosystems*. 16: 20-33.
- Everard, K.; Seabloom, E.W.; Harpole, W.S.; de Mazancourt, C. 2010. Plant use affects competition for nitrogen: why drought favors invasive species in California. *American Naturalist*. 175: 85-97.
- Farrow, R.A. 1979. Population dynamics of the Australian plague locust, *Chortoicetes terminifera* (Walker), in central western New South Wales. I. Reproduction and migration in relation to weather. *Australian Journal of Zoology*. 27: 717-45.
- Fay, P.A.; Carlisle, J.D.; Knapp, A.K. [and others]. 2003. Productivity responses to altered rainfall patterns in a C4-dominated grassland. *Oecologia*. 137: 245-251.
- Fehmi, J.S.; Kong, T.M. 2012. Effects of soil type, rainfall, straw mulch, and fertilizer on semi-arid vegetation establishment, growth and diversity. *Ecological Engineering*. 44: 70-77.
- Fehmi, J.S.; Niu, G.-Y.; Scott, R.L.; Mathias, A. 2014. Evaluating the effect of rainfall variability on vegetation establishment in a semidesert grassland. *Environmental Monitoring and Assessment*. 186: 395-406.
- Fernandez, C.; Vega, J.A. 2014. Efficacy of bark strands and straw mulching after wildfire in NW Spain: effects on erosion control and vegetation recovery. *Ecological Engineering*. 63: 50-57.
- Finch, D.M.; Smith, D.M.; LeDee, O. [and others]. 2012. Climate change, animal species, and habitats: Adaptation and issues (Chapter 5). In: Finch, D.M., ed. *Climate change in grasslands, shrublands, and deserts of the interior American West: a review and needs assessment*. Gen. Tech. Rep. RMRS-GTR-285. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 60-79.
- Finney, M.A.; McHugh C.W.; Stratton, R.D.; Riley, K.L. 2011. A simulation of probabilistic wildfire risk components for the continental United States. *Stochastic Environmental Research Risk Assessment*. 25: 973-1000.
- Flanders-Wanner, B.L.; White, G.C.; McDaniel, L.L. 2004. Weather and prairie grouse: dealing with effects beyond our control. *Wildlife Society Bulletin*. 32: 22-34.
- Floyd, M.L.; Clifford, M.; Cobb, N.S. [and others]. 2009. Relationship of stand characteristics to drought-induced mortality in three Southwestern pinyon-juniper woodlands. *Ecological Applications*. 19(5): 1223-1230.
- Floyd, M.L.; Hanna, D.D.; Romme, W.H. 2004. Historical and recent fire regimes in pinyon-juniper woodlands on Mesa Verde, Colorado, USA. *Forest Ecology and Management*. 198(1): 269-289.
- Floyd, M.L.; Romme, W.H.; Hanna, D.D. [and others]. 2008. Fire history of pinyon-juniper woodlands on Navajo Point, Glen Canyon National Recreation Area. *Natural Areas Journal*. 28(1): 26-36.
- Ford, P.L.; Chambers, J.K.; Coe, S.J.; Pendleton, B.C. 2012. Disturbance and climate change in the Interior West (Chapter 6). In: Finch, D.M., ed. *Climate change in grasslands, shrublands, and deserts of the interior American West: a review and needs assessment*. Gen. Tech. Rep. RMRS-GTR-285. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 80-96.
- Ford, P.L.; Johnson, G.V. 2006. Effects of dormant- vs. growing-season fire in shortgrass steppe: Biological soil crust and perennial grass responses. *Journal of Arid Environments*. 67: 1-14.
- Foti, R.; Ramirez, J.A.; Brown, T.C. 2012. Vulnerability of U.S. water supply to shortage: a technical document supporting the Forest Service 2010 RPA Assessment. Gen. Tech. Rep. 295. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 147 p.
- Franks S.J.; Sim S.; Weis A.E. 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences*. 104: 1278-1282.
- Frasier, G.W.; Cox, J.R.; Woolhiser, D.A. 1987. Wet-dry cycle effects on warm-season grass seedling establishment. *Journal of Range Management*. 40: 2-6.
- Fritcher, S.C.; Rumble, M.A.; Flake, L.D. 2004. Grassland bird densities in seral stages of mixed-grass prairie. *Journal of Range Management*. 57: 351-357.
- Fuhlendorf, S.D.; Briske, D.D.; Smeins, F.E. 2001. Herbaceous vegetation change in variable rangeland environments: The relative contribution of grazing and climatic variability. *Applied Vegetation Science*. 4: 177-188.

- Fuhlendorf, S.D.; Limb, R.F.; Engle, D.M.; Miller, R.F. 2011. Assessment of prescribed fires as a conservation practice. In: Briske, D.D., ed. Conservation benefits of rangeland practices: assessment, recommendations, and knowledge gaps. Lawrence, KS: U.S. Department of Agriculture, Natural Resources Conservation Service. Allen Press: 75-104.
- Funk J.L.; Zachary, V.A. 2010. Physiological responses to short-term water and light stress in native and invasive plant species in southern California. *Biological Invasions*. 12: 1685-1694.
- Gage, S.H.; Mukerji, M.K. 1977. A perspective of grasshopper population distribution in Saskatchewan and interrelationship with weather. *Environmental Entomology*. 6: 469-479.
- Galle, G.; Florez-Sarasa, I.; El Aououad, H.; Flexas, J. 2011. The Mediterranean evergreen *Quercus ilex* and the semi-deciduous *Cistus albidus* differ in their leaf gas exchange regulation and acclimation to repeated droughts and re-watering cycles. *Journal of Experimental Botany*. 62: 5207-5216.
- George, T.L.; Fowler, A.C.; Knight, R.L.; McEwen, L.C. 1992. Impacts of a severe drought on grassland birds in western North Dakota. *Ecological Applications*. 2(3): 275-284.
- Gillett, N.P.; Weaver, A.J.; Zwiers, F.W.; Flannigan, M.D. 2004. Detecting the effect of climate change on Canadian forest fires. *Geophysical Research Letters* 31: L18211. 4 p. doi:10.1029/2004GL020876. [Published online: September 29, 2004].
- Glenn, E.P.; Waugh, W.J.; Moore, D. [and others]. 2001. Revegetation of an abandoned uranium millsite on the Colorado Plateau, Arizona. *Journal of Environmental Quality*. 30: 1154-1162.
- Grantz, D.A.; Vaughn, D.L.; Farber, R.J. [and others]. 1998a. Wind barriers suppress fugitive dust and soil-derived airborne particles in arid regions. *Journal of Environmental Quality*. 27: 946-952.
- Grantz, D.A.; Vaughn, D.L.; Farber, R.J. [and others]. 1998b. Wind barriers offer short-term solution to fugitive dust. *California Agriculture*. 52: 14-18.
- Grayson, D.K. 2011. The Great Basin: a natural prehistory. Berkeley, CA: University of California Press. 875 p.
- Greb, B.W. 1980. Snowfall and its potential management in the semiarid central Great Plains. Akron, CO: U.S. Department of Agriculture, Science and Education Administration ARM-W-18. 64 p.
- Grissino-Mayer, H.D.; Baisan, C.H.; Morino, K.A.; Swetnam, T.W. 2002. Multi-century trends in past climate for the middle Rio Grande basin, AD 622-1922. Final Report 28C4800. Albuquerque NM: U.S. Department of Agriculture, Rocky Mountain Research Station. [Number of pages unknown].
- Groen, A.H.; Woods, S.W. 2008. Effectiveness of aerial seeding and straw mulch for reducing post-wildfire erosion, north-western Montana, USA. *International Journal of Wildland Fire*. 17: 559-571.
- Gullion, G.W. 1960. The ecology of Gambel's quail in Nevada and the arid southwest. *Ecology*. 41: 518-536.
- Guse, R. 2009. Lessons learned from recent prescribed burns in drought-stricken south Texas. Coastal Bend Prescribed Burn Association. http://www.prescribedburn.org/userfiles/file/lessons_learned_ray_guse_8-09.pdf. [Date accessed: May 5, 2014].
- Haddad, N.M.; Tilman, D.; Knops, J.M. 2002. Long-term oscillations in grassland productivity induced by drought. *Ecology Letters*. 5: 110-120.
- Haddock, P.G. 1962. Douglas-fir in Canada: seed collection zones based on geographic variation of populations as influenced by climate. Vancouver, BC: Faculty of Forestry, University of British Columbia. 11 p.
- Haglund, B.M. 1980. Proline and valine: cues which stimulate grasshopper herbivory during drought stress. *Nature*. 288: 697-698.
- Hajek, A.E.; St. Leger, R.J. 1994. Interactions between fungal pathogens and insect hosts. *Annual Review of Entomology*. 39: 293-322.
- Hall, D.B.; Anderson, D.C. 1999. Reclaiming disturbed land using supplemental irrigation in the Great Basin/Mojave Desert transition region after contaminated soils remediation: the Double Tracks Project. In: McArthur, E.D.; Ostler, W.K.; Wamboldt, C.L., eds. Proceedings: Shrubland Ecotones. Proceedings RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 260-265.
- Hallett, L.M.; Standish, R.J.; Hobbs, R.J. 2011. Seed mass and summer drought survival in a Mediterranean-climate ecosystem. *Plant Ecology*. 212: 1479-1489.
- Hansen, M.J.; Wilson, S.D. 2006. Is management of an invasive grass *Agropyron cristatum* contingent on environmental variation? *Journal of Applied Ecology*. 43: 269-280.
- Hardegree, S.P.; Jones, T.A.; Roundy, B.A. [and others]. 2011. Assessment of range planting as a conservation practice. In: Briske, D.D., ed. Conservation benefits of rangeland practices: assessment, recommendations, and knowledge gaps. Lawrence, KS: U.S. Department of Agriculture, Natural Resources Conservation Service. Allen Press: 171-212.
- Harju, S.M.; Olson, C.V.; Foy-Martin, L. [and others]. 2013. Occurrence and success of greater sage-grouse broods in relation to insect vegetation community gradients. *Human-Wildlife Interactions*. 7: 214-229.
- Harper, J.L. 1977. Population biology of plants. London: Academic Press. 892 p.
- Hart, C.R.; Carpenter, B.B. 2005. Stocking rate and grazing management. Rangeland Drought Management for Texans E-64: 05-01. College Station, TX: Texas Agricultural Experiment Station. 3 p.
- Hart, R.H.; Dean, J.G. 1986. Forage establishment—weather effects on stubble vs. fallow and fall vs. spring seeding. *Journal of Range Management*. 39: 228-230.
- He, J.J.; Cai, Q.G.; Tang, Z.J. 2008. Wind tunnel experimental study on the effect of PAM on soil wind erosion control. *Environmental Monitoring and Assessment*. 145: 185-193.
- Healy, W.M. 1985. Turkey poult feeding activity, invertebrate abundance, and vegetation structure. *Journal of Wildlife Management*. 49: 466-472.
- Heitschmidt, R.K.; Haferkamp, M.R.; Karl, M.G.; Hild, A.L. 1999. Drought and grazing: I. Effects on quantity of forage produced. *Journal of Range Management*. 52: 440-446.
- Hennessy, J.T.; Kies, B.; Gibbens, R.P.; Tromble, J.M. 1986. Soil sorting by forty-five years of wind erosion on a southern New Mexico Range. *Soil Science Society of America Journal*. 50: 319-294.
- Herman-Brunson, K.M.; Jensen, K.C.; Kaczor, N.W. [and others]. 2009. Nesting ecology of greater sage-grouse *Centrocercus urophasianus* at the eastern edge of their historic distribution. *Wildlife Biology*. 15(4): 395-404.
- Herweijer, C.; Seager, R.; Cook, E.R.; Emile-Geay, J. 2007. North American droughts of the last millennium from a gridded network of tree-ring data. *Journal of Climate*. 20: 1353-1376.
- Heschel, M.S.; Donohue, K.; Hausmann, N.; Schmitt, J. 2002. Population differentiation and natural selection for water-use efficiency in *Impatiens capensis* (Balsaminaceae). *International Journal of Plant Sciences*. 163: 907-912.

- Hewitt, G.B.; Onsager, J.A. 1983. Control of grasshoppers on rangeland in the United States—a perspective. *Journal of Range Management*. 36: 202-207.
- Hinzman, L.D.; Bettez, N.D.; Bolton, W.R. [and others]. 2005. Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change*. 72(3): 251-298.
- Hobbs, R.J.; Yates, S.; Mooney, H.A. 2007. Long-term data reveal complex dynamics in grassland in relation to climate and disturbance. *Ecological Monographs*. 77: 545-568.
- Holden, M.; Miller, C. 1995. New arid land revegetation techniques at Joshua Tree National Monument. In: Roundy, B.A.; McArthur, E.D.; Haley, J.S.; Mann, D.K., eds. *Proceedings: Wildland Shrub and Arid Land Restoration Symposium*. Gen. Tech. Rep. INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 99-101.
- Holloran, M.J.; Heath, B.J.; Lyon, A.G. [and others]. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. *Journal of Wildlife Management*. 69(2): 638-649.
- Holmgren, M.; Scheffer, M. 2001. El Niño as a window of opportunity for the restoration of degraded arid ecosystems. *Ecosystems*. 4: 151-159.
- Horning, M.E.; McGovern, T.R.; Darris, D.C. [and others]. 2010. Geneecology of *Holodiscus discolor* (Rosaceae) in the Pacific Northwest, USA. *Restoration Ecology*. 18: 235-243.
- Housman, D.C.; Powers, H.H.; Collins, A.D.; Belnap, J. 2006. Carbon and nitrogen fixation differ between successional stages of biological soil crusts in the Colorado Plateau and Chihuahuan Desert. *Journal of Arid Environments*. 66: 620-634.
- Howery, L.D. 1999. Rangeland management before, during, and after drought. University of Arizona Cooperative Extension report AZ1136. <http://extension.arizona.edu/sites/extension.arizona.edu/files/pubs/az1136.pdf>. [Date accessed: October 2015].
- Howery, L.D.; Provenza, F.D.; Banner, R.E.; Scott, C.B. 1998. Social and environmental factors influence cattle distribution on rangeland. *Applied Animal Behavioral Science*. 55: 231-244.
- Huberty, A.F.; Denno, R.F. 2004. Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology*. 85: 1383-1398.
- Hufford, K.M.; Mazer, S.J. 2003. Plant ecotypes: genetic differentiation in the age of ecological restoration. *Trends in Ecology and Evolution*. 18: 147-155.
- Hughes, M.K.; Brown, P.M. 1992. Drought frequency in central California since 101 BC recorded in giant sequoia tree rings. *Climate Dynamics*. 6: 161-167.
- Hulet, A.; Roundy, B.A.; Jessop, B. 2010. Crested wheatgrass control and native plant establishment in Utah. *Rangeland Ecology & Management*. 63: 450-460.
- Hurst, G.A.; Poe, W.E. 1985. Amino acid levels and patterns in wild turkey poults and their food items in Mississippi. *Proceeding of the National Wild Turkey Symposium*. 5: 133-143.
- Hurt, D.R. 1981. *An agricultural and social history of the Dust Bowl*. Chicago: Nelson Hall. 214 p.
- Ingram, J.; Bartels, D. 1996. The molecular basis of dehydration tolerance in plants. *Annual Review of Plant Physiology and Plant Molecular Biology*. 47: 377-403.
- Intergovernmental Panel on Climate Change (IPCC). 2007. *Climate change 2007: synthesis report*. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. (Core Writing Team: Pachauri, R.K.; Reisinger, A., eds.). Geneva, Switzerland: IPCC. 104 p.
- Jackson, L.E. 1985. Ecological origins of California's Mediterranean grasses. *Journal of Biogeography*. 12: 349-361.
- James, S.E.; Pärtel, M.; Wilson, S.D.; Peltzer, D.A. 2003. Temporal heterogeneity of soil moisture in grassland and forest. *Journal of Ecology*. 91: 234-239.
- Jensen, K.B.; Mott, I.W.; Robins, J.G. [and others]. 2012. Genetic improvement and diversity in Snake River wheatgrass (*Elymus wawaicensis*) (Poaceae: Triticeae). *Rangeland Ecology and Management*. 65: 76-84.
- Ji, L.; Peters, A.J. 2003. Assessing vegetation response to drought in the northern Great Plains using vegetation and drought indices. *Remote Sensing of Environment*. 87: 85-98.
- Joern, A.; Gaines, S.B. 1990. Population dynamics and regulation in grasshoppers. in: Chapman, R.F.; Joern, A. eds., *Biology of Grasshoppers*. John Wiley and Sons, Inc., New York, NY: 415-482.
- Johnson, D.A.; Asay, K.H. 1993. Viewpoint: selection for improved drought response in cool-season grasses. *Journal of Range Management*. 46: 194-202.
- Johnson, G.D.; Boyce, M.S. 1990. Feeding trials with insects in the diet of sage grouse chicks. *Journal of Wildlife Management*. 54: 89-91.
- Johnson, G.R.; Sorenson, F.C.; St. Clair, J.B.; Cronn, R.C. 2004. Pacific Northwest forest tree seed zones: a template for native plants? *Native Plants Journal*. 5: 131-140.
- Johnson, R.C.; Erickson, V.J.; Mandel, N.L. [and others]. 2010b. Mapping genetic variation and seed zones for *Bromus carinatus* in the Blue Mountains of eastern Oregon, USA. *Botany*. 88: 725-736.
- Johnson, R.C.; Hellier, B.C.; Vance-Borland, K.W. 2013. Geneecology and seed zones for tapertip onion in the U.S. Great Basin. *Botany*. 91: 686-694.
- Johnson, R.; Stritch, L.; Olwell, P. [and others]. 2010a. What are the best seed sources for ecosystem restoration on BLM and USFS lands? *Native Plants Journal*. 11: 117-132.
- Joly, K.; Duffy, P.A.; Rupp, T.S. 2012. Simulating the effects of climate change on fire regimes in Arctic biomes: implications for caribou and moose habitat. *Ecosphere*. 3(5): article 36. 18 p. <http://dx.doi.org/10.1890/ES12-00012.1>. [Published online: May 2, 2012].
- Joly, K.; Rupp, T.S.; Jandt, R.R.; Chapin, F.S., III. 2009. Fire in the range of the western Arctic caribou herd. *Alaska Park Science*. 8: 68-73.
- Jones, T.A.; Nielson, D.C.; Arredondo, J.T.; Redinbaugh, M.G. 2003. Characterization of diversity among 3 squirreltail taxa. *Journal of Range Management*. 56: 474-482.
- Jones, T.A.; Nielson, D.C.; Larson, S.R. [and others]. 2004. Registration of Toe Jam Creek bottlebrush squirreltail germplasm. *Crop Science*. 44: 1880-1881.
- Kachergis, E.; Derner, J.D.; Cutts, B.B. [and others]. 2014. Increasing flexibility in rangeland management during drought. *Ecosphere*. 5(6):77. <http://dx.doi.org/10.1890/ES13-00402.1>. [Published online: June 30, 2014].
- Kaczor, N.W.; Herman-Brunson, K.M.; Jensen, K.C. [and others]. 2011b. Resource selection during brood-rearing by Greater Sage-Grouse. In: Sandercock, B.K.; Martin, K.; Segelbacher, G., eds. *Ecology, conservation, and management of grouse*. Studies in Avian Biology No. 39. Berkeley, CA: University of California Press: 169-177.
- Kaczor, N.W.; Jensen, K.C.; Klaver, R.W. [and others]. 2011a. Nesting success and resource selection of greater sage-grouse. In: Sandercock, B.K.; Martin, K.; Segelbacher, G., eds. *Ecology, conservation, and management of grouse*. Studies in Avian Biology No. 39. Berkeley, CA: University of California Press: 107-118.

- Kasischke, E.S.; Turetsky, M.R. 2006. Recent changes in the fire regime across the North American boreal region—spatial and temporal patterns of burning across Canada and Alaska. *Geophysical Research Letters*. 33(9): L09703. 5 p. doi:10.1029/2006GL025677. [Published online: 3 May 2006].
- Kemp, W.P.; Cigliano, M.M. 1994. Drought and rangeland grasshopper species diversity. *Canadian Entomologist*. 126: 1075-1092.
- Kemp, W.P.; Sanchez, N.E. 1987. Differences in post-diapause thermal requirements for eggs of two rangeland grasshoppers. *Canadian Entomologist*. 119: 653-661.
- Khasanova, A.; James, J.J.; Drenovsky, R.E. 2013. Impacts of drought on plant water relations and nitrogen nutrition in dryland perennial grasses. *Plant Soil*. 372: 541-552.
- Kindscher, K.; Fraser, A. 2000. Planting forbs first provides greater species diversity in tallgrass prairie restorations (Kansas). *Ecological Restoration*. 18: 115-116.
- Knapp, A.K.; Smith, M.D. 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science*. 291: 481-484.
- Knowles, C.J. 1986. Some relationships of black-tailed prairie dogs to livestock grazing. *Western North American Naturalist*. 46: 198-203.
- Koerner, S.E.; Collins, S. L. 2014. Interactive effects of grazing, drought, and fire on grassland plant communities in North America and South Africa. *Ecology*. 95: 98-109.
- Kogan, F.N. 1995. Droughts of the late 1980s in the United States as derived from NOAA polar-orbiting satellite data. *Bulletin of the American Meteorological Society*. 76: 655-668.
- Kogan, M.; Bayer, D.E. 1996. Herbicide uptake as influenced by plant water status. *Pesticide Biochemistry and Physiology*. 56: 174-182.
- Kolb, K.J.; Sperry, J.S. 1999. Differences in drought adaptation between subspecies of sagebrush (*Artemisia tridentata*). *Ecology*. 80: 2373-2384.
- Kozłowski, T.T.; Pallardy, S.G. 1997. *Physiology of woody plants*. 2d ed. San Diego: Academic Press. 411 p.
- Krämer, S.; Miller, P.M.; Eddleman, L.E. 1996. Root system morphology and development of seedling and juvenile *Juniperus occidentalis*. *Forest Ecology and Management*. 86: 229-240.
- Kulpa, S.M. 2010. Identifying barriers to successful establishment of post-fire seeding in the Great Basin. Reno, NV: University of Nevada, Reno. 126 p. M.S. thesis.
- Kulpa S.M.; Leger E.A. 2013. Strong natural selection during plant restoration favors an unexpected suite of traits. *Evolutionary Applications*. 6: 510-523.
- Ladwig, L.M.; Collins, S.C.; Ford, P.L.; White, L.B. 2014. Chihuahuan Desert grassland responds similarly to fall, spring, and summer fires during prolonged drought. *Rangeland Ecology and Management*. 67(6): 621-628.
- Larcher, W. 2003. *Physiological plant ecology*. 4th ed. Berlin: Springer-Verlag. 513 p.
- Lauenroth, W.K.; Sala, O.E. 1992. Long-term forage production of North American shortgrass steppe. *Ecological Applications*. 2: 397-403.
- Lauridson, T.C.; Wilson, R.G.; Haderlie, L.C. 1983. Effect of moisture stress on Canada thistle (*Cirsium arvense*) control. *Weed Science*. 31: 674-680.
- Lawlor, D.W. 2013. Genetic engineering to improve plant performance under drought: physiological evaluation of achievements, limitations, and possibilities. *Journal of Experimental Botany*. 64(1): 83-108.
- Lawler, J.J.; Shafer, S.L.; White, D. [and others]. 2009. Projected climate-induced faunal change in the western hemisphere. *Ecology*. 90: 588-597.
- Leishman, M.R.; Westoby, M. 1994. The role of seed size in seedling establishment in dry soil-conditions—experimental-evidence from semiarid species. *Journal of Ecology*. 82: 249-258.
- Lesica, P.; Allendorf, F.W. 1999. Ecological genetics and the restoration of plant communities: mix or match? *Restoration Ecology*. 7: 42-50.
- Lewis, A.C. 1982. Leaf wilting alters a plant species ranking by the grasshopper *Melanoplus differentialis*. *Ecological Entomology*. 7: 391-395.
- Leys, J.; McTainsh, G. 1994. Soil loss and nutrient decline by wind erosion-cause for concern. *Australian Journal of Soil Water Conservation*. 7: 30-40.
- Li, J.; Okin, G.S.; Alvarez, H.E.; Epstein, H. 2007. Quantitative effects of vegetation cover on wind erosion and soil nutrient loss in a desert grassland of southern New Mexico, USA. *Biogeochemistry*. 85: 317-332.
- Lin, G.; Phillips, S.L.; Ehleringer, J.R. 1996. Monsoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau. *Oecologia*. 106: 8-17.
- Liu, J.; Shi, B.; Lu, Y. [and others]. 2012. Effectiveness of a new organic polymer sand-fixing agent on sand fixation. *Environmental Earth Sciences*. 65: 589-595.
- Littell, J.S.; McKenzie, D.; Peterson, D.L.; Westerling, A.L. 2009. Climate and wildfire area burned in western U.S. ecoregions, 1916-2003. *Ecological Applications*. 19: 1003-1021.
- Loik, M.E.; Breshears, D.D.; Lauenroth, W.K.; Belnap, J. 2004. A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the Western USA. *Oecologia*. 141: 269-281.
- Mack, R.N. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agro-Ecosystems*. 7(2):145-165.
- Madsen, M.D.; Petersen, S.L.; Fernelius, K.J. [and others]. 2012a. Influence of soil water repellency on seedling emergence and plant survival in a burned semi-arid woodland. *Arid Land Research and Management*. 26: 236-249.
- Madsen, M.D.; Petersen, S.L.; Roundy, B.A. [and others]. 2012b. Comparison of postfire soil water repellency amelioration strategies on bluebunch wheatgrass and cheatgrass survival. *Rangeland Ecology & Management*. 65: 182-188.
- Mariotte, P.; Vandenberghe, C.; Kardol, P. [and others]. 2013. Subordinate plant species enhance community resistance against drought in semi-natural grasslands. *Journal of Ecology*. 101: 763-773.
- Mattson, W.J.; Haack, R.A. 1987. The role of drought in outbreaks of plant-eating insects. *Bioscience*. 37: 110-118.
- Maxwell, R.S.; Hessler, A.E.; Cook, E.R.; Pederson, N. 2011. A multispecies tree ring reconstruction of Potomac River streamflow (950-2001). *Water Resources Research*. 47(5): W05512. 12 p. doi:10.1029/2010WR010019. [Published online: May 12, 2011].
- McKee, T.B.; Doesken, N.J.; Kleist, J. 1993. The relationship of drought frequency and duration to time scales. *Proceedings, Eighth Conference on Applied Climatology*, 17-22 January 1993, Anaheim, CA. American Meteorological Society: 179-184.

- Meko, D.M.; Woodhouse, C.A.; Baisan, C.A. [and others]. 2007. Medieval drought in the upper Colorado River Basin. *Geophysical Research Letters* 34(10): L10705. 5 p. doi:10.1029/2007GL029988. [Published online: May 24, 2007].
- Mensing, S.A.; Sharpe, S.E.; Tunno, I. [and others]. 2013. The late Holocene Dry Period: multiproxy evidence for an extended drought between 2800 and 1850 cal yr. BP across the central Great Basin, USA. *Quaternary Science Reviews*. 78: 266-282.
- Meyer, S.E. 1994. Germination and establishment ecology of big sagebrush: implications for community restoration. In: Monsen, S.B.; Kitchen, S.G., eds. *Proceedings—Ecology and Management of Annual Rangelands*. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 244-251.
- Milbau, A.; Scheerlinck L.; Reheul, D. [and others]. 2005. Ecophysiological and morphological parameters related to survival in grass species exposed to an extreme climatic event. *Physiologia Plantarum*. 125: 500-512.
- Milchunas, D.G.; Sala, O.E.; Lauenroth, W.K. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *The American Naturalist*. 132: 87-106.
- Miller, M.E.; Bowker, M.A.; Reynolds, R.L.; Goldstein, H.L. 2012. Post-fire land treatments and wind erosion—lessons from the Milford Flat Fire, UT, USA. *Aeolian Research*. 7: 29-44.
- Minnick, T.J.; Alward, R.D. 2012. Soil moisture enhancement techniques aid shrub transplant success in an arid shrubland restoration. *Rangeland Ecology & Management*. 65: 232-240.
- Mitchell, J.E.; Roberts, T.C., Jr. 1999. Distribution of pinyon–juniper in the Western United States. In: Monsen, S.B.; Stevens, R., eds. *Proceedings: ecology and management of pinyon–juniper communities within the interior West*. Ogden, UT: U.S. Department of Agriculture, Forest Service Proceedings RMRS-P-9. Rocky Mountain Research Station: 146–154.
- Monsen, S.B.; Stevens, R. 2004. Seedbed preparation and seeding practices. In: Monsen, S.B.; Stevens, R.; Shaw, N.L., eds. *Restoring western ranges and wildlands*. Gen. Tech. Rep. RMRS-GTR-136-vol-1. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 121-154.
- Montalvo, A.M.; McMillan, P.A.; Allen, E.B. 2002. The relative importance of seeding method, soil ripping, and soil variables on seeding success. *Restoration Ecology*. 10: 52-67.
- Morecroft, M.D.; Masters, G.J.; Brown, V.K. [and others]. 2004. Changing precipitation patterns alter plant community dynamics and succession in an ex-arable grassland. *Functional Ecology*. 18: 648-655.
- Morgan, J.A.; Derner, J. D.; Milchunas, D. G.; Pendall, E. 2008. Management implications of global change for Great Plains Rangelands. *Rangelands*. 30(3): 18-22.
- Moritz, M.A.; Parisien, M.-A.; Batllori, E. [and others]. 2012. Climate change and disruptions to global fire activity. *Ecosphere*. 3(6): Article 49. <http://dx.doi.org/10.1890/ES11-00345.1>. [Published online: June 12, 2012].
- Morrison, R.G.; Lownds, N.K.; Sterling, T.M. 1995. Picloram uptake, translocation, and efficacy in relation to water status of Russian knapweed (*Acroptilon repens*). *Weed Science*. 43: 34-39.
- Mukerji, M.K.; Gage, S.H. 1978. A model for estimating hatch and mortality of grasshopper egg populations based on soil moisture and heat. *Annals of the Entomological Society of America*. 71: 183-190.
- Mukherjee, J.R.; Jones, T.A.; Adler, P.B.; Monaco, T.A. 2011. Drought tolerance in two perennial bunchgrasses used for restoration in the Intermountain West, USA. *Plant Ecology*. 212: 461-470.
- Munson, S.M. 2013. Plant responses, climate pivot points, and trade-offs in water-limited ecosystems. *Ecosphere*. 4(9): Article 109. <http://dx.doi.org/10.1890/ES13-00132.1>. [Published online: September 23, 2013].
- National Wildfire Coordinating Group Fire Investigation Working Team. 2005. *Wildfire Origin & Cause Determination Handbook*. National Wildfire Coordinating Group Handbook 1. PMS 412-1. <http://www.nwcg.gov/sites/default/files/products/pms412-1.pdf>. [Date accessed: September 15, 2015].
- Naugle, D.E.; Aldridge, C.L.; Walker, B.L. [and others]. 2004. West Nile virus: pending crisis for greater sage-grouse. *Ecology Letters*. 7: 704-713.
- Nelson, D.W.; Hu, F.S. 2008. Patterns and drivers of Holocene vegetational change near the prairie-forest ecotone in Minnesota: revisiting McAndrews' transect. *New Phytologist*. 179: 449–459.
- Nyamai, P.A.; Prather, T.S.; Wallace, J.M. 2011. Evaluating restoration methods across a range of plant communities dominated by invasive annual grasses to native perennial grasses. *Invasive Plant Science and Management*. 4: 306-316.
- Office of Surface Mining (OSM). 1997. 20th anniversary of the surface mining law: a report on the protection and restoration of the Nation's land and water resources under the Surface Mining Law. <http://webharvest.gov/peth04/20041017083610/http://www.osmre.gov/annivrep.htm>. [Date accessed: May 7, 2014].
- Okin, G.S.; Murray, B.; Schlesinger, W.H. 2001. Degradation of sandy arid shrubland environments: observations, process modeling, and management implications. *Journal of Arid Environments*. 47: 123-144.
- Olson, K.C.; White, R.S.; Sindelar, B.W. 1985. Response of vegetation of the Northern Great Plains to precipitation amount and grazing intensity. *Journal of Range Management*. 38: 357-361.
- Ortega, Y.K.; Pearson, D.E.; Waller, L.P. [and others]. 2012. Population-level compensation impedes biological control of an invasive forb and indirect release of a native grass. *Ecology*. 93: 783-792.
- Orts, W.J.; Roa-Espinosa, A.; Sojka, R.E. [and others]. 2007. Use of synthetic polymers and biopolymers for soil stabilization in agricultural, construction, and military applications. *Journal of Materials in Civil Engineering*. 19: 58-66.
- Otkin, J.A.; Anderson, M.A.; Hain, C. [and others]. 2013. Examining rapid onset drought development using the thermal infrared-based evaporative stress index. *Journal of Hydrometeorology*. 14: 1057-1074.
- Passioura J.B. 1996. Drought and drought tolerance. *Plant Growth Regulation*. 20: 79-83.
- Pechanec, J.F.; Pickford, G.D.; Stewart, G. 1937. Vegetation of the upper Snake River Plains, Idaho. *Ecology*. 18: 490-505.
- Pechony, O.; Shindell, D.T. 2010. Driving forces of global wildfires over the past millennium and the forthcoming century. *Proceedings of the National Academy of Sciences*. 107: 19,167-19,170.
- Peñuelas J.; Sardans J.; Estiarte M. [and others]. 2013. Evidence of current impact of climate change on life: a walk from genes to the biosphere. *Global Change Biology*. 19: 2303-2338.
- Peters, R.L.; Darling, J.D.S. 1985. The greenhouse-effect and nature reserves. *Bioscience*. 35: 707-717.
- Pierson, F.B.; Blackburn, W.H.; Van Vactor, S.S. 2007. Hydrologic impacts of mechanical seeding treatments on sagebrush rangelands. *Rangeland Ecology & Management*. 60: 666-674.

- Pinchak, B.A.; Schuman, G.E.; Deput, E.J. 1985. Topsoil and mulch effects on plant-species and community responses of revegetated mined land. *Journal of Range Management*. 38: 262-265.
- Pinol, J.; Terradas, J.; Lloret, F. 1998. Climate warming, wildfire hazard, and wildfire occurrence in coastal eastern Spain. *Climatic Change*. 38: 345-357.
- Poirier, M.; Durand, J.L.; Volaire, F. 2012. Persistence and production of perennial grasses under water deficits and extreme temperatures: importance of intraspecific vs. interspecific variability. *Global Change Biology*. 18: 3632-3646.
- Polley, H.W.; Briske, D.D.; Morgan, J.A. [and others]. 2013. Climate change and North American rangelands: trends, projections, and implications. *Rangeland Ecology & Management*. 66: 493-511.
- Porensky, L.M.; Leger, E.A.; Davison, J. [and others]. 2014. Arid old-field restoration: Native perennial grasses suppress weeds and erosion, but also suppress native shrubs. *Agriculture Ecosystems & Environment*. 184: 135-144.
- Prose, B.L. 1987. Habitat suitability index models: plains sharp-tailed grouse. U.S. Fish Wildlife Service Biological Report. *Biological Report 82(10.142)*. 31 p.
- Ralphs, M.H.; Busby, F.E. 1979. Prescribed burning—vegetative change, forage production, cost, and returns on 6 demonstration burns in Utah. *Journal of Range Management*. 32: 267-270.
- Ramobo J.L.; Faeth, S.H. 1999. Effect of vertebrate grazing on plant and insect community structure. *Conservation Biology*. 13: 1047-105.
- Ratzlaff, T.D.; Anderson, J.E. 1995. Vegetal recovery following wildfire in seeded and unseeded sagebrush steppe. *Journal of Range Management*. 48: 386-391.
- Reich, P.B.; Wright, I.J.; Cavender-Bares, I. [and others]. 2003. The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences*. 164: S143-S164.
- Reeves, M.; Baggett, L.S. 2014. A remote sensing protocol for identifying rangelands with degraded productive capacity. *Ecological Indicators*. 43: 172-182.
- Reeves, M.C.; Mitchell, J.E. 2011. Extent of coterminous U.S. rangelands: quantifying implications of differing agency perspectives. *Rangeland Ecology and Management*. 64: 1-12.
- Reynolds, J.F.; Kemp, P.R.; Tenhunen, J.D. 2000. Effects of long-term rainfall variability on evapotranspiration and soil water distribution in the Chihuahuan Desert: a modeling analysis. *Plant Ecology*. 150: 145-159.
- Richards, R.T.; Chambers, J.C.; Ross, C. 1998. Use of native plants on Federal lands: policy and practice. *Journal of Range Management*. 51: 625-632.
- Richardson, P.J.; Horrocks, J.; Larson, D.W. 2010. Drought resistance increases with species richness in restored populations and communities. *Basic and Applied Ecology*. 11: 204-215.
- Riebsame, W.E.; Changnon, S.A., Jr.; Karl, T.R. 1991. Drought and natural resources management in the United States: impacts and implications of the 1987-89 drought. Boulder, CO: Westview Press. 174 p.
- Robichaud, P.R.; Pierson, F.B.; Brown, R.K.; Wagenbrenner, J.W. 2008. Measuring effectiveness of three postfire hillslope erosion barrier treatments, western Montana, USA. *Hydrological Processes*. 22: 159-170.
- Robichaud, P.R.; Jordan, P.; Lewis, S.A. [and others]. 2013a. Evaluating the effectiveness of wood shred and agricultural straw mulches as a treatment to reduce post-wildfire hillslope erosion in southern British Columbia, Canada. *Geomorphology*. 197: 21-33.
- Robichaud, P.R.; Lewis, S.A.; Wagenbrenner, J.W. [and others]. 2013b. Post-fire mulching for runoff and erosion mitigation Part I: effectiveness at reducing hillslope erosion rates. *Catena*. 105: 75-92.
- Roche, A.R.; Bovey, R.W.; Senseman, S.A. 2002. Water stress and triclopyr on clopyralid efficacy in honey mesquite. *Journal of Range Management*. 55: 266-269.
- Romme, W.H.; Allen, C.D.; Bailey, J.D. [and others]. 2009. Historical and modern disturbance regimes, stand structures, and landscape dynamics in piñon-juniper vegetation of the Western United States. *Rangeland Ecology & Management*. 62: 203-222.
- Rosentreter, R.; Belnap, J. 2003. Biological soil crusts of North America. In: Belnap, J.; Lange, O.L., eds. *Biological soil crusts: structure, function, and management*. Berlin: Springer: 31-50.
- Rotenberry, J.T.; Wiens, J.A. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. *Ecology* 61: 1228-1250.
- Roundy, B.A.; Heydari, H.; Watson, C. [and others]. 2001. Summer establishment of Sonoran Desert species for revegetation of abandoned farmland using line source sprinkler irrigation. *Arid Land Research and Management*. 15: 23-39.
- Roundy, B.A.; Winkel, V.K.; Khalifa, H.; Matthias, A.D. 1992. Soil-water availability and temperature dynamics after one-time heavy cattle trampling and land imprinting. *Arid Soil Research and Rehabilitation*. 6: 53-69.
- Rowe, H.I. 2010. Tricks of the trade: techniques and opinions from 38 experts in tallgrass prairie restoration. *Restoration Ecology*. 18: 253-262.
- Rumble, M.A.; Anderson, S.H. 1997. Variation in selection of microhabitats by Merriam's turkey brood hens. *Prairie Naturalist*. 28: 175-187.
- Rumble, M.A.; Gobeille, J.E. 1998. Bird community relationships to succession in green ash (*Fraxinus pennsylvanica*) woodlands. *American Midland Naturalist*. 140: 372-381.
- Rumble, M.A.; Gobeille, J.E. 2001. Small mammals in successional prairie woodlands of the northern Great Plains. Res. Pap. RMRS-RP-28. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 9 p.
- Rumble, M.A.; Gobeille, J.E. 2004. Avian use of successional cottonwood (*Populus deltoides*) woodlands along the middle Missouri River. *American Midland Naturalist*. 152: 165-177.
- Rundel, P.W.; Gibson, A.C. 1996. Adaptations of Mojave Desert plants, Chapter 3. In: *ecological communities and processes in a Mojave Desert ecosystem: Rock Valley, Nevada*. Cambridge, UK: Cambridge University Press: 55-83.
- Runia, T.J. 2013. Pheasant brood survey report—2013. South Dakota Department of Game Fish and Parks, Pierre, SD. <http://www.gfp.sd.gov/hunting/docs/pheasant-broodcount-report.pdf>. [Date accessed: November 2, 2015].
- Runyon, J.B.; Butler, J.L.; Friggens, M.M. [and others]. 2012. Invasive species and climate change (Chapter 7). In: Finch, D.M., ed. *Climate change in grasslands, shrublands, and deserts of the interior American West: a review and needs assessment*. Gen. Tech. Rep. RMRS-GTR-285. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 97-115.

- St. Clair, J.B.; Kilkenny, F.F.; Johnson, R.C. [and others]. 2013. Genetic variation in adaptive traits and seed transfer zones for *Pseudoroegneria spicata* (bluebunch wheatgrass) in the Northwestern United States. *Evolutionary Applications*. 6: 933-948.
- St. Clair, J.B.; Mandel, N.L.; Vance-Borland K.W. 2005. Geneecology of Douglas fir in western Oregon and Washington. *Annals of Botany*. 96: 1199-1214.
- Sala, O.E., Lauenroth, W.K. 1982. Small rainfall events: an ecological role in semiarid regions. *Oecologia*. 53: 301-304.
- Sala, O.E.; Parton, W.J.; Joyce, L.A.; Lauenroth, W.K. 1988. Primary production of the central grassland region of the United States. *Ecology*. 69: 40-45.
- Scheffer, M.; Carpenter, S.; Foley, J.A. [and others]. 2001. Catastrophic shifts in ecosystems. *Nature*. 413: 591-596.
- Schlesinger, W.H.; Ward, T.J.; Anderson J. 2000. Nutrient losses in runoff from grassland and shrubland habitats in southern New Mexico: II. Field plots. *Biogeochemistry*. 49: 69-86.
- Schmidt, C.P.; Belford, R.K. 1994. Increasing the depth of soil disturbance increases yields of direct drilled wheat on the sandplain soils of Western Australia. *Australian Journal of Experimental Agriculture*. 34: 777-781.
- Schreiber, L.A. 2013. Greater sage-grouse nest site selection, brood rearing, site selection and chick survival in Wyoming. Columbia, MO: University of Missouri. [Number of pages unknown]. M.S. thesis.
- Schuman, G.E.; Depuit, E.J.; Smith, J.A.; King, L.A. 1985. Reclamation of bentonite mined lands in the northern Great Plains. *Environmental Geochemistry and Health*. 7: 42-47.
- Schwinning, S.; Davis, K.; Richardson, L.; Ehleringer, J.R. 2002. Deuterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado Plateau. *Oecologia*. 130: 345-355.
- Schwinning, S.; Ehleringer, J.R. 2001. Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. *Journal of Ecology*. 89: 464-480.
- Schwinning, S.; Starr, B.I.; Ehleringer, J.R. 2005. Summer and winter drought in a cold desert ecosystem (Colorado Plateau) part I: effects on soil water and plant water uptake. *Journal of Arid Environments*. 60: 547-566.
- Seabloom, E.W. 2007. Compensation and the stability of restored grassland communities. *Ecological Applications*. 17: 1876-1885.
- Seager, R.; Mingfang, T.; Held, I. [and others]. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science*. 316: 1181-1184.
- Society for Ecological Restoration (SER). 2004. SER International Primer on Ecological Restoration, Version 2. <http://www.ser.org/resources/resources-detail-view/ser-international-primer-on-ecological-restoration>. [Date accessed: May 5, 2013].
- Shaw, J.D.; Steed, B.E.; DeBlander, L.T. 2005. Forest Inventory and Analysis (FIA) annual inventory answers the question: what is happening to pinyon-juniper woodlands? *Journal of Forestry*. 103: 280-285.
- Sheley, R.L.; James, J.J.; Rinella, M.J. [and others]. 2011. Invasive plant management on anticipated conservation benefits: a scientific assessment. In: Briske, D.D., ed. *Conservation benefits of rangeland practices: assessment, recommendations, and knowledge gaps*. Lawrence, KS: U.S. Department of Agriculture, Natural Resources Conservation Service. Allen Press: 291-336.
- Shinneman, D.J.; Baker, W.L. 2009. Historical fire and multidecadal drought as context for pinyon-juniper woodland restoration in western Colorado. *Ecological Applications*. 19(5): 1231-1245.
- Shishkoff, N.; Bruckart, W.L. 1996. Water stress and damage caused by *Puccinia jaceae* on two Centaurea species. *Biological Control*. 6: 57-63.
- Stabnikov, V.; Chu, J.; Myo, A.N.; Ivanov, V. 2013. Immobilization of sand dust and associated pollutants using bioaggregation. *Water Air and Soil Pollution*. 224(9): 1-9.
- Stafford, J.M.; Wendler, G.; Curtis, J. 2000. Temperature and precipitation of Alaska: 50 year trend analysis. *Theoretical and Applied Climatology*. 67: 33-44.
- Stahle, D.W.; Cook, E.R.; Cleaveland, M.K. [and others]. 2000. Tree-ring data document 16th century megadrought over North America. *Eos Transactions American Geophysical Union*. 81(12): 121-125. doi:10.1029/00EO00076. [Published online: June 3, 2011].
- Stambaugh, M.C.; Guyette, R.P.; McMurry E.R. [and others]. 2011. Drought duration and frequency in the U.S. corn belt during the last millennium (AD 992-2004). *Agricultural and Forest Meteorology*. 151: 154-162.
- Stradling, D.A.; Thygerson, T.; Walker, J.A. [and others]. 2002. Cryptogamic crust metabolism in response to temperature, water vapor, and liquid water. *Thermochimica Acta*. 394: 219-225.
- Streett, D.A.; McGuire, M.R. 1990. Pathogenic diseases of grasshoppers. In: Chapman, R.F.; Joern, A., eds. *Biology of grasshoppers*. New York: John Wiley: 483-516.
- Swemmer, A.J.; Knapp, A.K.; Snyman, H.A. 2007. Intra-seasonal precipitation patterns and above-ground productivity in three perennial grasslands. *Journal of Ecology*. 95: 780-788.
- Swetnam, T.W.; Betancourt, J.L. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *Journal of Climate*. 11: 3128-3147.
- Teague, W.R.; Duke, S.E.; Waggoner, J.A. [and others]. 2008. Rangeland vegetation and soil response to summer patch fires under continuous grazing. *Arid Land Research and Management*. 22: 228-241.
- Teague, W.R.; Dowhower, S.L.; Ansley, R.J. [and others]. 2010. Integrated grazing and prescribed fire restoration strategies in a mesquite savanna: I. vegetation responses. *Rangeland Ecology & Management*. 63: 275-285.
- Thomson, A.M.; Crowe, K.A.; Parker, W.H. 2010. Optimal white spruce breeding zones for Ontario under current and future climates. *Canadian Journal of Forest Research*. 40: 1576-1587.
- Thurow, T.L.; Taylor, C.A., Jr. 1999. Viewpoint: the role of drought in range management. *Journal of Range Management*. 52: 413-419.
- Thrupp A.C. 1927. Scientific seed collection. *Forestry Chronicles*. 3: 8.
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology*. 77: 350-363.
- Tilman, D.; Downing, J.A. 1994. Biodiversity and stability in grasslands. *Nature*. 367: 363-365.
- Tilman, D.; El Haddi, A. 1992. Drought and biodiversity in grasslands. *Oecologia*. 89: 257-264.
- Twidwell, D.; Rogers, W.E.; Fuhlendorf, S.D. [and others]. 2013. The rising Great Plains fire campaign: citizens' response to woody plant encroachment. *Frontiers in Ecology and the Environment*. 11: e64-e71.

- Uresk, D.W. 1987. Relation of black-tailed prairie dogs and control programs to vegetation, livestock, and wildlife. In: Capinera, J.L., ed. Integrated pest management on rangeland: a shortgrass prairie perspective. Boulder, CO: Westview Press: 312-323.
- Uresk, D.W. 1990. Using multivariate techniques to quantitatively estimate ecological stages in a mixed grass prairie. *Journal of Range Management*. 43: 282-285.
- Uresk, D.W.; Boldt, C.E. 1986. Effect of cultural treatments on regeneration of native woodlands on the northern Great Plains. *Prairie Naturalist*. 18: 193-202.
- Vallentine, J.F. 1989. Range development and improvements, Third Edition. San Diego, CA: Academic Press. 524 p.
- Vicente-Serrano, S.M.; Gouveia, C.; Camarero, J.J. [and others]. 2013. Response of vegetation to drought time-scales across global land biomes. *Proceedings of the National Academy of Sciences*. 110: 52-57.
- Volaire, F.; Barkaoui, K.; Norton, M. 2014. Designing resilient and sustainable grasslands for a drier future: adaptive strategies, functional traits and biotic interactions. *European Journal of Agronomy*. 52: 81-89.
- Vors, L.S.; Boyce, M.S. 2009. Global declines of caribou and reindeer. *Global Change Biology*. 15: 2626-2633.
- Walker, D.A.; Raynolds, M.K.; Daniëls, F.J. [and others]. 2005. The circumpolar Arctic vegetation map. *Journal of Vegetation Science*. 16(3): 267-282.
- Walter, J.; Nagy, L.; Hein, R. [and others]. 2011. Do plants remember drought? Hints toward a drought-memory in grasses. *Environmental and Experimental Botany*. 71: 34-40.
- Wang, S.Y.; Higgs, L.; Gillies, R.R.; Yoon, J.H. 2014. Probable causes of the abnormal ridge accompanying the 2013-2014 California drought: ENSO precursor and anthropogenic warming footprint. *Geophysical Research Letters*. 41(9): 3220-3226.
- Wangler, M.J.; Minnich, R.A. 1996. Fire and succession in pinyon-juniper woodlands of the San Bernardino Mountains, California. *Madroño*. 43: 493-514.
- Warrick, R.A. 1980. Drought in the Great Plains: a case study of research on climate and society in the USA. In: Ausubel, J.; Biswas, A.K., eds. Climatic constraints and human activities, IIASA Proceedings Series, Vol. 10. New York: Pergamon Press: 93-123.
- Watson, M.C.; Roundy, B.A.; Smith, S.E. [and others]. 1995. Water requirements for establishing native *Atriplex* species during summer in southern Arizona. In: Roundy, B.A.; McArthur, E.D.; Haley, J.S. Mann, D.K., eds. Proceedings: Wildland Shrub and Arid Land Restoration Symposium. Gen. Tech. Rep. INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 119-125.
- Weakley, H.E. 1965. Recurrence of drought in the Great Plains during the last 700 years. *Agricultural Engineering*. 46: 85.
- Weaver, J.E. 1954. North American prairie. Lincoln, NE: Johnson Publishing Company. 357 p.
- Weaver, J.E.; Albertson, F.W. 1936. Effects on the Great Drought on the prairies of Iowa, Nebraska, and Kansas. *Ecology*. 17: 567-639.
- Weaver, J.E.; Albertson, F.W. 1939. Major changes in grassland as a result of continued drought. *Botanical Gazette*. 100: 576-591.
- Weaver, J.E.; Albertson, F.W. 1940. Deterioration of midwestern ranges. *Ecology*. 21: 216-236.
- Weaver, J.E.; Albertson, F.W. 1943. Resurvey of grasses, forbs, and underground plant parts at the end of the Great Drought. *Ecological Monographs*. 13: 63-117.
- Weaver, J.E.; Stoddart, L.A.; Noll, W. 1935. Response of the prairie to the great drought of 1934. *Ecology*. 16: 612-629.
- Weiss, J.L.; Castro, C.L.; Overpeck, J.T. 2009. Distinguishing pronounced droughts in the Southwestern United States: seasonality and effects of warmer temperatures. *Journal of Climate*. 22(22): 5918-5932.
- Weltzin, J.F.; Loik, M.E.; Schwinning, S. [and others]. 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience*. 53: 941-952.
- Weninger, E.J.; Inouye, R.S. 2008. Insect community response to plant diversity and productivity in a sagebrush-steppe ecosystem. *Journal of Arid Environments*. 72(1): 24-33.
- West, N.E. 1983. Western intermountain sagebrush steppe semi-deserts. In: West, N.E., ed. *Ecosystems of the World*, 5th ed. Amsterdam, The Netherlands: Elsevier: 351-374.
- West, N.E. 1988. Intermountain deserts, shrub steppes, and woodlands. In: Barbour, M.G.; Billings, W.D., eds. *North American terrestrial vegetation*. Cambridge, England, United Kingdom: Cambridge University Press: 209-230.
- West, N.E.; Provenza, F.D.; Johnson, P.S.; Owens, M.K. 1984. Vegetation change after 13 years of livestock grazing exclusion on sagebrush semidesert in west central Utah. *Journal of Range Management*. 37: 262-264.
- West, N.E. 1999. Distribution, composition, and classification of current juniper-pinyon woodland and savannas across the western North America. In: Monsen, S.B.; Stevens, R., eds. *Proceedings: ecology and management of pinyon-juniper communities within the interior West*. Ogden, UT: U.S. Department of Agriculture, Forest Service Proceedings RMRS-P-9. Rocky Mountain Research Station: 20-23.
- Westerling, A.L.; Hidalgo, H.G.; Cayan, D.R.; Swetnam, T.W. 2006. Warming and earlier spring increases western U.S. forest wildfire activity. *Science*. 313(5789): 940-943. doi:10.1126/science.1128834. [Published online: July 6, 2006].
- Wiens, J.A. 1974. Climatic instability and the ecological saturation of bird communities in North American grasslands. *Condor*. 76: 385-400.
- Wiens, J.A.; Rotenberry, J.T. 1985. Response of breeding passerine birds to rangeland alteration in a North American shrubsteppe locality. *Journal of Applied Ecology*. 22: 655-668.
- Whisenant, S.G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. *Gen. Tech. Rep. INT-276*. In: McArthur, E.D.; Romney, E.M.; Smith, S.D.; Tueller, P.T., eds. *Symposium on cheatgrass invasion, shrub die-off and other aspects of shrub biology and management*. Ogden, UT: U.S. Department of Agriculture, Forest Service: 4-10.
- Whisenant, S.G.; Scifres, C.J.; Ueckert, D.N. 1984. Soil-water and temperature response to prescribed burning. *Great Basin Naturalist*. 44: 558-571.
- White, C.S.; Loftin, S.R. 2000. Response of 2 semiarid grasslands to cool-season prescribed fire. *Journal of Range Management*. 53: 52-61.
- White, T.C.R. 1976. Weather, food and plagues of locusts. *Oecologia*. 22: 119-134.
- Wilcox, B.P.; Thurow, T.L. 2006. Emerging issues in rangeland ecohydrology: vegetation change and the water cycle. *Rangeland Ecology & Management*. 59: 220-224.
- Williams, J.D.; Dobrowolski, J.P.; West, N.E.; Gillette, D.A. 1995. Microphytic crust influence on wind erosion. *Transactions of the ASAE*. 38: 131-137.

- Williams M.I.; Dumroese R.K. 2013.** Preparing for climate change: forestry and assisted migration. *Journal of Forestry*. 111: 287-297.
- Wilson, S.D.; Gerry, A.K. 1995.** Strategies for mixed-grass prairie restoration: Herbicide, tilling, and nitrogen manipulation. *Restoration Ecology*. 3: 290-298.
- Winkel, V.K.; Medrano, J.C.; Stanley, C.; Walo, M.D. 1995.** Effects of gravel mulch on emergence of galleta grass seedlings. Gen. Tech. Rep. INT-GTR-315. In: Roundy, B.A.; McArthur, E.D.; Haley, J.S.; Mann, D.K., eds. *Proceedings: Wildland Shrub and Arid Land Restoration Symposium*. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 130-134.
- Woodhouse, C.A.; Overpeck, J.T. 1998.** 2000 years of drought variability in the Central United States. *Bulletin of the American Meteorological Society*. 79: 2693-2714. .
- Worster, D. 1982.** *Dust bowl: the southern plains in the 1930s*. New York: Oxford University Press. 304 p.
- Yachi, S.; Loreau, M. 1999.** Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences USA*. 96: 1463-1468.
- Ying, C.C.; Yanchuk, A.D. 2006.** The development of British Columbia's tree seed transfer guidelines: purpose, concept, methodology, and implementation. *Forest Ecology and Management*. 227: 1-13.
- Young, K.R.; Roundy, B.A.; Eggett, D.L. 2013.** Tree reduction and debris from mastication of Utah juniper alter the soil climate in sagebrush steppe. *Forest Ecology and Management*. 310: 777-785.
- Zargar, A.; Sadiq, R.; Naser, B.; Khan, F.I. 2011.** A review of drought indices. *Environmental Reviews*. 19: 333-349.

Detecting and Monitoring Large-Scale Drought Effects on Forests: Toward an Integrated Approach

Steven P. Norman

Frank H. Koch

William W. Hargrove

S.P. Norman is a Research Ecologist, U.S. Department of Agriculture, Forest Service, Southern Research Station (SRS), Eastern Forest Environmental Threat Assessment Center (EFETAC), Asheville, NC 28801.

F.H. Koch is a Research Ecologist, U.S. Department of Agriculture, Forest Service, Southern Research Station (SRS), Eastern Forest Environmental Threat Assessment Center (EFETAC), Asheville, NC 28801.

W.W. Hargrove is a Research Ecologist, U.S. Department of Agriculture, Forest Service, Southern Research Station (SRS), Eastern Forest Environmental Threat Assessment Center (EFETAC), Asheville, NC 28801.

Introduction

Although drought is recognized as an important and overarching driver of ecosystem change, its occurrence and effects have been difficult to describe over large geographic areas (Hogg and others 2008, Panu and Sharma 2002). In forests, drought contributes to tree stress and mortality through the direct impacts of reduced moisture and high temperatures (Anderegg and others 2013, Wang and others 2012), and through indirect pathways such as increased disturbance from insects or fire (Martínez-Vilalta and others 2012, Mattson and Haack 1987, Meyn and others 2007, Raffa and others 2008, Schowalter and others 1986, Trouet and others 2010). Detecting drought effects on plant species demands detailed knowledge of where those species occur, but with few exceptions, only coarse vegetation maps are available for broad areas (Allen and others 2010). Long-term monitoring is helpful, but longer term assessments struggle with causal attribution. Numerous meteorologically based drought measures have been constructed to depict moisture deficits in agricultural contexts, but they may not accurately portray the effects of those deficits on forests, grasslands, or other natural vegetation types, where the constituent species may have diverse drought responses (Mishra and Singh 2010, Vicente-Serrano and others 2012). Furthermore, in order to examine those responses, meteorologically based approaches must make an inference about the impact of a given level of moisture deficit on the plants. Remote sensing-based measures are also available that exploit known differences in reflected radiation among stressed and unstressed vegetation (Peters and others 1991, Peters and others 2002, Zhang and others 2013), yet short-term stress may not be a precursor for ecological impacts that could take multiple seasons or even years to materialize.

Measures available from meteorological station data can be used to infer likely moisture and temperature impacts on trees or other vegetation (Vicente-Serrano and others 2012). When summarized for different time periods deemed relevant (e.g., with respect to tree mortality, multiple consecutive years of severe drought) (Guarín and Taylor 2005, Millar and others 2007), they can better approximate impacts like vegetation loss or cover change. Further assessments can come from direct measurements from remotely sensed or plot data (Ji and Peters 2003, Vicente-Serrano and others 2012, Vicente-Serrano and others 2013, Wullschlegel and Hanson 2006, Zhang and others 2013). With

advances in near-real-time meteorological and remotely sensed response technology, it is now possible to generate reasonable coarse-scale forecasts of certain drought effects, such as declines in crop yields (Arshad and others 2013, Hao and others 2014, Luo and Wood 2007). However, finer-scale translation of such expectations for forested areas remains challenging due to a lack of species- and community-specific long-term impact assessments (Carnicer and others 2011, Martínez-Vilalta and others 2012, Michaelian and others 2011). This chapter reviews the status and role of data mining approaches using diverse ancillary data sets that can be brought to bear on monitoring and assessment, and clarifies ways in which they can be leveraged to reduce the uncertainties associated with drought impacts in forested ecosystems.

Fundamental Challenges

Drought can have a range of species- and community-level consequences for forests, many of which are poorly understood (Hanson and Weltzin 2000, Mueller and others 2005). The drought responses that can be systematically monitored at regional scales are only a detectable subset of all those that likely occur or matter, and this introduces uncertainty into monitoring and assessment. Breadth and efficiency are often the practical tradeoffs of having depth of understanding. With such uncertainties, our expectations for broad-scale monitoring are somewhat different from what can be obtained through local field-based observations.

Broad-scale monitoring is intended to describe the scope and relative severity of coarse drought impacts, rather than to quantify effects directly with precision that often depend on local knowledge of topography, weather, or species responses. The coarse-scale expectations of such efforts justify application of relative drought indices instead of actual biophysical measurements such as soil moisture, temperature, or precipitation. In turn, broad-scale drought monitoring produces only relative likelihoods, but such insights may be the most relevant for a particular set of management questions.

To progress as an applied science, broad-scale drought monitoring must confront four fundamental challenges that are described below. Meeting these challenges will improve our ability to comprehend, predict, and address the risks posed to forests by drought.

Challenge 1: Measuring drought in ways that matter for different forests—Our conventional perceptions of drought and its effects have primarily

developed from how drought impacts agricultural production and water supplies (Wilhite and Glantz 1985). Yet the conventional meteorological measures of drought that estimate effects to field or stream may be less than optimal for characterizing drought impacts to forests.

When a broad-scale drought response is detected for forests, its implications are far more complex than mono-specific crop yield reduction or lowered water levels in reservoirs, where there is a clearer expectation of loss. Forests and their constituent species are highly variable in their tolerance of and response to drought, such that no single metric or indicator is likely to capture expected impacts (Martínez-Vilalta and others 2012, Mishra and Singh 2010, Svoboda and others 2004). Unlike annual field crops, most perennials within forest communities are tolerant of one or more years of moderate drought stress, and so scientists contend that multiyear measures of drought are needed (Allen and others 2010, Mishra and Singh 2010, Niinemets 2010, Panu and Sharma 2002, Wilhite and others 2007).

Interpretations of drought responses are especially difficult in areas of high compositional or structural complexity, as the sensitivity of deciduous and evergreen trees, shrubs, and grasses are generally not equivalent (Hanson and Weltzin 2000). Interpretation of drought effects becomes more challenging in areas that have been recently disturbed as these landscapes have vegetation in various stages of successional recovery with dominant species that may differ in their response to drought from one decade to the next (Sousa 1984). Similarly, it can be difficult to make sense of broad-scale drought responses in highly fragmented landscapes where forest, field, and developed areas occur in close proximity (Ewers and Didham 2006, Laurance 2004). We need clearer drought response indicators for these types of landscapes.

The ramifications of drought for species depend on when the drought occurs with respect to species' seasonal phenologies (Anderegg and others 2013). In the Eastern United States, spring and summer growth often responds to winter, spring, and summer temperature and precipitation, but summer and fall drought can shorten the growing season. A number of western tree species depend heavily on winter rains or snowpack to provide a pool of available soil moisture for the subsequent growing season, which is effectively shortened when this pool is reduced (Hanson and Weltzin 2000). The relative importance of heat and moisture stress may differ (Bréda and others 2006,

Mueller and others 2005, Orwig and Abrams 1997) due to fundamental regional differences in the evolutionary climatic environment. Because of these inherent climatic differences, regional patterns of species adaptations affect how meteorological drought is experienced, and how effects are shown (fig. 9.1).

Challenge 2: Establishing context from historical data—In an operational sense, drought is more than heat and dryness (chapter 2). It involves some measure of departure from baseline conditions for a given location and specified time period. Both spatial and temporal aspects of this definition are critical for accurate recognition and prediction of broad-scale drought effects. Extended periods of seasonal and interannual dryness are a normal part of many forest environments, particularly across much of the Western United States (fig. 9.1). Multiyear or decadal averages, as reflected in the term “normal,” can mask this climate variability, yet depending on the frequency and intensity of droughts that occur, both species and community attributes may be adapted to climatic extremes as much as, if not more than, any measure of central tendency.

Historical climate data provide both meteorological and biologically relevant context. Long-term paleoclimatological insights help contextualize the duration and intensity of recent drought events (chapter 2), but the relevance of historical drought patterns for contemporary forests and values can be difficult to ascertain where forest structure or composition have changed. From a meteorological perspective, the length of climatically meaningful baselines has been long debated (Lamb and Changon 1981, Livezey and others 2007, Wilks 2013), yet determining the period that is appropriate for understanding forest change may be far more difficult.

Commonly used 30-year baseline conditions may not be representative of the climate that existed when the longest lived trees established or developed. Tree species that produce many vegetative sprouts (as opposed to slower growing seedlings) after disturbance may subsequently have so many saplings that they retain demographic dominance in a site for centuries, regardless of the age of existing stems, and sprouting trees dominate many forest landscapes (Bellingham and Sparrow 2000, Bond and Midgley 2001, Del Tredici 2001, Vesik and Westoby 2004). Moreover, the relevant climate context for old forests may be longer than for adjacent areas affected by disturbance and recent succession. For example, the timing of drought

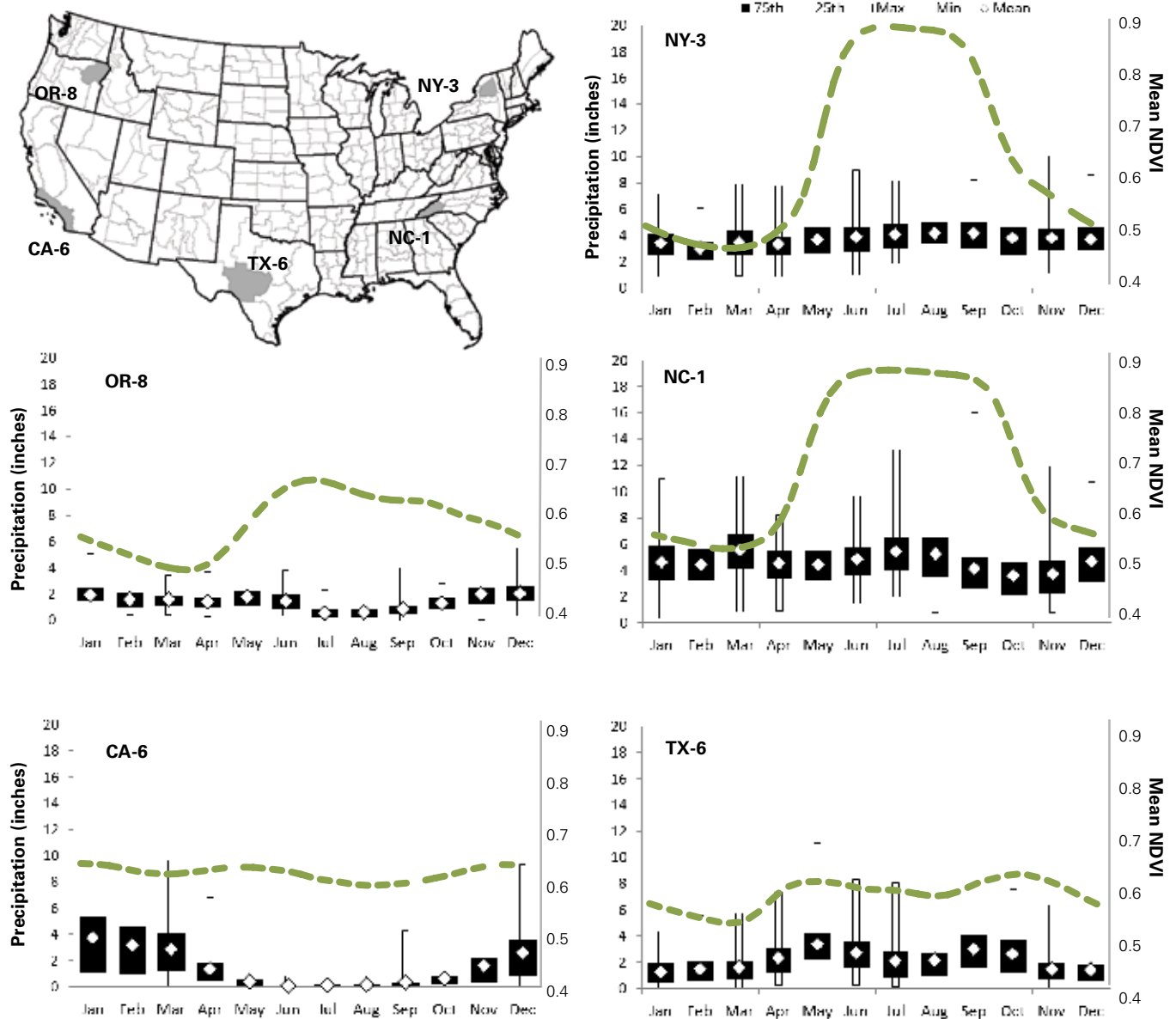


Figure 9.1—Regional differences in normal seasonal precipitation can affect how forests respond to drought. These graphs show historical variability in monthly precipitation for five National Climate Data Center (NCDC) Climate Divisions, 1895–2013, compared to the mean land surface phenology of forested Moderate Resolution Imaging Spectroradiometer (MODIS) pixels in those divisions as measured by the Normalized Difference Vegetation Index (NDVI) for the period 2000–2012. Box-whisker plots show the mean, extremes, and upper and lower quartiles of precipitation. Biweekly NDVI (green line) was derived from a National Land Cover Data (NLCD-2006) conditional filtering of majority forested *ForWarn*-MODIS data that included the following count of randomly selected cells: CA-6, n=110; NC-1, n=480; NY-3, n=474; OR-8, n=571; TX-6, n=247.

episodes during the late 20th century affected the establishment success of white pine (*Pinus strobus*) in old fields of the North-Central United States (Dovčiak and others 2005). Similarly, long-lasting cohorts of ponderosa pine (*Pinus ponderosa*) established during favorable climate windows in the Southwestern United States during the early 20th century (Savage and others 1996). Although forest changes caused by drought-associated mortality may be rapid (Mueller and others 2005, Wang and others 2012), we may need a long climatic perspective to make sense of observed changes over the lifespan of these forest dominants.

The relevance of past forest responses to drought for understanding those of the present is sometimes questionable, as the structure and composition of many forests has changed over the last century in response to logging, invasive insects, diseases and plants, fire exclusion, and livestock grazing (Norman and Taylor 2005, Nowacki and Abrams 2008). Increases in stand density and a decline in drought-tolerant species such as pines, oaks, and chestnut can make forests less resilient today than they were decades ago to drought or drought-associated disturbances such as fire (chapter 7). This potential shift in the implications of a given drought erodes the predictive capacity of efforts that rely only on meteorological data.

Trends in climate can pose serious problems for developing meaningful baselines (Wilks 2013). Such gradual transitions may reflect the progressive effects of a drying climate, and that rate of change is difficult to detect without long-term monitoring or broad-scale plot data (Woodall and others 2009). Mesophytic species may be expanding in importance from fire management, which could increase forest vulnerability if severe drought returns (Nowacki and Abrams 2008). Forests may be more vulnerable because of the increased water needs of denser stands or more mesophytic, less drought-tolerant species composition (Allen and Breshears 1998, Guarín and Taylor 2005, Savage 1997). While meteorological data provide insights into where meteorological trends are occurring (fig. 9.2), our knowledge of long-term trends in forest susceptibility is more limited.

Our primary broad-scale insights into how forests respond to drought comes from satellite observations, yet high-resolution satellite data have only been available for a third of the time that meteorological data have been collected on a wide scale. This shorter observation window limits what we can learn from historical

drought responses as shown through comparison of growing-season drought duration during the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite period with prior baseline periods (fig. 9.3). In this example, drought duration was derived from monthly National Oceanic and Atmospheric Administration (NOAA) National Climate Data Center (NCDC) Climate Division data (Guttman and Quayle 1996). Satellites that pass overhead frequently, such as Terra and Aqua that carry the MODIS sensor, can be used to identify short-term stress and longer term recovery or type conversion; however, their coarser resolution makes them less useful for monitoring species-specific stress in mixed stands over broad areas than less frequent, but higher resolution data. Derived products from satellite observations can help characterize similarities and differences among droughts, as observations coarsely quantify how forests are affected by drought and drought-associated disturbances.

Challenge 3: Capturing diverse drought effects—

As an indicator for a suite of other potential drought impacts, vegetation stress monitoring is efficient, even if it does not predict specific individual tree responses. Such efforts only capture a fraction of drought-induced effects to forests, but those aspects that can be monitored can be strong indicators of system dynamics overall. For example, morphological adaptations, such as deeper rooting, are nearly impossible to quantify from either a remote-sensing or field-based perspective, but defoliation or canopy stress can be readily monitored.

It is difficult to translate community-level observations to species- or population-level responses when the constituent species in a region vary in their susceptibility and tolerance to drought (Bigler and others 2007, Floyd and others 2009, Hanson and Weltzin 2000, McDowell and others 2008, McDowell and others 2011). Individual species drought responses can be wide-ranging, divergent, or delayed (chapter 3) (Archaux and Wolters 2006). Community-level responses include reduced productivity and altered composition or structure largely through selective mortality (chapter 4) (Archaux and Wolters 2006). Drought can also have secondary effects on the population dynamics of insects and diseases (chapter 6) (fig. 9.4), or on the occurrence, attributes, or consequences of wildfire (chapter 7), since stressed trees are often more susceptible. Drought stress induces ponderosa pine to leave stomates open at night, increasing exposure to ozone and other airborne pollutants (Grulke and others 2004). Grulke (2011) reported that drought stress increases

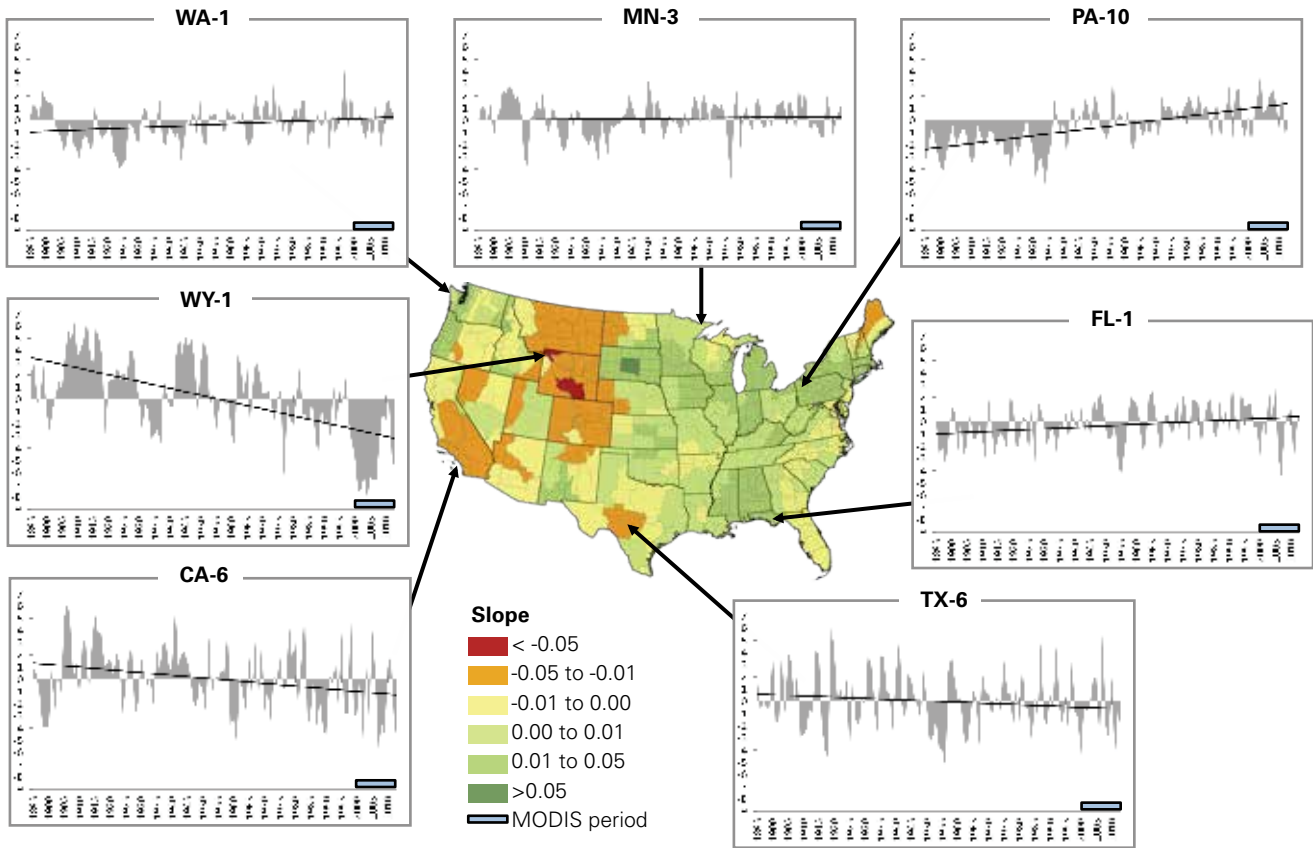


Figure 9.2—Long-term trends (black line) in the mean April–September Palmer Modified Drought Index (PMDI), 1895–2013, by National Climate Data Center (NCDC) Climate Division for the conterminous United States. Selected climate divisions are shown. The representativeness of the Moderate Resolution Imaging Spectroradiometer (MODIS) period relative to the past is suggested by the blue bar in the lower right of each inset graph.

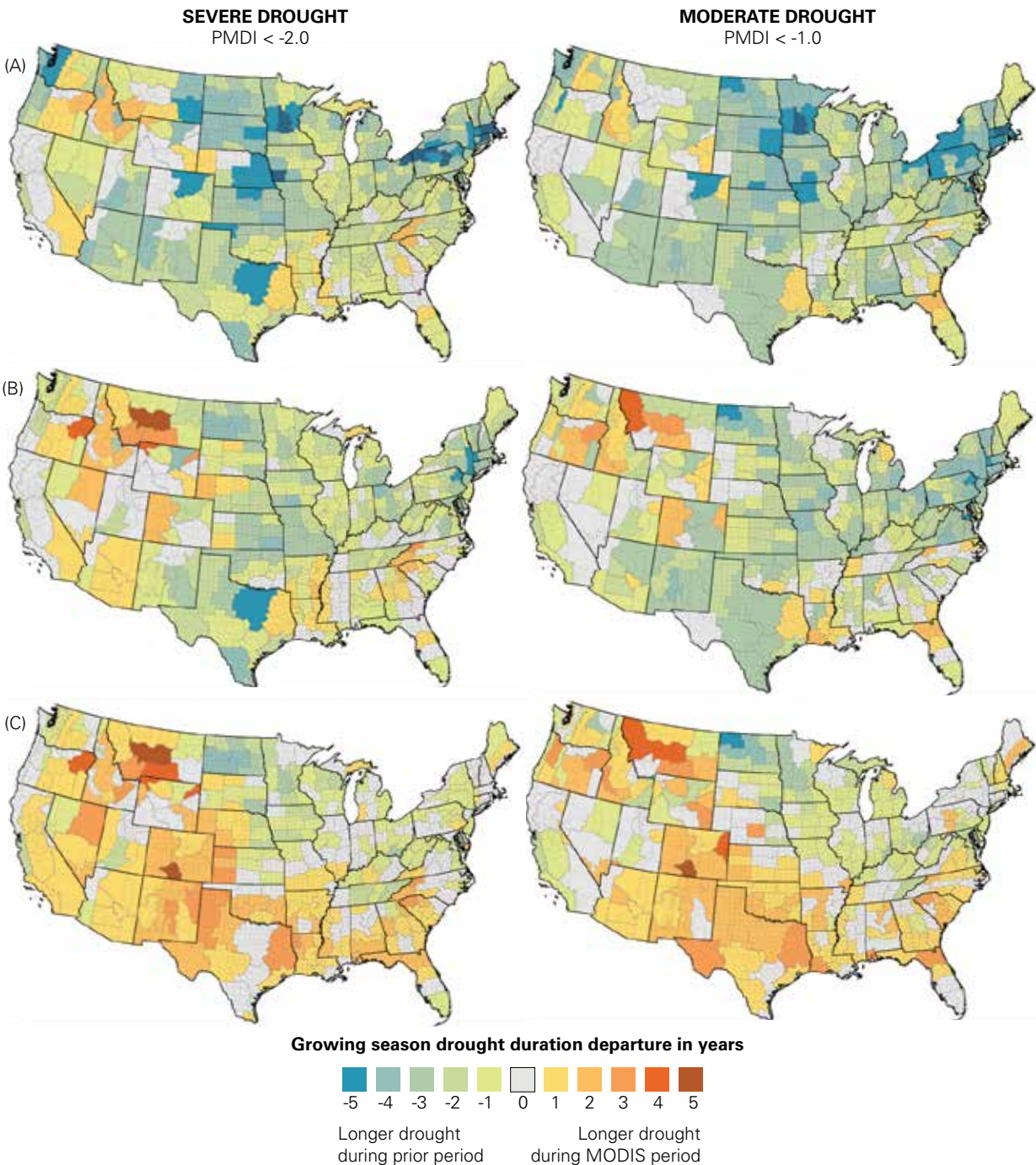


Figure 9.3—Annual departure, by National Climate Data Center (NCDC) Climate Division, of mean April–September Palmer Modified Drought Index (PMDI) drought duration for the Moderate Resolution Imaging Spectroradiometer (MODIS) period (2000–2013) compared to historical drought duration for three baseline periods: (A) 1900–1999, (B) 1950–1999, and (C) the 14 pre-MODIS years, 1986–1999. Differences at two levels of drought severity are shown: severe drought (PMDI < -2.0) and moderate (PMDI < -1.0).

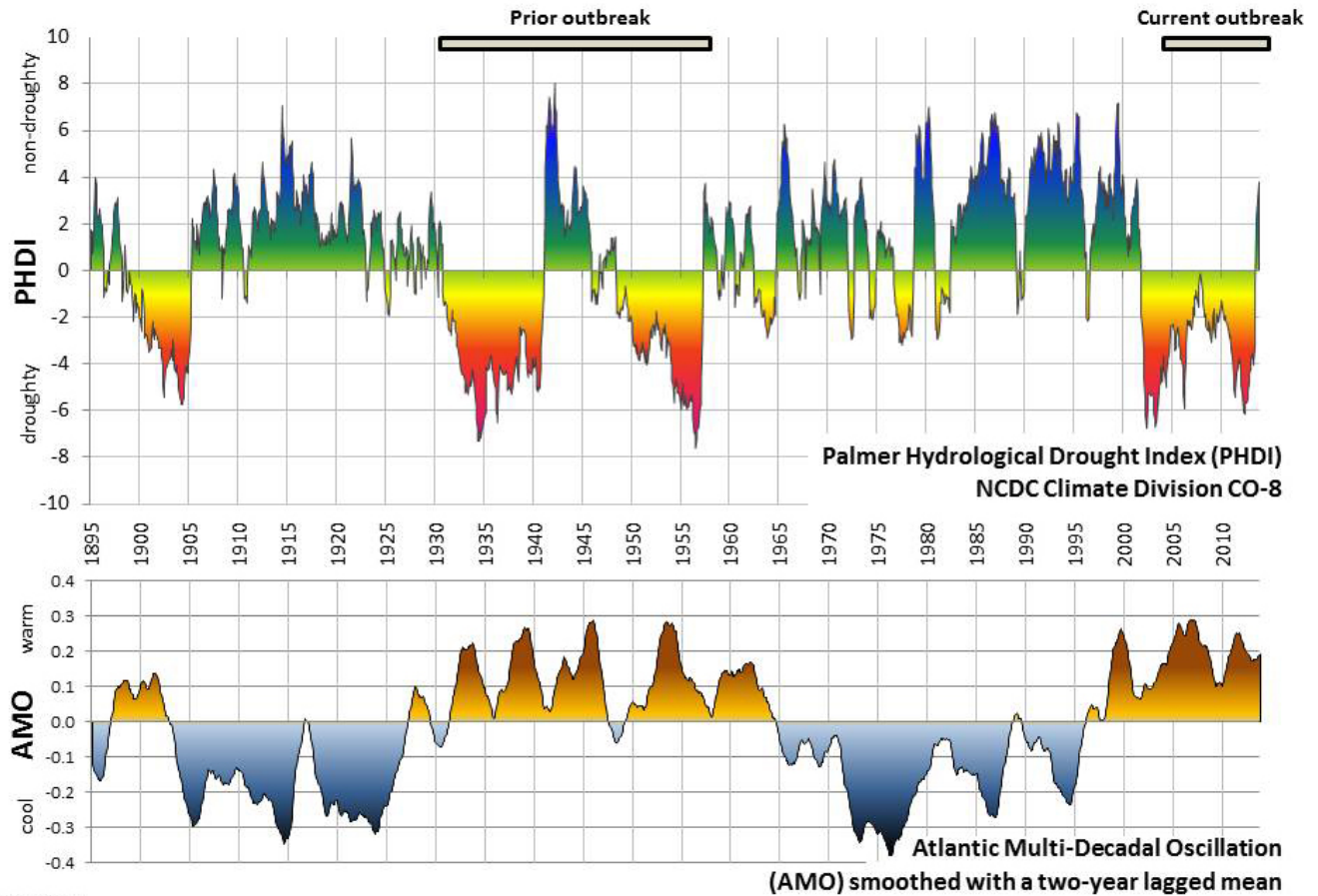


Figure 9.4—Variation in regional Palmer Hydrological Drought Index (PHDI) for northwestern Colorado and its relationship to outbreaks of the spruce beetle (*Dendroctonus rufipennis*). Regional drought is strongly influenced by hemispheric-scale variation in sea surface temperatures, particularly the Atlantic Multi-decadal Oscillation (AMO).

susceptibility to many pathogens that may be emerging with climatic change. While community-level response may not represent all impacts of concern, it provides the spatial pattern of likely effects across the landscape.

Variation in community-wide growing season stress may be the easiest drought-sensitive indicator to measure using remote sensing technologies. High-frequency observations can detect drought progression or near-real-time stress or mortality from wildfire or insects and disease (Hargrove and others 2009). From programmatic high-frequency datasets, measures of temperature and moisture-sensitive phenomena can be derived such as change in the onset of spring and fall and the duration of the growing season. These community-level measures of observed land surface phenological changes can be related to the responses of individual species and seasonal disturbances such as wildfire.

Some drought effects are difficult to recognize or track without ancillary information. The drought responses of different vegetation types are known to vary (Lobo and Maisongrande 2006, Sims and others 2014), so knowing the vegetation composition within particular remotely sensed grid map cells is critical for understanding both drought response and multiyear drought effects. Tree mortality can be delayed for years, and reduced vigor can invite second-order effects (Bigler and others 2007). This potential lag in response makes attribution more difficult without long-term datasets and modeling. Impacts from disturbance such as wildfire, insects, and diseases can be difficult to attribute to drought, since these are often a natural part of forests. With complex drivers in play, ancillary datasets can improve interpretations and predictions.

Conceptual models provide a graphical means of communicating these complex direct and indirect interactions. Figure 9.5 shows two example conceptual models for drought: a basic model of the direct relationships between drought, other drivers of forest disturbance, and their impacts (fig. 9.5A), as well as a more detailed model of the indirect relationships between drought and other landscape-level processes in the Interior West (fig. 9.5B). Within such models, contingencies can be structured as management options that can mitigate or prevent undesirable drought-associated effects. For example, in California's Yosemite National Park, where tree mortality has been associated with drought, drought susceptibility may have increased due to a fire management history

that has resulted in uncharacteristically dense stand structures that affect competition and water stress (Guarín and Taylor 2005). Thus, silvicultural methods such as mechanical thinning or fire may be viable options for improving stands and reducing the likelihood of drought-related tree mortality.

Challenge 4: Making drought-effect monitoring more applied—Broad drought-monitoring efforts capture changes to vegetation rather than impacts to individual trees. Detection of local effects is inferential due to the coarse nature of broad-scale observations. Local forest managers are usually aware when drought and drought-associated stresses are affecting their forests, yet recognizing and tracking drought effects becomes more difficult over States or regions. When large areas are affected by drought, the broad-scale need is often to identify those areas that are hardest hit and to prioritize areas for response. Such decisions can be greatly informed by relatively straightforward measures derived from systematic drought monitoring efforts.

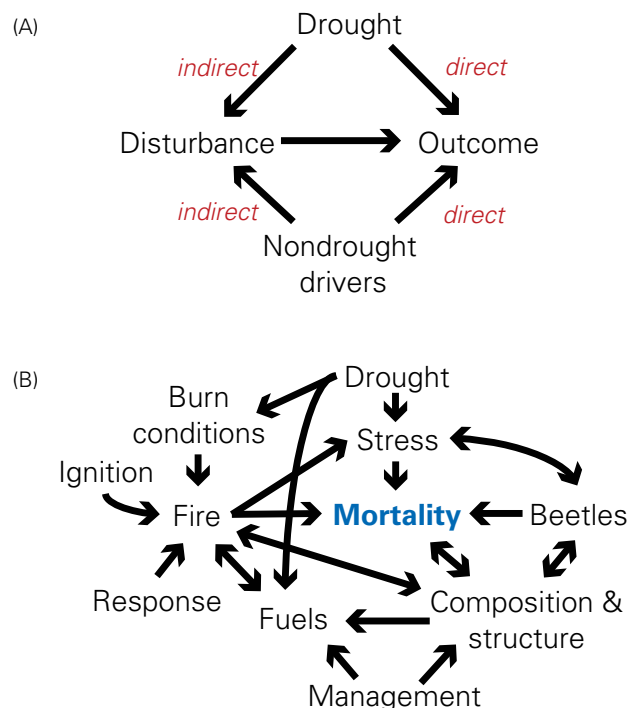


Figure 9.5—Conceptual models show how outcomes can result from direct and indirect climate effects or from unrelated nondrought drivers, such as land use change, management actions, or succession or other biological processes (A). For specific environments such as the dry forests of the Interior West, causal models can organize and communicate more explicitly the complex interconnectedness of landscape processes such as drought, fire, beetles, and management on tree mortality (B).

Near-real-time drought-effect monitoring has been implemented for agricultural and grazing systems that are sensitive to seasonal and short-term drought effects (Brown and others 2008). Efforts have also been developed to improve fire hazard assessments using near-real-time information about the state of drought-sensitive fuels (Schneider and others 2008). These systems are highly applicable to areas with relatively homogenous, drought-sensitive vegetation types, but where land use is mixed, drought-effects monitoring systems are less likely to provide clear information for forest managers. Forests, especially those with an evergreen component, are generally less sensitive to drought than are grasslands or crops. In areas of more fragmented land use, this variable sensitivity makes it far more difficult to interpret drought effects. Geographic patterns in observed stress responses could result from actual differences in drought intensity or they could be from different sensitivities caused by the mix of cover type. Year-to-year changes in land use make interpretation more difficult. Use of ancillary datasets can help to filter out these less reliable areas entirely, or can be used to develop vegetation-specific models calibrated to their drought sensitivities (Lobo and Maisongrande 2006).

Finer resolution imagery can be useful for identifying specific drought responses, particularly for localized areas. While even fine-resolution imagery can harbor a mix of cover types that can hamper interpretations of drought effects, the mixture of grass, shrub, trees, or crops generally decreases at finer spatial resolutions (fig. 9.6). Small inholdings of drought-sensitive

vegetation could also be important drought indicators in mixed landscapes, particularly where meteorological station data are lacking.

While local needs often benefit from high-resolution drought monitoring products, these come at a computational cost, which usually involves reduced product frequency (fig. 9.7). To detect and monitor forest drought stress, coarse-resolution products can be effective, but for questions of tree mortality or other detailed impacts, finer resolution research may be necessary. Such local management questions may require local assessments that are calibrated and tempered with information gathered in the field.

Existing Approaches Used for Broad-Scale Drought Impact Detection and Monitoring

Extended periods of extreme drought result from persistent continental- to global-scale climate patterns that affect landscapes and regions. The large extent and contiguity of potential drought impacts helps us identify where drought is occurring because long-term meteorological or stream gauge data are sparse and their use normally requires interpolation. Drought can also be inferred from satellite-based observations of temperature or precipitation, though not without difficulties. Further insights into drought occurrence can be harvested from drought effects to sensitive vegetation as observed from satellites, yet vegetation change can also be caused by factors other than drought, such as disturbance. While these individual approaches for detecting and tracking

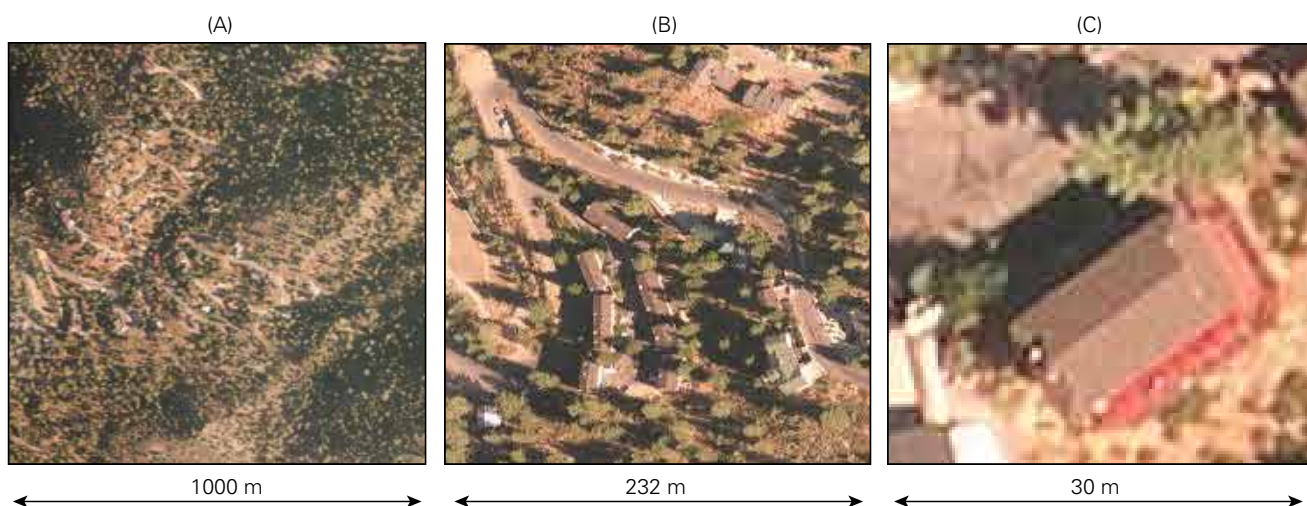


Figure 9.6—Mixed vegetation or land cover types that can result from different spatial resolutions, including: (A) 1000 m, (B) 232 m, and (C) 30 m grid cell widths. Products delivered at these resolutions would only provide one value for each unit area above, which typically decrease in diversity from left to right depending on the patch size of the vegetation.

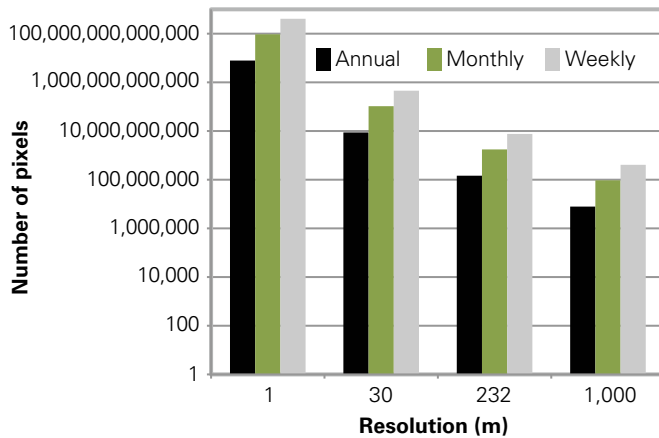


Figure 9.7—Potential tradeoffs between spatial and temporal resolution measured in terms of the number of pixels per year needed to cover the conterminous United States with a remotely sensed product set of a given frequency and spatial resolution. Standard vegetation products from Landsat are at 30-m resolution, while products from Moderate Resolution Imaging Spectroradiometer (MODIS) are 232-m resolution, and products from Advanced Very High Resolution Radiometer are 1000-m resolution.

drought have limitations, integrated monitoring systems can combine their particular strengths (Lawrimore and others 2002, Steinemann 2003, Svoboda and others 2002, Svoboda and others 2004, Tadesse and others 2005). It should be noted, however, that none of these integrated systems specifically focus on drought stress in forested ecosystems.

Meteorology-Based Measures of Drought

Primary meteorological measurements are not themselves the strongest predictors of drought effects. Various combinations of mostly temperature and precipitation measurements have been formulated into indices that are designed to provide drought-specific interpretations (table 9.1). These indices can be calculated directly at the locations of meteorological stations, producing a point-based map, or from gridded datasets (e.g., interpolated station data or reanalysis files). Although all of the indices in table 9.1 estimate the degree of moisture deficit in some context, they are typically associated with a particular class of drought—meteorological, agricultural, or hydrological drought (chapter 2). Some indices, such as the Surface Water Supply Index (SWSI), have distinctive formulations that are clearly applicable to one drought class (hydrological drought, in this case). For other indices, however, these class associations appear to derive from subtle differences in how the indices operate through time. For instance, the Palmer Hydrological Drought Index (PHDI) rebounds less quickly from moisture surpluses

or deficits than the similarly calculated Palmer Drought Severity Index (PDSI), which is generally considered a meteorological drought index (Palmer 1965). Likewise, the related Palmer Z-index (considered an index of agricultural drought) is more responsive to short-term moisture anomalies than either the PHDI or PDSI.

Most of the indices in table 9.1 are, like the PDSI, calculated using a water-balance approach between precipitation and potential evapotranspiration (PET). Indeed, many of the indices in table 9.1 represent direct modifications of the PDSI in response to perceived limitations. For instance, Heddinghaus and Sabol (1991) introduced Palmer Modified Drought Index (PMDI), a revised version of the PDSI. Their revision addressed one of the major areas of criticism regarding the PDSI: the determination of wet and dry spells. The PMDI yields a continuous measure that is less volatile than the PDSI, such that it can accurately capture a linear combination of temperature and precipitation effects across broad geographic regions (fig. 9.8).

A notable departure from the PDSI and other water-balance-based indices is the Standardized Precipitation Index (SPI). The SPI characterizes moisture conditions during multiple, well-defined time windows; it is also considered more consistent across geographic space. Nonetheless, it only uses precipitation data, which could be an important limitation in the face of increasing recognition that high temperatures exacerbate drought impacts on forest mortality (Allen and others 2010, Breshears and others 2005, McDowell and others 2008, Mitchell and others 2014, Vicente-Serrano and others 2013, Williams and others 2013). The Standardized Precipitation Evapotranspiration Index (SPEI) incorporates temperature into the water-balance equation via PET, but also follows the multi-temporal implementation of the SPI. The SPEI has outperformed the PDSI for monitoring drought impacts on “vulnerable systems” (i.e., for capturing impacts on indicator variables such as streamflow, soil moisture, forest growth, and crop yields), and appears to be better than the SPI at capturing drought conditions during the summer, when drought monitoring is arguably most critical (Vicente-Serrano and others 2012).

Ultimately, no meteorology-based drought index—regardless of its specific strengths or limitations—is appropriate in all circumstances. For national- or regional-scale analysis of drought, no single indicator is likely to be sufficient (Steinemann 2003). The U.S. Drought Monitor (DM), developed by the National

Table 9.1—Major meteorological (i.e., weather-station-based) drought indices used in the United States and elsewhere

Index	Key citation(s)	Type ^a	Foundation	Components/inputs	Remarks
Palmer Drought Severity Index (PDSI)	Palmer (1965)	M	Water balance model	Precipitation and temperature; Accounting done with five parameters: precipitation, evapotranspiration (ET) potential evapotranspiration (PET), soil moisture loss and recharge, and runoff	Preceded by a number of less sophisticated indices; like many other indices, enabled by the work of Thornthwaite (1948) on modeling PET; the PDSI has often been criticized but has been widely accepted despite its limitations
Palmer Hydrological Drought Index (PHDI)	Palmer (1965)	H	Water balance model	Precipitation and temperature; calculated during an intermediate step when computing PDSI	Very similar to the PDSI; uses same water balance model, but rebounds less quickly from a moisture deficit or surplus than the PDSI
Palmer Moisture Anomaly Index (Z-index)	Palmer (1965)	A	Water balance model	Precipitation and temperature; also calculated as an intermediate step when computing PDSI	Reflects departure of weather in a particular month from the average moisture climate for that month, regardless of conditions in prior or subsequent months; more responsive to short-term moisture anomalies than the PDSI or PHDI
Crop Moisture Index (CMI)	Palmer (1968)	A	Water balance model	Precipitation and temperature; uses weekly means	Also developed by Palmer; effective at measuring agricultural drought during the growing season; like the Z-index, focuses on short-term moisture conditions
Keetch-Byram Drought Index (KBDI)	Keetch and Byram (1968); Burgan (1988)	M	Water budget model	Precipitation and soil moisture	Forest Service product; developed for wildfire managers in the Southeastern United States, but implemented as a stand-alone drought index by Burgan (1988); values (hundredths of inches) range from 0 (no soil moisture depletion) to 800 (completely saturated soil)
Surface Water Supply Index (SWSI)	Shafer and Dezman (1982); revised by Garen (1993)	H	Available surface water including snowmelt	Measurements for snowpack, precipitation, streamflow, reservoir storage	Statistical properties poorly understood; difficult to compute; mostly used for western United States river basins (i.e., places where snowmelt strongly influences streamflow)
Soil Moisture Anomaly Index	Bergman and others (1988)	A	Water balance model	Uses PET (Thornthwaite 1948)	Developed for global-scale climate monitoring; values change at an intermediate rate somewhere between the CMI (fast) and the PDSI (slow)
Palmer Modified Drought Index (PMDI)	Heddinghaus and Sabol (1991)	M	Water balance model	Same inputs as PDSI. Still uses X1 and X3 terms, but in a slightly different fashion (see next box)	Operational modification of the PDSI; modified rules for index response during wet and dry spells; prevents sudden flipping from positive to negative index values (and vice versa); modified index is continuous and likely to be normally distributed
Standardized Precipitation Index (SPI)	McKee and others (1993)	M	Precipitation probability	Precipitation only; standardized departure with respect to a rainfall probability distribution	Typically calculated for multiple time windows (e.g., 1, 3, 6, 9, and 12 months); main criticism is that it only includes precipitation
Soil Moisture Percentiles	Andreadis and others (2005)	H	Available soil moisture	Modeled soil moisture values	Modeled values from precipitation and soil information, which across regions or continents may lack detail/accuracy
Standardized Precipitation Evapotranspiration Index (SPEI)	Vicente-Serrano and others (2010)	M	Water balance model	Precipitation and temperature	Multi-scale (i.e., incorporates multiple time windows) like the SPI, but also includes temperature via PET (calculated using the Thornthwaite method)

^aType: M = meteorological, H = hydrological, A=agricultural.

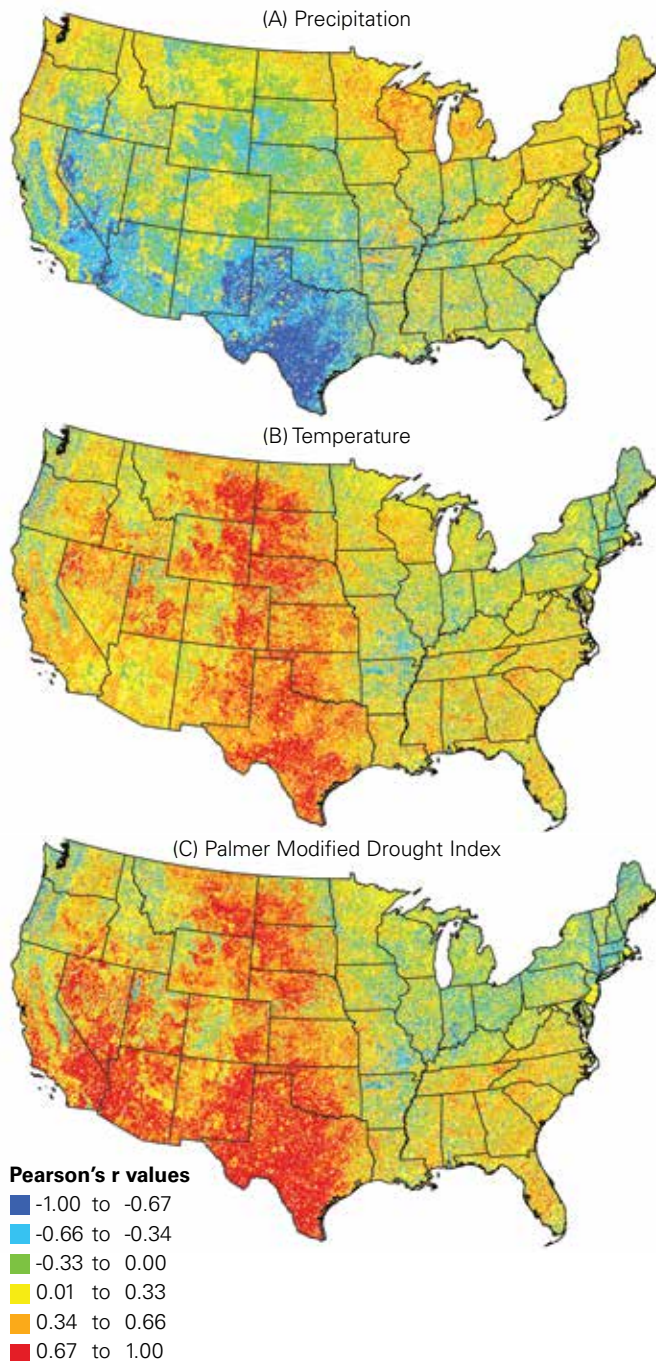


Figure 9.8—Correlations (Pearson's r) between mean March–September Moderate Resolution Imaging Spectroradiometer (MODIS)-based *ForWarn* Normalized Difference Vegetation Index (NDVI) and National Land Cover Data Climate Division mean monthly March–September for (A) temperature, (B) precipitation, and (C) Palmer Modified Drought Index (PMDI), 2000–2012, based on 250,000 random points sampled with a 1-km buffer.

Drought Mitigation Center (NDMC) with cooperation from the U.S. Department of Commerce and U.S. Department of Agriculture (Svoboda and others 2002), and the related North American Drought Monitor (NADM) (Lawrimore and others 2002), were designed to integrate six key and numerous supplementary indicators—some from station data, others via remote sensing—to estimate drought severity, albeit subjectively. The PDSI and the SPI are key indicators in the U.S. and North American Drought Monitors, while the Crop Moisture Index (CMI), the Keetch-Byram Drought Index (KBDI), and the Surface Water Supply Initiative (SWSI) are among the supplementary indicators (see table 9.1).

Strengths and weaknesses of meteorology-based indices—The primary strengths of meteorology-based indices are that precise monthly meteorological data are widely available for most portions of the United States, and regional data extend back in time a century or more to provide a relatively consistent climate context. Individual monthly temperature station records in the Global Historical Climatology Network (GHCN) date to as early as 1701 (Lawrimore and others 2011). Observations from 69 countries and territories were available by 1880. A fairly robust station network was in place for the continental United States (and Hawaii) by the late 1800s (Menne and others 2012).

Satellites are comparatively expensive to manage and to maintain a calibrated and continuous record (Lawrimore and others 2011, Mendelsohn and others 2007, Menne and others 2012). However, the low spatial density of meteorological stations necessitates the use of spatial interpolation, which, despite significant methodological advances in recent decades (Daly and others 2002, Daly and others 2008), can fail in heterogeneous terrain and microclimates. The GHCN daily dataset has data from more than 80,000 weather stations worldwide, but about two-thirds of the stations only record precipitation, and not temperature (Menne and others 2012). By comparison, the GHCN monthly mean temperature dataset provides data for 7,280 stations from 226 countries and territories, plus ongoing monthly updates for more than 2,000 stations (Lawrimore and others 2011). The continental United States has one of the greatest temperature station densities, both historically and currently of any World region (Menne and others 2012). GHCN stations represent only about 10 percent of all weather stations available in the United States (Daly and others 2008), although missing data are still an analytical impediment.

Another issue is that the formulations of most meteorology-based indices are biased in favor of crops that are harvested after a single growing season. Few of these indices carry much information about historical conditions, and when they do, it is on the order of months rather than years. For example, the SPI considers a 12-month history; the SPEI is the longest, with a 24-month “memory.” Trees are more resilient to drought effects, making it necessary to track antecedent moisture conditions over the prior several years (see fig. 9.4). Few researchers have devised and regularly employed drought indices that include multiyear prior conditions of the sort needed when gauging forest impacts. Koch and others (2013a, 2013b, 2014, 2015) have used a set of drought indices consisting of 1-, 3-, and 5-year histories for an annual chapter in the last four national reports issued by the U.S. Department of Agriculture, Forest Service, Forest Health Monitoring program.

Fundamentally, with a meteorology-based approach to characterizing drought, impacts are inferred rather than measured directly. Anderegg and others (2013) argued that we have yet to link any meteorology-based drought measure to forest damage or mortality at broader spatial scales. Drought indices are not designed to predict levels of drought damage or mortality in forests or any other vegetation type—just moisture deficit, in an abstract sense. This problem is universal, regardless of the selected drought index or the spatial and temporal coverage provided by stations for the area of interest. Impacts on vegetation due to drought conditions can only be inferred, since vegetation responses are not measured by stations.

Nevertheless, Mitchell and others (2014) highlighted a possible way to employ meteorology-based indices to identify geographic areas where drought-induced tree mortality is most likely. They looked at 41 different forest die-off events across Australia (in different forest types over a period of about 80 years) and found 3 things they had in common: (1) water deficits, (2) maximum temperatures outside of 98 percent of the observed range in drought intensity, and (3) the presence of at least 1 heat wave (3 consecutive days above the 90th percentile for maximum temperature). While these specific threshold values may not translate to new locations—Australian ecosystems are more water-limited than many U.S. forest ecosystems—the concept laid out by Mitchell and others (2014) is worth further research. Toward this end, moisture and temperature extremes for the United States are reasonably well documented from weather station

data or from spatially interpolated products such as the gridded maps produced by the PRISM Climate Group at Oregon State University (Daly and others 2002, Daly and others 2008).

Remote Sensing-Based Measures of Drought Impacts

Various remote sensing-based indices have been proposed and utilized to detect drought occurrence and severity (table 9.2). The continuous gridded nature of these remotely sensed indices is an innate advantage over the meteorological indices shown in table 9.1, which are derived from dispersed meteorological stations. This advantage is counterbalanced, however, by the relatively brief observational history that any particular class of satellite sensors provides. New orbital sensors have substantially different characteristics, yet may not share overlapping periods of operation to calibrate with the sensors that they are replacing. The decade-or-more service lifetimes of MODIS and Advanced Very High Resolution Radiometer (AVHRR) are considered long records for remote sensing platforms, yet they are short with regard to tree lifetimes and forest successional dynamics.

In contrast to meteorology-based measures of drought, remote sensing indices measure certain impacts of drought to vegetation and disturbance directly (Deshayes and others 2006). Sensors integrate vegetation conditions across the entire grid cell at the resolution of the sensor, averaging across vegetation types and plant species. Because of these basic distinctions from ground-based measurements, and because these indices represent an emergent vegetation property, the trajectory of such integrating measures across seasons has been referred to as Land Surface Phenology (LSP) (de Beurs and Henebry 2004), and interannual differences in the timing and magnitude of LSP have been suggested as potential indicators of environmental change.

Conceived initially by Rouse and others (1973) but popularized by Tucker (1979), the Normalized Difference Vegetation Index (NDVI) has proven to be useful both alone and as a component of other indices, and also as a fertile starting point, since many variants of this index have been devised. Chief among its advantages is the automatic normalization for differences in sun-and-sensor geometry that is provided by the “difference-over-sum” format of its arithmetic construction, a form that has been frequently borrowed for other indices. NDVI is colloquially referred to as “greenness”

Table 9.2—Remote sensing indices for drought detection and monitoring

Index	Formula	Purpose	Strengths	Weaknesses	Reference
Normalized Difference Vegetation Index (NDVI)	$(\text{NIR}-\text{Red})/(\text{NIR}+\text{Red})$ National Inventory Report (NIR)	Monitor vegetation condition and health	Self-normalizing across different sun-sensor geometries	Affected by soil color; may saturate at high vegetation densities	Tucker (1979)
Normalized Difference Vegetation Moisture Index (NDMI)	$(\text{NIR}-\text{MIR})/(\text{NIR}+\text{MIR})$ Miscellaneous Inventory Report (MIR)	Uses MIR, which is sensitive to leaf moisture	Measures vegetation water relative to chlorophyll	Not all sensor platforms have MIR band	Wilson and Sader (2002)
Ratio to Mean NDVI (RMNDVI)	$((\text{NDVI}_i - \text{NDVI}_{\text{mean}})/\text{NDVI}_{\text{mean}}) * 100\%$	Percentage change relative to mean of last n years	Depicts current status relative to a multi-year history	Mean greenness may not show sensitivity to drought impacts	Vegscape
Ratio to Previous NDVI (RPNDVI)	$((\text{NDVI}_i - \text{NDVI}_{i-1})/\text{NDVI}_i) * 100\%$	Percentage change relative to this time last year	Depicts current status relative to prior year	Prior year may not be representative of “normal”; seasonal timing may be shifted	Vegscape
Enhanced Vegetation Index (EVI)	$((\text{NIR}-\text{Red})/(\text{NIR}+6\text{Red}-7.5\text{Blue}+1)) * 2.5$	Lower saturation risk	Lessens soil background effect	Atmospheric effects; requires standardization	Huete and others (2002)
Soil-Adjusted Vegetation Index (SAVI)	$((\text{NIR}-\text{Red})/(\text{NIR}+\text{Red}+\mathbf{L})) * (1+\mathbf{L})$ Correction Factor (L)	Corrects NDVI when vegetative cover is low and soil color is visible	Adds a soil “brightness” correction factor, L ; when L =0, SAVI=NDVI	Must know amount of vegetation to set L , and this is somewhat circular	Huete (1988)
Vegetation Condition Index (VCI)	$((\text{NDVI}_i - \text{NDVI}_{\text{min}})/(\text{NDVI}_{\text{max}} - \text{NDVI}_{\text{min}})) * 100\%$	Shows current value relative to dynamic range of previous years	Normalizes current value to past range	Shows other disturbances besides drought; Divisor grows with additional history	Kogan (1995)
Mean-Referenced Vegetation Condition Index (MVCI)	$((\text{NDVI}_i - \text{NDVI}_{\text{mean}})/\text{NDVI}_{\text{mean}}) * 100\%$	Shows current value relative to mean of previous years	Normalizes current value to past mean	Change from mean of past years is relatively insensitive	Vegscape
MODIS Global Disturbance Index (MGDI)	$(\text{LST}_{\text{max}, i} / \text{EVI}_{\text{post LST max}, i}) / (\text{LST}_{\text{max}, n-1} / \text{EVI}_{\text{post max}, n-1})$ Land Surface Temperature (LST)	Detects large-scale vegetation disturbances; separate annual and historical formulations	Disturbances cause LST and EVI to exceed normal variability	Requires annual and historical maximum composite LST and EVI data; current year excluded from denominator	Mildrexler and others 2007), Mildrexler and others (2009)

Note: All are calculated on a cell-by-cell basis, often with respect to past values in that same cell. There are many variants of the Normalized Difference Vegetation Index (NDVI) not covered here, including the Normalized Built-up Index (NDBI), the Normalized Difference Water Index (NDWI) and Modified NDWI (MNDWI), the Normalized Difference Soil Index (NDSI), the Modified Soil Adjusted Vegetation Index (MSAVI and MSAVI2), the Transformed Soil Adjusted Vegetation Index (TSAVI), the Anomaly Vegetation Index (AVI), the Crop Moisture Index (CVI), and uncounted others. We treat the modeled multivariate VegDRI and GIDMaPS indices separately as Drought Detection System entries in table 9.3 (Zhang and others 2013).

although Tucker (1979) never used this term himself. A majority of remote sensing indices attempt to track drought impacts on growth by tracking changes in this “greenness” using the logic that observed changes in photosynthetic machinery can be used to infer drought impacts indirectly (albeit more directly than the purely meteorological indices shown in table 9.1). Classical NDVI, however, saturates at high vegetation densities, giving rise to the “Enhanced” and “Soil-Adjusted” variants (table 9.2).

Most of the remote sensing indices rely on changes in “greenness” (sometimes in concert with leaf moisture or land surface temperature) relative to the same value calculated for the equivalent time interval in a previous year or years. This common construction represents an intention to compare a current value with an historical “normal.” This “normal” may be the local value at the same time the previous year [i.e., NDVI or Ratio to Previous NDVI (RPNDVI)]; it may be the ratio to mean (or RMNDVI), median, or maximum value from a number of prior years; or it may be scaled to the full dynamic range of the local value (i.e., VCI). Differences in the mechanism used to characterize this normal baseline are responsible for much of the proliferation of variant forms of these basic indices. Indeed, it may be more challenging to quantify the normal, expected trend than it is to monitor the current status. Development of the standard against which drought or greenness departures are measured may represent the most difficult part of drought detection, whether by meteorology-based or remotely sensed impact metrics.

The appropriateness and temporal equivalency of a “same date” comparison strategy across years relies on the stationarity of seasonal progressions in LSP. However, LSP is known to shift dynamically across years (Hargrove and others 2009). The degree of these seasonal phenology shifts will affect the detection sensitivity of drought indices based on such interannual comparisons, yet an earlier-than-normal fall season may be an indicator of drought (Hwang and others 2014). In the spring, where greenup is typically temperature limited, drought could result in either higher or lower values or both depending on what portion of the spring is considered. Such broad swings in detection sensitivity serve to demonstrate the confounded nature of drought impacts with other types of disturbances, including climatic effects (see Challenge 3 above).

Several indices evaluate the current situation relative to the mean of prior years. While the mean may

characterize the entire prior distribution, the goal of a detection index is unlikely to be detection of a shift in the entire distribution itself. Comparisons with multiyear median may be only marginally more sensitive. It may be more effective to detect an onset of drought based on comparisons with maximum historical greenness, but this comparison will show increasing sensitivity as current greenness is compared with ever-higher values from particularly verdant prior years experiencing unusually favorable conditions.

A key need is to translate remotely observed changes in vegetation to actual impacts on the ground, such as tree mortality, annual growth reduction, or changes related to secondary disturbance risks, such as annual fuels for wildfire or insect and disease responses. Because short-term vegetation responses may not necessarily equate to long-term impacts, the multiyear monitoring capabilities that remote sensing provides are critical for detecting substantive lasting change apart from short-term drought responses related to immediate reductions in seasonal greenness.

Limitations of Remote Sensing-Based Approaches: An Illustrative Example

Remote sensing-based methods for drought detection and monitoring are not a panacea. Interpretation of results shown by remotely sensed products may not be straightforward, and interpretations can be complicated by both the technical aspects of the sensor technologies, as well as by the intricacies and interconnections of the ecological processes.

A recent example highlights the magnitude of controversy that is possible surrounding interpretation of forest drought impacts from remote sensing observations. Impressed by global simulation results with the Hadley Center model in particular (Cox and others 2004), the Intergovernmental Panel on Climate Change (IPCC) AR4 report (IPCC 2007) issued warnings suggesting that the rain forests of the Amazon might collapse under climatic change, being replaced by savanna-like vegetation (Nepstad and others 2008). In addition to the radical transformation of the ecosystem and loss of biodiversity, Phillips and others (2009) claimed that massive Amazon tree mortality would temporarily change the forest from a carbon dioxide (CO₂) sink (2 billion tons absorbed yearly) to a carbon monoxide (CO) source (3 billion tons released).

In part to test short-term predictions of decreases in forest photosynthesis following drought, Saleska and

others (2007) examined MODIS Enhanced Vegetation Index from 2000–2006, and reported that Amazon forests actually became greener during the severe drought that occurred in the region in 2005. Myneni and others (2007) found that Amazon forests become greener in the dry season due to an increase in leaf area index. Huete and others (2006) suggested that photosynthesis in Amazon forests might be limited by light availability, and that the observed increase of greenness during the dry season is stimulated by increased sunlight. Huete and others (2006) speculated that the normal dry season may be the forests' most productive time of year because the rain clouds clear up and more sunlight reaches the forest, in the same way that some areas in the United States show positive correlations between drought and NDVI (see fig. 9.8). They also suggested that soil water content was not a limiting factor for Amazon greenness. Saleska and others (2007) concluded that Amazon forests might be more resilient to climate changes than ecosystem models assume.

These counterintuitive findings were immediately challenged by other studies, which concluded that the 2005 drought had no impact on the greenness of Amazon forests. Samanta and others (2011) found “no evidence of large-scale greening of intact Amazon forests during the 2005 drought.” They suggested that the previous findings were attributable to artefacts resulting from contamination of satellite-based observations by clouds and aerosols. Zhou and others (2014) showed widespread decline in greenness of Congolese forests over the last decade, even though such forests are probably more drought-tolerant, with their drier conditions and higher composition of semi-evergreen trees.

Recently, Morton and others (2014) showed that the apparent increase in greenness in Amazon forests could be explained by seasonal variations in lighting caused by changes in sun-sensor geometry. They suggested that it is soil moisture rather than light that determines the balance between photosynthesis and respiration in Amazon forests [summarized in Soudani and François (2014)]. These results tip the balance back toward interpretations that the Amazon is very sensitive to rainfall and, as the IPCC report indicated, may be prone to conversion and loss in a warmer, drier future in the tropics.

The emergence of such a surprising amount of controversy might discourage those considering a

remote sensing perspective on drought detection and monitoring. However, tropical forests represent one of the most challenging of all locations for remote sensing work (Asner and Alencar 2010). A combination of complicating factors in tropical forest exacerbates the interpretation of remote imagery in these locations. High tree diversity in Amazonian forests leads to mixed responses from differential plant sensitivity, and there are potential saturation issues for some greenness-based indices. Clouds are nearly ever-present, and aerosols and terpenes may be in high concentration, as are particulates, soot, and smoke from fires. Most importantly, not many long-term ground observations and datasets exist, with few exceptions (Phillips and others 2009). This alignment of challenges may make tropical locations one of the worst-case remote sensing scenarios (Huete and Saleska 2010). More straightforward and direct interpretations of drought might be expected in temperate or boreal locations. An all-data approach, where remote sensing methods are leveraged with other ancillary data streams, including ground-based measurements, may represent the most promising approach for detecting and monitoring drought in these and other, less-challenging locations.

Existing Systems for Drought Detection and Monitoring

Table 9.3 shows 11 existing systems for detecting and monitoring drought, all of which include remote sensing as a fundamental component. The geographic extent that is monitored ranges from single countries to continents to the globe. Systems can be identified that are primarily the product of meteorologists, agricultural scientists, computational scientists, remote sensing specialists, and even political and social policy analysts. Not surprisingly, each system retains and exhibits the approaches, interests, and perspectives of the group producing and operating it. Some have a practical emphasis, while others are more research-oriented. Systems benefiting from the participation of more than a single one of these domain perspectives are likely to be the most useful in the long term. Although the oldest system has been operational for nearly 3 decades, the majority have been initiated within the last 5 years. There is a clear tendency among these newer systems to take a multivariate approach to drought detection rather than relying on one or a few indicators. Many of the drought systems are designed primarily for detecting food and agricultural drought effects, including verification for crop insurance settlements. Some of the tree-based systems are aimed at carbon accounting

Detection system	Operated by	Year started	Spatial extent	Release frequency	Input data
Famine Early Warning Systems Network (FEWS Net)	U. S. Agency for International Development (USAID)	1985	Africa, Asia, Central America, and the Central Tropics	Every 20 days; predictions 6–12 months ahead	Subjective combination of agro-climatology, production, market data, nutrition, and scenario development
Vegetation Drought Response Index (VegDRI)	USGS (Earth Resources Observation Systems) (EROS), Univ. of Nebraska Lincoln, USDA Forest Service Resource and Monitoring Analysis (RMA)	7 States in 2006, CONUS in 2009	Conterminous United States	Weekly	AVHRR and eMODIS NDVI, combined with PDSI and SPI drought indices, land cover, soil water capacity, elevation, ecological setting, using three seasonal Regression Tree models
ForWarn	Forest Service, National Aeronautic Space Administration (NASA) Stennis Space Center (SSC)	2010	Conterminous United States	Every 8 days	Moderate Resolution Imaging Spectroradiometer (MODIS), Modis Vegetation Index Algorithm (MOD13), Vegetation Indices for Operational Drought Monitoring (eMODIS)
Forest Disturbance Mapper (FDM)	Forest Service Remote Sensing Application Center (RSAC)/ Forest Service Forest Health Technology Enterprise Team (FHTET)	2010	Conterminous United States	Every 8 days	Forest type map, USGS map zones, local MODIS downloads
United States Drought Monitor	Forest Service, NOAA, and Univ. Nebraska Lincoln	1999	Conterminous United States	Weekly	Rain, snow, observer reports on wildlife and crop effects
North American Drought Monitor	USDA, NOAA, University of Nebraska-Lincoln (UNL), National Meteorological Service (SMN) Mexico, National Water Commission (CNA) Mexico, Agrifood Canada, Meteorological Service Canada	2002	Canada, Mexico, United States	Bi-weekly	Subjective maps from the three member countries, which may not line up at international borders
Global Drought Monitoring Portal (GDMP)	NOAA NCDC	2012 startup, seeking global participation	Global	Monthly	Thresholded Global Precipitation Climatology Center SPI with up to 24-month history, other metrics where available
Vegscape Vegetation Condition Explorer/ CropScape	USDA National Agricultural Statistics Service (NASS)/ George Mason	2013/2011	Conterminous United States	Daily, weekly, bi-weekly composites	MODIS NDVI, Enhanced Vegetation Index (EVI)
Global Agricultural Monitoring (GLAM) Production System/Global Inventory Monitoring and Modeling Studies (GIMMS)	NASA Goddard, USDA Foreign Agricultural Service (FAS)	2001 Terra, 2002 Aqua	Global	Every 8 days	MODIS Terra and Aqua, treated separately
Global Integrated Drought Monitoring and Prediction System (GIDMaPS)	Univ. California, Irvine	2013	Global, 1980–2014, coarse resolution	Monthly	Precipitation and soil moisture from simulations and remote sensing, including Modern Era-Retrospective Analysis for Research and Applications (MERRA), North American Land Data Assimilation System (NLDAS), Global Drought Climate Data Record (GLDAS), and Global Drought Climate Data Record (GDCDR) historical data sets
ALERTS 1.0/ Planetary Skin	NASA Ames, Univ. of Minnesota, National Space Research Institute (INPE) Brazil, Planetary Skin Institute	In development, beta available	Global, 1 km	Biweekly	MODIS NDVI, Land Surface Temperature (LST)

Purpose	Meteorology or vegetation effects	Algorithm	Web site URL
Drought effects on food security	Vegetation, specifically food	Based originally on AVHRR in Northern Africa; has grown beyond a strictly remote sensing system	www.fews.net
Monitor vegetation stress to improve preparedness and response	Vegetation	AVHRR and eMODIS VegDRI index from CART; Percent of Average Seasonal Greenness (PASG) ratio is relative to 20-year mean Seasonal Greenness	vegdi.unl.edu , vegdi.cr.usgs.gov ; Web viewer at vegdi.cr.usgs.gov/viewer/viewer.htm
Broad forest change detection, tracking, and recovery	Vegetation	% NDVI difference between current NDVI versus given NDVI baseline	forwarn.forestthreats.org ; Web viewer at forwarn.forestthreats.org/fcav
Assist IDS flight planning and map disturbances	Vegetation	Difference of current vs. historical spectral reflectances, followed by calculation of NDMI in Western United States, or NDVI in Eastern United States	foresthealth.fs.usda.gov/portal ; Web viewer at foresthealth.fs.usda.gov/portal/Flex/FDM
Monitor broad-scale drought impacts	Meteorology/ Vegetation (inferred)	Subjectively combine inputs into five Drought Intensity categories	droughtmonitor.unl.edu
Monitor broad-scale drought impacts at continental scale	Meteorology/ Vegetation (inferred)	Experts balance conflicts from three countries into five subjective Drought Intensity categories	www.drought.gov/nadm ; Web viewer at gis.ncdc.noaa.gov/map/drought/NA
Provide a global snapshot of water scarcity	Meteorology	A combination of existing continental-scale drought systems, with efforts to harmonize at country borders	gis.ncdc.noaa.gov/map/drought/Global
Monitor crop vegetation conditions	Vegetation	Compares NDVI change ratio to previous year, to median and to mean NDVI	nassgeodata.gmu.edu/vegscope
Monitor global food production	Vegetation	% NDVI anomaly, calculated from historical all-year mean NDVIs	glam1.gsfc.nasa.gov
Drought prediction and probability that drought will persist	Meteorology	SPI, SSI, or Multivariate Standardized Drought Index (MSDI), mapped as five levels of wetness and five levels of drought	drought.eng.uci.edu
Improve detection, awareness, and decisionmaking	Vegetation	Multi-resolution Global Water Stress Index Algorithm	www.planetaryskin.org , www.planetaryskin.org/rd-programs/resource-nexus/global-land-change-detection , viewer at ourplanetaryskin.org/ps/is/cs/run.php?uid=guest

Table 9.3—Existing operational and experimental systems for detecting the extent and severity of drought Forest Service Forest Inventory Analysis (FIA), Insect and Disease Survey (IDS), National Oceanic and Atmospheric Administration (NOAA) Historical Climatology Network (HCN) meteorological stations, U.S. Geological Survey (USGS) Stream Gauge network, and SNOwpack TElemetry (SNOTEL) are related networks that, while providing invaluable ancillary information, are not specifically designed to detect or monitor extent, duration, or impact of drought

or global deforestation, while others monitor drought effects on forests, particularly tree mortality.

Integrating Broad Monitoring With Assessment

Remote sensing platforms see everything; this is simultaneously both an advantage and a drawback of these methods. Observing all vegetation types, all disturbances, and all locations synoptically on a regular interval maximizes the likelihood of understanding the local situation. Nevertheless, remote sensing methods also see nondrought disturbance effects, both abiotic and biotic, and these can be difficult to distinguish and disentangle. Local information, history, and expertise can greatly inform the conclusions made from remote data, and may be a requisite for the successful use of remote sensing to detect drought impacts. Remote sensing platforms alone are insufficient for most drought assessment purposes. However, as discussed in the following sections, they can be extremely useful for drought assessment when combined with ancillary datasets.

Land Surface Phenology Datasets

Phenology, the timing of foliage greenup and browndown, can provide one of the earliest indications of drought effects. In particular, comparison of current greenness with historical phenological behavior can show departures from expected trajectories caused by drought (Hargrove and others 2009). However, such phenological differences might be caused by other, nondrought effects, or might be delayed significantly from when original drought events occurred. These operational difficulties mirror the conceptual difficulties in isolating indirect from direct drought stressors (fig. 9.5).

Drought detectability using remote sensing is variable over time and space. Drought response is not just a function of weather, but also of spatial variation in phenological cover types and fractional vegetation cover, which is often imperfectly known. Conifers remain green even while dormant, while deciduous woody plants and grasses can have an extended period of brown dormancy that can mimic drought conditions (Volaire and Norton 2006). Vegetation response to drought is muted outside the growing season, although winter drought can cause needle loss and reduction in net primary productivity in conifers that can theoretically be detected remotely (Berg and Chapin 1994). This disparate responsiveness of land surface phenology can

be isolated, but drought effects become confounded when the composition of a grid cell is mixed. It can be challenging to know when the remote sensing signal is changing due to disturbance or successional recovery and when it is changing from drought.

High-frequency land surface phenology datasets provide a means to interpret drought responses, particularly for reliably drought-sensitive vegetation types. In open-canopy forests, savannas, or forest edges, increased grass, shrub, or herb cover can increase drought sensitivity. Deciduous trees may respond to drought by earlier leaf senescence (Hwang and others 2014). Although senescence can also be triggered by frost (Vitasse and others 2009), an unusually early onset of leaf browning and/or abscission may serve as a season-specific indicator of drought in some forests. High-frequency land surface phenology datasets may provide a number of drought indicators that can distinguish drought responses among cover types.

In high-elevation or mountainous areas, winter variation in snowpack extent and duration provides an important, albeit temporally delayed source of precipitation that can be monitored. At high elevations, limited snowpack has been associated with the early onset of spring green-up (Hu and others 2010), although this may result from warmer temperatures. Winter drought can extend the subsequent wildfire season and can reduce fuel moisture (Littell and others 2009, Westerling and others 2006). Early green-up may also affect drought-associated insects and diseases (Ayres and Lombardero 2000). The delayed effects of snowpack variation are captured in the next growing season by existing phenological datasets that track NDVI and other vegetation indices (table 9.4).

Insect and Disease Surveys

The Insect and Disease Surveys (IDS) aerial survey program (table 9.4), administered by the Forest Service Forest Health Protection (FHP) program could serve as a national-scale source of geospatial data about biotic impacts triggered by drought. In some cases, IDS data also document direct impacts from drought and other abiotic disturbance agents. Under the program, surveyors use aerial sketch-mapping hardware and software to delineate geospatial features (typically polygons) that depict forest health impacts such as tree mortality or defoliation. The surveyors assign disturbance agent codes, as well as certain measures of the intensity of the impact (e.g., trees per acre defoliated), to each feature. The IDS data are compiled

Table 9.4—Ancillary datasets that may be useful for interpretation during drought detection and monitoring

Dataset	Developers/owners	Contents	Value added for drought detection	Reference
National Land Cover Database (NLCD); NLCD 2011 Forest Service Tree Canopy product	USGS, along with the Multi-Resolution Land Characteristics (MRLC) Consortium	16-class Landsat-based 30-m resolution land cover database for the United States; updated every 5 years; Tree Canopy product provides estimated percent canopy cover plus standard error	Shows vegetation and land cover types to assist estimation of drought impacts across areas with variable sensitivity; enables land cover conditional filtering of drought impacts	www.mrlc.gov/
Snowpack/SNOTEL	NOAA	Ground-based remote sensing of snow accumulations	Future drought impacts in areas dependent on snowmelt water	www.noahis.noaa.gov/nsa
MODIS hotspots showing recent wildfires	NASA, Remote Sensing Applications Center (RSAC) Active Fire Mapping Program	Thermal detection of wildfires at 1-km resolution	Fire may be the final outcome of drought; separates fire effects from extreme drought effects	activefiremap.fs.fed.us
Monitoring Trends in Burn Severity (MTBS) and GeoMac	Remote Sensing Applications Center (RSAC) and USGS	Mapped perimeters of past wildfires, with burn severity estimates	Fire may be the final outcome of drought; separates fire effects from extreme drought effects	www.mtbs.gov , www.geomac.gov
Active fire maps	Incident Information System (INCIWEB)	Status of active wildfires and large prescribed burns	Fire progression maps show effects of near-real-time drought conditions	www.inciweb.org
Historical Insect and Disease Survey (IDS) maps	Forest Health Technology Enterprise Team (FHTET)	Aerial disturbance surveys from aircraft for a portion of U.S. forests	Shows the pattern and landscape position of pest mortality and defoliation events	www.fs.fed.us/foresthealth/technology
Stream depth and flow	USGS Stream Gauge Network	Depth and amount of flow of rivers and streams	Monitor changes in runoff and surface flow downstream of drought areas	waterdata.usgs.gov
LANDFIRE Disturbance database	USDA Forest Service LANDFIRE	Vegetation and fuel disturbances 1999-2010	Separate other disturbances and harvests from drought mortality	www.landfire.gov/disturbance.php
Forest Inventory and Analysis (FIA)	USDA Forest Service	Inventoried forest plots in a statistical design, remeasured every 5/10 years	Shows long-term cumulative effects and mortality of drought	www.fia.fs.fed.us
Phenology data, phenoregion maps	USGS, USDA Forest Service	NDVI and other vegetation indices, statistically created maps of multivariate clusters of NDVI through time	Shows departure from normal timing of greenness, maps major vegetation types having similar phenology behavior, empirically determined	phenology.cr.usgs.gov , forwam.foresthreats.org , White and others (2005)

Note: These data sets and systems, while not directly useful in drought detection, may provide useful surrogate information when used conjointly to support core data in a multivariate "big data" approach to drought detection and monitoring. Most of these data sources are restricted in extent to the United States.

on an annual basis, and so they are not sources of near-real-time information.

Meddens and others (2012) noted several additional obstacles to using the IDS data. First, the amount of forest surveyed varies from year to year, and not all forests are surveyed; flights are targeted at areas where disturbances are most likely to have occurred (in response to ground reports), so it is possible that some affected areas are missed. Second, IDS polygons are delineated broadly, and they typically also include healthy trees. Hence, the severity of a disturbance is not reported consistently. IDS observations are recorded by different observers having a wide range of skills and experience, which introduces further variability in the reported severity and extent of a disturbance.

A related obstacle is a lack of standardized causal attribution. Depending on the aerial surveyor, IDS polygons could be labeled as having been caused by drought, or instead, by insect activity driven by drought. Causal attribution is assigned from the air, with limited field validation. IDS data users must consider multiple agents when trying to ascertain the extent of an impact. For instance, when analyzing pinyon and juniper mortality in the Southwestern United States, Breshears and others (2005) combined IDS polygons attributed to various bark beetles as well as drought. To circumvent these ambiguities, IDS data are probably best used to delineate general geographic regions where multiple years of forest damage and/or mortality have been attributed to a complex of biotic and abiotic agents associated with drought (Huang and Anderegg 2012). These regions can then be adopted as the setting for further retrospective analysis into relationships between the agents, using ancillary data sources (Williams and others 2010, Williams and others 2013).

Wildfire Mapping Datasets

Wildfire often causes tree mortality and initiates successional recovery that destabilizes the historical pattern of climate sensitivity of communities within burned areas. Despite being an indirect outcome of drought (Westerling and others 2006), burned areas are likely to provide a less consistent measure of direct drought effects than are adjacent undisturbed areas. Increases in grass or shrub cover after fire may make burned landscapes more climate-sensitive than when they were dominated by dense conifers. Existing wildfire datasets (see table 9.4) can be used to isolate burned portions of the landscape that may differ in their drought response for a more accurate understanding

of the system in post-fire years. As with insect and disease data, burned areas can be selectively masked for regional interpretations of drought responses, or they could be targeted for understanding the cumulative effects of drought and disturbance.

The 2011–12 Texas drought and drought-associated fires illustrate how remote-sensing-based change monitoring can be better interpreted with ancillary wildland fire data. This Texas drought was remarkable (Nielson-Gammon 2012) because of its severity and duration, and because of the extensive area burned during the 2011 wildfire season (fig. 9.9). Where and when they co-occur, drought and wildfire may have additive or redundant effects on reducing NDVI. For two nearby MODIS pixels in figure 9.10, the effects of fire and drought are at least partially additive. The NDVI of these two pixels tracks each other closely for years prior to 2011, suggesting they had quite similar vegetation, and the 2011 drought effects were likely identical given their proximity. However, the immediate reduction from burning and drought clearly exceeded that of drought alone, and this effect persisted through 2012.

Retrospective analyses of drought effects across different vegetation types provide coarse-filter insights into differential responses. For a random sample of MODIS pixels across west Texas, annual variation in NDVI clearly varies by majority vegetation type, as filtered by the National Land Cover Database (fig. 9.11). Shrub- and grass-dominated areas have greater year-to-year amplitude in NDVI, which is consistent with expectations of their greater climate sensitivity than forests. All vegetation types show a general decline that could be an indication of widespread mortality caused by the 2011 Texas drought.

Land Use/Land Cover Datasets

Changes in land use and land cover are typically so fine-scale that they are unlikely to influence more coarse-scale estimates of climate departure. But taken over decades, extensive areas of certain regions have experienced substantive urban and infrastructural development (Riitters and others 2002, Riitters and Wickham 2003). Conversion from forest to nonforest land cover often increases dominance by grass, shrubs, and ruderal or early-successional species that are generally more responsive to drought than are many forests. In areas that have experienced these changes, baselines from long-term, remotely sensed time series may be less desirable than efforts to model effects based on recent land cover over shorter periods. For the

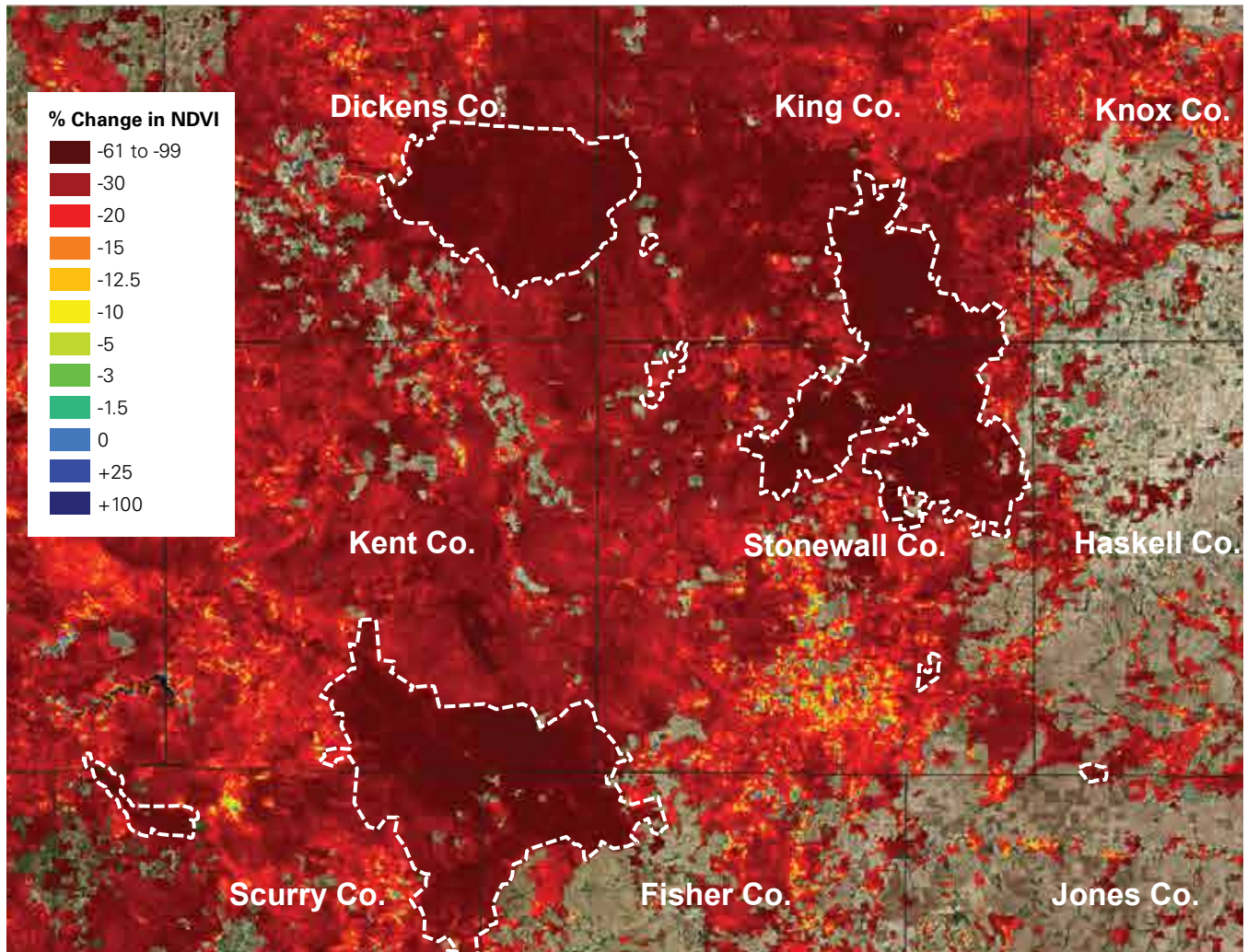


Figure 9.9—*ForWarn* change in Normalized Difference Vegetation Index (NDVI) from the All Year Mean Baseline for the 3-week period ending August 28, 2011, showing the severity of drought and wildfire on nonagricultural lands across northcentral Texas. Wildfire boundaries for 2011 are shown by dashed white lines.

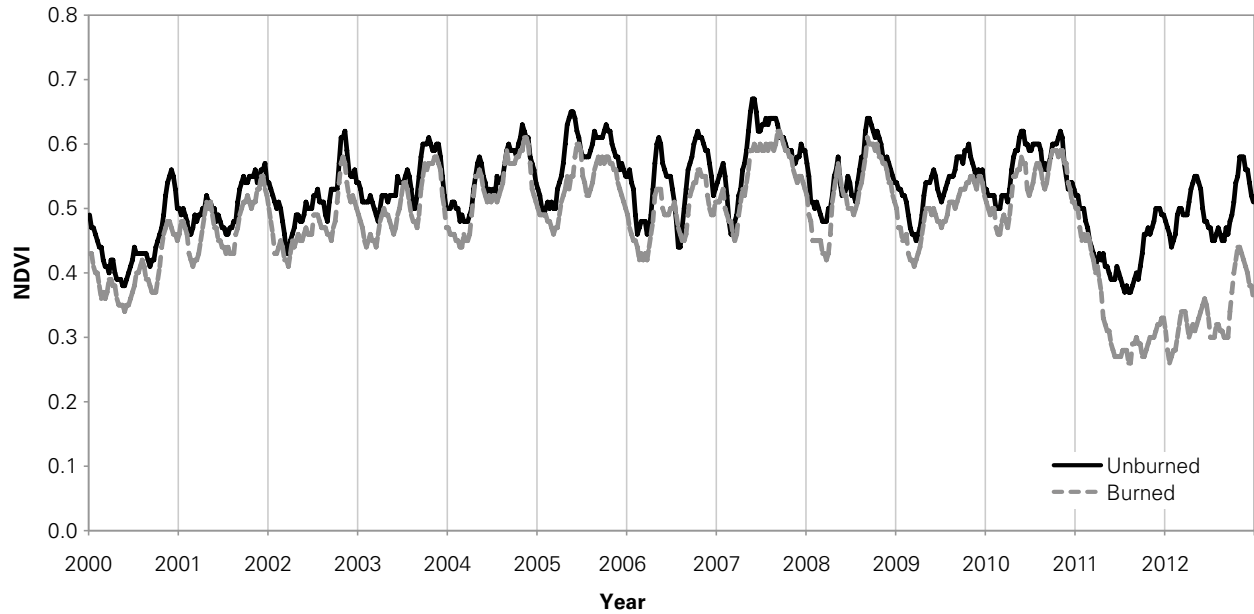


Figure 9.10—A comparison of two nearby woodland *ForWarn* pixels in west Texas on similar sites, one that burned and one that did not during 2011. Note that effects persisted through 2012 on both sites, but that the cumulative effects of drought and wildfire were more pronounced than drought alone. Site locations: unburned site location 31.8295, -100.6636; burned site location: 31.8390, -100.6455.

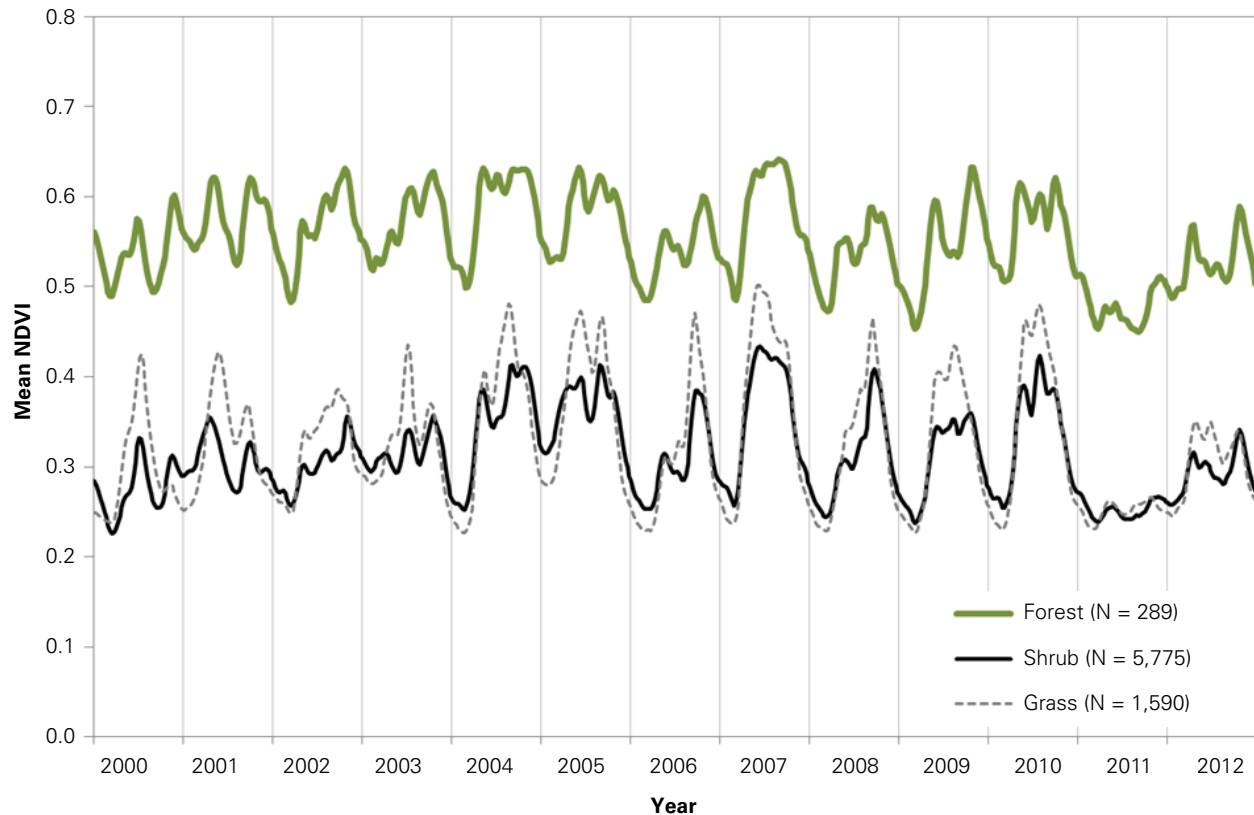


Figure 9.11—Mean NDVI for a random sample of unburned majority forest, shrub, or grass pixels within Texas climate divisions 1, 2, 5, and 6 (west Texas) using the *ForWarn* dataset. Note the extreme decline in NDVI during the 2011 drought that affected all vegetation types.

United States, the National Land Cover Database (NLCD) (see table 9.4) provides complete national coverage for multiple time steps (1992, 2001, 2006, and 2011), allowing analysts to distinguish patterns of land cover change that may be pertinent for interpreting drought response.

More subtle changes in forest management, crop type, or livestock grazing intensity can be difficult to monitor and assess. Crop types and livestock grazing intensity can fluctuate with changes in market prices in ways that confound drought response. Similarly, broad-scale forest restoration that involves stand thinning via mechanical means or prescribed fire has the potential to reduce a forest's sensitivity to drought as grass and shrubs are removed; yet restoration efforts are rarely extensive enough to be widely detected except when they involve wildfire use. Far less logging has occurred over the last decade on most Forest Service lands, suggesting that there was far more drought-sensitive early successional habitat during the 1980s than exists in the 2000s. As large wildfires become increasingly common in the West, extensive areas of forest could become far more drought-sensitive than they were earlier. Certain derived land use/land cover datasets, such as the percent tree canopy cover layer developed by the Forest Service for the 2011 NLCD, may offer limited insight into these landscape dynamics.

“Big Data” Integration: A Contextual Learning Approach to Drought

To understand broad-scale drought impacts, both meteorology-based measures of drought and remote sensing observations need interpretation, and, as we have seen, interpretations are not straightforward. Many ancillary spatial datasets may be useful for selecting, masking out, or simply interpreting different effects that are observed (table 9.4). As noted above, identifying areas that have been affected or not affected by disturbance provides an effective way to isolate direct and indirect drought effects. Comparisons of different vegetation types, whether as specific dominant forest species types, or generally as evergreen, conifer, or mixed forest types, are useful for understanding how drought responsiveness and effects differ on the ground.

At a national scale, conditional filtering of sites based on their drought sensitivity and disturbance history can provide insights into the regional relationships between drought and NDVI (fig. 9.12). While the

MODIS NDVI period is limited to 2000–present, most filtered or masked vegetation types show a strong response of reduced NDVI with increasing drought, with some exceptions. The NDVI response of northeastern hardwood forests runs counter to expectations, perhaps because this area has not experienced the drought and temperature extremes as have hardwood forests of the Southeast (figs. 9.2 and 9.8). With their evergreen attributes, conifers only show some sensitivity to drought stress (fig. 9.12). In contrast, grass and shrublands show as highly sensitive to drought, particularly in areas that have experienced extreme drought during the MODIS period. The sensitivities described here, of course, are with respect to the speed and magnitude of NDVI responses. Such responses are useful to the degree that they reflect actual vegetation impact from realized drought stresses.

Using a random sample of 250,000 MODIS-*ForWarn* grid cells out of the 14.6 million cells in the conterminous United States, we found that 20.4 percent of the continental U.S. forest area was mapped as disturbed by wildfire, insects, or diseases between 2000 and 2012 (estimated using IDS, Monitoring Trends in Burn Severity (MTBS), and GeoMac data; see table 9.4). The drought response of these areas may be misleading for certain analyses, particularly when disturbance or drought occurs nonuniformly during the analysis period. For example, a gradual increase in NDVI associated with post-disturbance succession and recovery may overwhelm any reduction in NDVI caused by drought (see fig. 9.10). By masking out disturbed forests, however, the response of the remaining areas is more likely to relate to direct drought effects (fig. 9.12A).

The majority of the remote sensing indices in table 9.2 scale or proportionalize the absolute changes in greenness into relative terms. Usually the scaling divisor is some metric of total greenness (or range of greenness) in this location. Such formulations suggest a conceptual model (implicit or otherwise) that trees, which are “greener” than grasses, for example, are somehow better able to withstand a particular absolute decrease in greenness than their less-green grass counterparts. Thus, the estimated impact of a drought that causes a uniform absolute decrease in greenness will be reported by such indices as relatively more severe for grasses, since it represents a greater proportion of their total greenness, and relatively less severe for trees.

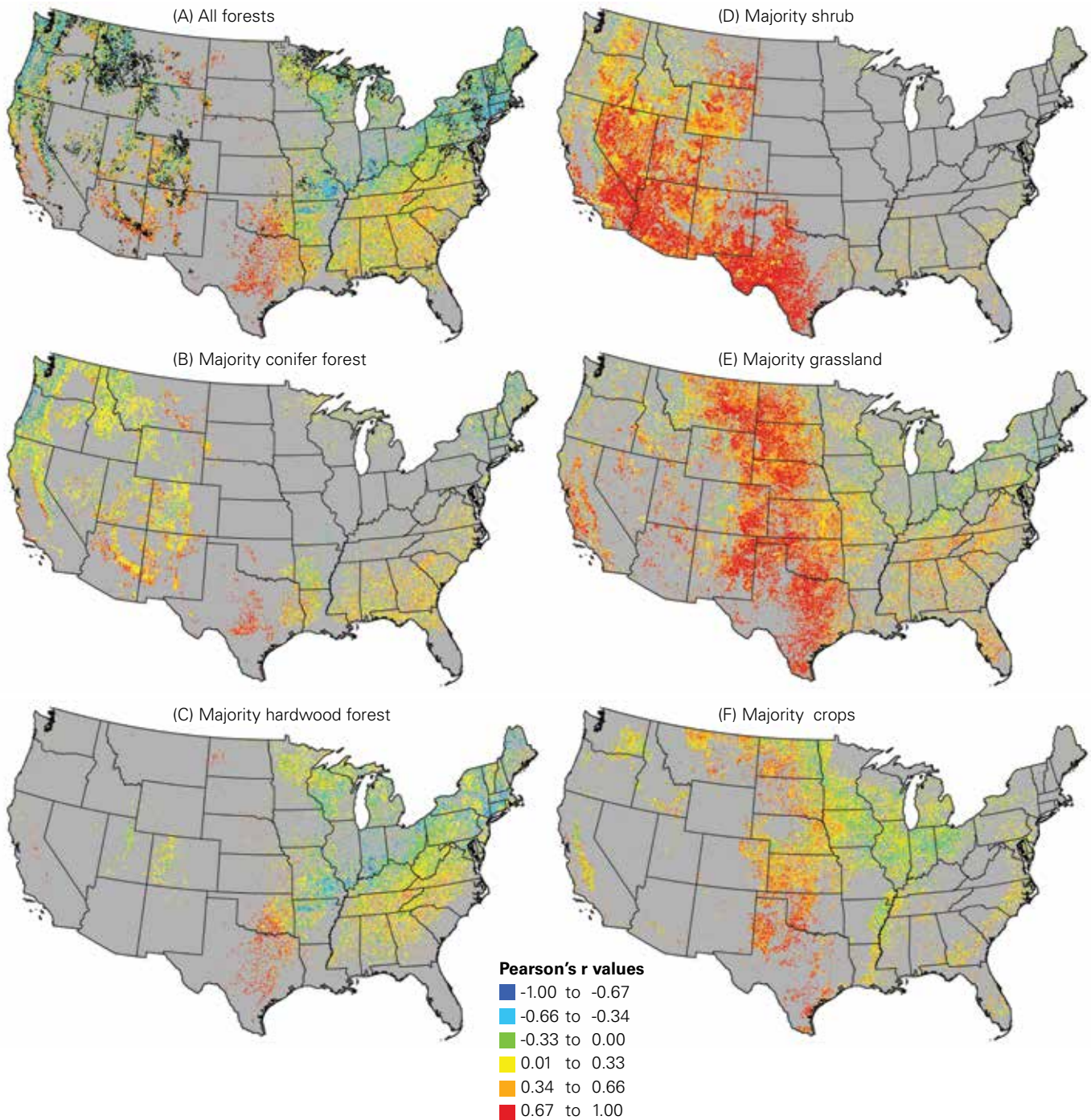


Figure 9.12—Correlations (Pearson's r) between mean March–September Moderate Resolution Imaging Spectroradiometer (MODIS)-based *ForWarn* Normalized Difference Vegetation Index (NDVI) and National Land Cover Data Climate Division mean monthly March–September Palmer Modified Drought Index (PMDI) for majority land cover types derived from the NLCD showing areas of known disturbance by wildland fire or biotic insect or disease in black for (A) all forests, (B) majority conifer, (C) majority hardwood, (D) majority shrub, (E) majority grassland, and (F) majority crops, 2000–2012. Wildland fire was derived from <http://www.MTBS.gov> (2000–2012) and <http://www.GeoMac.gov> (2013) (accessed September 1, 2014); insect and disease disturbance was compiled from Forest Service Forest Health Protection (FHP) Insect and Disease Survey (IDS) data. Data shown are based on 250,000 random points, sampled with a 1-km buffer.

Yet such relative sensitivities are diametrically opposite to the differential drought response patterns across vegetation types demonstrated here (Lobo and Maisongrande 2006, Sims and others 2014; see also Challenge 3). Figure 9.12 shows a version of fig. 9.8C that has been filtered by vegetation type. Small stature, low biomass vegetation types like grasses and shrubs are the quickest to show decreases in greenness under drought conditions, but grass and herbaceous perennials can recover quickly following an end to drought. In contrast, when drought leads to tree or shrub mortality, full recovery may take decades. Thus, grasses are a sensitive indicator vegetation type that may be useful as a harbinger of regional drought stress (Sims and others 2014). The NDVI of conifer-dominated forests are relatively unresponsive to drought. For example, at higher elevations, the coastal Northwest, and in New England, NDVI may actually increase as PMDI decreases (fig. 9.12). Weighting the severity of effects by scaling with absolute greenness would seem to be counter-indicated, and also acts to reduce the sensitivity of indices to drought effects on trees.

As noted earlier, remote sensing provides a coarse-filter type approach. Observations are frequent, extensive, and continuous in space, but are not detailed (fig. 9.7), and average across many vegetation types. Sensors are not species-specific and integrate across all vegetation growing in an area to produce a single value. Such integration may actually be advantageous, averaging out noise and measuring land surface phenology as a repeatable, emergent property of the entire vegetated ecosystem. An ideal drought detection approach would leverage both the extent and the temporal completeness of remote sensing approaches, while at the same time utilizing the longer historical record of meteorological records, which offer longer histories than remote sensing platforms. Ironically, the length of the MODIS or AVHRR record is considered long by remote sensing standards, yet it is very short relative to the depth of the climatic records, much less tree lifespans within forests. For even longer comparisons, one must employ other, even more-removed proxies, like tree-ring data (Herweijer and others 2007).

Combining Remote Sensing With Context-Based Learning

The broad spatial coverage and frequent, multiyear temporal sampling are powerful strengths of remote sensing approaches to the analysis of drought effects. It is not possible to do experiments on drought at the landscape scale. The extent is too large to randomize,

to replicate, or to apply droughts as experimental treatments [but see the Walker Branch Throughfall Displacement Experiment near Oak Ridge, TN, described by Hanson and others (2003)]. An inability to apply the classical scientific method does not, however, prevent a remote sensing approach to drought effects from making progress (Hargrove and Pickering 1992). Scientific progress on drought effects at large scales is simply limited to inference, based on what we can see happening. In this, remote sensing of drought is similar to a scientific field like astronomy, in which rich observation without the possibility of direct manipulation is the only avenue for advancement.

We suggest that a filtering approach that carefully considers both vegetative and climatic conditions can leverage the strengths of extensive drought data collected with remote sensing to best advantage. The identification of past situations whose drought outcomes might be informative or discriminating forms the keystone of this approach. A cycle starting with the postulation of an hypothesis, followed by identification and selection of relevant past “natural” experiments, followed by observation of the outcomes that resulted could be expected to produce inferences about the general principles at work, which would, in turn, result in refinement or rejection of hypotheses, beginning the cycle anew.

Such context-based learning, involving the isolation and examination of relevant prior circumstances, would leverage the availability of “big data” volumes of historical observations. Essentially, it is a form of empirical data mining. This type of time sequence approach is sometimes called space-for-time substitution, an approach that has been employed elsewhere in large-scale ecology (Pickett 1989). Figure 9.12 demonstrates the utility of such a filtering approach by showing the differential responses of various vegetation types to drought.

Empowered by ancillary datasets, powerful post hoc opportunistic analyses of drought may be possible when advantage can be taken of past droughts that are embedded within these specific relevant contexts of particular past times and locations. Such observation-based approaches carry with them the dangers of pseudoreplication, or at least an inability to replicate at will (Hurlbert 1984). Nevertheless, a strategy of coarse filtering by vegetation type, antecedent conditions, and drought severity could obtain targeted insights based on the weight of evidence from past outcomes.

Searching an extensive database of observations for the occurrence and review of particularly relevant chronosequences in time and space might be an effective way to make observation-based progress in our understanding of drought effects.

We advocate a data-mining, “big data” approach for detection and monitoring of drought impacts, relying primarily on remote sensing platforms, but also leveraging the longer term meteorological data and ancillary datasets for context-based interpretation. Figure 9.13 shows a conceptual model of how a “big data” approach might be used in developing a system for monitoring drought impacts in forests. This type of circumstantial data harvesting is the method most likely to increase our understanding of the impacts of drought stress on forests. Such a cycle might even advance our scientific understanding of landscape-scale drought effects with greater efficiency than classical experimental approaches (Tilman 1989). The strategy is empirical, allowing patterns to emerge passively from the data, without preconceived notions or hypotheses. Despite their neutrality and passive observational

nature, space-for-time filtering approaches can be highly constructive, as they will generate large numbers of testable hypotheses for the next round of conditional analysis.

Unambiguous establishment of causation (even in a limited pragmatic sense of learning to recognize correlated antecedent conditions) is difficult using these observational methods. Drought impacts are confounded and are difficult or impossible to disentangle without the use of relevant ancillary data (see fig. 9.13). With drought, however, this difficulty in separating proximate from ultimate drivers may not matter. Managers may be satisfied to monitor combined cumulative primary and secondary drought effects, unless they feel that they possess management options that would be effective against one or more of the separated drivers. Managers will want to recognize individual drivers only if they believe that they know how to relieve or mitigate some of the potential drivers. Otherwise, in practical terms, it is the sum total of the cumulative effects that acts to reduce the productivity of their forests.

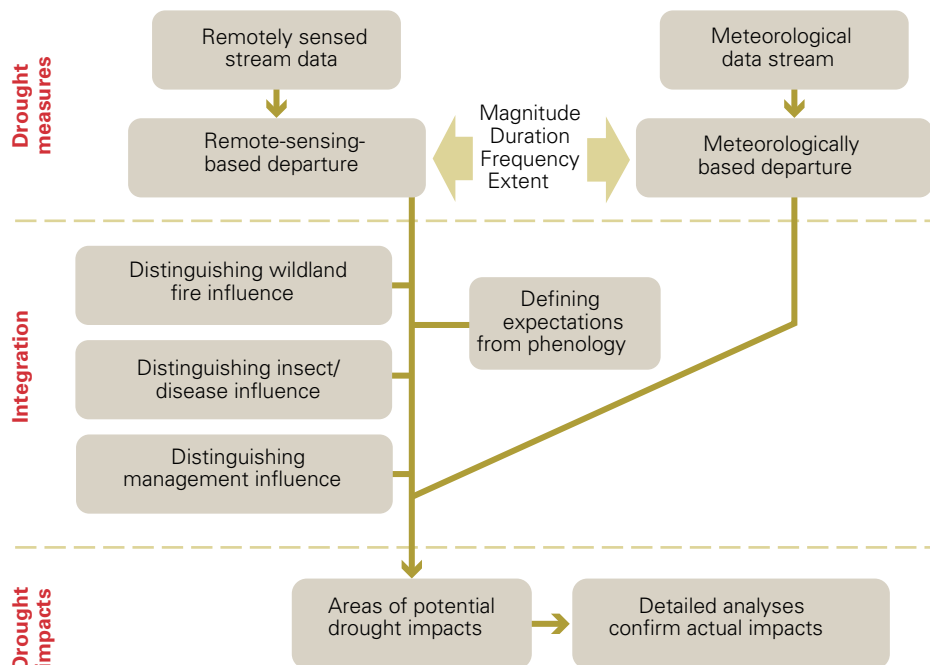


Figure 9.13—Conceptual model of how a “big data” integration approach might be employed in a system for monitoring drought impacts in forests. Fundamentally, areas of potential impacts occur where and when signals from both the remotely sensed and meteorological data streams coincide. Because the remotely sensed data stream documents all kinds of departures from normal vegetation conditions, the integration phase must include ancillary data that can distinguish departures unrelated or only indirectly related to drought. Detailed confirmatory analyses might include, for example, using Forest Inventory and Analysis (FIA) data retrospectively to look for tree growth declines or increases in tree mortality in areas where drought impacts were predicted.

Many of the newest generation of remote-sensing-based drought monitoring systems (table 9.3) are adopting such multivariate approaches. These multivariate approaches mirror appropriately the multivariate nature of drought effects and impacts themselves (as shown in fig. 9.5B). However, we must avoid subjective or quantitative “black box” solutions that infer impacts. We must move beyond such blind methods if we are to increase our basic understanding of complex drought impacts and the processes controlling them. A filtering approach that isolates particular conditions of vegetation and weather before, during, and after drought can, by looking across space, provide needed “experiments” that can yield insights into drought responses under more stringent conditions, isolating particular effects. Combined with ground-based sampling and monitoring data, such a hybrid approach can inform and enlighten our understanding of drought effects on forests.

Embedding Local Monitoring

Large-scale drought monitoring may not be capable of addressing local drought effects with the desired precision, even when the portions of broad landscapes that are likely to be hardest hit can be efficiently identified by large-scale monitoring efforts. Intensive local assessments can fill in the gaps that are not captured by coarse-scale monitoring (fig. 9.13). These efforts may consist of detailed mapping using high-resolution imagery that may or may not be calibrated with plot data or systematic plot inventories to capture changes of concern, such as reduced growth or tree mortality.

The Forest Inventory and Analysis (FIA) program administers an annualized system of field plot inventories. Under this system, first implemented in the late 1990s, plots are remeasured systematically on a cycle ranging from 5 (Eastern United States) to 10 years (Western United States). Thus, in the Western United States, one-tenth of the established FIA plot locations in any given State are sampled each year. These annual samples attempt to be free of geographic bias (Shaw and others 2005), appear to be sufficient for annual time series analysis of forest growth and mortality, and are able to detect relatively low levels of forest change (Shaw and others 2005). However, because of the temporal remeasurement interval, it may be impractical to link a short-term (e.g., single-year) drought event to mortality or any other impact observed on a plot, since the timing of that impact (i.e., exactly when during the several years since the plot was last visited) cannot

be determined (Liknes and others 2012). Long-term trends (i.e., more than a decade) typically must be studied using a combination of annualized and older periodic inventory data between which there may have been methodological differences. In addition, there is roughly 1 FIA plot per 6,000 forested acres, and there are about 130,000 forested plots nationwide. FIA data are probably best suited to analysis of status and trends at broader spatial scales (Shaw and others 2005). Plot density may be insufficient to detect impacts that are patchy in nature, even if they are manifested over a relatively large geographic region (Liknes and others 2012). Unfortunately, drought-induced tree mortality is often patchy (Allen and others 2010).

Despite such limitations, Gustafson and Sturtevant (2013) concluded that a drought-induced tree mortality signal in the upper Great Lakes region could be uncovered using FIA data. Gustafson (2014) similarly used FIA data to construct predictive models of drought-induced tree mortality (based in part on correlation with the NDSI and SPI in the Northeastern United States). He found that the reliability of these models varied substantially; models for drought-intolerant tree species performed most poorly. Gustafson hypothesized that this may have occurred because long drought periods did not occur in the Northeast during the period when FIA inventories were available.

A major challenge when using FIA data is the inability to ascertain the actual cause of mortality or any other forest health change (Gustafson and Sturtevant 2013). If plots are disturbed, FIA field crews do have the option to assign damage agent codes, and drought is one possible code. However, these codes are reported inconsistently, and, as with the IDS data, field crews may label a disturbed plot according to the primary agent (drought) or the secondary disturbance agent (insect or disease activity). They can also assign multiple agent codes, which might provide some data filtering opportunities. The coarse temporal FIA remeasurements probably lead most field crews to assign secondary damage agents, concealing that these impacts may have been triggered initially by drought.

Ultimately, the best use of FIA data may be for retrospective analyses linking tree mortality and reduced growth to possible explanatory drivers, including drought. For this approach, FIA data might be used in concert with a variety of other data sources, including tree-ring data, remote sensing, meteorological drought index maps, and others. A number of studies

have employed this multivariate approach (Dietze and Moorcroft 2011, Klos and others 2009, Shaw and others 2005, Williams and others 2013). Additionally, through specially commissioned FIA remeasurement surveys, it may be possible to quantify areas experiencing major forest impacts in terms of trees lost and extent of the affected area, as was done by the Texas A&M Forest Service after the exceptional Texas drought in 2011. Final estimates of tree losses and subsequent economic impacts were released within a year (Nielson-Gammon 2012).

Summary

There is much recent interest in understanding how drought effects forests in part because drought and drought-associated forest disturbances are expected to increase with climatic change (Adams and others 2009, Allen and others 2010, Anderegg and others 2012, Breshears and others 2005, Breshears and others 2009, Carnicer and others 2011, Martínez-Vilalta and others 2012, Westerling and others 2006). Yet our ability to systematically and accurately recognize drought effects to forests over broad scales is limited. The most compelling research efforts mostly focus on catastrophic droughts rather than episodic droughts of moderate severity. The collective outcomes of more routine occurrences of moderate drought may be just as important and as impactful as rare, exceptional drought events. In any case, better tools, systems, and indices for dealing operationally with more commonplace drought events of moderate intensity are needed by forest managers and other resource professionals.

Drought is a value-laden term as concerns about particular impacts are implicit in the measures designed and baselines employed. No standard or universal definition is possible or even desirable, given the range of possible effects. Disentangling the various impacts of drought with different measures and ancillary data is part of the extraordinary challenge of dealing with drought effectively. With broad-scale monitoring, it is not possible to cleanly distinguish the effects of drought from the recipients of those effects, as moisture stress is not expressed uniformly across vegetation types (fig. 9.12). The relative composition of vegetation types must be considered in order to gauge the impact of any drought event accurately. In addition to utilizing nonforest species as indicator types that can be used to show what drying or wetting effects trees may be

experiencing, it may become possible to utilize the extreme sensitivity of grasses to drought as a means to “standardize” drought intensity universally across all vegetation types, including trees. Understanding drought impacts on trees may require a longer history and a longer period of calculating baselines. Similarly, drought metrics for trees may require a longer, multiyear “memory” of antecedent conditions in order to be useful. New indices specific to trees are needed, because while metrics repurposed from agricultural crop use may work well for forests, these drought indices could be adapted in ways that increase their relevance for forests, in particular. Adaptations might include reformulating drought measures to capture long-duration multiyear drought, targeting drought measures to the sensitive seasons of the year based on phenological insights, or embracing baselines that relate better to the nonequilibrium nature of forested ecosystems.

Taking a broad view, drought effects to forests include direct and secondary effects that must all be addressed to understand each individually and the effects of climate extremes more fully. While wildfire, insects, and diseases can only partially be attributable to drought (fig. 9.5B), a change in drought-sensitive disturbance regimes may be the primary means by which drought alters forests in coming decades. While some drought-sensitive disturbances can be monitored using the same types of systems used for monitoring changes in productivity or mortality, attribution back to drought as the prime mover often requires integration of independent wildfire and insect and disease inventories and datasets.

Because of their inherently multivariate nature, efforts to characterize drought effects on forest landscapes will necessarily involve the integration of information, as knowledge of species, communities, disturbances, and mitigating factors are obtained from a multitude of different programmatic efforts. Interpretation is not inherent in monitoring when indicators are sensitive but coarse, and “big data” help translate observations to effects of specific concern (fig. 9.13). To make large-scale drought monitoring and assessment more accessible, we need an integrating framework for organizing knowledge that efficiently narrows down what is and is not likely to be a drought effect. This knowledge can help prioritize applied efforts for drought mitigation, adaptation, or response more generally.

Literature Cited

- Adams, H.D.; M. Guardiola-Claramonte, G.A.; Barron-Gafford J.C. [and others]. 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences*. 106: 7063-7066.
- Allen, C.D.; Breshears, D.D. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences*. 95: 14,839-14,842.
- Allen, C.D.; Macalady, A.K.; Chenchouni, H. [and others]. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*. 259: 660-684.
- Anderegg, L.D.L.; Anderegg, W.R.L.; Berry, J.A. 2013. Not all droughts are created equal: translating meteorological drought into woody plant mortality. *Tree Physiology*. 33: 672-683.
- Anderegg, W.R.L.; Berry, J.A.; Smith, D.D. [and others]. 2012. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *Proceedings of the National Academy of Sciences*. 109(1): 233-237.
- Andreadis, K.M.; Clark, E.A.; Wood, A.W. [and others]. 2005. Twentieth-century drought in the conterminous United States. *Journal of Hydrometeorology*. 6: 985-1001.
- Archaux, F.; Wolters, V. 2006. Impact of summer drought on forest biodiversity: what do we know? *Annals of Forest Science*. 63: 645-652.
- Arshad, S.; Morid, S.; Mobasheri, M.R. [and others]. 2013. Monitoring and forecasting drought impact on dryland farming areas. *International Journal of Climatology*. 33: 2068-2081.
- Asner, G.P.; Alencar, A. 2010. Drought impacts on the Amazon forest: the remote sensing perspective. *New Phytologist*. 187: 569-578.
- Ayres, M.P.; Lombardero, M.A.J. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Science of The Total Environment*. 262: 263-286.
- Bellingham, P.J.; Sparrow, A.D. 2000. Resprouting as a life history strategy in woody plant communities. *Oikos*. 89: 409-416.
- Berg, E.E.; Chapin, F.S. 1994. Needle loss as a mechanism of winter drought avoidance in boreal conifers. *Canadian Journal of Forest Research*. 24: 1144-1148.
- Bergman, K.H.; Sabol, P.; Miskus, D. 1988. Experimental indices for monitoring global drought conditions. In: *Proceedings of the Thirteenth Annual Climate Diagnostics Workshop*, Cambridge, MA. Washington: U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Weather Service: 190-196.
- Bigler, C.; Gavin, D.G.; Gunning, C.; Veblen, T.T. 2007. Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains. *Oikos*. 116: 1983-1994.
- Bond, W.J.; Midgley, J.J. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology and Evolution*. 16: 45-51.
- Bréda, N.; Huc, R.; Granier, A.; Dreyer, E. 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*. 63: 625-644.
- Breshears, D.D.; Cobb, N.S.; Rich, P.H. [and others]. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences*. 102: 15,144-15,148.
- Breshears, D.D.; Myers, O.B.; Meyer, C.W. [and others]. 2009. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Frontiers in Ecology and the Environment*. 7: 185-189.
- Brown, J.A.; Wardlow, B.D.; Tadesse, T. [and others]. 2008. The Vegetation Drought Response Index (VegDRI): a new integrated approach for monitoring drought stress in vegetation. *GIScience & Remote Sensing*. 45: 16-46.
- Burgan, R.E. 1988. 1988 revisions to the 1978 National Fire-Danger Rating System. Res. Pap. SE-273. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 144 p.
- Carnicer, J.; Coll, M.; Ninyerola, M. [and others]. 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the National Academy of Sciences*. 108: 1474-1478.
- Cox, P.M.; Betts, R.A.; Collins, M. [and others]. 2004. Amazonian forest dieback under climate-carbon cycle projections for the 21st century. *Theoretical and Applied Climatology*. 78: 137-156.
- Daly, C.; Gibson, W.P.; Taylor, G.H. [and others]. 2002. A knowledge-based approach to the statistical mapping of climate. *Climate Research*. 22: 99-113.
- Daly, C.; Halbleib, M.; Smith, J.I. [and others]. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology*. 28: 2031-2064.
- de Beurs, K.M.; Henebry, G.M. 2004. Land surface phenology, climatic variation, and institutional change: Analyzing agricultural land cover change in Kazakhstan. *Remote Sensing of Environment*. 89: 497-509.
- Del Tredici, P. 2001. Sprouting in temperate trees: a morphological and ecological review. *The Botanical Review*. 67: 121-140.
- Deshayes, M.; Guyon, D.; Jeanjean, H. [and others]. 2006. The contribution of remote sensing to the assessment of drought effects in forest ecosystems. *Annals of Forest Science*. 63: 579-595.
- Dietze, M.C.; Moorcroft, P.R. 2011. Tree mortality in the eastern and central United States: patterns and drivers. *Global Change Biology*. 17: 3312-3326.
- Dovčiak, M.; Frelich, L.E.; Reich, P.B. 2005. Pathways in old-field succession to white pine: seed rain, shade, and climate effects. *Ecological Monographs*. 75: 363-378.
- Ewers, R.M.; Didham, R.K. 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*. 81: 117-142.
- Floyd, M.L.; Clifford, M.; Cobb, N.S. [and others]. 2009. Relationship of stand characteristics to drought-induced mortality in three southwestern pinyon-juniper woodlands. *Ecological Applications*. 19: 1223-1230.
- Garen, D.C. 1993. Revised surface-water supply index for western United States. *Journal of Water Resources Planning and Management*. 119: 437-454.
- Grunke, N.E. 2011. The nexus of host and pathogen phenology: understanding the disease triangle with climate change. *New Phytologist*. 189: 8-11.

- Grunke, N.E.; Alonso, R.; Nguyen, T. [and others] C. 2004. Stomata open at night in pole-sized and mature ponderosa pine: implications for O₃ exposure metrics. *Tree Physiology*. 24: 1001-1010.
- Guarín, A.; Taylor, A.H. 2005. Drought triggered tree mortality in mixed conifer forests in Yosemite National Park, California, USA. *Forest Ecology and Management*. 218: 229-244.
- Gustafson, E.J. 2014. Applicability of predictive models of drought-induced tree mortality between the Midwest and Northeast United States. *Forest Science*. 60: 327-334.
- Gustafson, E.J.; Sturtevant, B.R. 2013. Modeling forest mortality caused by drought stress: implications for climate change. *Ecosystems*. 16: 60-74.
- Guttman, N.B.; Quayle, R.G. 1996. A historical perspective of U.S. climate divisions. *Bulletin of the American Meteorological Society*. 77: 293-303.
- Hanson, P.J.; Huston, M.A.; Todd, D.E. 2003. Walker Branch Throughfall Displacement Experiment. In: Hanson, P.J.; Wullschlegel, S.D., eds. *North American temperate deciduous forest responses to changing precipitation regimes*. New York: Springer: 8-31.
- Hanson, P.J.; Weltzin, J.F. 2000. Drought disturbance from climate change: response of United States forests. *The Science of the Total Environment*. 262: 205-220.
- Hao, Z.; AghaKouchak, A.; Nakhjiri, N.; Farahmand, A. 2014. Global integrated drought monitoring and prediction system. *Scientific Data*. 1: 140001. doi: 10.1038/sdata.2014.1. [Published online: March 11, 2004].
- Hargrove, W.; Pickering, J. 1992. Pseudoreplication: a sine qua non for regional ecology. *Landscape Ecology*. 6: 251-258.
- Hargrove, W.W.; Spruce, J.P.; Gasser, G.E.; Hoffman, F.M. 2009. Toward a national early warning system for forest disturbances using remotely sensed canopy phenology. *Photogrammetric Engineering and Remote Sensing*. 75: 1150-1156.
- Heddinghaus, T.R.; Sabol, P. 1991. A review of the Palmer Drought Severity Index and where do we go from here? In: *Proceedings of the Seventh Conference on Applied Climatology*. Boston, MA: American Meteorological Society: 242-246.
- Herweijer, C.; Seager, R.; Cook, E.R.; Emile-Geay, J. 2007. North American droughts of the last millennium from a gridded network of tree-ring data. *Journal of Climate*. 20: 1353-1376.
- Hogg, E.H.; Brandt, J.P.; Michaelian, M. 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. *Canadian Journal of Forest Research*. 38: 1373-1384.
- Hu, J.I.A.; Moore, D.J.P.; Burns, S.P.; Monson, R.K. 2010. Longer growing seasons lead to less carbon sequestration by a subalpine forest. *Global Change Biology*. 16: 771-783.
- Huang, C.-Y.; Anderegg, W.R.L. 2012. Large drought-induced aboveground live biomass losses in southern Rocky Mountain aspen forests. *Global Change Biology*. 18: 1016-1027.
- Huete, A.; Didan, K.; Miura, T. [and others]. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment*. 83: 195-213.
- Huete, A.R. 1988. A soil-adjusted vegetation index (SAVI). *Remote Sensing of Environment*. 25: 295-309.
- Huete, A.R.; Didan, K.; Shimabukuro, Y.E.P. [and others]. 2006. Amazon rainforests green-up with sunlight in dry season. *Geophysical Research Letters*. 33(6): L06405. 4 p. doi: 10.1029/2005GL025583. [Published online: March 22, 2006].
- Huete, A.R.; Saleska, S.R. 2010. Remote sensing of tropical phenology: issues and controversies. *International Archives of the Photogrammetry, Remote Sensing and Spatial Information Science*. 38: 539-541.
- Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*. 54: 187-211.
- Hwang, T.; Band, L.E.; Miniati, C.F. [and others]. 2014. Divergent phenological response to hydroclimate variability in forested mountain watersheds. *Global Change Biology*. 20: 2580-2595.
- Intergovernmental Panel on Climate Change (IPCC). 2007. *Climate Change 2007. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press. 976 p.
- Ji, L.; Peters, A.J. 2003. Assessing vegetation response to drought in the northern Great Plains using vegetation and drought indices. *Remote Sensing of Environment*. 87: 85-98.
- Keetch, J.J.; Byram, G.M. 1968. A drought index for forest fire control. Res. Pap. SE-38. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 35 p.
- Klos, R.J.; Wang, G.G.; Bauerle, W.W.; Rieck, J.R. 2009. Drought impact on forest growth and mortality in the southeast USA: an analysis using Forest Health and Monitoring data. *Ecological Applications*. 19: 699-708.
- Koch, F.H.; Smith, W.D.; Coulston, J.W. 2013a. An improved method for standardized mapping of drought conditions. In: Potter, K.M.; Conkling, B.L., eds. *Forest Health Monitoring: national status, trends, and analysis 2010*. Gen. Tech. Rep. SRS-176. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 67-83.
- Koch, F.H.; Smith, W.D.; Coulston, J.W. 2013b. Recent drought conditions in the conterminous United States. In: Potter, K.M.; Conkling, B.L., eds. *Forest Health Monitoring: national status, trends, and analysis 2011*. Gen. Tech. Rep. SRS-185. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 41-58.
- Koch, F.H.; Smith, W.D.; Coulston, J.W. 2014. Drought patterns in the conterminous United States and Hawaii. In: Potter, K.M.; Conkling, B.L., eds. *Forest Health Monitoring: national status, trends, and analysis 2012*. Gen. Tech. Rep. SRS-198. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 49-72.
- Koch, F.H.; Smith, W.D.; Coulston, J.W. 2015. Drought patterns in the conterminous United States 2012. In: Potter, K.M.; Conkling, B.L., eds. *Forest Health Monitoring: national status, trends, and analysis 2013*. Gen. Tech. Rep. SRS-207. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 55-69.
- Kogan, F.N. 1995. Droughts of the late 1980s in the United States as derived from NOAA polar-orbiting satellite data. *Bulletin of the American Meteorological Society*. 76: 655-668.
- Lamb, P.J.; Changon, S.A. 1981. On the "best" temperature and precipitation normals: the Illinois situation. *Journal of Applied Meteorology*. 20: 1383-1390.
- Laurance, W.F. 2004. Forest-climate interactions in fragmented tropical landscapes. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 359: 345-352.
- Lawrimore, J.; Heim, R.R.; Svoboda, M. [and others]. 2002. Beginning a new era of drought monitoring across North America. *Bulletin of the American Meteorological Society*. 83: 1191-1192.

- Lawrimore, J.H.; Menne, M.J.; Gleason, B.E. [and others]. 2011. An overview of the global historical climatology network monthly mean temperature data set, version 3. *Journal of Geophysical Research*. 116(D19): D19121. 18 p. doi:10.1029/2011JD016187. [Published online: October 15, 2011].
- Liknes, G.C.; Woodall, C.W.; Perry, C.H. 2012. Using inventory data to determine the impact of drought on tree mortality. In: McWilliams, W.; Roesch, F.A., eds. *Monitoring across borders: 2010 joint meeting of the Forest Inventory and Analysis (FIA) Symposium and the Southern Mensurationists*, Knoxville, TN, 5-7 October 2010. e-Gen. Tech. Rep. SRS-157. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 109-112.
- Littell, J.S.; McKenzie, D.; Peterson, D.L.; Westerling, A.L. 2009. Climate and wildfire area burned in western U.S. ecoregions, 1916–2003. *Ecological Applications*. 19: 1003-1021.
- Livezey, R.E.; Vinnikov, K.Y.; Timofeyeva, M.M. [and others]. 2007. Estimation and extrapolation of climate normals and climatic trends. *Journal of Applied Meteorology and Climatology*. 46: 1759-1776.
- Lobo, A.; Maisongrande, P. 2006. Stratified analysis of satellite imagery of SW Europe during summer 2003: the differential response of vegetation classes to increased water deficit. *Hydrology and Earth System Sciences*. 10: 151-164.
- Luo, L.; Wood, E.F. 2007. Monitoring and predicting the 2007 U.S. drought. *Geophysical Research Letters*. 34: L22702. 6 p. doi:10.1029/2007GL031673. [Published online: November 20, 2007].
- Martínez-Vilalta, J.; Lloret, F.; Breshears, D.D. 2012. Drought-induced forest decline: causes, scope and implications. *Biology Letters*. 8: 689-691.
- Mattson, W.J.; Haack, R.A. 1987. The role of drought in outbreaks of plant-eating insects. *BioScience*. 37: 110-118.
- McDowell, N.G.; Beerling, D.J.; Breshears, D.D. [and others]. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology and Evolution*. 26: 523-532.
- McDowell, N.G.; Pockman, W.T.; Allen, C.D. [and others]. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist*. 178: 719-739.
- McKee, T.B.; Doesken, N.J.; Kleist, J. 1993. The relationship of drought frequency and duration to time scales. In: *Proceedings of the Eighth Conference on Applied Climatology*. Boston: American Meteorological Society: 179-184.
- Meddens, A.J.H.; Hicke, J.A.; Ferguson, C.A. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the Western United States. *Ecological Applications*. 22: 1876-1891.
- Mendelsohn, R.; Kurukulasuriya, P.; Basist, A. [and others]. 2007. Climate analysis with satellite versus weather station data. *Climatic Change*. 81: 71-83.
- Menne, M.J.; Durre, I.; Vose, R.S. [and others]. 2012. An overview of the global historical climatology network-daily database. *Journal of Atmospheric and Oceanic Technology*. 29: 897-910.
- Meyn, A.; White, P.S.; Buhk, C.; Jentsch, A. 2007. Environmental drivers of large, infrequent wildfires: the emerging conceptual model. *Progress in Physical Geography*. 31: 287-312.
- Michaelian, M.; Hogg, E.H.; Hall, R.J.; Arsenault, E. 2011. Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Global Change Biology*. 17: 2084-2094.
- Mildrexler, D.J.; Zhao, M.; Heinsch, F.A.; Running, S.W. 2007. A new satellite-based methodology for continental-scale disturbance detection. *Ecological Applications*. 17: 235-250.
- Mildrexler, D.J.; Zhao, M.; Running, S.W. 2009. Testing a MODIS global disturbance index across North America. *Remote Sensing of Environment*. 113: 2103-2117.
- Millar, C.I.; Westfall, R.D.; Delany, D.L. 2007. Response of high-elevation limber pine (*Pinus flexilis*) to multiyear droughts and 20th-century warming, Sierra Nevada, California, U.S.A. *Canadian Journal of Forest Research*. 37: 2508-2520.
- Mishra, A.K.; Singh, V.P. 2010. A review of drought concepts. *Journal of Hydrology*. 391: 202-216.
- Mitchell, P.J.; O'Grady, A.P.; Hayes, K.R.; Pinkard, E.A. 2014. Exposure of trees to drought-induced die-off is defined by a common climatic threshold across different vegetation types. *Ecology and Evolution*. 4: 1088-1101.
- Morton, D.C.; Nagol, J.; Carabajal, C.C. [and others]. 2014. Amazon forests maintain consistent canopy structure and greenness during the dry season. *Nature*. 506: 221-224.
- Mueller, R.C.; Scudder, C.M.; Porter, M.E. [and others]. 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. *Journal of Ecology*. 93: 1085-1093.
- Myneni, R.B.; Yang, W.; Nemani, R.R. [and others]. 2007. Large seasonal swings in leaf area of Amazon rainforests. *Proceedings of the National Academy of Sciences*. 104: 4820-4823.
- Nepstad, D.C.; Stickler, C.M.; Soares-Filho, B.S.; Merry, F. 2008. Interactions among Amazon land use, forests and climate: prospects for a near-term forest tipping point. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 363: 1737-1746. doi:10.1098/rstb.2007.0036. [Published online: February 11, 2008].
- Nielsen-Gammon, J.W. 2012. The 2011 Texas drought. *Texas Water Journal*. 3: 59-95.
- Niinemets, Ü. 2010. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. *Forest Ecology and Management*. 260: 1623-1639.
- Norman, S.P.; Taylor, A.H. 2005. Pine forest expansion along a forest-meadow ecotone in northeastern California, USA. *Forest Ecology and Management*. 215: 51-68.
- Nowacki, G.J.; Abrams, M.D. 2008. The demise of fire and "mesophication" of forests in the Eastern United States. *BioScience*. 58: 123-138.
- Orwig, D.A.; Abrams, M.D. 1997. Variation in radial growth responses to drought among species, site, and canopy strata. *Trees*. 11: 474-484.
- Palmer, W.C. 1965. *Meteorological drought*. Research Paper No. 45. Washington, DC: U.S. Department of Commerce, Weather Bureau. 58 p.
- Palmer, W.C. 1968. Keeping track of crop moisture conditions, nationwide: the new Crop Moisture Index. *Weatherwise* 21(4): 156-161.
- Panu, U.S.; Sharma, T.C. 2002. Challenges in drought research: some perspectives and future directions. *Hydrological Sciences Journal*. 47(S1): S19-S30. doi:10.1080/02626660209493019. [Published online: December 29, 2009].

- Peters, A.J.; Rundquist, D.C.; Wilhite, D.A. 1991. Satellite detection of the geographic core of the 1988 Nebraska drought. *Agricultural and Forest Meteorology*. 57: 35-47.
- Peters, A.J.; Walter-Shea, E.A.; Ji, L. [and others]. 2002. Drought monitoring with NDVI-based Standardized Vegetation Index. *Photogrammetric Engineering and Remote Sensing*. 68: 71-75.
- Phillips, O.L.; Aragão, L.E.O.C.; Lewis, S.L. [and others]. 2009. Drought sensitivity of the Amazon Rainforest. *Science*. 323: 1344-1347.
- Pickett, S.T.A. 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E., ed. *Long-term studies in ecology: approaches and alternatives*. New York: Springer-Verlag: 110-135.
- Raffa, K.F.; Aukema, B.H.; Bentz, B.J. [and others]. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience*. 58: 501-517.
- Riitters, K.H.; Wickham, J.D. 2003. How far to the nearest road? *Frontiers in Ecology and the Environment*. 1: 125-129.
- Riitters, K.H.; Wickham, J.D.; O'Neill, R.V. [and others]. 2002. Fragmentation of Continental United States Forests. *Ecosystems*. 5: 815-822.
- Rouse, J.W.; Haas, R.H.; Schell, J.A.; Deering, D.W. 1973. Monitoring vegetation systems in the Great Plains with ERTS. In: Freden, S.C.; Mercanti, E.P.; Becker, M.A., eds. *Third Earth Resources Technology Satellite-1 Symposium*. Vol. I. NASA SP-351. Washington, DC: National Aeronautic Space Administration: 309-317.
- Saleska, S.R.; Didan, K.; Huete, A.R.; da Rocha, H.R. 2007. Amazon forests green-up during 2005 drought. *Science*. 318(5850): 612.
- Samanta, A.; Ganguly, S.; Myneni, R.B. 2011. MODIS enhanced vegetation index data do not show greening of Amazon forests during the 2005 drought. *New Phytologist*. 189: 11-15.
- Savage, M. 1997. The role of anthropogenic influences in a mixed-conifer forest mortality Episode. *Journal of Vegetation Science*. 8: 95-104.
- Savage, M.; Brown, P.M.; Feddema, J. 1996. The role of climate in a pine forest regeneration pulse in the Southwestern United States. *Ecoscience*. 3: 310-318.
- Schneider, P.; Roberts, D.A.; Kyriakidis, P.C. 2008. A VARI-based relative greenness from MODIS data for computing the Fire Potential Index. *Remote Sensing of Environment*. 112: 1151-1167.
- Schowalter, T.D.; Hargrove, W.W.; Crossley, D.A. 1986. Herbivory in forested ecosystems. *Annual Review of Entomology*. 31: 177-196.
- Shafer, B.A.; Dezman, L.E. 1982. Development of a surface water supply index (SWSI) to assess the severity of drought conditions in snowpack runoff areas. In: Henderson, T.J. *Proceedings of the 50th Annual Western Snow Conference*. Western Snow Conference, Reno, NV. Fort Collins, CO: Colorado State University: 164-175.
- Shaw, J.D.; Steed, B.E.; DeBlander, L.T. 2005. Forest Inventory and Analysis (FIA) annual inventory answers the question: what is happening to pinyon-juniper woodlands? *Journal of Forestry*. 103: 280-285.
- Sims, D.A.; Brzostek, E.R.; Rahman, A.F. [and others]. 2014. An improved approach for remotely sensing water stress impacts on forest C uptake. *Global Change Biology*. 20: 2856-2866.
- Soudani, K.; François, C. 2014. Remote sensing: a green illusion. *Nature*. 506: 165-166.
- Sousa, W.P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics*. 15: 353-391.
- Steinemann, A. 2003. Drought indicators and triggers: a stochastic approach to evaluation. *Journal of the American Water Resources Association*. 39: 1217-1233.
- Svoboda, M.D.; LeCompte, D.; Hayes, M.J. [and others]. 2002. The drought monitor. *Bulletin of the American Meteorological Society*. 83: 1181-1190.
- Svoboda, M.D.; Hayes, M.J.; Wilhite, D.A.; Tadesse, T. 2004. Recent advances in drought monitoring. In: 14th Conference on Applied Climatology, Seattle, WA, 10-16 January 2004. American Meteorological Society. Paper J2.4. 4 p.
- Tadesse, T.; Brown, J.F.; Hayes, M.J. 2005. A new approach for predicting drought-related vegetation stress: integrating satellite, climate, and biophysical data over the U.S. central plains. *ISPRS Journal of Photogrammetry and Remote Sensing*. 59: 244-253.
- Thornthwaite, C.W. 1948. An approach towards a rational classification of climate. *Geographical Review*. 38: 55-94.
- Tilman, D. 1989. Ecological experiments: strengths and conceptual problems. In: Likens, G.E., ed. *Long-term studies in ecology: approaches and alternatives*. New York: Springer-Verlag: 136-157.
- Trouet, V.; Taylor, A.H.; Wahl, E.R. [and others]. 2010. Fire-climate interactions in the American West since 1400 CE. *Geophysical Research Letters*. 37:L04702. 5 p. doi:10.1029/2009GL041695. [Published online: February 25, 2010].
- Tucker, C.J. 1979. Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sensing of Environment*. 8: 127-150.
- Vesk, P.A.; Westoby, M. 2004. Sprouting ability across diverse disturbances and vegetation types worldwide. *Journal of Ecology*. 92: 310-320.
- Vicente-Serrano, S.M.; Beguería, S.; López-Moreno, J.I. 2010. A multiscale drought index sensitive to global warming: the Standardized Precipitation Evapotranspiration Index. *Journal of Climate*. 23: 1696-1718.
- Vicente-Serrano, S.M.; Beguería, S.; Lorenzo-Lacruz, J. [and others]. 2012. Performance of drought indices for ecological, agricultural, and hydrological applications. *Earth Interactions*. 16: 1-27.
- Vicente-Serrano, S.M.; Gouveia, C.; Camarero, J.J. [and others]. 2013. Response of vegetation to drought time-scales across global land biomes. *Proceedings of the National Academy of Sciences*. 110: 52-57.
- Vitasse, Y.; Porté, A.; Kremer, A. [and others]. 2009. Responses of canopy duration to temperature changes in four temperate tree species: relative contributions of spring and autumn leaf phenology. *Oecologia*. 161: 187-198.
- Volaire, F.; Norton, M. 2006. Summer dormancy in perennial temperate grasses. *Annals of Botany*. 98: 927-933.
- Wang, W.; Peng, C.; Kneeshaw, D.D. [and others]. 2012. Drought-induced tree mortality: ecological consequences, causes, and modeling. *Environmental Reviews*. 20: 109-121.
- Westerling, A.L.; Hidalgo, H.G.; Cayan, D.R.; Swetnam, T.W. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science*. 313: 940-943.

- White, M.A.; Hoffman, F.; Hargrove, W.W.; Nemani, R.R. 2005.** A global framework for monitoring phenological responses to climate change. *Geophysical Research Letters*. 32: L04705. 4 p. doi:10.1029/2004GL021961. [Published online: February 18, 2005].
- Wilhite, D.; Svoboda, M.; Hayes, M. 2007.** Understanding the complex impacts of drought: a key to enhancing drought mitigation and preparedness. *Water Resources Management*. 21: 763-774.
- Wilhite, D.A.; Glantz, M.H. 1985.** Understanding: the drought phenomenon: the role of definitions. *Water International*. 10: 111-120.
- Wilks, D.S. 2013.** Projecting “normals” in a nonstationary climate. *Journal of Applied Meteorology and Climatology*. 52: 289-302.
- Williams, A.P.; Allen, C.D.; Macalady, A.K. [and others]. 2013.** Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change*. 3: 292-297.
- Williams, A.P.; Allen, C.D.; Millar, C.I. [and others]. 2010.** Forest responses to increasing aridity and warmth in the southwestern United States. *Proceedings of the National Academy of Sciences*. 107: 21,289-21,294.
- Wilson, E.H.; Sader, S.A. 2002.** Detection of forest harvest type using multiple dates of Landsat TM imagery. *Remote Sensing of Environment*. 80: 385-396.
- Woodall, C.W.; Oswald, C.M.; Westfall, J.A. [and others]. 2009.** An indicator of tree migration in forests of the Eastern United States. *Forest Ecology and Management*. 257: 1434-1444.
- Wullschlegel, S.D.; Hanson, P.J. 2006.** Sensitivity of canopy transpiration to altered precipitation in an upland oak forest: evidence from a long-term field manipulation study. *Global Change Biology*. 12: 97-109.
- Zhang, Y.; Peng, C.; Li, W. [and others]. 2013.** Monitoring and estimating drought-induced impacts on forest structure, growth, function, and ecosystem services using remote-sensing data: recent progress and future challenges. *Environmental Reviews*. 21: 103-115.
- Zhou, L.; Tian, Y.; Myneni, R.B. [and others]. 2014.** Widespread decline of Congo rainforest greenness in the past decade. *Nature*. 509: 86-90.

Ecohydrological Implications of Drought

James M. Vose
Chelcy Ford Miniat
Charles H. Luce

CONTRIBUTORS

Heidi Asbjornsen, Peter V. Caldwell,
John L. Campbell, Gordon E. Grant,
Daniel J. Isaak, Steven P. Loheide, and Ge Sun

J.M. Vose is a Research Ecologist, U.S. Department of Agriculture, Forest Service, Southern Research Station (SRS), Center for Integrated Forest Science (CIFS), North Carolina State University, Department of Forestry and Environmental Resources, Raleigh, NC 27695.

C.F. Miniat is a Research Ecologist, U.S. Department of Agriculture, Forest Service, Southern Research Station (SRS), Center for Watershed Science, Coweeta Hydrologic Laboratory, Otto, NC 28763.

C.H. Luce is a Research Hydrologist, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Boise, ID 83702.

H. Asbjornsen is an Associate Professor, University of New Hampshire, Department of Natural Resources, Durham, NH 03824; **P.V. Caldwell** is a Research Hydrologist, U.S. Department of Agriculture, Forest Service, Southern Research Station, Center for Watershed Science, Coweeta Hydrologic Laboratory, Otto, NC 28763; **J.L. Campbell** is a Research Ecologist, U.S. Department of Agriculture, Forest Service, Northern Research Station (NRS), Center for Research on Ecosystem Change, Durham, NH 03824;

G.E. Grant is a Research Hydrologist, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station (PNW), Ecological Process and Function Program, Forestry Science Laboratory, Corvallis, OR 97331; **D.J. Isaak** is a Research Fish Biologist, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Boise, ID, 83702; **S.P. Loheide** is an Associate Professor, University of Wisconsin, Civil and Environmental Engineering, Madison, WI 53706; **G. Sun** is a Research Hydrologist, U.S. Department of Agriculture, Forest Service, Southern Research Station (SRS), Eastern Forest Environmental Threat Assessment Center (EFETAC), Raleigh, NC 27695.

Introduction

Ecohydrology focuses on the interactions and interrelationships between hydrological processes and the structure and function of vegetation (Breshears 2005, Rodriguez-Iturbe 2000). It builds on a long history of watershed science that quantified how changes in vegetation (e.g., through purposeful manipulation, succession, or natural disturbances) alters water and streamflow dynamics at catchment scales (Bosch and Hewlett 1982, Vose and others 2014). Recent papers have broadened the scope to include understanding soil moisture dynamics (D’Odorinco and others 2010, Emanuel and others 2010), human-dominated landscapes (Jackson and others 2009), and the sensitivity of ecosystem transitions after disturbance (Viglizzo and others 2014). In this chapter, we focus on how drought affects the interrelationships among forest structure and function, hydrologic processes, and streamflow dynamics.

Forests naturally grow where water is sufficient to support perennial woody vegetation, as forest evapotranspiration (ET) is typically much greater than other vegetation types (Frank and Inouye 1994, Sun and others 2011). Where precipitation (P) inputs substantially exceed ET losses, surface water draining forest land is typically of high quality and supports many human uses, including drinking water, agriculture, and industrial activities (Binkley and Brown 1993, Vose and others 2011). Forests also maintain relatively clean and cold water and are important for supporting aquatic ecosystems, particularly coldwater fishes (Peterson and others 2013, Rieman and others 2003). In addition to being important for providing high-quality surface water supply, forests modulate the quantity and timing of streamflows by intercepting and transpiring precipitation (Sun and others 2011) and influence snowmelt timing (Cristea and others 2013). Forests are also commonly important areas for groundwater recharge (Price 2011) and flood mitigation (Beschta and others 2000, Jones and Perkins 2010).

In simple terms, drought means less water—less water for plants and less water for streams. In some regions, seasonal droughts are common, and forest and stream ecosystems often adapt to these somewhat predictable disturbances through various physiological, morphological, and behavioral adaptations (Lytle and Poff 2004, McDowell and others 2008). In contrast, multiyear or severe droughts are less predictable, and hydrological

and biogeochemical responses can be substantial (Lake 2003). This is especially true when very low precipitation is combined with warmer temperatures (Difflenbaugh and others 2015). The relationships among drought, surface water flow, soil water availability, and groundwater recharge are not straightforward for most forest ecosystems due to several factors, including the role of vegetation in the forest water balance. Hydrologic responses to drought can be either mitigated or exacerbated by forest vegetation depending upon vegetation water use and how drought affects forest population dynamics.

We can conceptualize a simple framework for assessing the drought sensitivity of a forest catchment by describing it as a series of four hydrologic pools: (1) vegetation, (2) soil, (3) groundwater, and (4) streams (fig. 10.1). Examining the sensitivity of streamflow to drought can be framed by looking at the duration that water is held in each pool and how much evaporative or transpiration losses occur from those pools. The first pool to intercept P is the vegetation surface (i.e., leaves, stems, boles). Some of the intercepted P (10–40 percent) evaporates back into the atmosphere. The wide range in intercepted P lost to evaporation is primarily related to vegetation surface area and rainfall characteristics, with a greater percentage of P intercepted with larger surface area and during light rain events (Eagleson 2002, Waring and Schlesinger 1985). Precipitation that is not intercepted (i.e., throughfall and stemflow) enters the forest floor where some (or all) may evaporate from the litter layer, or it may

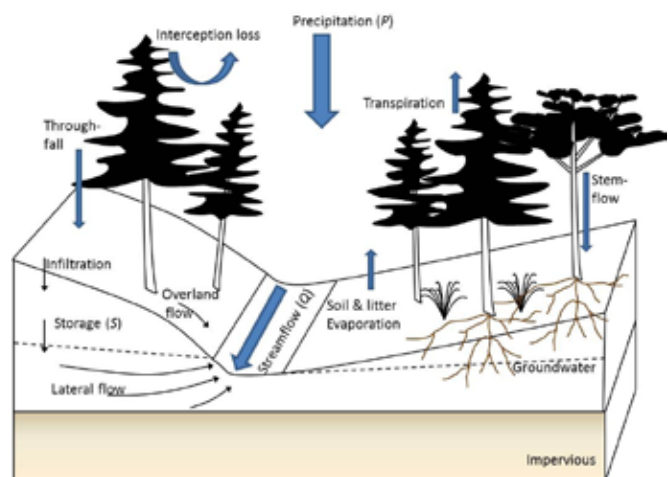


Figure 10.1—Conceptualization of major water pools and fluxes in a forested catchment. The catchment water balance can be viewed as partitioning of precipitation into evapotranspirative and drainage fluxes.

move across the leaf/soil surface as overland flow. The remainder enters the soil water storage pool. Stored soil water can be evaporated or transpired by plants before becoming streamflow or recharging groundwater. While some water is temporarily stored in the roots and boles, most of the soil water taken up by tree roots moves through the internal vegetation pool quickly and returns to the atmosphere. For some forests, roots capture much of the water that does not freely drain to groundwater within a brief period after precipitation (Brooks and others 2009). If roots can access groundwater, they can deplete groundwater pools. However, when groundwater pools contain sufficient water, they can provide long-term base flows (Tague and Grant 2009), buffering streamflow against long periods without P .

The connections among the pools can be expressed using a simple water balance equation:

$$Q = P - ET - \Delta S$$

where Q represents streamflow and is the balance of precipitation inputs (P) after losses to evapotranspiration (ET), which is the sum of interception, transpiration, and soil evaporation, and changes in storage (ΔS). Over the short term, all four variables can change dramatically; however, over the long term (e.g., annually), change in ΔS is typically minor and is therefore often assumed to be zero. Thus, Q can be estimated as P minus ET . The assumption that changes in storage are zero under severe drought conditions may not be correct in some instances and may yield incorrect interpretations of the impacts of drought on Q using $P - ET$ approaches (Creutzfeldt and others 2012, Vose and Swank 1994). Regardless, Q can change in response to drought directly through reductions in P and indirectly via ET responses to changing evaporative energy and water availability; however, these responses are especially complex.

For a particular watershed, drought effects on Q can vary greatly in space and time depending on the timing of reduced precipitation inputs (growing season versus nongrowing season), the magnitude of precipitation deficit, and watershed characteristics (e.g., vegetation, watershed size and configuration, terrain features, soil depth and storage capacity, and hydrogeology). For example, on shorter time scales, ET can exceed P , particularly when water used in ET is derived from soil water stores or deeper groundwater stores, rather than recent or local P (Loheide and others 2005, Lubczynski and Gurwin 2005).

In this chapter, we (1) review the relationships between meteorological and hydrologic drought; (2) examine how differences in forest species composition and structure impact evapotranspiration, and we interpret these changes in the context of mitigating or exacerbating hydrologic drought; and (3) discuss the impacts of hydrologic drought on watershed processes and water quality.

Relationship Between Meteorological Drought and Hydrologic Drought

Meteorological drought is defined as the degree and duration of dryness relative to the average (chapter 2); the effects of meteorological drought on streamflow may differ across and within forest ecosystems. Hydrologic drought, defined as decreases in streamflow below a threshold level (chapter 2), is complex and difficult to relate to meteorological drivers. In this section, we describe how catchment characteristics and precipitation patterns influence the relationship between meteorological and hydrologic drought.

Catchment-Scale Sensitivity to Meteorological Drought

The catchment water-balance equation provides a conceptual framework for evaluating differential sensitivities of ET and Q to drought. In general, sensitivity depends most strongly on temporal and spatial storage in soil and groundwater pools, as well as snowpack in snow-dominated ecosystems. For example, in places with deep soils and hence greater soil water storage, there may be an apparent reduced sensitivity of ET and Q to reduced precipitation (Boggs and others 2013, Ohnuki and others 2008) that may help enhance resilience to drought (Taylor and others 2013). In contrast, steep, coarse, and shallow soils that cannot retain water may represent systems with high ET and Q sensitivity to reduced precipitation. If accessible by trees roots, soil stores are more vulnerable to ET , so they deplete more rapidly and approach a state of near zero discharge much sooner (Fan and Miguez-Macho 2011).

The sensitivity of low flows to meteorological drought in places with deep or substantial groundwater storage should be thought of in two ways (Tague and Grant 2009). In terms of absolute flow, they are more sensitive than systems with little storage because they generally sustain greater baseflow than systems with shallow and tight bedrock, and even a small fractional decline in low flows can be a large amount of water. In

contrast, places with little baseflow cannot decline far in absolute terms, simply because there is already so little runoff. However, when cast as a percent change due to either drought duration or precipitation recharge, the systems with greater groundwater storage are less sensitive. This differs from sensitivity to variations in the soil store, as we defined it, because water stored in soils (generally places where roots are more abundant) is vulnerable to ET , but deep groundwater is not.

Streamflow from forests where the snowpack makes up a large proportion of annual P is more sensitive to precipitation declines. When the annual precipitation is delivered as meltwater in one relatively large pulse, runoff generation is more efficient, and variations in potential ET have little effect on the total annual runoff, which is essentially dependent on how much snow accumulates and then melts. Similarly, if most of the precipitation falls in the cold season, it is less vulnerable to evaporation and is converted more efficiently to runoff. In such cases, ET may vary little as a function of precipitation, but variations in P will be transmitted to runoff reliably on an annual scale (Berghuijs and others 2014, Wolock and McCabe 1999), similar to more humid

locations (Milly and Dunne 2002) and locations with greater seasonality in P (Wolock and McCabe 1999).

High degrees of snow heterogeneity caused by drifting or large elevation ranges in a basin provide substantial buffering of Q variation through the year because deep drifts and high-elevation snowpacks do not melt until late in the summer (Luce and others 1998, Wolock 2003). Snowpack meltwater is slowly released during warmer periods in these systems, making them less vulnerable to variations in summertime precipitation. Buffering from snow heterogeneity is probably most pronounced in the high mountains of the Western United States (Clark and others 2011). We illustrate the spatial variability of drought sensitivity impacts on water yield as a response to a uniform reduction of precipitation in figure 10.2 (Sun and others 2015).

Interactions With Precipitation Patterns

Reduced P not only affects Q through the amount of water available, but also through its timing. For example, in snowpack-dominated areas of the Western United States, a low snowfall winter creates a shallower snowpack that takes less time to melt and can create

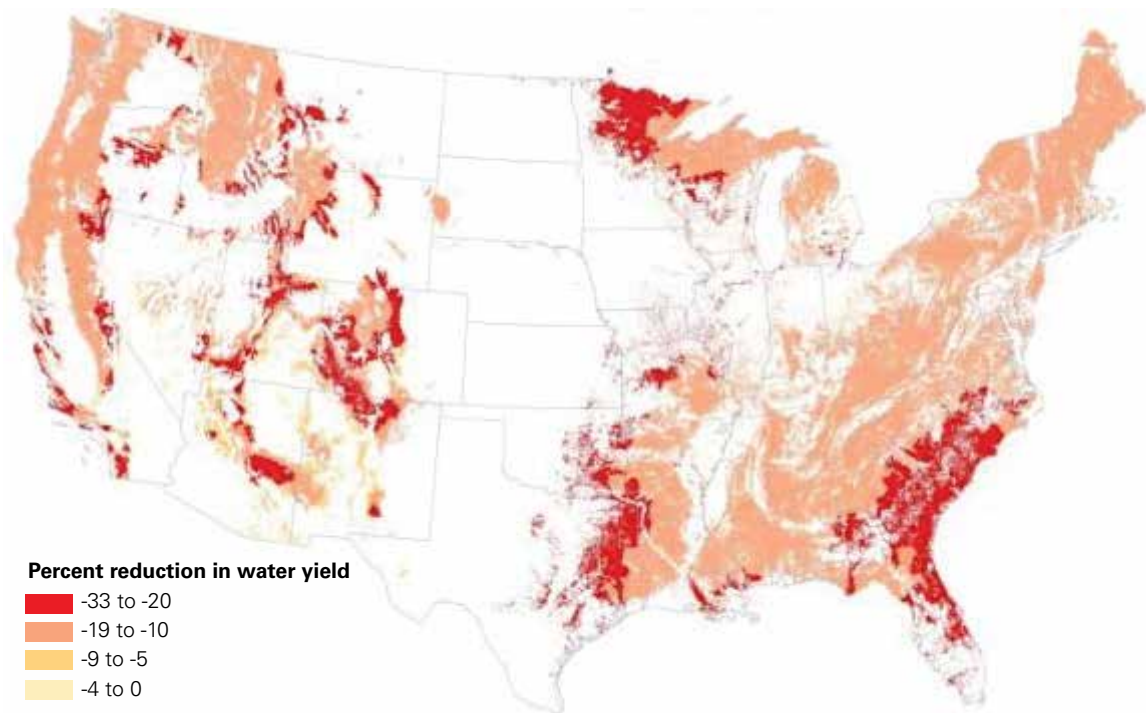


Figure 10.2—Spatial distribution of annual forest water yield response (percent reduction in water yield) to a 10-percent decrease in precipitation across the conterminous United States. Darker shades represent a greater percent reduction relative to lighter shades. Simulation results at the U.S. Geological Survey HUC-8 scale are presented at 1-km resolution by a mask of forest land cover (Source: Sun and others 2015).

an expectation for lower flows in late summer (Cayan and others 2001, Stewart and others 2005, Tague and Grant 2009). While low elevation snowpacks are more sensitive to temperature in determining the melt timing (Mote 2006), the effect of P variability on center of timing of outflow can be quite pronounced from high elevation basins (Luce and Holden 2009). Warming can also shift the elevation of the transition zone between rain and snow, and rain on snow events (Surfleet and Tullos 2013), both of which impact streamflow timing. The synoptic weather patterns giving rise to prolonged drought can also shape the nature of P events, making the relationship between hydrologic drought and meteorological drought dynamic (Potter and Chiew 2011). If limited ET occurs due to dry land surface conditions, convective storms may produce less intense P and less P during a given storm. The reduction in P has implications for a greater proportion being intercepted by canopies or held in soil, reducing runoff. Water added to wet soils or vegetation is more likely to contribute to recharge compared to periodic wetting of a relatively dry soil or canopy. Higher interception evaporation maximizes the potential for recirculation of water between land and atmosphere, but also exacerbates Q responses during prolonged dry periods.

Species Composition, Vegetation Dynamics, and Drought Interactions With Streamflow

Understanding and predicting the complex interactions among species, vegetation dynamics, and streamflow requires integrating atmospheric conditions, above- and belowground plant physiological processes, forest stand dynamics, soil water availability, and streamflow generation processes. Many of these components are discussed in detail in other chapters of this assessment (i.e., chapter 2 characterizes drought for forests and rangelands; chapter 3 summarizes the physiological responses of forest tree species to drought; and chapter 4 addresses drought impacts on forest structure, dynamics, and diversity).

Assessing the ecohydrological implications of drought requires quantification and understanding of how the individual components interact to determine hydrologic responses. Due to the challenges associated with linking ecological and hydrological processes, much of our insight into ecohydrologic feedbacks has been derived from quantifying short-term, species-specific physiological processes from experimental studies; linking and projecting long-term vegetation dynamics;

and interpreting long-term streamflow dynamics under varying ecohydrological conditions.

Vegetation structure and species composition directly impact the hydrologic cycle because they exert significant control on several hydrologic fluxes: evaporation, transpiration, canopy interception, forest floor interception, infiltration, overland flow, groundwater recharge, and streamflow (fig. 10.1). Given that transpiration can represent up to approximately 70 percent of ET (Schlesinger and Jasechko 2014) and ET can represent >100 percent of P (e.g., when ET includes stored soil water or groundwater sources) (Sanford and Selnick 2012), changes in transpiration (e.g., due to shifts in species assemblages) can substantially impact stand water balance and downstream water supply. If drought frequency and duration increase, these will likely lead to significant changes in vegetation structure and species composition. While some trees will die as a direct consequence of moisture stress and cavitation (chapter 3), the interaction between drought and other stressors such as insects and pathogens may be an even more important driver of drought-related mortality (chapter 6).

Extreme droughts and heat waves have already triggered widespread tree mortality globally (Allen and others 2010, Weed and others 2013), and there is observational evidence that forests across all biomes might be equally vulnerable to drought (Choat and others 2012). The detailed physiological mechanisms and thresholds that determine when mortality or dieback will occur for different species are addressed in chapter 3. Here we provide an overview of the potential impacts of drought on species assemblages and consequences for ecohydrological processes, while highlighting examples from different regions within the United States that illustrate possible scenarios for future change.

Generally, when mortality rates increase for a particular species or set of species, whether due to climatic, biotic, or other drivers, stand density of live mature trees decreases and stand leaf area index and productivity decline. This process may either occur abruptly, as in the case of rapid mortality in response to an acute stressor [e.g., eastern hemlock (*Tsuga canadensis*) mortality following attack by hemlock woolly adelgid (*Adelges tsugae*), or western juniper (*Juniperus occidentalis*) mortality following severe drought], or gradually, as in the case of chronic diseases that slowly diminish the health of host trees [such as with beech bark disease (*Neonectria* spp.) infecting American

beech (*Fagus grandifolia* Ehrh.]). Extensive research in mesic forest ecosystems has shown that a reduction in forest cover generally reduces stand transpiration and leads to an increase in streamflow (Bethlahmy 1974, Bosch and Hewlett 1982, Hadley and others 2008, Stednick 1996, Zhang and others 2001); however, these forest-streamflow relationships are less well understood in semi-arid regions and are potentially very different than mesic regions (Wilcox and Thurow 2006). In northern temperate regions, the reduction in canopy cover leads to greater snow accumulation and more rapid snowmelt due to decreased canopy interception and increased solar radiation reaching the forest floor (Boon 2012, Pugh and Small 2012). Depending on the temporal and spatial dynamics of the die-off process, resources that become available after tree mortality are eventually utilized by existing co-dominant mature trees and/or existing or newly regenerating seedlings and saplings in the understory and mid-story; often (but not always) these changes are associated with a shift in species composition.

Because different species and functional groups vary in their ecophysiological traits that influence water use patterns (chapter 3), changes in species assemblages can alter hydrological processes from the stand to the watershed scales. Below, we highlight examples from different regions of the United States of species shifts resulting from global change drivers to illustrate the potential ecohydrological impacts.

Northeastern Region

Although the Northeastern United States is expected to experience an increase in total annual precipitation (mostly in the winter and spring), and an increase in large rainfall events, it is also projected to have more prolonged rainless periods, particularly in mid- to late-summer (Swain and Hayhoe 2014). While the mixed deciduous-coniferous forest ecosystems that dominate the Northeast are more limited by radiation and nutrients than water (Vadeboncoeur 2010), paleoecological evidence suggests that previous droughts have strongly influenced changes in species assemblages and ecosystem dynamics; consequently, such extreme events may be outside the range of species' capacities for adaptation and resilience (Pederson and others 2014). Future drought stress will likely be concomitant with biotic stressors that also may be outside the physiological tolerance of these forests (Dietze and Moorcroft 2011, Groffman and others 2012, Lovett and others 2006). Thus, the ecohydrological effects of tree mortality due to these multiple stressors are particularly

relevant for managing water resources in the Northeast. Here, we discuss two species affected by such climate change-biotic agent interactions specifically within the context of increasing drought stress and potential ecohydrological implications.

Eastern hemlock, an ecologically important species throughout much of its geographical range, is currently experiencing rapid decline due to the hemlock woolly adelgid (HWA), an exotic insect that has invaded forests from Georgia to Maine (Fitzpatrick and others 2012). The primary factor limiting the spread of HWA is overwintering temperatures; increasing winter temperature has accelerated the invasion process and associated hemlock mortality (Paradis and others 2008). Once attacked, eastern hemlock trees usually die within 4–5 years (Young and others 1995); thus, HWA infestations create an acute disturbance event that abruptly changes stand structure and composition.

The most likely scenario for these forests is that hemlock will be replaced by broadleaved deciduous species (Ellison and others 2005, Ford and others 2012). Research shows that this shift in the dominant species will result in higher annual transpiration rates and total ET, in turn causing small decreases in streamflow during the growing season and increased peakflow after large storm events in the dormant season due to decreased canopy interception (Brantley and others 2013, Brantley and others 2014, Ford and Vose 2007). Another hydrologic control of these dense evergreen canopies is their insulating effect on snowcover (Lustenhouwer and others 2012); consequently, hemlock loss and subsequent warming air temperatures will likely alter snowmelt and runoff dynamics during the winter-spring transition period. Post mortality regeneration may offset these impacts to some degree, but impacts will be long lasting if the evergreen canopy is replaced with a deciduous canopy. Finally, while the above studies show that hydrologic impacts of hemlock loss are likely, eastern forests may experience minimal long-term effects on carbon fluxes (Albani and others 2010) because although there can be rapid mortality of hemlock trees following HWA invasion, subsequent replacement by other species—such as red maple (*Acer rubrum* L.), birch (*Betula* spp.), oaks (*Quercus* spp.) and American beech (*Fagus grandifolia* Ehrh.)—also occurs relatively rapidly (Cobb 2010, Ford and others 2012).

American beech has experienced decline since the early 20th century due to beech bark disease (BBD), which is caused by infestation by the exotic scale insect,

Cryptococcus fagisuga (Lind.), and subsequent infection by one or more fungi (Kasson and Livingston 2012). In contrast to HWA, BBD is a chronic disturbance that slowly diminishes the host tree's vitality and health, but usually does not directly cause mortality. Evidence also suggests that a prolonged period of mild winters and drier-than-normal late summers (including a major drought) triggered a significant growth decline and mortality in BBD-infected trees in Maine (Kasson and Livingston 2012); this suggests that the disease lowers the resistance of trees to other stressors. Predictions for future BBD-affected stands are that other associated or co-dominant species, particularly sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*), will replace this species (Forrester and others 2003, Hancock and others 2008, Lovett and others 2013).

Given the slow progression rate of BBD, the shift in forest structure and species composition is expected to also occur gradually, which is confirmed by the lack of a significant change observed in aboveground net primary production in BBD-affected stands in the Catskills region of New York (Hancock and others 2008). Consequently, impacts on the hydrologic cycle may also be gradual (Busby and Canham 2011). Moreover, because many of the associated species (e.g., sugar maple, yellow birch) have similar ecological characteristics and functions to American beech, including transpiration, leaf hydraulic traits, and vulnerability to cavitation (Hoffmann and others 2011, Wullschlegel and others 2001), these changes may not significantly alter stand transpiration and, hence, runoff and streamflow dynamics, although effects will likely vary across different forests and geographic regions.

Western Mountain Region

Recent warming trends and more prolonged and frequent droughts have accelerated the spread and intensity of attacks by mountain pine beetle (MPB) (*Dendroctonus ponderosae*) and increased the susceptibility of host trees, resulting in widespread mortality of five-needle pine and affecting more than 600,000 km² of coniferous forests in western North America since 1996 (Weed and others 2013). Forests that are already water stressed appear to be more vulnerable to severe MPB attacks (Kaiser and others 2013). Because these outbreaks often kill nearly all of the canopy trees within forest stands, they influence the energy balance of the land surface and potentially affect many hydrologic processes (Potts 1984, Pugh and Gordon 2013). MPB-infested watersheds will likely experience a decrease in ET, but an increase in

snow accumulation and earlier and faster snowmelt; combined, these processes would lead to increases in runoff volume and a change in timing (Mikkelsen and others 2013). As a whole, MPB-infested watersheds would be at greater risk for flooding in the spring and drought in the summer (Mikkelsen and others 2013).

Similarly, increased wildfire in western U.S. forests (chapter 7) would be expected to change water yield, timing, and flood potential in basins after fire. Small basins (on the order of 10–20 km²) have shown substantial increases in post-fire debris flows and flooding (Cannon and others 2001, Istanbuluoglu and others 2004, Moody and Martin 2009). However, increases in post-fire flooding have not been noted for large basins on the order of 2,000 km², despite a great enough portion of the basin burning to cause increases in basin water yield by 5 percent (Luce and others 2012).

Southwestern Pinyon-Juniper Woodlands

One region and vegetation type most severely affected by extreme drought and heat events—often in combination with associated increases in stress from biotic agents—is the pinyon-juniper woodlands of the Southwest United States. As a result of these extreme events, this vegetation type has experienced major changes in mortality rates and species composition throughout much of this region, with significant ecohydrological consequences. For instance, widespread mortality has occurred in pinyon pine populations, while western juniper trees have exhibited relatively high survival (Plaut and others 2012) (chapter 3 for mechanisms). During the 2000–2002 severe drought event, streamflow from southwestern watersheds decreased following tree die-off, likely due to increases in the understory vegetation after release from competition and shade, and subsequent reductions in overland flow (Guardiola-Claramonte and others 2011). Widespread vegetation die-off can have contrasting ecohydrological impacts in water-limited versus high rainfall regions; these observations underscore the need for more research to understand the vegetation-drought-hydrology interactions and feedbacks that determine watershed scale effects on streamflow dynamics (Adams and others 2012).

Southern Region

Extensive forest areas in the Southern United States have experienced severe droughts in recent years causing widespread tree mortality in many regions (Elliott and Swank 1994, Klos and others 2009). Some tree species and size classes are more vulnerable than others (chapter

4), suggesting the potential for drought-mediated shifts in both species composition and structure. For example, Klos and others (2009) reported higher drought-related mortality in pine and mesophytic species groups (e.g., *Liriodendron tulipifera*, *Acer* spp., *Betula*, *Fagus*, *Magnolia*) than in oaks (*Quercus* spp.). In contrast, Clinton and others (1993) documented a higher mortality in larger and older oak (especially *Quercus coccinea*) associated with interactions between drought and root pathogens.

Tree-level sapflow data suggest wide variation in whole-tree daily water use among species groups, and different sensitivities to water stress depending on xylem anatomy. A two- to three-fold difference among species (holding tree size constant) in mean daily water use can occur in these forests (Ford and others 2011b), with oaks (e.g., *Quercus rubra*, *Quercus prinus*) generally having lower water use than more mesophytic species (e.g., *Betula lenta*, *Liriodendron tulipifera*) (figs. 10.3 and 10.4). While oaks and hickories have a potential for high water use based on the diameter of their xylem conduits, field observations across the region suggest that these species operate under a fraction of this potential, thus lending support for their low observed water use (fig. 10.4). These tree-based data suggest that drought-related shifts in species composition may impact streamflow, as has been demonstrated by sapflow and ecohydrological studies on species such as eastern hemlock (discussed earlier), and in small paired

watershed studies of hardwood to pine conversions (Ford and others 2011b); however, drought-related changes in species composition may be much more difficult to detect, especially in diverse stands and at larger spatial scales (Patterson and others 2013).

Range Shifts in Major Ecosystem Types in Response to Climate Change

Thus far we have focused the discussion on the ecohydrological impacts of tree mortality of certain species due to drought and interactions with biotic agents; but model projections and some empirical evidence suggest that entire communities will shift their range in response to climate change. In the New England region, models project that by the late 21st century 71–100 percent of boreal conifer forests will be lost; the range of mixed oak-hickory forests will shift northward by 100–200 km and expand by 149–431 percent; and northern deciduous hardwoods will decrease in area by 26 percent (Iverson and Prasad 2001, Tang and Beckage 2010, Tang and others 2012). However, within a community type, individual species' responses will depend on phenology and physiology, with some species benefiting more from decreased stomatal conductance and increased water use efficiencies in response to rising carbon dioxide (CO₂) (Tjoelker and others 1998).

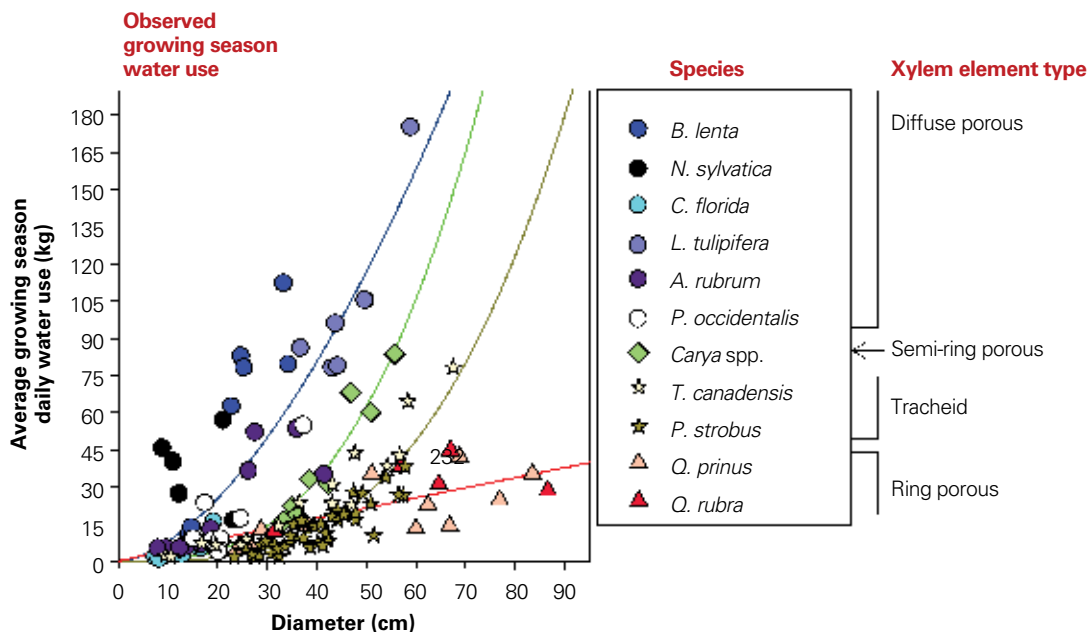


Figure 10.3—Average growing season daily water use across species sampled in the Coweeta Basin. (Source: Ford and others 2011).

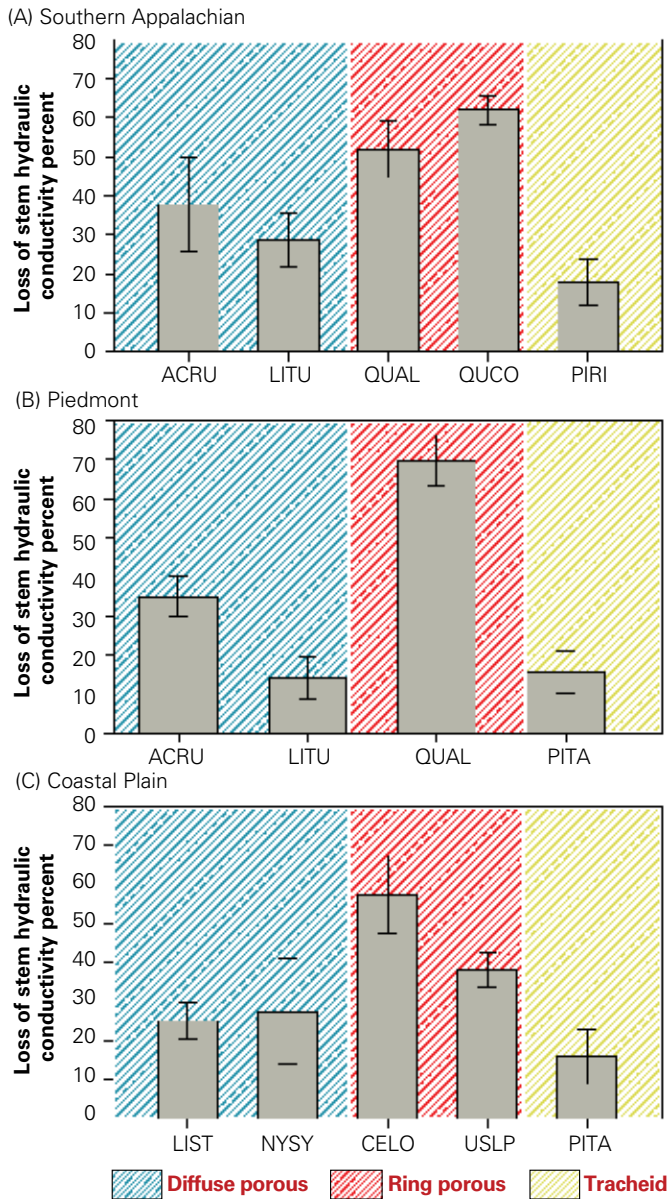


Figure 10.4— Percent loss of hydraulic conductivity (PLC) for co-occurring species varied by xylem type across a regional gradient from (A) Southern Appalachian forests to (B) Piedmont forests to (C) Coastal Plain forests. Ring-porous trees had >50 percent dysfunction under the same soil water potentials as diffuse porous and tracheid-type species. Evidence suggests that mortality occurs when plants experience >80 percent dysfunction. Bars represent the mean PLC across five individuals from each species sampled three times throughout the growing season (May, August, and October 2010). Bars are standard error. PLC was determined using a flowmeter (Xyl'em, Bronkhorst, France) and the following equation: $\{[ks(max) - ks(P)] / ks(max)\}$, where $ks(P)$ is the hydraulic conductivity at the time of sampling from the field, and $ks(max)$ is the conductivity determined after fully saturating the sample under vacuum for 24 hours or with high positive pressure. ACRU=red maple; LITU=tulip poplar; LIST=sweetgum; NYSY=black gum; QUAL=white oak; QUCO=scarlet oak; CELO=sugarberry; USLP=American elm; PIRI=pitch pine; PITA=loblolly pine. (Source: unpublished data; C.F. Miniati and J.M. Vose. On file with: C.F. Miniati, Coweeta Hydrologic Laboratory, 3160 Coweeta Lab Road, Otto, NC 28763; cfminiati@fs.fed.us).

For example, species with evergreen sclerophyllous leaves that characteristically have high mesophyll resistance are predicted to benefit more from increased CO_2 concentrations compared to deciduous broadleaved species (Niinemets and others 2011). The amount of time required for communities to reach a new equilibrium is uncertain; however, observations from past migration rates suggest that species may not keep pace with their climate envelopes (Loarie and others 2009).

Changes in future rainfall patterns may also affect the competitive interactions among species and thus affect the outcome of range shifts (Clark and others 2014a, Clark and others 2014b). For example, because northern deciduous hardwoods tend to be physiologically less drought tolerant than mixed oak-hickory, an increase in precipitation [as predicted by Swain and Hayhoe (2014)] may favor the former and enable them to persist to a greater extent within their current range. Because trees are long-lived, range shifts of forest ecosystems will be a slow process; however, initial shifts are already being detected in the understory regeneration. For instance, Fisichelli and others (2014) showed that seedlings and saplings of temperate forest tree species are establishing across local ecotones into boreal forest patches in central North America, a process facilitated by warmer temperatures.

Boreal conifer regeneration has been negatively correlated with the regional temperature gradient and only displayed high abundance at the boreal end of local ecotones at cool northern sites, suggesting a reduced range for boreal forests in the future (Fisichelli and others 2014). In the Western United States, models project shifts in major vegetation types in response to climate change (Bachelet and others 2001). In addition to climate, an overarching influence on future vegetation types for the Western United States is fire and biotic disturbances (Hicke and others 2012, McKenzie and others 2004). Using models that combine changing fire regimes and climate, Halofsky and others (2013) project an overall decline in cool needle-leaf and subalpine forest vegetation types, and an increase in xeromorphic shrubland types.

Predicting how these changes will impact hydrologic processes at larger spatial scales presents a considerable challenge. Although tree-level physiological data and small watershed studies suggest a strong interaction between vegetation type, structure, and hydrologic processes, we do not know how these interactions and gradual changes will play out at larger landscapes and longer time scales.

Groundwater Interactions With Drought

When available to tree roots, groundwater may help vegetation avoid drought-induced effects (Ehleringer and Dawson 1992). This strategy is well-known in groundwater-dependent ecosystems (Orellana and others 2012) such as wetlands and riparian forests (Busch and others 1992, Thorburn and others 1992), but has also been recognized in upland systems (Dickson and Tomlinson 1996, Miller and others 2010), which can be referred to as groundwater-influenced ecosystems.

Groundwater-dependent ecosystems dominated by phreatophytes, plants dependent on groundwater for their water supply (Meinzer 1927, Robinson 1958), are well studied. Examples include deep-rooted trees and shrubs including cottonwood (*Populus* spp.), willow (*Salix* spp.), salt cedar (*Tamarix* spp.), greasewood (*Adenostoma fasciculatum*, *Baccharis sarothroides*, *Glossopetalon spinescens*, *Larrea tridentate*, and *Sarcobatus vermiculatus*), and mesquite (*Prosopis* spp.). Phreatophytes can be obligate or facultative depending on whether they rely on perennial access or intermittent access to groundwater to avoid drought (Smith and others 1998), with examples in the latter category including sagebrush (*Artemisia* spp.) and rabbitbrush (*Chrysothamnus* spp.) (Nichols 1994). Phreatophytes (particularly those in arid regions) also employ a diverse array of other drought-avoidance and drought-tolerance strategies to survive dry periods including control of the magnitude and timing of leaf area, osmotic potential, leaf conductance, and maintenance of turgor at low leaf water potential (Nielsen and others 1984).

The groundwater subsidies, as defined by Lowry and Loheide (2010), are provided to groundwater-dependent and groundwater-influenced ecosystems buffering them from adverse effects of drought. Maps depicting estimates of depth to groundwater (see fig. 4 in Fan and others 2013) reveal that it is generally <5 m across vast regions of the United States, which is within the critical range required to help offset the impacts of drought in forests and many other ecosystems (Lowry and Loheide 2010, Maxwell and Kollet 2008, Soylu and others 2014). Even when groundwater is not regionally shallow, riparian and other areas may have shallow groundwater (Fan and others 2013) resulting in local areas where groundwater is not sufficient to buffer drought. Heterogeneity in

groundwater depth across the landscape suggests the potential for management and protection strategies aimed at specific resources as the landscape becomes further fragmented into natural, urban, and agricultural systems (Jackson and others 2009).

Challenges to Predicting the Impacts of Drought on Hydrological Processes

Sensitivity analysis and empirical data suggest that the magnitude of hydrologic responses to droughts, due to climate warming or/and reduction in precipitation, vary tremendously under different regimes (Lu and others 2013, Ma and others 2008). Predicting short-term responses to moderate- and short-duration droughts is generally straightforward, especially if drought does not change above- and belowground forest structure. For example, at monthly or annual time scales over large areas, hydrologic models can capture much of the drought-related streamflow dynamics that occur simply as a direct result of reduced precipitation, or indirectly using an empirical soil moisture feedback (Caldwell and others 2012, Sun and others 2011).

In addition to climatic dryness (potential ET/P), terrain characteristics, land cover types, biomass, and soils all influence the potential impacts of droughts on watershed hydrology. This complexity poses considerable challenges for predicting the impacts of drought on hydrological processes. Adding leaf-level physiological responses (either mechanistically or empirically) and soil moisture dynamics can increase predictive ability (Hanson and others 2004), although often these are “big-leaf” models that homogenize canopy variation and belowground responses.

Considerable uncertainty can result if models are unable to accurately account for above- and belowground structural and functional vegetation responses that can occur after severe and/or long-term drought (Luo and others 2008, Tague and others 2013). Examples of long-term vegetation responses to drought include reduced leaf area index from abscission or mortality, altered root-to-shoot ratios (Joslin and others 2007), differential species responses in mixed species stands (Ford and others 2011a), and changing species composition (Anderegg and others 2013, Klos and others 2009). All of these factors drive or feed back to ET, ultimately influencing stand water balance and streamflow.

One of the limitations of physically based modeling approaches is that changes in vegetation structure (e.g., reduced leaf area, changing root distributions, etc.) and function (e.g., shifts to species with different mechanisms for regulation of water use) that may occur in response to severe drought are often not explicitly incorporated in the framework and require direct empirical investigation to understand (Powell and others 2013). For example, short-term droughts (e.g., <1 year) may dry up depression forested wetlands in the Southeastern United States, but hydrologic processes recover quickly and trees are rarely subject to water stress due to changes in soil water storage in wetlands (Lu and others 2009, Sun and others 2010). However, long-term droughts could alter wetland hydrology to an extent that causes permanent changes in plant community composition and fire regimes (De Steven and Toner 2004) resulting in altered hydrologic processes at larger spatial scales. Furthermore, lumped parameter ecosystem models that intend to describe the effects of soil water on ecological processes such as carbon cycling, often treat soil water and nutrient movement in a rather simplified fashion. For example, lateral flow and topographic effects on soil water distribution on the landscape are usually not accounted for in ecosystem models (Govind and others 2009); however, modeling approaches that account for subsurface hydrologic connectivity suggest strong spatial controls on ecosystem processes (Emanuel and others 2010, Hwang and others 2009).

More accurate predictions of the impacts of severe and longer term drought (especially when vegetation changes occur) will require models that couple hydrologic and ecosystem processes in a dynamic context with appropriate feedbacks (Law 2014). It is expected that ecosystem-specific models are needed to more fully determine hydrologic responses to extreme droughts, especially recent observations of “exceptional drought” arising from the combination of very low precipitation and warmer temperatures (Diffenbaugh and others 2015). This is not a trivial expectation, as it requires models that couple leaf-level physiology, above- and belowground whole-tree responses, root dynamics and soil water access, stand level responses, and physical hydrology (Tague and others 2013) and usually results in complex models that are difficult to parameterize and calibrate over large spatial scales.

Drought Impacts on Water Quality

Droughts not only affect the quantity of water in and flowing from forest ecosystems, but also water quality, having important implications for stream ecosystem services. Drought affects water quality both directly and indirectly. Direct impacts are primarily physical, as reduced streamflow concentrates nutrients and sediment, and warms more quickly. Indirect effects include a combination of terrestrial, riparian, and instream processes that impact sediment and nutrient concentrations and fluxes. The impacts of drought on terrestrial biogeochemical cycling processes are discussed in chapter 5. Here we focus primarily how those and other drought-related impacts influence water quality in forest streams.

Importance of Intermittent and Ephemeral Streams

Much of our understanding of the linkages among drought, streamflow, and water quality is derived from gauged perennial streams; less information is available on the impacts of drought on ephemeral and intermittent streams, despite the fact that these streams are a critical component of the hydrologic network in forested watersheds and river systems (Acuña and others 2014, Larned and others 2010, Lowe and Likens 2005). In terms of ecohydrological functions, intermittent and ephemeral streams serve critical roles for elemental cycling, connecting materials and energy exchange in watersheds (Lowe and Likens 2005) and river networks, and providing unique habitat for plants (Katz and Moore 2011) and aquatic and terrestrial species (McDonough and others 2011). They are most common in arid and semi-arid regions of the United States (Levick and Rogers 2008), but also occur frequently in the headwaters of forested watersheds in all regions (Hansen 2001, Larned and others 2010).

Intermittent streams are typically seasonal, and surface flows occur in response to snowmelt or elevated groundwater resulting from high precipitation or reduced ET, whereas ephemeral streams flow as a result of discharging groundwater and in response to runoff events (McDonough and others 2011). Due to their dependence on precipitation and/or snowmelt, intermittent and ephemeral streams are particularly vulnerable to drought (Palmer and others 2008). Increasing the duration or frequency of drought will

increase and alter periods of “no-flow” conditions and change hydrologic processes and aquatic habitats (Godsey and others 2014, Jaeger and Olden 2012).

These changing flow regimes are likely to have important implications for the timing and quantity of carbon, nutrient, and sediment exchanges with the perennial stream network, and alter habitat availability for fish and other aquatic organisms (Brooks 2009). Species that utilize ephemeral and intermittent streams already have adaptations to survive dry periods; however, whether these traits will allow for survival under longer, more frequent, and more extreme droughts is uncertain (Robson and others 2011) but of concern (Acuña and others 2014, Brooks 2009). For example, a prolonged drought had a much greater impact on fish and invertebrates in ephemeral and intermittent streams than in perennial streams in a Mediterranean climate (Beche and others 2009).

Stream Chemistry and Sediment

The terrestrial biogeochemical consequences of drought (chapter 5) are closely linked to changes in vegetation and hydrology (Dahm and others 2003). However, the effects on water quality can be highly variable depending on the characteristics of the site and broader region. The role of tree species on nutrient cycling is well documented (Finzi and others 1998, Pastor and others 1984); therefore, shifts in species composition may affect biogeochemical processes in soil that ultimately impact the chemical composition of streamwater (chapter 5). For example, Wurzbarger and Miniati (2014) found that tree species that have the ability to form nitrogen gas (N_2)-fixing nodules in their roots do so more under conditions of moderate drought, adding a new source of nitrogen (N) into these systems that could be available for uptake and eventual leaching and stream export.

Drought may also affect the productivity of vegetation, having implications for stream chemistry. For example, Lutz and others (2012) suggested that streamwater nitrate concentrations are affected by temporal trends in fine root production and mortality during drought. In the early stages of drought, root production may initially increase as trees attempt to access soil water over broader areas (Hendrick and Pregitzer 1996), resulting in lower streamwater nitrate concentrations. Following drought, root mortality returns N to the system, resulting in higher stream nitrate concentrations. Secondary influences of drought on disturbances such as wildfire can also impact water chemistry and sediment (Goode

and others 2012, Smith and others 2011, Spencer and others 2003) (chapter 7 includes discussion of how drought affects fire severity and probability).

The combination of biological and hydrologic controls on water quality results in high complexity and spatial heterogeneity in response to drought. Concentrations of a particular solute in streamwater can increase at one location while decreasing at another. Droughts can have a concentrating effect on solutes in streamwater due to the limited volume of water. However, the flux of solutes in streamwater is generally lower during drought periods because less water is moving through the watershed. As streamflow declines, nutrients moving downstream are cycled more rapidly (Fisher and others 1998). This more rapid uptake of solutes within streams can have a strong influence on their concentration. For example, high streamwater silica concentrations are often observed during dry periods because silica is derived from mineral weathering and tends to increase when groundwater inputs dominate (Johnson and others 1969). However, several studies have reported declines in the concentration of dissolved silica during drought (Wall and others 1998, Williams and Melack 1997).

Wall and others (1998) determined that the low silica concentrations during a drought at Canajoharie Creek, New York, could only be attributed to in-stream processing, resulting from uptake by diatoms. Reduced streamflow velocity also enhances sediment and particulate organic matter deposition (Acuña and others 2007, Wood and Armitage 1999). Fine sediment deposition during drought has been shown to negatively affect stream organisms, such as macroinvertebrates and fish (Hakala and Hartman 2004, Kaller and Hartman 2004, Kemp and others 2011, Wood and Armitage 1997). In cases where streamflow ceases entirely, water becomes stagnant, and sediment, organic matter, and nutrients can accumulate in the pools that form. Severely reduced or eliminated flow, along with warmer temperatures, may promote algal growth (Caramujo and others 2008) and reduce dissolved organic carbon (DOC) in streams (Everard 1996). In most cases, the concentration and flux of DOC in streamwater are low during drought years compared to normal or wetter years. The reduced export of DOC during droughts has been attributed to factors such as diminished flow and changing flow paths (Eimers and others 2008, Portal and others 2009, Schindler and others 1997, Worrall and Burt 2008), decreased organic matter solubility during acidic episodes (Clark and others 2005, Clark and others

2006), and decreased production of DOC due to the inhibition of microbial processes associated with dry or acidic conditions during drought (Scott and others 1998).

Subsurface hydrologic flowpaths can also play a critical role in regulating the concentration of solutes in streamwater. During droughts, groundwater continues to travel along deep, long flowpaths, whereas less water flows along shallow groundwater paths. As the water residence time increases along these deep flowpaths, the contact time between groundwater and bedrock lengthens. This results in a higher concentration of streamwater solutes derived from geological weathering of bedrock. In contrast, during high flows, water tends to move more rapidly through upper soil horizons, resulting in higher concentrations of elements derived from organic matter, such as carbon (C) and nitrogen (N) (Raymond and Saiers 2010, Swistock and others 1989). Local lithology largely determines which elements will become more concentrated in streamwater during drought.

While it is typically difficult to determine when a drought begins, droughts are often punctuated by a more abrupt ending, at which point their biogeochemical impacts are most apparent. The first flush of water following drought has high concentrations of products that have accumulated in the soil (Burt and others 2014). Aerobic processes in the vadose zone produce nitrate, sulfate, and DOC that are transported to surface waters when a drought ends. The flushing of solutes can last for multiple storms, as saturated zones enlarge and hydrologic connections expand. Some solutes can have complex responses to drought, such as potassium, which has been shown to be influenced by changes in flowpaths, sediment transport, and the chemical properties of streamwater (Stott and Burt 1997). Other solutes with more predictable responses to drought are those that are sensitive to oxidation-reduction reactions. For example, sulfate and nitrate tend to exhibit the strongest and most predictable responses to drought, especially in streams that drain wetland and riparian zones, which are typically saturated.

Stream Temperature

Streamwater temperature is a critical water quality parameter that affects the chemical, biological, and ecological processes and functions of watersheds (Caissie 2006), and it influences the growth and distribution of aquatic organisms (Hester and Doyle 2011, Mohseni and others 2003). Droughts impact streamwater temperatures primarily by decreasing

stream discharge (flow volume and velocity) and increasing solar radiation (exacerbating wildfires and limiting vegetation density), and to a lesser extent by changing atmospheric (precipitation, air temperature) and streambed factors (groundwater input). The low flows associated with droughts during warm periods cause stream temperatures to increase because thermal capacity is lower when flow volume decreases (Hockey 1982, Webb 1996, Webb and others 2003) and slower water velocities allow streams to more strongly equilibrate to local climatic conditions (Isaak and others 2012, Meier and others 2003).

Warmer waters hold less dissolved oxygen, and drought conditions concentrate aquatic organisms in smaller habitat volumes. Droughts, therefore, can cause significant stress to fish and other aquatic organisms by increasing metabolic costs and the intensity of interspecific competitive interactions. For some highly valued, coldwater species like trout and salmon, temperatures often define the geographic extent of their habitat, and drought conditions may temporarily constrain those habitats or even incur direct mortalities during extreme events. The lethal temperature limit for a coldwater trout species such as eastern brook trout (*Salvelinus fontinalis*) is approximately 25 °C (Bjornn and Reiser 1991, Hokanson and others 1977); but, reduced growth begins to occur at temperatures well below this limit. Most aquatic organisms are ectothermic, so the limitations imposed by temperature and dissolved oxygen during droughts have broad implications for the growth and survival of individuals in many species (Bjornn and Reiser 1991), including coldwater species.

Atmospheric, topographic, and vegetative shade; streambed; and stream and groundwater discharge factors all play a role in stream temperature dynamics. Atmospheric factors are most influential on larger streams and less so in smaller headwater streams. For example, Evans and others (1998) found that 82 percent of the heat energy exchange in a stream with a 109-km² drainage area in the United Kingdom occurred at the air/water interface, while 15 percent occurred at the streambed interface. In smaller headwater streams, temperature dynamics are more strongly controlled by the amount of local groundwater (Deitchman and Loheide 2012) and the role of topographic and vegetative shade in mediating the solar radiation that a stream receives (Johnson 2003, Luce and others 2014). Solar radiation is the single largest energy input to most streams, accounting for as much as 97 percent of the total energy gains (Evans and others 1998).

Management Options for Minimizing the Impacts of Drought on Water Quantity and Quality

The concept of managing forests to augment annual streamflow is not new (Douglass 1983); however, recent severe drought in many areas of the United States has increased awareness of the relationship among forest disturbance and management, drought, and streamflow (Ford and others 2011b, Jones and others 2012). Since harvesting often increases annual water yield, it has been suggested that the effects of drought could be mitigated by cutting forests (McLaughlin and others 2013). A major challenge in managing forests to enhance water supply is that a large proportion of the watershed has to be cut in order to increase annual runoff (Bosch and Hewlett 1982). Consequently, the potential increases in streamflow through forest cutting are minimal due to limitations on the amount of land that can be harvested at any given time (Kattelman and others 1983).

Streamflow responses are often short term due to rapid forest regrowth (e.g., especially in the Eastern United States) (Swank and others 2014), and the aggrading post-cut forest may actually have lower streamflow than the uncut forest (Ford and others 2011b). Additionally, because of the unpredictable nature of droughts, it is impractical to plan the timing of harvesting operations so that the streamflow response occurs rapidly enough to offset the effect of drought. Furthermore, in contrast to management actions that are intended to augment streamflow, increasing drought stress in some forest ecosystems may warrant management strategies that retain water (and hence reduce streamflow) on the landscape in order to keep trees alive (Grant and others 2013).

Replanting cut forests with species that consume less water is a longer term solution that may be warranted in some cases, if it is economically feasible and does not adversely affect other forest management objectives, such as forest productivity, carbon sequestration, wildlife habitat, and water quality (King and others 2013). In snow-dominated, coniferous forests of the Western United States, small patch cuts and thinning have been shown to enhance snow accumulation by reducing snow interception and evaporation (Ffolliott and others 1989, Meiman 1987); however, these responses are transient as regrowing forests fill in the openings. Since much of the water supply in the West originates as snowmelt

from montane ecosystems, managing subalpine forests to enhance snow accumulation may alleviate the effects of drought in this region.

As with other natural disturbances, droughts are difficult to prepare for because they are unpredictable. However, there are management options that may be implemented to minimize the impacts of drought on water quality. In more developed areas, an obvious measure is to limit streamwater withdrawals (Meier and others 2003, Webb and Nobilis 1995) and wastewater discharge during periods of low flow, and encourage reuse of treated wastewater to help reduce higher temperature effluent volume from entering streams (Kinouchi and others 2007). In forested areas, efforts should focus on minimizing inputs of sediments and nutrients into the stream. It may be beneficial to plan the timing of management activities so they do not disturb streams during low-flow periods and to avoid vulnerable areas during droughts. Another management option is to practice riparian buffer conservation and restoration strategies that will maintain or increase shading from solar radiation (Burton and Likens 1973, Kaushal and others 2010, Peterson and Kwak 1999, Swift and Baker 1973); buffering stream temperatures against drought becomes important because removal and alteration of riparian vegetation increases stream temperatures (Beschta and others 1987, Groom and others 2011), particularly following timber harvest (Sun and others 2004, Swift and Baker 1973, Swift and Messer 1971, Wooldridge and Stern 1979) and wildfires (Dunham and others 2007, Isaak and others 2010). Other mitigation strategies, such as releases of cold water from the hypolimnions (i.e., the lower layers of water) of deep reservoirs, can have a significant cooling effect in downstream reaches (Null and others 2013), as can discharge of municipal wastewater from underground pipes, which may cool streams in the summer (Bogan and others 2003).

Conclusions

Forest vegetation has a strong influence over the water balance and biogeochemical cycling processes that determine streamwater quality. Hence, understanding and predicting how drought will impact hydrological processes requires linking vegetation drought responses across fine (e.g., stomatal regulation) and coarse scales (e.g., community dynamics at watershed scales). Where impacts are large and sudden, and species diversity is less complex (such as widespread drought-mediated mountain pine beetle mortality in the Western United

States), assessing short- and long-term responses may be possible with existing models (Tague and others 2013). However, where impacts are smaller scale and longer term (such as selective mortality in eastern U.S. forests), predicting impacts will be much more difficult and uncertain. If drought frequency and severity increases as expected (Swain and Hayhoe 2014), understanding the ecohydrological implications will become even more critical. To improve understanding, we recommend several areas of research need:

- Better understanding of species' differences in water use and sensitivity to drought, as well as the thresholds that determine species' physiological capacity to survive drought.
- Better understanding of competitive interactions among species, especially novel species combinations that might result with climate change or other disturbance regimes.
- Better understanding of belowground processes (e.g., root dynamics, hydraulic lift, and soil water access) that interact with drought responses.
- Improved ability to scale from tree-level, plots, and small watersheds to landscape scales in order to better understand and predict the ecohydrological consequences of tree-level responses to water balance and streamflow dynamics.
- Better understanding of the impacts of multiple co-occurring stressors on drought responses.
- Better understanding of how water quality is influenced by subsurface flow paths and hydrological connectivity.
- Improved ecohydrological models that couple hydrologic, ecosystem, and plant physiological processes in a dynamic context with appropriate feedbacks.
- Increased efforts to monitor the effectiveness of management options to mitigate droughts.
- Better understanding of the effectiveness of post-disturbance (e.g., direct and indirect effects of drought) restoration for improving watershed function.

Literature Cited

- Acuña, V.; Datry, T.; Marshall, J. [and others]. 2014. Why should we care about temporary waterways? *Science*. 343: 1080-1081.
- Acuña, V.; Giorgi, A.; Muñoz, I. [and others]. 2007. Meteorological and riparian influences on organic matter dynamics in a forested Mediterranean stream. *Journal of the North American Benthological Society*. 26: 54-69.
- Adams, H.D.; Luce, C.H.; Breshears, D.D. [and others]. 2012. Ecohydrological consequences of drought- and infestation-triggered tree die-off: insights and hypotheses. *Ecohydrology*. 5: 145-159.
- Albani, M.; Moorcroft, P.R.; Ellison, A.M. [and others]. 2010. Predicting the impact of hemlock woolly adelgid on carbon dynamics of Eastern United States forests. *Canadian Journal of Forest Research*. 40: 119-133.
- Allen, C.D.; Macalady, A.K.; Chenchouni, H. [and others]. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*. 259: 660-684.
- Anderegg, W.R.L.; Kane, J.M.; Anderegg, L.D.L. 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change*. 3: 30-36.
- Bachelet, D.; Neilson, R.P.; Lenihan, L.M.; Drapek, R.J. 2001. Climate change effects on vegetation distribution and carbon budget in the United States. *Ecosystems*. 4: 164-185.
- Beche, L.A.; Connors, P.G.; Resh, V.H.; Merenlender, A.M. 2009. Resilience of fishes and invertebrates to prolonged drought in two California streams. *Ecography*. 32: 778-788.
- Berghuijs, W.R.; Woods, R.A.; Hrachowitz, M. 2014. A precipitation shift from snow towards rain leads to a decrease in streamflow. *Nature Climate Change*. 4: 583-586.
- Beschta, R.; Bilby, R.E.; Brown, G.W. [and others]. 1987. Stream temperature and aquatic habitat: fisheries and forestry interactions. In: Salo, E.O.; Cundy, T.W., eds. *Streamside management: forestry and fishery interactions*. Institute of Forest Resources, Contribution No. 57. Seattle: University of Washington: 191-232.
- Beschta, R.L.; Pyles, M.R.; Skaugset, A.E.; Surfleet, C.G. 2000. Peakflow responses to forest practices in the western cascades of Oregon, USA. *Journal of Hydrology*. 233: 102-120.
- Bethlahmy, N. 1974. More streamflow after a bark beetle epidemic. *Journal of Hydrology*. 23: 185-189.
- Binkley, D.; Brown, T.C. 1993. Forest practices as nonpoint sources of pollution in North America. *Water Resources Bulletin*. 29: 729-740.
- Bjornn, T.C.; Reiser, D.W. 1991. Habitat requirements of salmonids in streams. In: Meehan, W.R., ed. *Influences of forest and rangeland management on salmonid fishes and their habitats*. Special Publication no. 19. Bethesda, MD: American Fisheries Society: 83-138.
- Bogan, T.; Mohseni, O.; Stefan, H.G. 2003. Stream temperature-equilibrium temperature relationship. *Water Resources Research*. 39 (9): 12 p. doi:10.1029/2003WR002034. [Published online: September 2003].
- Boggs, J.; Sun, G.; Jones, D.; McNulty, S.G. 2013. Effect of soils on water quantity and quality in Piedmont forested headwater watersheds of North Carolina. *Journal of the American Water Resources Association*. 49: 132-150.

- Boon, S. 2012. Snow accumulation following forest disturbance. *Ecohydrology*. 5: 279-285.
- Bosch, J.M.; Hewlett, J.D. 1982. A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration. *Journal of Hydrology*. 55: 3-23.
- Brantley, S.; Ford, C.R.; Vose, J.M. 2013. Future species composition will affect forest water use after loss of eastern hemlock from southern Appalachian forests. *Ecological Applications*. 23: 777-790.
- Brantley, S.T.; Miniati, C.F.; Elliott, K.J. [and others]. 2014. Changes to southern Appalachian water yield and stormflow after loss of a foundation species. *Ecohydrology*. 8(3): 518-528. doi:10.1002/eco.1521. [Published online: August 5, 2014].
- Breshears, D.D. 2005. An ecologist's perspective of ecohydrology. *Bulletin of the Ecological Society of America*. 86(4): 296-300.
- Brooks, R.T. 2009. Potential impacts of global climate change on the hydrology and ecology of ephemeral freshwater systems of the forests of the Northeastern United States. *Climatic Change*. 95: 469-483.
- Brooks, J.R.; Barnard, H.R.; Coulombe, R.; McDonnell, J.J. 2009. Ecohydrologic separation of water between trees and streams in a Mediterranean climate. *Nature Geoscience*. 3: 100-104.
- Burt, T.P.; Worrall, F.; Howden, N.J.K.; Anderson, M.G. 2014. Shifts in discharge-concentration relationships as a small catchment recovers from severe drought. *Hydrological Processes*. 29(4): 498-507. doi:10.1002/hyp.10169. [Published online: March 1, 2014].
- Burton, T.M.; Likens, G.E. 1973. Effect of strip-cutting on stream temperatures in Hubbard Brook Experimental Forest, New Hampshire. *Bioscience*. 23: 433-435.
- Busby, P.E.; Canham, C.D. 2011. An exotic insect and pathogen disease complex reduces aboveground tree biomass in temperate forests of eastern North America. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*. 41: 401-411.
- Busch, D.E.; Ingraham, N.L.; Smith, S.D. 1992. Water uptake in woody riparian phreatophytes of the Southwestern United States: a stable isotope study. *Ecological Applications*. 2: 450-459.
- Caissie, D. 2006. The thermal regime of rivers: a review. *Freshwater Biology*. 51: 1389-1406.
- Caldwell, P.V.; Sun, G.; McNulty, S.G. [and others]. 2012. Impacts of impervious cover, water withdrawals, and climate change on river flows in the conterminous U.S. *Hydrology and Earth System Sciences*. 16: 2839-2857.
- Cannon, S.H.; Bigio, E.R.; Mine, E. 2001. A process for fire-related debris flow initiation, Cerro Grande fire, New Mexico. *Hydrological Processes*. 15: 3011-3023.
- Caramujo, M.-J.; Mendes, C.R.B.; Cartaxana, P. [and others]. 2008. Influence of drought on algal biofilms and meiofaunal assemblages of temperate reservoirs and rivers. *Hydrobiologia*. 598: 77-94.
- Cayan, D.R.; Kammerdiener, S.A.; Dettinger, M.D. [and others]. 2001. Changes in the onset of spring in the Western United States. *Bulletin of the American Meteorological Society*. 82: 399-415.
- Choat, B.; Jansen, S.; Brodrribb, T.J. [and others]. 2012. Global convergence in the vulnerability of forests to drought. *Nature*. 491: 752-755. doi:10.1038/nature11688. [Published online: November 21, 2012].
- Clark, J.M.; Chapman, P.J.; Adamson, J.K.; Lane, S.N. 2005. Influence of drought-induced acidification on the mobility of dissolved organic carbon in peat soils. *Global Change Biology*. 11: 791-809.
- Clark, J.M.; Chapman, P.J.; Heathwaite, A.L.; Adamson, J.K. 2006. Suppression of dissolved organic carbon by sulfate induced acidification during simulated droughts. *Environmental Science and Technology*. 40: 1776-1783.
- Clark, J.S.; Bell, D.M.; Kwit, M.C.; Zhu, K. 2014a. Competition-interaction landscapes for the joint response of forests to climate change. *Global Change Biology*. 20: 1979-1991.
- Clark, J.S.; Gelfand, A.E.; Woodall, C.W.; Zhu, K. 2014b. More than the sum of the parts: forest climate response from joint species distribution models. *Ecological Applications*. 24: 990-999.
- Clark, M.P.; Hendriks, J.; Slater, A.G. [and others]. 2011. Representing spatial variability of snow water equivalent in hydrologic and land-surface models: A review. *Water Resources Research*. 47(7): W07539. 23 p. doi:10.1029/2011WR010745. [Published online: July 21, 2011].
- Clinton, B.D.; Boring, L.R.; Swank, W.T. 1993. Canopy gap characteristics and drought influences in oak forests of the Coweeta Basin. *Ecology*. 74: 1551-1558.
- Creutzfeldt, B.; Ferre, T.; Troch, P. [and others]. 2012. Total water storage dynamics in response to climate variability and extremes: inference from long-term terrestrial gravity measurement. *Journal of Geophysical Research-Atmospheres*. 117 (D8): D08112. 17 p. doi:10.1029/2011JD016472. [Published online: April 27, 2012].
- Cristea, N.C.; Lundquist, J.D.; Loheide, S.P. [and others]. 2013. Modelling how vegetative cover affects climate change impacts on streamflow timing and magnitude in the snowmelt-dominated upper Tuolumne Basin, Sierra Nevada. *Hydrological Processes*. 28(12): 3896-3918. doi: 10.1002/hyp9909. [Published online: July 9, 2013].
- Dahm, C.N.; Baker, M.A.; Moore, D.I.; Thibault, J.R. 2003. Coupled biogeochemical and hydrological responses of streams and rivers to drought. *Freshwater Biology*. 48: 1219-1231.
- D'Odorico, P.; Liao, F.; Porporato, A. [and others]. 2010. Ecohydrology of terrestrial ecosystems. *Bioscience*. 60(11): 898-907.
- De Steven, D.; Toner, M.M. 2004. Vegetation of upper coastal plain depression wetlands: environmental templates and wetland dynamics within a landscape framework. *Wetlands*. 24: 23-42.
- Deitchman, R.; Loheide, S.P. 2012. Sensitivity of thermal habitat of a trout stream to potential climate change, Wisconsin, United States. *Journal of the American Water Resources Association*. 48: 1091-1103.
- Dickson, R.; Tomlinson, P. 1996. Oak growth, development and carbon metabolism in response to water stress. *Annals of Forest Science*. 53: 181-196.
- Dietze, M.C.; Moorcroft, P.R. 2011. Tree mortality in the Eastern and Central United States: patterns and drivers. *Global Change Biology*. 17: 3312-3326.
- Diffenbaugh, N.S.; Swain, D.L.; Touma, D. 2015. Anthropogenic warming has increased drought risk in California. *Proceedings of the National Academy of Sciences*. 112(13): 3931-3936.
- Dunham, J.B.; Rosenberger, A.E.; Luce, C.H.; Rieman, B.E. 2007. Influences of wildfire and channel reorganization on spatial and temporal variation in stream temperature and the distribution of fish and amphibians. *Ecosystems*. 10: 335-346.
- Eagleson, P.S. 2002. *Ecohydrology: Darwinian expression of vegetation form and function*. Eos Transactions of the American Geophysical Union. Cambridge, UK: Cambridge University Press. 345 p.
- Ehleringer, J.R.; Dawson, T.E. 1992. Water uptake by plants: perspectives from stable isotope composition. *Plant, Cell & Environment*. 15: 1073-1082.

- Eimers, M.C.; Watmough, S.A.; Buttle, J.M.; Dillon, P.J. 2008. Examination of the potential relationship between droughts, sulphate and dissolved organic carbon at a wetland-draining stream. *Global Change Biology*. 14: 1-11.
- Elliott, K.J.; Swank, W.T. 1994. Impacts of drought on tree mortality and growth in a mixed hardwood forest. *Journal of Vegetation Science*. 5: 229-236.
- Ellison, A.M.; Bank, M.S.; Clinton, B.D. [and others]. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment*. 9: 479-486.
- Emanuel, R.E.; Epstein, H.E.; McGlynn, B.L. [and others]. 2010. Spatial and temporal controls on watershed ecohydrology in the northern Rocky Mountains. *Water Resources Research*. 46: W11553. 14 p. doi:11510.11029/12009wr008890. [Published online: November 24, 2010].
- Evans, E.C.; McGregor, G.R.; Petts, G.E. 1998. River energy budgets with special reference to river bed processes. *Hydrological Processes*. 12: 575-595.
- Everard, M. 1996. The importance of periodic droughts for maintaining diversity in the freshwater environment. *Freshwater Forum*. 7: 33-50.
- Fan, Y.; Li, H.; Miguez-Macho, G. 2013. Global patterns of groundwater table depth. *Science*. 339: 940-943.
- Ffolliott, P.F.; Gottfried, G.J.; Baker, M.B. 1989. Water yield from forest snowpack management: Research findings in Arizona and New Mexico. *Water Resources Research*. 25: 1999-2007.
- Finzi, A.C.; Van Breeman, N.; Canham, C.D. 1998. Canopy tree-soil interactions within temperate forests: species effects on soil carbon and nitrogen. *Ecological Applications*. 8: 440-446.
- Fisher, S.G.; Grimm, N.B.; Martí, E. [and others]. 1998. Material spiraling in river corridors: a telescoping ecosystem model. *Ecosystems*. 1: 19-34.
- Fischelli, N.A.; Frelich, L.E.; Reich, P.B. 2014. Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures. *Ecography*. 37: 152-161.
- Fitzpatrick, M.C.; Preisser, E.L.; Porter, A. 2012. Modeling range dynamics in heterogeneous landscapes: invasion of the hemlock woolly adelgid in eastern North America. *Ecological Applications*. 22: 472-486.
- Ford, C.R.; Elliott, K.J.; Clinton, B.D. [and others] 2012. Forest dynamics following eastern hemlock mortality in the southern Appalachians. *Oikos*. 121: 523-536.
- Ford, C.R.; Hubbard, R.M.; Vose, J.M. 2011a. Quantifying structural and physiological controls on variation in canopy transpiration among planted pine and hardwood species in the southern Appalachians. *Ecohydrology*. 4: 183-195.
- Ford, C.R.; Laseter, S.H.; Swank, W.T.; Vose, J.M. 2011b. Can forest management be used to sustain water-based ecosystem services in the face of climate change? *Ecological Applications*. 21: 2049-2067.
- Ford, C.R.; Vose, J.M. 2007. *Tsuga canadensis* (L.) Carr. mortality will impact hydrologic processes in southern Appalachian forest ecosystems. *Ecological Applications*. 17: 1156-1167.
- Forrester, J.A.; McGee, G.G.; Mitchell, M.J. 2003. Effects of beech bark disease on aboveground biomass and species composition in a mature northern hardwood forest, 1985 to 2000. *Journal of the Torrey Botanical Society*. 130: 70-78.
- Frank, D.A.; Inouye, R.S. 1994. Temporal variation in actual evapotranspiration of terrestrial ecosystems: patterns and ecological implications. *Journal of Biogeography*. 21: 401-411.
- Godsey S.E.; Kirchner, J.W.; Tague, C.L. 2014. Effects of changes in winter snowpacks on summer low flows: case studies in the Sierra Nevada, California, USA. *Hydrologic Processes*. 28: 5048-5064.
- Goode, J.R.; Luce, C.H.; Buffington, J.M. 2012. Enhanced sediment delivery in a changing climate in semi-arid mountain basins: Implications for water resource management and aquatic habitat in the northern Rocky Mountains. *Geomorphology*. 139-140: 1-15. doi: 10.1016/j.geomorph.2011.06.021. [Published online: July 14, 2011].
- Govind, A.; Chen, J.M.; Margolis, H. [and others]. 2009. A spatially explicit hydro-ecological modeling framework (BEPS-TerrainLab V2.0): model description and test in a boreal ecosystem in Eastern North America. *Journal of Hydrology*. 367: 200-216.
- Groffman, P.M.; Rustad, L.E.; Templer, P.H. [and others]. 2012. Long-term integrated studies show complex and surprising effects of climate change in the northern hardwood forest. *Bioscience*. 62: 1056-1066.
- Groom, J.D.; Dent, L.; Madsen, L.J. 2011. Stream temperature change detection for State and private forests in the Oregon Coast Range. *Water Resources Research*. 47(1): W01501. 12 p. doi: 10.1029/2009WR009061. [Published online: January 8, 2011].
- Grant, G.E.; Tague, C.L.; Allen, C.D. 2013. Watering forests for the trees: an emerging priority for managing water in forest landscapes. *Frontiers in Ecology and Environment*. 11: 314-321. doi:10.1890/120209. [Published online: May 30, 2013].
- Guardiola-Claramonte, M.; Troch, P.A.; Breshears, D.D. [and others]. 2011. Decreased streamflow in semi-arid basins following drought-induced tree die-off: a counter-intuitive and indirect climate impact on hydrology. *Journal of Hydrology*. 406: 225-233.
- Hadley, J.L.; Kuzeja, P.S.; Daley, M.J. 2008. Water use and carbon exchange of red oak- and eastern hemlock-dominated forests in the northeastern USA: implications for ecosystem-level effects of hemlock woolly adelgid. *Tree Physiology*. 28: 615-627.
- Hakala, J.P.; Hartman, K.J. 2004. Drought effect on stream morphology and brook trout (*Salvelinus fontinalis*) populations in forested headwater streams. *Hydrobiologia*. 515: 203-213.
- Halofsky, J.E.; Hemstrom, M.A.; Conklin, D.R. [and others]. 2013. Assessing potential climate change effects on vegetation using a linked model approach. *Ecological Modelling*. 266: 131-143.
- Hancock, J.E.; Arthur, M.A.; Weathers, K.C.; Lovett, G.M. 2008. Carbon cycling along a gradient of beech bark disease impact in the Catskill Mountains, New York. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*. 38: 1267-1274.
- Hansen, W.F. 2001. Identifying stream types and management implications. *Forest Ecology and Management*. 143: 39-46.
- Hanson, P.J.; Amthor, J.S.; Wullschleger, S.D. [and others]. 2004. Oak forest carbon and water simulations: Model intercomparisons and evaluations against independent data. *Ecological Monographs*. 74: 443-489.
- Hendrick, R.L.; Pregitzer, K.S. 1996. Temporal and depth-related patterns of fine root dynamics in northern hardwood forests. *Journal of Ecology*. 48: 167-176.
- Hester, E.T.; Doyle, M.W. 2011. Human impacts to river temperature and their effects on biological processes: a quantitative synthesis. *Journal of the American Water Resources Association*. 47: 571-587.
- Hicke, J.A.; Allen, C.D.; Desai, A.R. [and others]. 2012. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. *Global Change Biology*. 18: 7-34.

- Hockey, J.B.; Owens, I.F.; Tapper, N.J. 1982. Empirical and theoretical models to isolate the effect of discharge on summer water temperatures in the Hurunui River. *Journal of Hydrology* (New Zealand). 21: 1–12.
- Hoffmann, W.A.; Marchin, R.M.; Abit, P.; Lau, O.L. 2011. Hydraulic failure and tree dieback are associated with high wood density in a temperate forest under extreme drought. *Global Change Biology*. 17: 2731-2742.
- Hokanson, K.E.F.; Kleiner, C.F.; Thorslund, T.W. 1977. Effects of constant temperatures and diel temperature-fluctuations on specific growth and mortality-rates and yield of juvenile rainbow-trout, *Salmo-Gairdneri*. *Journal of the Fisheries Research Board of Canada*. 34: 639-648.
- Hwang, T.; Band, L.; Hales, T.C. 2009. Ecosystem processes at the watershed scale: extending optimality theory from plot to catchment. *Water Resources Research*. 45(11): W11425. 20 p. doi:10.1029/2009WR007775. [Published online: November 21, 2009].
- Isaak, D.J.; Luce, C.H.; Rieman, B.E. [and others]. 2010. Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. *Ecological Applications*. 20: 1350-1371.
- Isaak, D.J.; Wollrab, S.; Horan, D.; Chandler, G. 2012. Climate change effects on stream and river temperatures across the Northwest U.S. from 1980-2009 and implications for salmonid fishes. *Climatic Change*. 113: 499-524.
- Istanbulluoglu, E.; Tarboton, D.G.; Pack, R.T.; Luce, C.H. 2004. Modeling of the interactions between forest vegetation, disturbances, and sediment yields. *Journal of Geophysical Research-Earth Surface*. 109(F1): F01009. 22 p. doi: 10.1029/2003JF000041. [Published online: February 19, 2004].
- Iverson, L.R.; Prasad, A.M. 2001. Potential changes in tree species richness and forest community types following climate change. *Ecosystems*. 4: 186-199.
- Jackson, R.B.; Jobbagy, E.G.; Noretto, M.D. 2009. Ecohydrology in a human-dominated landscape. *Ecohydrology*. 2: 383-389.
- Jaeger, K.L.; Olden, J.D. 2012. Electrical resistance sensor arrays as a means to quantify longitudinal connectivity of rivers. *River Research and Applications*. 28: 1843-1852.
- Johnson, N.M.; Likens, G.E.; Bormann, F.H. [and others]. 1969. A working model for the variation in streamwater chemistry at the Hubbard Brook Experimental Forest, New Hampshire. *Water Resources Research*. 5: 1353-1363.
- Johnson, S.L. 2003. Stream temperature: scaling of observations and issues for modelling. *Hydrological Processes*. 17: 497-499.
- Jones, J.A.; Perkins, R.M. 2010. Extreme flood sensitivity to snow and forest harvest, western Cascades, Oregon, United States. *Water Resources Research*. 46: W12512. 21 p. doi: 10.1029/2009WR008632. [Published online: December 3, 2010].
- Joslin, J.D.; Gaudinski, J.B.; Torn, M.S. [and others]. 2007. Fine-root turnover patterns and their relationship to root diameter and soil depth in a C-14-labeled hardwood forest. *New Phytologist*. 172: 523-535.
- Kaiser, K.E.; McGlynn, B.L.; Emanuel, R.E. 2013. Ecohydrology of an outbreak: mountain pine beetle impacts trees in drier landscape positions first. *Ecohydrology*. 6: 444-454.
- Kaller, M.D.; Hartman, K.J. 2004. Evidence of a threshold level of fine sediment accumulation for altering benthic macroinvertebrate communities. *Hydrobiologia*. 518: 95–104.
- Kasson, M.T.; Livingston, W.H. 2012. Relationships among beech bark disease, climate, radial growth response and mortality of American beech in northern Maine, USA. *Forest Pathology*. 42: 199-212.
- Kattelmann, R.C.; Berg, N.H.; Rector, J. 1983. The potential for increasing streamflow from Sierra Nevada watersheds. *Journal of the American Water Resources Association*. 19: 395-402.
- Katz, D.L.; Moore, M.R. 2011. Dividing the waters: an empirical analysis of interstate compact allocation of transboundary rivers. *Water Resources Research*. 47: W06513. 15 p. doi: 10.1029/2010WR009736. [Published online: June 15, 2011].
- Kaushal, S.S.; Likens, G.E.; Jaworski, N.A. [and others]. 2010. Rising stream and river temperatures in the United States. *Frontiers in Ecology and the Environment*. 8: 461-466.
- Kemp, P.; Sear, D.; Collins, A. [and others]. 2011. The impacts of fine sediment on riverine fish. *Hydrological Processes*. 25: 1800-1821.
- King, J.S.; Ceulemans, R.; Albaugh, J.M. [and others]. 2013. The challenge of lignocellulosic bioenergy in a water-limited world. *Bioscience*. 63: 102-117.
- Kinouchi, T.; Yagi, H.; Miyamoto, M. 2007. Increase in stream temperature related to anthropogenic heat input from urban wastewater. *Journal of Hydrology*. 335: 78-88.
- Klos, R.J.; Wang, G.G.; Bauerle, W.L.; Rieck, J.R. 2009. Drought impact on forest growth and mortality in the Southeast USA: an analysis using Forest Health and Monitoring data. *Ecological Applications*. 19: 699-708.
- Lake, P.S. 2003. Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology*. 48: 1161-1172.
- Larned, S.T.; Datry, T.; Arscott, D.B.; Tockner, K. 2010. Emerging concepts in temporary-river ecology. *Freshwater Biology*. 55: 717-738.
- Law, B.E. 2014. Regional analysis of drought and heat impacts on forests: current and future science directions. *Global Change Biology*. 20: 3595-3599.
- Levick, S.; Rogers, K. 2008. Patch and species specific responses of savanna woody vegetation to browser exclusion. *Biological Conservation*. 141: 489-498.
- Loarie, S.R.; Duffy, P.B.; Hamilton, H. [and others]. 2009. The velocity of climate change. *Nature*. 462: 1052-1055.
- Loheide, S.P.; Butler, J.J.; Gorelick, S.M. 2005. Estimation of groundwater consumption by phreatophytes using diurnal water table fluctuations: a saturated-unsaturated flow assessment. *Water Resources Research*. 41(7): W07030. 14 p. doi: 10.1029/2005WR003942. [Published online: July 27, 2005].
- Lovett, G.M.; Arthur, M.A.; Weathers, K.C.; Griffin, J.M. 2013. Effects of introduced insects and diseases on forest ecosystems in the Catskill Mountains of New York. *Effects of Climate Change and Invasive Species on Ecosystem Integrity and Water Quality*. 1298: 66-77.
- Lovett, G.M.; Canham, C.D.; Arthur, M.A. [and others]. 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. *Bioscience*. 56: 395-405.
- Lowe, W.H.; Likens, G.E. 2005. Moving headwater streams to the head of the class. *Bioscience*. 55: 196-197.
- Lowry, C.S.; Loheide, S.P. 2010. Groundwater-dependent vegetation: quantifying the groundwater subsidy. *Water Resources Research*. 46(6): W06202. doi:10.1029/2009WR008874. [Published online: July 17, 2010].
- Lu, J.B.; Sun, G.; McNulty, S.G.; Comerford, N.B. 2009. Sensitivity of pine flatwoods hydrology to climate change and forest management in Florida, USA. *Wetlands*. 29: 826-836.
- Lu, N.; Sun, G.; Feng, X.M.; Fu, B.J. 2013. Water yield responses to climate change and variability across the North-South Transect of Eastern China (NSTEC). *Journal of Hydrology*. 481: 96-105.

- Lubczynski, M.W.; Gurwin, J. 2005. Integration of various data sources for transient groundwater modeling with spatio-temporally variable fluxes—Sardon study case, Spain. *Journal of Hydrology*. 306: 71-96.
- Luce, C.H.; Morgan, P.; Dwire, K. [and others]. 2012. Climate change, forests, fire, water, and fish: building resilient landscapes, streams, and managers. Gen. Tech. Rep. RMRS-GTR-290. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 207 p.
- Luce, C.H.; Staab, B.; Kramer, M. [and others]. 2014. Sensitivity of summer stream temperatures to climate variability in the Pacific Northwest. *Water Resources Research*. 50: 3428-3443.
- Luce, C.H.; Holden, Z.A. 2009. Declining annual streamflow distributions in the Pacific Northwest United States, 1948-2006. *Geophysical Research Letters*. 36(16): L16401. 6 p. doi: 10.1029/2009GL039407. [Published online: August 22, 2009].
- Luce, C.H.; Tarboton, D.G.; Cooley, R.R. 1998. The influence of the spatial distribution of snow on basin-averaged snowmelt. *Hydrological Processes*. 12: 1671-1683.
- Luo, Y.Q.; Gerten, D.; Le Maire, G. [and others]. 2008. Modeled interactive effects of precipitation, temperature, and carbon dioxide (CO₂) on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biology*. 14: 1986-1999.
- Lustenhower, M.N.; Nicoll, L.; Ellison, A.M. 2012. Microclimatic effects of the loss of a foundation species from New England forests. *Ecosphere*. 3(3): article 26. 16 p. doi: 10.1890/ES12-00019.1. [Published online: March 26, 2012].
- Lutz, B.D.; Mulholland, P.J.; Bernhardt, E.S. 2012. Long-term data reveal patterns and controls on streamwater chemistry in a forested stream: Walker Branch, Tennessee. *Ecological Monographs*. 82: 367-387.
- Lytle, D.A.; Poff, N.L. 2004. Adaptation to natural flow regimes. *Trends in Ecology and Evolution*. 19(2): 94-100.
- Ma, Z.M.; Kang, S.Z.; Zhang, L. [and others]. 2008. Analysis of impacts of climate variability and human activity on streamflow for a river basin in arid region of northwest China. *Journal of Hydrology*. 352: 239-249.
- Maxwell, R.M.; Kollet, S.J. 2008. Interdependence of groundwater dynamics and land-energy feedbacks under climate change. *Nature Geoscience*. 1: 665-669.
- McDonough, O.T.; Hosen, J.D.; Palmer, M.A. 2011. Temporary streams: the hydrology, geography, and ecology of non-perennially flowing waters. In: Elliot, H.S.; Martin, L.E., eds. *River ecosystems: dynamics, management and conservation*. Hauppauge, NY: Nova Science Publishers: 259-289.
- McKenzie, D.; Gedalof, Z.; Peterson, D.L.; Mote, P. 2004. Climatic change, wildfire, and conservation. *Conservation Biology*. 18: 890-902.
- McLaughlin, D.L.; Kaplan, D.A.; Cohen, M.J. 2013. Managing forests for increased regional water yield in the southeastern U.S. Coastal Plain. *Journal of the American Water Resources Association*. 49: 953-965.
- Meier, W.; Bonjour, C.; Wuest, A.; Reichert, P. 2003. Modeling the effect of water diversion on the temperature of mountain streams. *Journal of Environmental Engineering (ASCE)*. 129: 755-764.
- Meiman, J.R. 1987. Influence of forests on snowpack accumulation. In: Troendle, C.A.; Kaufmann, M.R.; Hamre, R.H.; Winokur, R.P., eds. *Management of subalpine forests: building on 50-years of research*. Gen. Tech. Rep. RM-GTR-149. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 61-67.
- Meinzer, O.E. 1927. Plants as indicators of ground water. *Water Supply Paper 577*. Washington, DC: U.S. Geological Survey. 95 p.
- Mikkelsen, K.M.; Maxwell, R.M.; Ferguson, I. [and others]. 2013. Mountain pine beetle infestation impacts: modeling water and energy budgets at the hill-slope scale. *Ecohydrology*. 6: 64-72.
- Miller, G.R.; Chen, X.; Rubin, Y. 2010. Groundwater uptake by woody vegetation in a semiarid oak savanna. *Water Resources Research*. 46(10): W10503. 14 p. doi: 10.1029/2009WR008902. [Published online: October 6, 2010].
- Milly, P.C.D.; Dunne, A. 2002. Macroscale water fluxes—2. Water and energy supply control of their interannual variability. *Water Resources Research*. 38(10): I206. 9 p. doi: 10.1029/2001WR000760. [Published online: October 23, 2002].
- Mohseni, O.; Stefan, H.G.; Eaton, J.G. 2003. Global warming and potential changes in fish habitat in U.S. streams. *Climatic Change*. 59: 389-409.
- Moody, J.A.; Martin, D.A. 2009. Synthesis of sediment yields after wildland fire in different rainfall regimes in the Western United States. *International Journal of Wildland Fire*. 18: 96-115.
- Mote, P.W. 2006. Climate-driven variability and trends in mountain snowpack in western North America. *Journal of Climate*. 19: 6209-6220.
- Nichols, W.D. 1994. Groundwater discharge by phreatophyte shrubs in the Great Basin as related to depth to groundwater. *Water Resources Research*. 30: 3265-3274.
- Niinemets, U.; Flexas, J.; Penuelas, J. 2011. Evergreens favored by higher responsiveness to increased carbon dioxide (CO₂). *Trends in Ecology & Evolution*. 26: 136-142.
- Nilsen, E.T.; Sharifi, M.R.; Rundel, P.W. 1984. Comparative water relations of phreatophytes in the Sonoran Desert of California. *Ecology*. 65: 767-778.
- Null, S.E.; Ligare, S.T.; Viers, J.H. 2013. A method to consider whether dams mitigate climate change effects on stream temperatures. *Journal of the American Water Resources Association*. 49: 1456-1472.
- Ohnuki, Y.; Kimhean, C.; Shinomiya, Y.; Toriyama, J. 2008. Distribution and characteristics of soil thickness and effects upon water storage in forested areas of Cambodia. *Hydrological Processes*. 22: 1272-1280.
- Orellana, F.; Verma, P.; Loheide, S.P.; Daly, E. 2012. Monitoring and modeling water-vegetation interactions in groundwater-dependent ecosystems. *Reviews of Geophysics*. 50(3): RG3003. 24 p. doi: 10.1029/2011RG000383. [Published online: July 24, 2012].
- Palmer, M.A.; Liermann, C.A.R.; Nilsson, C. [and others]. 2008. Climate change and the World's river basins: anticipating management options. *Frontiers in Ecology and the Environment*. 6: 81-89.
- Paradis, A.; Elkinton, J.; Hayhoe, K.; Buonaccorsi, J. 2008. Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America. *Mitigation and Adaptation Strategies for Global Change*. 13: 541-554.
- Pastor, J.; Aber, J.D.; McClaugherty, C.A.; Melillo, J.M. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology*. 65: 256-268.
- Patterson, L.A.; Lutz, B.D.; Doyle, M.W. 2013. Characterization of drought in the South Atlantic, United States. *Journal of the American Water Resources Association*. 49: 1385-1397.

- Pederson, N.; Dyer, J.M.; McEwan, R.W. [and others]. 2014. The legacy of episodic climatic events in shaping temperate, broadleaf forests. *Ecological Monographs*. 84(4): 599-620. doi: 10.1890/13-1025.1. [Published online: November 2014].
- Peterson, D.P.; Wenger, S.J.; Rieman, B.E.; Isaak, D.J. 2013. Linking climate change and fish conservation efforts using spatially explicit decision support tools. *Fisheries*. 38: 112-127.
- Peterson, J.T.; Kwak, T.J. 1999. Modeling the effects of land use and climate change on riverine smallmouth bass. *Ecological Applications*. 9: 1391-1404.
- Plaut, J.A.; Yopez, E.A.; Hill, J. 2012. Hydraulic limits preceding mortality in a pinyon-juniper woodland under experimental drought. *Plant, Cell & Environment*. 35: 1601-1617.
- Portal, P.; Koprivnjak, J.F.; Molot, L.A.; Dillon, P.J. 2009. Humic substances—part 7: the biogeochemistry of dissolved organic carbon and its interactions with climate change. *Environmental Science and Pollution Research*. 16: 714-726.
- Potter, N.J.; Chiew, F.H.S. 2011. An investigation into changes in climate characteristics causing the recent very low runoff in the southern Murray-Darling Basin using rainfall-runoff models. *Water Resources Research*. 47(12): W00G10. 12 p. doi: 10.1029/2010WR010333. [Published online: October 18, 2011].
- Potts, D.F. 1984. Hydrologic impacts of a large-scale mountain pine-beetle (*Dendroctonus-Ponderosae* Hopkins) epidemic. *Water Resources Bulletin*. 20: 373-377.
- Powell, T.L.; Galbraith, D.R.; Christoffersen, B.O. [and others]. 2013. Confronting model predictions of carbon fluxes with measurements of Amazon forests subjected to experimental drought. *New Phytologist*. 200: 350-364.
- Price, K. 2011. Effects of watershed topography, soils, land use, and climate on baseflow hydrology in humid regions: a review. *Progress in Physical Geography*. 35: 465-492.
- Pugh, E.; Gordon, E. 2013. A conceptual model of water yield effects from beetle-induced tree death in snow-dominated lodgepole pine forests. *Hydrological Processes*. 27: 2048-2060.
- Pugh, E.; Small, E. 2012. The impact of pine beetle infestation on snow accumulation and melt in the headwaters of the Colorado River. *Ecohydrology*. 5: 467-477.
- Raymond, P.A.; Saiers, J.E. 2010. Event controlled DOC export from forested watersheds. *Biogeochemistry*. 100: 197-209.
- Rieman, B.; Lee, D.; Burns, D. [and others]. 2003. Status of native fishes in the Western United States and issues for fire and fuels management. *Forest Ecology and Management*. 178: 197-211.
- Robinson, T.W. 1958. Phreatophytes. Geological Survey Water Supply Paper 1423. Washington, DC: U.S. Government Printing Office. 84 p.
- Robson, B.J.; Chester, E.T.; Austin, C.M. 2011. Why life history information matters: drought refuges and macroinvertebrate persistence in non-perennial streams subject to a drier climate. *Marine and Freshwater Research*. 62: 801-810.
- Rodriguez-Iturbe, I. 2000. Ecohydrology: a hydrologic perspective of climate-soil-vegetation dynamics. *Water Resources Research*. 36(1): 3-9.
- Sanford W.E.; Slenick, D.L. 2013. Estimation of actual evapotranspiration across the conterminous United States using a regression based on climate and land cover data. *Journal of the American Water Resources Association*. 49(1): 217-230.
- Schindler, D.W.; Curtis, P.J.; Bayley, S.E. [and others]. 1997. Climate-induced changes in the dissolved organic carbon budgets of boreal lakes. *Biogeochemistry*. 36: 9-28.
- Schlesinger, W.H.; Jasechko, S. 2014. Transpiration in the global water cycle. *Agricultural and Forest Meteorology*. 189: 115-117.
- Scott, M.J.; Jones, M.N.; Woof, C.; Tipping, E. 1998. Concentrations and fluxes of dissolved organic carbon in drainage water from an upland peat system. *Environment International*. 24: 537-546.
- Smith, S.D.; Devitt, D.A.; Sala, A. [and others]. 1998. Water relations of riparian plants from warm desert regions. *Wetlands*. 18: 687-696.
- Smith, H.G.; Sheridan, G.J.; Lane, P.N. [and others]. 2011. Wildfire effects on water quality in forest catchments: a review with implications for water supply. *Journal of Hydrology*. 396: 170-192.
- Soylu, M.E.; Kucharik, C.J.; Loheide, S.P. 2014. Influence of groundwater on plant water use and productivity: development of an integrated ecosystem—variably saturated soil water flow model. *Agricultural and Forest Meteorology*. 189: 198-210.
- Spencer, C.N.; Gabel, K.O.; Hauer, F.R. 2003. Wildfire effects on stream food webs and nutrient dynamics in Glacier National Park, USA. *Forest Ecology and Management*. 178: 141-153.
- Stednick, J.D. 1996. Monitoring the effects of timber harvest on annual water yield. *Journal of Hydrology*. 176: 79-95.
- Stewart, I.T.; Cayan, D.R.; Dettinger, M.D. 2005. Changes toward earlier streamflow timing across western North America. *Journal of Climate*. 18: 1136-1155.
- Stott, R.E.; Burt, T.P. 1997. Potassium chemistry of a small upland stream following a major drought. *Hydrological Processes*. 11: 189-201.
- Surfleet, C.G.; Tullos, D. 2013. Variability in effect of climate change on rain-on-snow peak flow events in a temperate climate. 479: 24-34.
- Sun, G.; Riedel, M.; Jackson, R. [and others]. 2004. Influences of management of Southern forests on water quantity and quality. In: Rauscher, H.M.; Johnsen, K., eds. *Southern Forest Sciences: past, current, and future*. Gen. Tech. Rep. SRS-75. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 394 p.
- Sun, G.; Noormets, A.; Gavazzi, M.J. [and others]. 2010. Energy and water balance of two contrasting loblolly pine plantations on the lower coastal plain of North Carolina, USA. *Forest Ecology and Management*. 259: 1299-1310.
- Sun, G.; Caldwell, P.; Noormets, A. [and others]. 2011. Upscaling key ecosystem functions across the conterminous United States by a water-centric ecosystem model. *Journal of Geophysical Research-Biogeosciences*. 116(G3): G00J05. 16 p. doi: 10.1029/2010JG001573. [Published online: May 21, 2011].
- Sun, G.; Caldwell, P.V.; McNulty, S.G. 2015. Modelling the potential role of forest thinning in maintaining water supplies under a changing climate across the conterminous United States. *Hydrological Processes*. 15 p. doi: 10.1002/hyp.10469. [Published online: April 1, 2015].
- Swain, S.; Hayhoe, K. 2014. CMIP5 projected changes in spring and summer drought and wet conditions across North America. *Climate Dynamics*. 44(9): 2737-2750. doi: 10.1007/s00382-014-2255-9. [Published online: August 12, 2014].

- Swank, W.T.; Knoepp, J.D.; Vose, J.M. [and others]. 2014. Response and recovery of water yield and timing, stream sediment, abiotic parameters, and stream chemistry following logging. In: Swank, W.T.; Webster, J.R., eds. Long-term response of a forest watershed ecosystem: clearcutting in the Southern Appalachians. New York: Oxford University Press: 35-56.
- Swift, L.W., Jr.; Baker, S.E. 1973. Lower water temperatures within a streamside buffer strip. Research Note SE-193. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 7 p.
- Swift, L.W.; Messer, J.B. 1971. Forest cuttings raise temperatures of small streams in Southern Appalachians. *Journal of Soil and Water Conservation*. 26: 111-116.
- Swistock, B.R.; DeWalle, D.R.; Sharpe, W.E. 1989. Sources of acidic stormflow in an Appalachian headwater stream. *Water Resources Research*. 25: 2139-2147.
- Tague, C.; Grant, G.E. 2009. Groundwater dynamics mediate low-flow response to global warming in snow-dominated alpine regions. *Water Resources Research*. 45(7): W07421. 12 p. doi: 10.1029/2008WR007179. [Published online: July 23, 2009].
- Tague, C.L.; Choate, J.S.; Grant, G. 2013. Parameterizing sub-surface drainage with geology to improve modeling streamflow responses to climate in data limited environments. *Hydrology and Earth System Sciences*. 17: 341-354.
- Taylor, R.G.; Scanlon, B.; Doll, P. [and others]. 2013. Groundwater and climate change. *Nature. Climate Change* 3: 322-328.
- Tang, G.P.; Beckage, B. 2010. Projecting the distribution of forests in New England in response to climate change. *Diversity and Distributions*. 16: 144-158.
- Tang, G.P.; Beckage, B.; Smith, B. 2012. The potential transient dynamics of forests in New England under historical and projected future climate change. *Climatic Change*. 114: 357-377.
- Thorburn, P.; Walker, G.; Hatton, T. 1992. Are river red gums taking water from soil, groundwater or streams? In: Adelaide, SA, ed. Proceedings: National Conference on Vegetation and Water Management. Canberra, Australia: Greening Australia: 37-42.
- Tjoelker, M.G.; Oleksyn, J.; Reich, P.B. 1998. Seedlings of five boreal tree species differ in acclimation of net photosynthesis to elevated CO₂ and temperature. *Tree Physiology*. 18: 715-726.
- Vadeboncoeur, M.A. 2010. Meta-analysis of fertilization experiments indicates multiple limiting nutrients in northeastern deciduous forests. *Canadian Journal of Forest Research*. 40: 1766-1780.
- Viglizzo, E.F.; Noretto, M.D.; Jobbagy, E.G. 2014. The ecohydrology of ecosystems in transition: a meta-analysis. *Ecohydrology*. 8(5): 911-921. doi: 10.1002/eco.1540. [Published online: August 7, 2014].
- Vitvar, T.; Burns, D.A.; Lawrence, G.B. [and others]. 2002. Estimation of baseflow residence times in watersheds from the runoff hydrograph recession: method and application in the Neversink watershed, Catskill Mountains, New York. *Hydrological Processes*. 16: 1871-1877.
- Vose, J.M.; Sun, G.; Ford, C.R. [and others]. 2011. Forest ecohydrological research in the 21st century: what are the critical needs? *Ecohydrology*. 4: 146-158.
- Vose, J.M.; Swank, W.T. 1994. Effects of long-term drought on the hydrology and growth of a white-pine plantation in the Southern Appalachians. *Forest Ecology and Management*. 64: 25-39.
- Wall, G.R.; Phillips, P.J.; Riva-Murray, K. 1998. Seasonal and spatial patterns of nitrate and silica concentrations in Canajoharie Creek, New York. *Journal of Environmental Quality*. 27: 381-389.
- Waring, R.H.; Schlesinger, W.H. 1985. Forest ecosystems: concepts and management. Orlando, FL: Academic Press. 340 p.
- Webb, B.W. 1996. Trends in stream and river temperature. *Hydrological Processes*. 10: 205-226.
- Webb, B.W.; Clack, P.D.; Walling, D.E. 2003. Water-air temperature relationships in a Devon river system and the role of flow. *Hydrological Processes*. 17: 3069-3084.
- Webb, B.W.; Nobilis, F. 1995. Long-term water temperature trends in Austrian rivers. *Hydrological Sciences Journal*. 40: 83-96.
- Weed, A.S.; Ayres, M.P.; Hicke, J.A. 2013. Consequences of climate change for biotic disturbances in North American forests. *Ecological Monographs*. 83: 441-470.
- Westerling, A.L.; Hidalgo, H.G.; Cayan, D.R.; Swetnam, T.W. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science*. 313: 940-943.
- Wilcox, B.P.; Thurow, T.L. 2006. Emerging issues in rangeland ecohydrology: vegetation change and the water cycle. *Rangeland Ecology & Management*. 59: 220-224.
- Williams, M.R.; Melack, J.M. 1997. Effects of prescribed burning and drought on the solute chemistry of mixed-conifer forest streams of the Sierra Nevada, California. *Biogeochemistry*. 39: 225-253.
- Wolock, D.M.; McCabe, G.J. 1999. Explaining spatial variability in mean annual runoff in the conterminous United States. *Climate Research*. 11: 149-159.
- Wolock, D.M. 2003. Base-flow index grid for the conterminous United States. [Digital data set]. USGS Open File Report 03-263. Reston, VA: U.S. Geological Survey. <http://water.usgs.gov/lookup/getspatial?bf148grd>. [Date accessed: October 19, 2015].
- Wood, P.J.; Armitage, P.D. 1997. Biological effects of fine sediment in the lotic environment. *Environmental Management*. 21: 203-217.
- Wood, P.J.; Armitage, P.D. 1999. Sediment deposition in a small lowland stream— management implications. *Regulated Rivers: Research & Management*. 15: 199-210.
- Wooldridge, D.D.; Stern, D. 1979. Relationships of silvicultural activities and thermally sensitive forest streams. Report DOE 79-5a-5. Seattle, WA: University of Washington, College of Forest Resources. 90 p.
- Worrall, F.; Burt, T.P. 2008. The effect of severe drought on the dissolved organic carbon (DOC) concentration and flux from British rivers. *Journal of Hydrology*. 361: 262-274.
- Wullschlegel, S.D.; Hanson, P.J.; Todd, D.E. 2001. Transpiration from a multi-species deciduous forest as estimated by xylem sap flow techniques. *Forest Ecology and Management*. 143: 205-213.
- Wurzburger, N.; Miniat, C.F. 2014. Drought enhances symbiotic dinitrogen fixation and competitive ability of a temperate forest tree. *Oecologia*. 174: 1117-1126.
- Young, R.F.; Shields, K.S.; Berlyn, G.P. 1995. Hemlock woolly adelgid (Homoptera: Adelgidae): stylet bundle insertion and feeding sites. *Annals of the Entomological Society of America*. 88: 827-835.
- Zhang, L.; Dawes, W.R.; Walker, G.R. 2001. Response of mean annual evapotranspiration to vegetation changes at catchment scale. *Water Resources Research*. 37: 701-708.

Economics and Societal Considerations of Drought

Jeffrey P. Prestemon
Linda Kruger

CONTRIBUTORS

Karen L. Abt, J.M. Bowker, Consuelo Brandeis,
David E. Calkin, Geoffrey H. Donovan, Charlotte Ham,
Thomas P. Holmes, Jeffrey Kline, and Travis Warziniack

J.P. Prestemon is a Research Forester, U.S. Department of Agriculture, Forest Service, Southern Research Station (SRS), Forest Economics and Policy Research, Forestry Sciences Laboratory, Research Triangle Park (RTP), NC 27709.

L. Kruger is a Research Social Scientist, Alaska Native and American Indian Special Emphasis Program Manager, and Tribal Liaison, Pacific Northwest Research Station (PNW), U.S. Department of Agriculture, Forest Service, Juneau Forestry Sciences Laboratory, Juneau, AK 99801.

K.L. Abt is a Research Economist, U.S. Department of Agriculture, Forest Service, Southern Research Station (SRS), RTP, NC 27709; **J.M. Bowker** is a Research Social Scientist, U.S. Department of Agriculture, Forest Service, SRS, Athens, GA 30605; **C. Brandeis** is a Research Forester, U.S. Department of Agriculture, Forest Service, Southern Research Station (SRS), Knoxville, TN 37919; **D.E. Calkin** is a Research Forester, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Missoula, MT 59802; **G.H. Donovan** is a Research Forester, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station (PNWRS), Portland, OR 97204; **C. Ham** is a Postdoctoral Scholar, North Carolina State University, Department of Forestry and Environmental Resources, Raleigh, NC 27709; **T.P. Holmes** is a Research Economist, U.S. Department of Agriculture, Forest Service, Southern Research Station (SRS), RTP, NC 27709; **J. Kline** is a Research Forester, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station (PNWRS), Corvallis, OR 97331; **T. Warziniack** is a Research Economist, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Ft. Collins, CO 80526.

Introduction

The economic and social effects of drought are diverse and related to physical characteristics of drought, including spatial extent, severity, duration, and frequency that combine to determine drought's overall effects on society. Most of the attention given to economic and social impacts of drought focuses on adverse consequences, but technology, public policies, economic activity, and social systems are largely adapted to the historical occurrence of drought—at least within the normal range. This chapter covers traditional impacts from drought, and also highlights possible adaptations, noting when adaptation may be difficult due to growing stresses on water resources in response to changes in global climate and regional demographics.

Droughts of particular combinations of severity, duration, and spatial extent occur at varying frequency—say, once in 50 years or once in 100 years. These dimensions can be relatively stationary in a location's climate, or they can change along with climate. The multiple dimensions of any given drought determine its effects on forest and rangeland systems, on society, and on the economy (Hornbeck 2012, McLeman and others 2014). Short, local, or mild droughts may have effects that are imperceptible in the larger forest and rangeland sector because of adaptation to these variations in water status and flows. The historical occurrence of these “average” droughts have created the conditions that determined forest and rangeland characteristics as well as the land use, technology, and production patterns of the associated human communities.

In contrast to the adaptations that society has made to more typical droughts, the United States has experienced droughts that were extreme in one or more of their characteristics, with significant consequences for technology, policies, economic activity in water-sensitive sectors, and social systems. Extreme droughts could occur more often or more widely in the United States in the future (Wuebbles and others 2014). Predictions from Wuebbles and others (2014) include significant drying in the winter and spring months in the North American monsoon region of the West (affecting mainly Arizona, New Mexico, and parts of Utah and Colorado). For the Southeastern United States, models project greater interannual variability in precipitation. Models project overall average drying of the continental United States throughout the 21st century, relative to 20th century conditions. Much of the projected drying in the Southeastern United States would occur

through overall higher average temperatures, leading to increased evapotranspiration, compared to the average levels observed in recent history.

Wuebbles and others (2014) refer to shifts in distributions of precipitation and temperature—and hence drought—in ways that make droughts either longer in duration, more severe, more frequent, or, potentially, more widespread. The overall implication is that the likelihood of large magnitude droughts could be higher in the coming decades. As a result, we might expect society in general and local economies in particular to be challenged more regularly and more forcefully to adapt to these climate changes. Adaptation could entail the development of new and application of existing technologies, policies, and resource management approaches that can aid water-sensitive economic sectors—and society more broadly—to better withstand the negative consequences of drought.

In this chapter, we discuss how drought affects economic and social systems and then evaluate some specific effects of drought on forest and rangeland economies and societies. We describe a conceptual model of social and economic systems that defines where and how droughts are expected to influence these systems, and we examine social and economic resilience and the policies and programs that have been enacted to promote and maintain resilience. We address the direct effects of drought on the timber products sector, forest and rangeland water supplies, and the rangeland sector; and the indirect effects of drought on wildfire suppression expenditures. Finally, we examine nonmarket effects that include changes in recreation, effects on urban communities, and effects on tribal values and lifeways.

General Economic and Social Effects of Drought in Forests and Rangelands

An Economic and Social Conceptual Model of Drought

We begin by describing a conceptual model of drought impacts on the economy and society more broadly (fig. 11.1). The model shows how market and nonmarket goods and services are produced by an economy interacting with nature and how drought affects that production. Figure 11.1 shows that society has two broad classes of inputs that can be used to obtain desired goods and services: free inputs and purchased inputs. Free inputs are those that nature

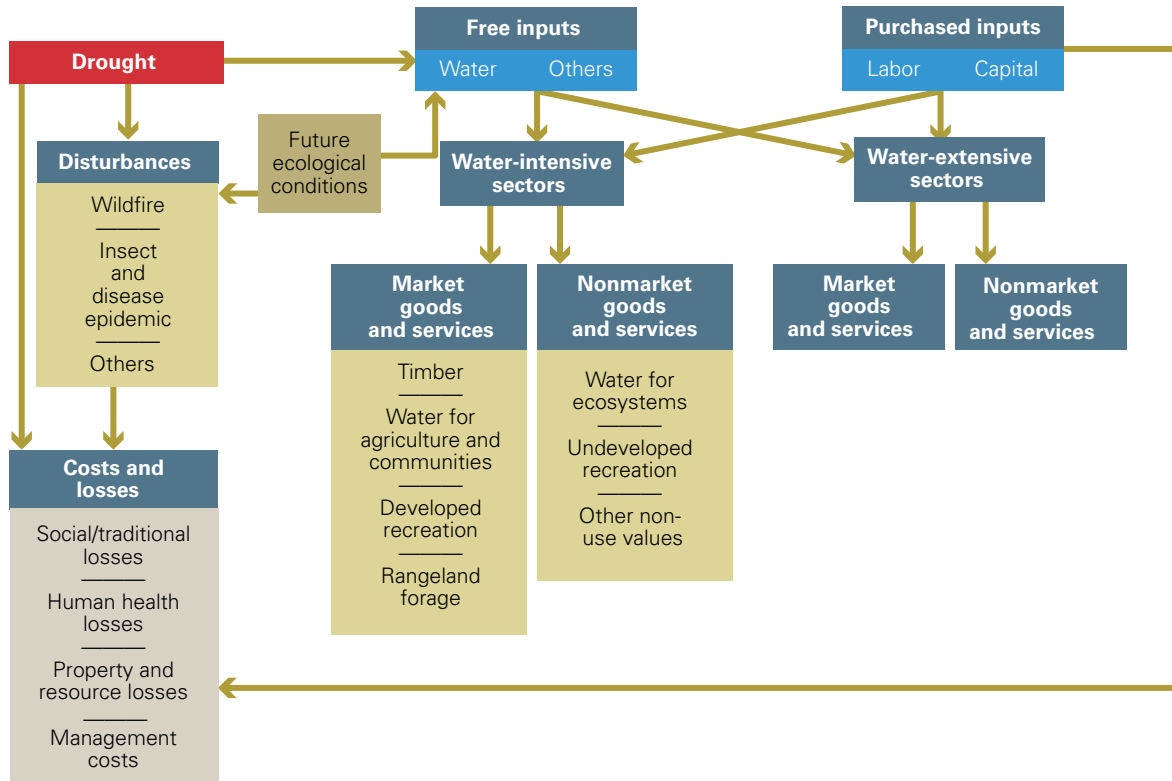


Figure 11.1—A conceptual model of an economy and society, which can produce and consume goods and services that are either water-intensive or water-extensive, and are affected by drought. (Colored boxes within encompassing squares are subcategories or examples).

provides (but humans can alter them subsequently and intervene to affect their distribution or character), such as water and sunshine and air. Purchased inputs, including capital and labor, are provisioned by society.¹ Two parts of society, described as sectors, are either water-intensive or water-extensive.² Each of these two sectors produces market and nonmarket goods and services. Drought alters the quantities (and qualities) of free inputs that are available to produce goods and services in both sectors, thus altering production possibilities and shifting supply curves in the markets for goods and services that depend on them. Drought also directly and indirectly results in costs and losses. Direct losses include the flows of timber, range forage, and water services. Direct costs include research (Miao and Popp 2014) and actions (e.g., construction)

designed to reduce the extent of losses. Indirect losses derive from changes in ecological conditions, which means that drought changes the quantities of free inputs available to society for future production of goods and services. In terms of market goods and services that are water-intensive, possible categories of goods and services (there could be more) include timber (requiring water to grow), water for agriculture and communities (direct human consumption), developed recreation (e.g., downhill skiing, motorized water-based sports), and undeveloped recreation (e.g., cross-country skiing, nonmotorized water-based sports).³ Nonmarket goods and services in forests and rangelands that are water-intensive include ecosystem health, plant and animal habitat, and the general quality of landscape esthetics.

¹ Capital and labor, however, embody some water themselves, but this does not alter the general principles laid out in this conceptual model.

² A water-intensive sector is one for which some form of water is a major input to producing an output. A water-extensive sector is one for which water is a minor input, perhaps only embodied in the capital and labor used to produce the output.

³ We note that the terms “water-intensive” and “water-extensive” are most often associated with agriculture and cropping systems, and thus entirely appropriate in most parts of the economy that we examine in this chapter. Recreation activities, on the other hand, might more accurately be classified as “water-dependent” or “nonwater-dependent.”

Much of the research on the economic effects of drought on forests and rangelands has focused on quantifying how drought might affect the quantities and market values of the goods and services shown in the subcategories (mustard and gray boxes) in figure 11.1, as opposed to quantifying the effects on the economic value of market production and consumption (welfare). Our conceptual model attempts to address Logar and van den Bergh's (2013) criticism that while there have been many attempts to quantify the "costs" of drought, there is no comprehensive framework for understanding drought's effects on an entire economy or society in terms of overall economic welfare. Taking this broad perspective, Logar and van den Bergh (2013) delineate the societal effects of drought into three categories: (1) direct, focusing on costs and losses on primary producing sectors that consume and manage water; (2) indirect, by altering the amounts of inputs available for production in other sectors and by adding effects on disturbances such as wildfires and insect and disease epidemics, which themselves affect free inputs available to society and also induce allocation of purchased inputs for management; and (3) nonmarket, including effects on human and ecosystem health and social and cultural values.

Table 11.1 combines our conceptual model with the categorization advanced by Logar and van den Bergh (2013). As such, it lists several categories of goods and services production that could represent some of the subcategories (mustard and gray boxes) shown in figure 11.1. The forest and rangeland-related market goods and services that are water-intensive include timber production, forest and rangeland water supply sources, and rangeland production. The nonmarket effects coincide with those in the water-intensive nonmarket goods and services box shown in figure 11.1. Table 11.1 indicates whether the effect is direct, indirect, and/or nonmarket as well as the specific effects that occur and sometimes can be measured. In latter sections of this chapter, we provide some examples of effects found by researchers in most of these categories.

Figure 11.1 does not show many of the dynamics of society, specifically how drought that affects production of one category of good or service may change conditions faced in the production of another good or service. This chapter's appendix provides a graphical description of how drought can lead to shifts in supply and demand, affecting equilibrium market prices and quantities and economic welfare (Just and others 1982) in water-intensive and water-extensive parts of an

economy. The appendix also describes how neoclassical economics would approach quantification of the effects of drought on markets for goods and services produced by forests and rangelands.

The economic effects of drought are complex because of the interplay among physical, social, and technological responses to drought. For example, drought lowers output in the water-intensive sectors of an economy, lowering wages, the price of capital (interest rates), and the prices of other inputs to production in the water-intensive sector, such as land. Drought also leads to lower income through its negative effects on the price of capital and labor (wage rates). Water-extensive sectors, however, can benefit from drought, as the costs of labor and capital decline; output increases while the prices of goods in those sectors decrease. Nevertheless, the overall effect on the economy, when both water-intensive and water-extensive sectors are combined, is to reduce wages, interest rates, and income. New technology introduced to the water-intensive sector can help to mitigate the negative effects of drought, allowing for more efficient use of water for each unit of water-intensive good output. Technology can be introduced through efforts of either the private sector or the public sector. It should be noted that capital markets are large and fluid, so technology investments would put only very slight upward pressure on interest rates.

There are a few notable studies on describing societies' responses to drought and their ability to mitigate negative impacts through new investments in technology. Banerjee and others (2013) describe the direct and indirect economic effects of drought from an ecosystems perspective, quantifying the "Millennium Drought" in Australia (1997–2010). The study focuses on quantifying impacts, not on measuring how economic welfare (see appendix) was affected by drought or how it would be in the future as a result of drought-related investments. It does, however, list the expenditures on mitigation and investments designed to help the region withstand future droughts with lower overall negative consequences for economic welfare. The study indicated that AU\$810 million [US\$745 million, at 2010 exchange rates (OZF-REX Foreign Exchange Services 2014)] was spent during the drought to mitigate the drought's effects and to better withstand future droughts. Expenditures included those by the national government to build a new system of integrated water pipelines to more efficiently allocate water among agricultural and potable water users.

Table 11.1—Economic and societal effects of drought in forests and rangelands

Type of effect	Economic subsector or aspect	Mechanism	Effects
Direct and indirect	Timber products sector	Reduced net volume growth	Lower income and employment, altered land use away from active forestry
Direct and indirect	Forest- and rangeland-based water	Reduced water quantity and quality	Lower consumption quantities, lower water quality, shifted water provision timing, higher water prices and treatment costs
Indirect	Wildfire management	Higher wildfire activity	Increased expenditures on suppression, fuels management, prevention, and post-fire mitigation by public and private landowners; greater losses of natural resources, reduced overall economic output in the economy due to wildfire-related evacuations, morbidity, and mortality
Indirect	Insect and disease management	Increased insect and disease activity	Increased expenditures on monitoring, suppression, and mitigation by public agencies and private individuals; higher prices and lower overall output and spatio-temporal shifts in production of valued ecosystem goods and services
Indirect	Rangeland sector	Reduced growth of vegetation needed by livestock and wildlife	Lower livestock production, higher livestock prices; lower wildlife populations and therefore fewer opportunities for hunting
Indirect	Urban and residential communities	Reduced growth to landscape plants, increased tree mortality, higher vulnerability to other disturbances	Lower property values, reduced shading resulting in higher energy costs, deterioration in human health and welfare
Nonmarket	Recreation sector	Altered ability of forests and rangelands to provide various types of recreation opportunities	Shifts in spending by recreationists across time, space, type, and to other sectors; lower fish populations and fewer fishing opportunities
Nonmarket	Human health	Increased air particulate matter	Increased rates of respiratory illness-related admissions to medical facilities due to wind-blown dust and wildfire smoke
Nonmarket	Indigenous cultures	Altered provision of water-affected ecosystem goods and services valued by indigenous cultures	Changes in the consumption and therefore the religious experiences available; altered rates of consumption of nontimber forest products
Nonmarket	Wildlife habitat	Reduced quantity and quality of habitat with potential endangerment or extinction of at-risk species	Increased management cost for species identified as threatened or endangered; potential cost of management restrictions on identified critical habitat; potential loss of genetic diversity

The South Australian government also bought water allocations from agricultural users and used this water to meet critical human needs and protect important drought-threatened riparian habitat. Mitigation costs also included expenditures by the South Australian government to repair levees damaged by floodplain subsidence; modify bridges, ferry landings, and pipelines to low-flow conditions; repair roads damaged by subsidence-related slumping and collapse; build new monitoring systems for threatened infrastructure; buy new and more efficient irrigation infrastructure; lime drought-exposed lakebeds to help reduce drought-related soil acidification; revegetate drought-exposed lakebeds; and buy water from the water market to create an environmental water reserve.

The Banerjee and others (2013) study described the extensive efforts of Australian government entities to mitigate and adapt to drought in anticipation that future droughts might be as severe. The study provides a specific example of how drought affected the production of goods and services and stimulated actions by government to help mitigate it. A study by Hornbeck (2012) details some of the economic and social effects of the American Dust Bowl of the 1930s, a drought that had large economic and social consequences, as well. This study is informative of how scientists can use historical data to analyze drought's economic effects. The study also highlights the consequences of an inability to anticipate or respond to severe drought: the region affected was not resilient enough to absorb its impacts without profound economic and social change. Hornbeck (2012) compares the long-run fates of low-, medium- and high-erosion counties in the affected region of the Great Plains. One effect was the reallocation of farmland from water-intensive to less water-intensive uses (especially from crops to pasture for livestock). However, the majority of the Dust Bowl's effects in the agricultural sector were manifested in significant net out-migration of people from affected regions and associated reductions in income, rather than through reallocations of resources to other sectors locally such as to industry or through investments into new technologies. As a result, agricultural sector impacts are quantified through changes in land values, which embody the long-run expected value of profits from these agricultural uses. In the affected region, land values declined by 30 percent in highly eroded counties and by 17 percent in medium-eroded counties, when compared to less-eroded counties. Further, losses in land values in most affected counties persisted at least into the 1990s—60 years. Hornbeck (2012) emphasizes that there were spatial

effects tied to soil losses, creating shifts in production from more-eroded to less-eroded counties, coupled with an overall decline in output and hence higher prices, which resulted in land value increases in the latter that partially compensated for the land value losses in the former. Maladaptation by farmers to dustbowl conditions and the buildup of farm debt created additional vulnerability of the local population. In summary, drought (as with any natural disaster) can result in spatial as well as spatio-temporal reallocations of resources within affected sectors, which can mitigate overall losses to the sector. Moreover, drought can force reallocations across sectors, and these effects can be quantified by changes in incomes generated in each sector.

Societal and Economic Resilience

The experience of the 1930s Dust Bowl in America highlights the importance of societal and economic resilience in the face of large-scale and intense disturbances. In general, ecosystem stress due to drought increases societal and economic costs (such as those associated with emigration from drought-stricken areas) and losses (such as diminished land values resulting from reduced productivity) (Hornbeck 2012). The ability to withstand and recover from ecosystem stresses with minimal costs and losses reflects the degree of societal and economic resilience (Holmes and others 2014). For typical drought conditions, societal and economic resilience may be fairly high. For example, when confronted with normal dry spells, homeowners typically increase irrigation of their lawns and other landscaping to a degree sufficient to alleviate vegetative stress. Although simple actions such as these may entail costs and losses, they often are relatively modest. Further, resilience to typical drought conditions is high because a low-cost technology (irrigation) is usually accessible due to prevailing institutions (such as markets and public water supplies) and prior knowledge is adequate. However, as the severity, duration, and spatial extent of drought conditions increase, routine mitigation actions based on prior knowledge and accessible technology may not always produce the desired effect, and communities may incur substantial cost plus loss amounts. In particular, societal and economic cost plus loss amounts may increase at an increasing rate with greater ecosystem stress as the ability to mitigate damages is reduced and resilience is gradually exceeded. This dynamic process is shown graphically in figure 11.2, where the horizontal axis measures any or a combination of the three dimensions of ecosystem stress (severity, duration, spatial extent). Modest cost plus loss amounts associated with typical

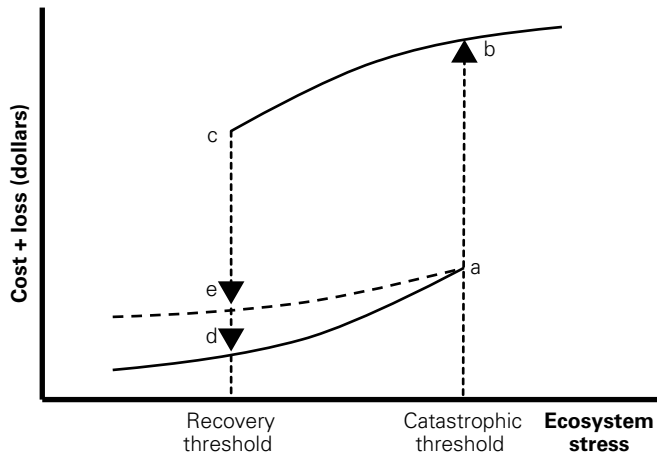


Figure 11.2—Economic impacts resulting from increasing levels of a disturbance may entail catastrophic surprises, and economic systems may fail to fully recover.

drought conditions are illustrated by points along the lower curve (moving along the curve from point d to a). The increasing slope indicates that as the capacity to manage greater ecosystem stress is diminishing, cost plus loss amounts are rapidly increasing.

Extreme levels of ecosystem stress may cause a dramatic upward shift in the cost-plus-loss function as the services provided by ecosystems degenerate and societal and economic resilience is exceeded (illustrated by the move from point a to point b on the upper curve in fig. 11.2). Even as the level of ecosystem stress subsides, communities may continue to invest in recovery efforts, keeping cost-plus-loss amounts on the upper curve in the figure (moving from point b to point c). However, over time, damage mitigation investments are diminished and communities recover, perhaps fully (illustrated by the recovery threshold and the move from c to d in the figure). When the damage to ecosystems is sufficiently severe, communities may fail to fully recover (moving from point c to point e).

Using the American Dust Bowl of the 1930s as an example, we see evidence of this dynamic process of ecological stress, catastrophic societal and economic loss, and (partial) recovery. Although the Great Plains historically experienced episodic periods of drought, an emerging cadre of “agricultural capitalists” willing to take entrepreneurial risks resulted in the Great Plow-up (Worster 1986), pushing much of the southern Great Plains beyond an unstable cropland-grassland equilibrium (McLeman and others 2014). Combined with the severe drought of the 1930s, enormous

societal and economic costs and losses were exacted (e.g., associated with the costs of human migration, foreclosure of homes, and lost agricultural and other business income). Recent evidence shows that, despite the economic adjustments that occurred in the region since the 1930s, communities that experienced the worst drought conditions have not fully recovered (Hornbeck 2012).

People generally learn from their experience and make efforts to find ways to adapt to threatening environmental conditions, which increases societal and economic resilience. One strategy for increasing resilience is to create flexible institutions that can readily adapt to ecosystem stresses. For example, Welsh and others (2013) demonstrated how formal rules (water laws), in combination with informal rules governing local use of common-pool resources, have been effective in adapting to drought conditions by farmers in the Western United States. Another strategy for increasing social and economic resilience is to develop new technologies that are less vulnerable to ecosystem stresses. Using a statistical model linking historical droughts with patent applications for drought-resistant crops, Miao and Popp (2014) show how historical drought events have spurred innovation in agricultural biotechnology.

The societal and economic resilience in forest and rangelands to drought depends upon efforts to improve the adaptive capacity of communities across many spatial scales. Three adaptation strategies are suggested. First, increased knowledge of the impacts of drought on trees and forests and rangeland plants (including a better understanding of drought-fire-pest interactions) may help predict the timing, location, and severity of ecosystem stress so that pre-emptive mitigating actions can be taken. A second strategy would be the development of drought-resistant tree and rangeland plant species, but these investments will probably only occur if drought stress is anticipated to substantially reduce the productivity of important tree crops. Third, the development of institutions, such as local communication networks among forest and rangeland stakeholders, may facilitate more rapid and better informed responses to emerging ecosystem stressors such as drought.

Programs and Policies To Address Resilience

U.S. society has faced drought conditions throughout its history. As the United States grew economically and in population, local, State, and Federal governments created institutions that work to reduce

the overall negative impacts from droughts and other natural phenomena—in short, to help to create a more economically and socially resilient society by building new economic policy infrastructure. The Federal Emergency Management Agency responds to large-scale disasters such as floods, hurricanes, and earthquakes to help victims. Firefighting agencies exist to mitigate the overall losses caused by wildfires on public and private lands. In the agricultural sector, programs have been developed—from price supports to crop insurance—to help farmers cope with natural disasters, from insect epidemics to hail storms to drought.

Although there are numerous programs and policies that address drought, drought impacts, and drought assistance, few of these are tailored for forest landowners. Livestock grazing is an exception where some forest and rangeland owners could receive assistance but only due to damage to the livestock—not forest products. The Agriculture Act of 2014⁴ includes a provision that now allows orchardists (including Christmas tree farm operators) to qualify for drought assistance based on demonstrated damages.

Drought assistance programs are designed to relieve some of the financial burden to farmers, ranchers, and local governments that result from serious or severe droughts. Typically, a severe drought in a county will trigger an emergency notice, which will enable assistance to affected farmers [see USDA Farm Service Agency (2014) for a more complete description of the process]. Most of these programs are longstanding and have served farmers for decades (Western Drought Coordination Council, USDA Farm Service Agency, and Federal Emergency Management Agency 1999). No programs exist to specifically address issues of forest lands that are affected by drought.

Lessons from the Dust Bowl led to the creation of the Prairie States Forestry Project, in which the Forest Service, U.S. Department of Agriculture promoted the planting of trees along edges of croplands to shelter wheat fields from blowing winds and slow the displacement of soil. Between 1937 and 1942, when the project ended, the Forest Service planted nearly 220 million trees creating 18,600 miles of windbreaks that occupied 238,000 acres on 30,000 farms (Munns and Stoeckeler 1946). It also led to the purchase of lands for soil conservation, many of which form the heart of

designated national grasslands, which are also managed by the Forest Service.

Continuing Federal interest in the impacts of drought on communities is demonstrated by the November 2013 Executive Order regarding preparedness for Climate Change (Office of the White House 2013a), which led to the introduction of the National Drought Resilience Partnership (Office of the White House 2013b). The primary focus of these actions is on streamlining the provision of Federal assistance (and the accompanying expenditures by the Federal Government) to private landowners (mostly farmers, some ranchers, and a few Christmas tree farmers) and on increasing the resiliency of local communities that face increasing stress from drought.

There is evidence that landowners who face higher drought risk are more likely to participate in Federal land management programs that help landowners drought-proof their farms and ranches (Wallander and others 2013). Measuring damage to a forest from drought, however, is problematic: there is no easily referenced counterfactual to show that it was actually the drought that reduced forest growth, and thus income, by a specific amount. Further, any program that reduces the losses experienced by individuals, through payments or other forms of assistance, carries with it issues of moral hazard (where covered individuals undertake greater risks as a consequence of having losses covered by others) and adverse selection (where individuals seeking coverage have above-average risk profiles).

Government programs in response to natural disturbances such as drought are one way in which resilience can be increased. Because such programs are not widely applied to the forest and rangeland sector, there is a paucity of research that elaborates drought's effects on the sector. The following part of this chapter provides some details on how drought does affect water-intensive parts of the sector.

Examples of Drought Effects on the Forest and Rangeland Sectors

The above discussion provides context for a description of the effects of drought on specific segments of the forest and rangeland dependent economy and its social systems. In the following sections, we provide a general summary of the effects of droughts on the forest and rangeland sectors. Detailed discussions of many of these

⁴ Agriculture Act of 2014. P.L. 113-79 (February 7, 2014).

effects are provided in other chapters of this report. In this chapter, we discuss direct, indirect, and nonmarket effects, as suggested in Logar and van den Bergh (2013). Note, however, that adding up the costs and losses and other effects into an overall economic impact is not appropriate from an economics perspective. As noted above, “impact” depends on the many dimensions of drought. Moreover, there is much that is not understood about how drought affects the markets (and hence market prices or unit values) of the goods and services provided by forest and rangeland ecosystems.

Little is known about how drought redistributes wealth, and the production and consumption of goods and services across space, time, or economic sectors. For example, the costs incurred in firefighting are gains to the markets for firefighting inputs (e.g., fire engines, airplanes, firefighting labor). Likewise, the losses experienced in the market for one kind of recreation might reappear as gains in the market for another kind of recreation, due to substitutions across recreation types. Also, because humans are adaptable, societal changes induced by drought often have uncertain overall effects on the human condition, even if we can measure the effects on specific segments of society. Our examples, while classified according to direct, indirect, or nonmarket effects of drought (Logar and van den Bergh 2013), do not always fit neatly within this structure. For example, trees in forests can be killed by drought (a direct effect), but the effects of their loss is manifested in part in how their loss affects timber products supply and demand conditions, which translate into economic losses in that market. Moreover, not all effects are precisely quantified in these examples, nor are all even quantifiable given existing methods or data.

Direct Effects of Drought in Forest and Rangeland Sectors

The timber products industry—The timber products industry is directly responsible for close to 1.2 million U.S. jobs and over 72 billion dollars in labor income. Based on estimates from a contribution analysis of the U.S. forest sector using IMPLAN (IMPact analysis for PLANning) software and 2012 dataset (MIG 2012), economic activity associated with the forest sector generates an additional 4 million jobs with \$210 billion of associated labor income, constituting 2 percent of the U.S. economy (MIG 2012). Droughts can affect the forest industry through their effect on forest inventories, which are assumed to affect the supply function for stumpage. Lower inventories lead to a contraction of supply and a corresponding increase in the market

price and a decrease in the quantity of production. The magnitude of these effects on any particular forest parcel depends, in part, on the severity, duration, and frequency of drought events; the economy-wide effects depend on the spatial extent of the drought. Droughts can negatively impact forest inventories in two ways: (1) by increasing mortality, and (2) by reducing growth. Prolonged periods of dry conditions increase the likelihood of forest fires; increase tree vulnerability to pests and diseases; and, due to water stress, can lead to higher mortality of saplings and seedlings (Elliott and Swank 1994, Hanson and Weltzin 2000).

Although droughts occur periodically across the United States, an increase in frequency, severity, and duration could significantly affect forest species composition and live tree volumes. Prolonged periods of water stress not only increase the likelihood of tree mortality and pest outbreaks, but they can also lead to gradual changes in forest composition (chapters 3, 4, and 6) (Hanson and Weltzin 2000). During the drought experienced in South Carolina in 1998–2000, State foresters reported regeneration success that was 5 to 20 percent below the historical average (Knutson and Hayes 2001). Faced with higher rates of artificial regeneration failure, forest landowners can respond by introducing drought-resistant seedlings or by using natural regeneration methods. Although extreme, the possibility of landowners changing land use also exists. Lower success in tree establishment could lead to an age class gap over a prolonged drought, which could be a factor contributing to the current South Carolina shortage of small-diameter feedstock for pulp mills, oriented strand board mills, and other small-timber uses (Abt and others 2013). Pulp mills contribute a significant portion of the jobs in the primary wood processing industry; therefore, changes to the supply chain could trigger notable negative impacts.

The eventual decrease in forest inventories resulting from prolonged droughts could lead local industries to expand their procurement zones. However, transportation costs can limit a mill’s ability to increase its procurement area. Given that product prices are set at the regional or national level, higher costs of roundwood inputs could make the affected mills less competitive, resulting in mill closures. Additionally, extended periods of water shortages could lead to higher electricity costs, affecting mill operating costs. Mills needing water in their production process, such as pulp and paper mills, could have their operations hampered and profits reduced (English 2007).

When viewed at a landscape scale, the effects of drought vary widely across stands because of the varying mix of species and site types. Several factors determine how drought affects tree growth, including tree species, forest composition, soil characteristics, and site hydrology. Studies show that pine species respond to water stress by reducing their growth rate, often by up to 30 percent (Amateis and others 2013, Vose and Swank 1994). For hardwood species, resilience to drought varies from high (e.g., oaks) to low (e.g., tulip poplar) (Elliott and Swank 1994, Klos and others 2009, Orwig and Abrams 1997). During a severe drought, trees on mesic sites likely experience higher competition than trees on xeric sites more adapted to drier conditions, leading to more severe impacts in the former sites than the latter (Orwig and Abrams 1997).

Ultimately, drought's tendency to reduce tree growth and increase tree mortality can potentially lead to job losses and income declines in rural, forest-dependent communities that are more acute than in more diversified, urban areas. For instance, Waters and others (1994) evaluation of a wood supply shock found a significant difference in job losses between a metropolitan area and the surrounding rural area, with the rural area experiencing the highest drop in employment and likely negative growth given higher difficulty for replacement of lost jobs.

Forest droughts that lead to large disturbance events, such as wildfire, can produce time-dependent impacts in the forest sector and the local economy. For example, wildfires can generate positive short-term impacts in local communities where external resources are brought in to fight the fires and where post-fire timber salvage and burn area rehabilitation activities generate economic activity (Nielsen-Pincus and others 2014). For instance, the salvage recovery plan for the 2006 fire affecting a section of the Malheur National Forest in Grant County, Oregon, estimated employment impacts ranging from 3 to 8 percent, depending on the volume of wood recovered (USDA Forest Service 2008).

Butry and others (2001) predicted that owners of salvaged timber would gain \$33 to \$61 million in salvage revenues following the drought-driven, half-million acres of wildfires in northeast Florida in May and June of 1998. Prestemon and others (2006) determined that post-wildfire salvage in the Bitterroot National Forest following the drought-enhanced 2000 Bitterroot Fire in western Montana would also generate more than \$10 million of net benefits to the local economy, mainly

through higher profits earned by wood processors that are partially offset by lower profits earned by owners of unburned timber in the region. Prestemon and Holmes (2008) estimated that post-wildfire salvage from the 2002 Biscuit Fire in southwest Oregon would generate from about \$24 million at low salvage rates to \$265 million in salvage sales at high salvage rate. In the long term, however, large wildfires can result in significant timber market losses (Prestemon and others 2006; Prestemon and Holmes 2008), with attendant employment declines (Nielsen-Pincus and others 2014).

Studies on the effects of policy-related harvest restrictions can inform the expected spatial effects of long-duration and large-scale droughts. Studies by Guan and Munn (2000) and Wear and Murray (2004) documented shifts in forest industry capital investment and production from the Pacific Northwest to the Southeastern United States as the result of efforts by Federal decisionmakers to protect spotted owl habitat and other ecosystem values. Waters and others (1994) analysis found that such restrictions resulted in an estimated 22-percent employment loss in the timber industry of western Oregon.

Forest and rangeland based water supplies—

National forests are the single largest source of fresh water in the United States, accounting for 14 percent of all runoff. Over 900 cities rely on water originating from National Forest lands (Sedell and others 2000). These amounts vary widely by location across the United States. In the West, where most of the water originates in the mountains, half of all water originates in National forests. In Colorado, the percentage of water originating from National forests climbs to almost 70 percent. In the Mississippi River basin, by comparison, only 2–5 percent of water originates on National Forest land (Brown and others 2008). Weidner and Todd (2011) show how runoff from all forests affects communities by weighting water yield by the population served. They show a high dependence on forested watersheds throughout the Eastern United States, Rocky Mountains, Cascades, and Sierra Nevada (fig. 11.3).

Forests and rangelands are critical to water flow regulation and groundwater recharge (chapter 10). These ecosystems help regulate the supply of water by stabilizing surface flow (i.e., reducing streamflow flashiness) and allowing more subsurface recharge. When drought happens in forest or rangeland, vegetation will grow more slowly; in a severe drought, vegetation may die. Extensive mortality may increase

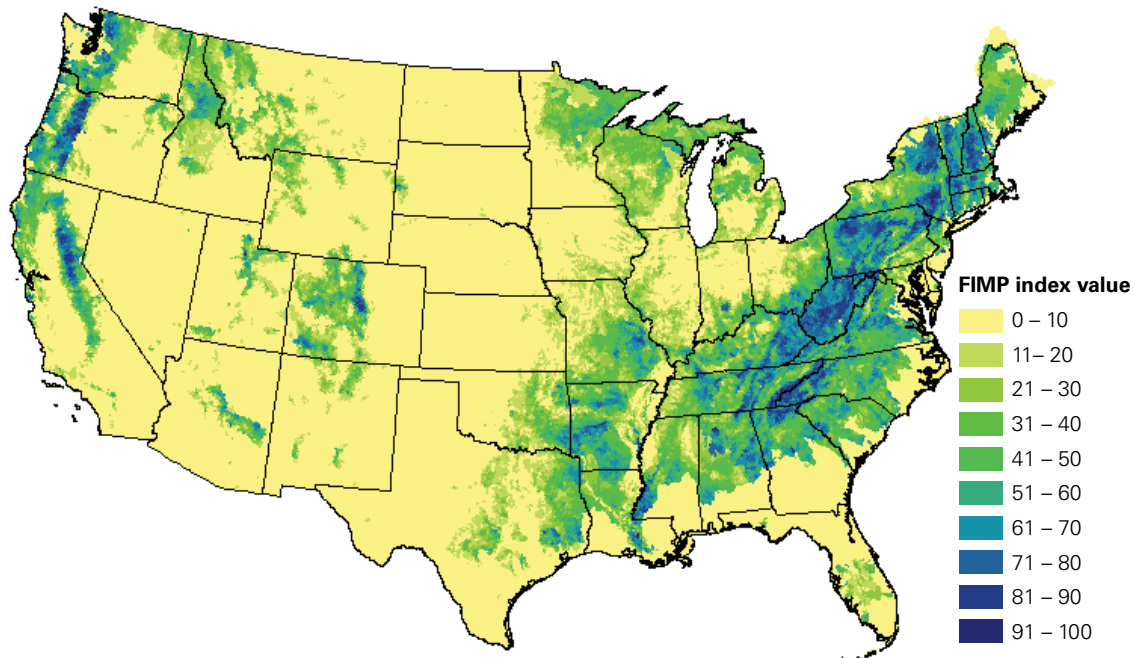


Figure 11.3—Index of forest importance (FIMP) to surface drinking water; higher values (shown in shades of blue) indicate greater importance (Source: Sedell and others 2000).

overall streamflow; however, flows will be likely more variable and groundwater recharge reduced (chapter 10). The end result is that the marginal cost of water (i.e., the cost of providing an additional unit of water) to downstream communities is higher when the forests and rangelands at the water supply source are under drought.

The increase in the marginal cost of water connects to three characteristics of U.S. drinking water markets. First, demand for water is inelastic—i.e., water consumers change their consumption little in response to water price changes, at least within the range of prices set by local water authorities (Dalhuisen and others 2003, Espey and others 1997). Research shows that a 10-percent increase in the marginal price (the price charged for an additional unit) of water is expected to reduce residential water demand by 3–4 percent in the short run and by 6 percent in the long run (Olmstead and Stavins 2009). Conversely, reducing water demand by 20 percent in the short run would require water prices to increase by 50 percent. Second, prices set by water authorities are typically below, and sometimes well below, the marginal costs of supplying water. This means that many water-providing agencies do not cover their production costs with the prices that are charged to consumers. Third, water is typically perceived to be

a public good—it should be available to everyone and be clean and abundant—so efforts to recover costs through price increases are met with public and political opposition. Such price increases carry with them issues of legality, political constraints, and equity due to the larger-than-average impact to low-income households (Agthe and Billings 1987, Mansur and Olmstead 2012, Renwick and Archibald 1998).

The full economic cost of water includes costs of storage, transmission, and treatment, as well as opportunity costs associated with other uses and maintaining instream flows. Boland and Whittington (2000) note that significant efficiency and equity gains could be achieved by setting a single price that raises enough revenue to not only cover costs but provide enough funds to redistribute the extra revenues in the form of rebates back to low-income households. Alternatively, tier-based pricing schemes, called increasing block tariffs, could allow quantities deemed to be of subsistence value to be priced lower and larger quantities to be priced high enough to be responsive to price signals (Olmstead and others 2007). Such pricing policies, particularly if made flexible to respond to reduced water supplies, could therefore also help reduce consumption during times of drought. Further, pricing policies can provide the revenue for investments

that are longer run solutions to drought-induced water shortages, including water reservoirs and tertiary water treatment facilities that produce water for reuse following initial consumption.

The net effect of these three market characteristics—inelastic water demand, water prices set below costs, and the public good view of water—is that water markets typically use quantity controls when shortages loom, despite evidence that quantity controls are economically inefficient compared to cost-based pricing policies (Brennan and others 2007, Collinge 1994, Krause and others 2003, Timmins 2003). Quantity controls can result in the amount of water demanded exceeding the amount of water available, especially in dry years when water is scarce. The larger the scarcity, the greater the divergence between marginal cost and price. For many communities, water shortages are already common. In 2015, for example, Governor Jerry Brown issued the first-ever executive order for mandatory water restrictions in California. The order requires a statewide 25-percent reduction in potable urban water use compared to 2013 usage. It also prohibits irrigation with potable water of ornamental turf on public street medians and outside of newly constructed homes and buildings without drip or microspray systems (Executive Department, State of California 2015). As long as municipal water prices lie below the true cost of supply, there will always be a perceived shortage among the 86 percent of U.S. households that get their water from municipal water companies.

Because of public and political opposition to higher water prices, and given that quantity controls create shortages, water authorities and communities gravitate toward measures that do not directly involve pricing policies or additional quantity controls. These measures are directed toward water conservation. Conservation policies focus on technologies to improve efficiency of water use and on rationing outdoor water use. Lawn-watering restrictions are commonplace in drought-stricken western communities. Governments have mandated the use of more water-efficient technologies, as well: Federal law requires new toilets, the largest user of in-home water, to use no more than 1.6 gallons per flush, a 73-percent decrease from the 6 gallons many older toilets use. Communities also subsidize adoption of water-efficient lawn irrigation systems (City of San Diego 2014, Kjellgren and others 2000) and the switch from older to new water-efficient toilets (Benbear and others 2013). While such policies are more palatable to the public, the fact that households

achieve these water use reductions through regulations and incentives rather than through pricing policies implies that these measures are economically suboptimal, creating losses in consumer benefits (economic welfare) from water consumption (Brennan and others 2007, Collinge 1994, Krause and others 2003, Timmins 2003).

Insights into the underlying causes of water disputes and the reason for tight water regulation emerge by examining not just the marginal cost of water provision but also by examining the value that consumers place on the water that they consume. Values tend to be higher in places where water is scarcer. In particular, the differences in amounts of water provisioned by forests, along with the types of water uses in the basin, affect its marginal value (the value to the consumer of an additional unit of water consumed). This implies that the effects of drought are felt economically more acutely during times of water scarcity, including during droughts. Brown (2004) reports rough estimates of marginal values of instream flow for water resource regions throughout the country (table 11.2). Although users should consider that these values are rough approximations, the values are useful for comparing relative values among regions, and they illustrate how marginal values vary due to both the quantity of water in the region and how the community is using that water. Small changes in the quantity of water in New England or in the Mississippi River basin, where people and communities consider that water is abundant, are not likely to have a great concern because the value of a lost unit of water is small. Conversely, the quantity (and value) of water in relatively water-scarce regions such as the Lower Colorado River basin can have significant impacts, because the value of a lost unit of water is considered much larger.

Effects of drought on rangeland production—

Drought in rangelands affects society and the economy by (1) reducing forage and water available for livestock grazing, and (2) by reducing overall vegetative land cover, which can lead to wind erosion and water erosion. In range management, drought is defined as the level of soil moisture that causes extreme plant stress and wilt (Carr 1966). Thus, the severity of drought in the rangeland sector is also a function of the timing of both water supply and plant demand. Drought also depends on temperature and wind through its effects on plant water demand and soil infiltration, soil texture, and soil depth. These variables are part of the Palmer (1968) Crop

Table 11.2—Marginal value of instream flow by water resource region (WRR) (year 2003 dollars per acre-foot per year)

Water resource region	Off-stream	Hydroelectric	Instream
New England	0.62	1.73	5.01
Mid-Atlantic	3.09	1.03	4.91
South-Atlantic-Gulf	1.87	1.56	5.03
Great Lakes	6.3	5.54	4.88
Ohio	3.17	0.71	4.96
Tennessee	3.18	7.02	5.16
Upper Mississippi	4.08	0.72	4.98
Lower Mississippi	0.4	0.35	4.75
Souris-Red-Rainy	0.29	0.26	6.45
Missouri	20.99	4.29	16.82
Arkansas-White-Red	4.08	2.05	7.7
Texas-Gulf	13.25	0.54	7.49
Rio Grande	16.54	1.42	28.26
Upper Colorado	13.32	17.79	26.32
Lower Colorado	25.56	16.19	42.46
Great Basin	36.08	1.31	16.52
Pacific Northwest	1.45	9.44	9.34
California	10.95	10.64	23.07

Source: Brown (2004).

Moisture Index, which reflects expected weekly evapotranspiration and plant specific needs (Meyer and others 1993).

A chief concern for long-term sustainability of rangeland is topsoil health and its ability to retain water (Mannering 1981, Marshall 1973). Semi-arid environments often have insufficient vegetative cover to protect the soil from wind and water erosion, whose effects are amplified by grazing (Dankwerts and King 1984, Robinson 1982). On western U.S. rangelands, typical erosion rates can be up to 1 mm/year (Mannering 1981), though topsoil only replenishes at a rate of less than 0.1 mm/year (Pimental and others 1976, 1995).

Because animal stocking rates are generally determined by expected precipitation, degradation can occur quickly if drought occurs and grazing persists. Some of this erosion can be mitigated by vegetative buffers (Lee and others 2003, Osborne and Kovacic 1993).

The role of irrigation in rangeland and agriculture—

Although soil conservation practices and modern irrigation have reduced the impact of episodic droughts, the effects of severe drought remain a prominent concern in rangeland-dependent communities. Nationally, irrigation accounts for 37 percent of total freshwater withdrawals (Barber and others 2009). In the West where water is scarce, 90 percent of water consumption is for irrigated agriculture. During the drought of 2002, direct Federal aid in South Dakota reached \$100 million, and the total estimated impact was as high as \$1.4 billion (Dierson and others 2002, Dierson and Taylor 2003). That same year, impacts to Missouri's agricultural sector were \$251 million (Ding and others 2010).

Quantifying the economic effects of drought on crop and livestock production requires an accurate description of water markets. Water demand characterization requires measurement of the benefits of water used in the production of market goods and services, including for irrigation. Prices in the water sector are quantified by measuring the shadow price of water, that is, the change in net profits given a small change in water use by the water demanding goods and services market. Measuring the shadow price of water is done frequently in production economics with mathematical programming (Scheierling and others 2006), field experiments, and hedonic methods (Colby 1989, Young 2005).

Increasing water scarcity has led farmers to invest in water-saving techniques such as improved drip irrigation systems. In 1984, 71 percent of irrigation in the West was done with inefficient gravity-fed furrows. By 2008, that percentage had fallen to 48 percent; pressurized sprinkler systems represented 52 percent of irrigation water. This technology adoption in irrigation explains how, although total irrigated acres increased in the West by 2.1 million acres from 2004 to 2008, the water used in irrigation decreased by 100,000 acre-feet during that period (Schaible and Aillery 2012). Decreased use of water in agriculture, and the associated decrease in runoff of fertilizers and pesticides, has the added benefit of increasing downstream water quality (Warziniack 2014).

In spite of its widespread use in the water-scarce Western United States, most studies show that irrigation is an inefficient, low-value use of water, and the price of water charged to farmers is so low that it rarely factors into on-farm production decisions. The average price of an acre-foot of water in the West (\$24 or \$66 per acre of cropland) is lower than the cost of power to pump it out of the ground and distribute it through a sprinkler system (\$76 for groundwater and \$38 for surface water). Because of the low price charged for water for agriculture, water used for irrigation is often leased during wet years, when supply is plentiful and demand for other uses is low (Brown 2006).

Societal structural barriers exist to achieving more economically efficient water allocation in forest and rangeland systems in the United States. Economically efficient allocation of water would equate the value of a unit of water across uses, including instream uses for ecological sustainability. In reality, value between uses diverges substantially for two reasons. First, in the West, the doctrine of prior appropriation determines allocations, and while water rights are transferable, market transactions are limited by geographic structure of rivers and water pathways, costs of storing and transferring water, and impacts to other water users along the waterway. Second, most water use is highly subsidized, so when prices are charged, they rarely reflect the full cost of provision. Water rights that are leased or sold in markets are characterized by seniority and location, making each water right a unique good with high transaction costs.

Brown (2006) reviews 1,380 transactions in Western water markets between 1990 and 2003. He finds that water markets are far from competitive. Only three States (California, Colorado, and Texas) saw significant transactions during the period studied, representing two-thirds of all water transfers. Over half the sales were to municipal areas to satisfy the needs of fast growing cities, such as those along the Colorado Front Range, near Las Vegas, and near Reno. As well, over half of the sellers were irrigators. The median lease price for municipal uses was \$56 per megaliter (ML, 1 million liters), or 4.6 times that paid for irrigation (\$12/ML). The median sale prices were \$2,120/ML for municipal uses and \$1,917/ML for irrigation. Despite numerous studies suggesting agriculture-to-urban transfer of water rights would be welfare improving, few transfers have actually taken place (Brewer and others 2007, Brown 2006, Howe 1997). Reasons for

the limited number of transfers include lack of markets, legal restrictions, and reluctance to further constrain local agriculture.

Research also indicates that government efforts to achieve ecological goals through water allocation and purchase decisions can have effects that create new conflicts while moving water allocations toward greater equity. Eleven percent of water rights purchases studied in Brown (2006) were for environmental purposes, sold for a median price of \$706/ML. Most of these (105 of the 113) purchases were by government entities for the protection of aquatic species. And while regulations such as the Endangered Species Act⁵ may require minimum flows for species preservation, instream water is also valued for its contribution to recreation and for riparian and wetland restoration. In a study of 67 river basins in the United States with significant irrigation, the marginal value of instream water for fishing exceeded that for irrigation in 51 basins (Hansen and Hallam 1991). Loomis and others (2000) found the benefits of purchasing water leases and farmland easements to restore a section of the Platte River near Denver outweighed the costs.

Indirect Effects of Drought in Forest and Rangeland Sectors: Federal Wildfire Expenditures

Forest and rangeland management is significantly affected by drought, and perhaps most acutely in its management of wildfires. Longstanding western drought is a likely cause of recent increased wildfire activity in forests and rangelands in much of the Western United States (Westerling and others 2003). Aside from sometimes justified increased investments to manage landscapes to be more resilient to wildfire (USDA Forest Service 2000), greater wildfire activity generally leads to increased expenditures needed for suppressing fires (Prestemon and others 2008).

To characterize the importance of the fire-suppression effect of drought in forests and rangelands, we compared Forest Service regional fire suppression average expenditures during drought years with average expenditures during nondrought years. The Palmer Hydrological Drought Index (PHDI) was selected as a “real time” measure of drought (Alley 1984) because it captures persistent, long-term effects that impact surface and subsurface water supply levels (Heim 2002). The index is available from the National Oceanic

⁵ Endangered Species Act of 1973. P.L. 93-205. (December 28, 1973), as amended through P.L. 107-136 (January 24, 2002). 16 U.S.C. 1531.

Table 11.3—Fiscal year suppression expenditures (2014 dollars in millions) on USDA Forest Service lands in the United States, by region, regional aggregate, and in total according to drought status (1995–2013)

Region	Factor ^a	Average expenditures	Average expenditures during drought	Average expenditures not during drought	t-test p-value	Fire season
R1	5	92	139	28	0.01	June, July, Aug.
R2	4	39	57	14	0.01	June, July, Aug., Sept.
R3	2	95	107	59	0.02	May, June, July
R4	3	85	127	38	0.01	June, July, Aug., Sept.
R5	2	272	340	178	0.02	Oct. (-1), July, Aug., Sept.
R6	2	136	181	95	0.02	June, July, Aug.
R8	3	41	57	22	0.01	March, April, May, June
R9	2	13	16	9	0.04	March, April, May
West (R1-6)	2	718	959	386	0.01	
East (R8-9)	2	53	63	26	0.01	
Total (R1-9)	2	771	831	450	0.04	

^aFactor = Average expenditures during drought/average expenditures not during drought.

Note: there is no Region 7.

higher fire-related damages due to affected forests and rangelands and associated communities.

Nonmarket Effects of Drought in the Forest and Rangeland Sectors

Recreation impacts—Recreation services in forests and rangelands are provided by a combination of nature, labor, and capital. While service markets exist, such as the market for developed downhill skiing services (i.e., offering a place, the snow, the ski lifts, and associated built facilities), the majority of research in the economics of recreation has focused on recreation activities—specifically, valuing those activities and understanding what factors affect the benefits that the activities provide to those who participate in them. So discussion on recreation in this section is limited to describing how drought could affect recreation activities.

A limited amount of research has shown that drought conditions affect outdoor recreation activities in the United States, generally, and in forests and rangelands in particular. Notable studies include those by Creel and Loomis (1992), who quantified the overall recreational benefits of water; Ward and others (1996), who focused

in particular on the connections between drought and water recreation, with evidence from California; and Thomas and Wilhelmi (2013), who examined all forms of recreation and tourism in southwestern Colorado. Drought can lower reservoir levels and therefore reduce the availability of water-based activities (such as fishing and recreational boating) and lakeside activities (such as swimming and camping). In the Ward and others (1996) study, the “use-value” marginal value estimates of water per acre-foot in reservoirs of California varied from \$6 to \$700/year. This range covers previous estimates for wetland areas in the San Joaquin Valley of California quantified by Creel and Loomis (1972), \$348/acre-foot/year.

Thomas and Wilhelmi (2013), using a limited-resource survey and two focus groups, identified how drought in southwest Colorado affects the recreation sector. One finding was that drought affects winter recreation differently than summer recreation, due to dependence especially on snow in the winter (i.e., downhill and cross-country skiing, snowboarding, and snowmobiling) and on water and a wide variety of other resource values provided in the summer (i.e., boating/rafting/

canoeing, fishing, hiking, camping, horseback riding, wildlife viewing, off-road vehicle driving). In the winter, lower snowfall from drought generally reduces the economic net benefits in the recreation sector. In summer, drought can worsen water-based activities but conceivably can increase the provision of some dryland activities such as hiking and camping, owing to the greater number of rain-free days. In all times of the year, drought can alter animal migration patterns and thereby affect hunting and wildlife viewing. Drought may also have effects on insect and disease outbreaks in forests, affecting aesthetic values, and it can yield dry vegetation that is more prone to large and intense wildfires, which can force campground and forest closures, reducing summer recreational uses. Drought-induced reduction in tourism results in fewer jobs and lower economic output compared to nondrought periods.

While targeted studies have examined drought effects on recreation at fine spatial scales or for particular resources, recreation research from the most recent Resources Planning Act Assessment (Bowker and others 2012) indicates that prolonged drought in parts of the United States can have effects on a broad set of recreation activities. Bowker and others (2012) projected the probability of an individual's participation in various recreation activities as a function of socio-demographic and climate variables (including precipitation, potential evapotranspiration, and temperature). From their analysis, they concluded that: (1) in climate scenarios involving drier overall conditions in forests and rangelands, snow-dependent recreation activities are the most negatively affected of any category of recreation; and (2) there are some kinds of recreation activities that benefit from drier conditions, including nature center and historic site visitation, motorized off-road vehicle use, and adult equestrian participation.

Despite previous research efforts, a thorough understanding of the effects of a drought on recreation is lacking, which hampers our ability to fully characterize the overall effects of drought on this sector. Data are needed that can connect the levels of specific types of recreation at specific locations to the weather or climate conditions existing at the time and place of the specific activity. Although Bowker and others (2012) and other studies have advanced understanding of a few key relationships, a comprehensive understanding of drought effects across the entire spectrum of recreation activities would require additional recreation (panel) data. Panel data would quantify how drought in one time and place affects each specific type of recreation activity

occurring in that same time and place, as well as how it affects participation in all activities in other locations and in future time periods. As Thomas and Wilhelm (2013) and Thomas and others (2013) emphasize, estimates of recreation impacts from drought would be overestimated if these within- and across-activity spatio-temporal substitution opportunities available to recreationists are not accounted for.

Urban and residential communities—Most studies of the effects of water stress and high temperatures on tree and forest mortality have been designed to detect changes in background mortality and large scale die-off events in wildland forest areas (Allen and others 2010). Although drought-induced forest mortality in wildlands can alter the supply of ecosystem goods and services, large magnitude drought events can also alter the benefits experienced by people where most live and work—in cities. Evidence suggests that trees in cities are significantly affected by drought, and their responses lead to changes in the services that city trees provide. For example, the drought and heat event associated with the American Dust Bowl drought in 1934 killed approximately 20 percent of the trees in Manhattan, KS, and damaged another 30 percent (Stiles and Melchers 1935). Although the pre-drought tree density varied considerably across the urban forest, as many as 235 trees per city block were recorded in residential areas, so the overall number of affected trees was large. The city and property owners therefore incurred considerable expenses to remove and eventually replace many of the affected trees.

To our knowledge, the economic consequences of tree mortality due to drought and high temperatures have not been quantified. However, there is a growing body of research documenting how trees provide a variety of benefits to homeowners and residential and urban communities. Trees have been shown to enhance property values (Anderson and Cordell 1988; Donovan and Butry 2010, 2011) and lower crime rates in urban areas (Donovan and Prestemon 2012, Kuo and Sullivan 2001, Troy and others 2012). Tree shading has been found to reduce energy use in homes (Akbari and others 1997, Donovan and Butry 2009, McPherson and Simpson 2003), in this way mitigating some of the negative effects of the heat and sun associated with many droughts. Urban forests also have been shown to benefit stormwater management in built-up areas, reducing flooding and water-handling costs for cities and their residents (Sanders 1986, Wang and others 2008, Xiao and others 1998).

With respect to tree mortality, the loss of trees is connected to worsened human and urban environments and lowered house values. Recent research links tree mortality caused by pests to adverse public health outcomes (Donovan and others 2011, 2013; Lovasi and others 2008; Nowak and others 2014). Research also has documented how tree mortality resulting from other natural disturbances in residential forests is capitalized into property values. Losses in values are in the range of 1 to 10 percent of a home's value (Holmes and others 2010, Kovacs and others 2011). We anticipate that similar losses in value would result from drought-induced tree mortality.

Homeowners living within forests are often willing to incur expenses, such as irrigation, to help protect tree health, although such options may be limited when municipal water restrictions are enforced. Trees killed by drought conditions are generally removed when they threaten the safety of homeowners or other residents. Hazard trees that are removed may be replaced with different species that may be more drought resistant, although much remains to be learned about the selection of trees that improve the resilience of urban trees to drought conditions (Clark and Kjelgren 1990).

Although it is not currently known whether water deficits are more severe in urban trees than in trees growing in rural areas, there is growing concern that urban land uses create novel stresses on urban forests (Carreiro and Tripler 2005). Given the recognized high economic value of residential forests across the urban-rural gradient, greater attention to policies and potential technologies that improve urban forest resilience in the face of drought could yield positive net benefits.

Impacts of Drought on Tribal Values and Lifeways

There are 566 federally recognized tribes and more than 34 State-recognized tribes in the United States. These tribes, distributed across both drought-prone and mesic ecosystems throughout the country, are diverse in their cultural practices, the structure of their tribal economies, and their degree of dependence on forest and rangeland ecosystems. Hence, the effects of drought on tribal values and lifeways (defined here as the customs and practices of tribal societies) vary across all of these dimensions. In some places and for some peoples, the effects of drought are compounded and complicated by ongoing social, economic, and rapid ecosystem changes, making scientific attribution of the effects of drought alone difficult. Effects of drought, however, would likely be more acute for local populations whose

livelihoods are most tightly connected to natural resources. For example, American Indians and Alaska Natives (AIAN) are particularly vulnerable because of their resource-based economic activities and spiritual and cultural values (Wildcat 2013).

General impacts of drought on tribes in the United States

As for all potentially drought-affected sectors or parts of an economy or community, it is important to identify risk, potential impacts, and vulnerabilities, especially related to water supply and water rights. Ongoing drought in the Western United States, where most tribal lands exist, is expected to continue to affect tribal health, culture, economies, and infrastructure. Competing demands for dwindling water resources challenge Federal trust responsibilities. Complicating factors, warming streams and hydrologic cycle changes affect fish populations important to tribal diets and ceremonies. Because of their natural resource dependence for income, employment, and cultural practices, many tribes are also vulnerable to higher rates of forest and rangeland disturbances, including invasive species spread, increased occurrences of epidemic pest populations and their associated damages, and wildfires. These disturbances increase forest mortality and reduce the quality and quantity of forest products valued by tribes (Voggeser and others 2013). Tribal elders have voiced concern for "bio-cultural" loss, defined as "the intimate innate connection that exists between tribal language, customs, and traditions and the biological health of their land, resources, and its inhabitants" (Collins and others 2010).

In order to successfully address environmental change, many scholars, tribal leaders, and agencies charged with consulting with tribes are calling for the incorporation of traditional ecological knowledge (TEK) in monitoring and assessing environmental change impacts, developing tribal community adaptation plans, and for "respectful partnering and collaboration of indigenous peoples and their communities with nonindigenous governments and organizations" (Wildcat 2013). Incorporating traditional values and TEK in these ways can support the perpetuation of traditional lifeways.

Relatedly, a workshop on climate change and drought on western native lands (Collins and others 2010) identified the ways that data and institutions could be marshalled to help mitigate overall impacts. The workshop participants concluded that inadequate communication of current conditions and potential impacts to tribes has resulted in a lack of attention to

drought-related issues. Participants called for increasing documentation of impacts and data collection and monitoring in an effort to build awareness and bring attention to potential impacts and related needs. Participants also identified critical needs, such as for:

“...reliable resources to support tribal drought planning and response; methods for integrating local and traditional knowledge into environmental monitoring and planning; education and outreach programs about drought, climate change, and water scarcity; and technical training opportunities related to climate monitoring for tribal resource managers...” (Ferguson and others 2011).

Finally, workshop participants identified four priorities for developing a regional drought early warning system: (1) integrate tribal observations and data into national and State monitoring efforts; (2) ensure maintenance and sustainability of existing observation networks; (3) facilitate data sharing and access; and (4) explore ways to use existing data and provide technical training for tribal staff (Ferguson and others 2011).

The Forest Service notes that this call for collaboration is now a catalyst to developing tools and sponsoring webinars and face-to-face training in climate adaptation planning and strategies, which make partnerships through the Tribal Climate Change Project (University of Oregon 2015) mutually beneficial to all involved. Partners include the Institute for Tribal Environmental Professionals at Northern Arizona University, the Pacific Northwest Tribal Climate Change Network at the University of Oregon, and the Forest Service Pacific Northwest Research Station.

The National Wildlife Federation suggests that drought may result in the most pervasive climate-related changes to impact tribes (Curry and others 2011). It could be the most pervasive because water is the foundation for tribal lifeways, economies, subsistence, and treaty rights (Curry and others 2011). In addition, water is considered by many as a traditional food (Lynn and others 2012). Cozzetto and others (2013) synthesize this argument (*italics in original*):

“Water is sacred. This is tradition. In contrast to the non-tribal utilitarian view of water, Native Americans revere water and water is life. It is integral to many Native American practices such as purification and blessing rituals and is used to acknowledge all relations and to establish connection to Mother

Earth and Father Sky. Water is a holistic and integrating component connecting continents, humans, animals, and plants through a continuous cycle of liquid, solid, and vapor states. Without water, life would not exist as we know it. Water is the one thing we all need, all of us, all of life. As Native Americans, we honor and respect the tradition of water and must protect it always.”

Indigenous peoples depend on a wide variety of native species for food, medicine, ceremonies, community, and economic health. “The indigenous relationship between food and people is intimately tied to the cultural, physical, emotional, psychological, and spiritual health of tribal communities” (Lynn and others 2013). Drought tends to reduce the production of traditional foods, and this reduction is compounded by ongoing background effects of disease, pollution, invasive species, and unsustainable resource management activities. Declining ability to access and harvest traditional foods is leading to increasing health problems including obesity, diabetes, heart disease, and cancer (Lynn and others 2013). Disruption in resource availability and drought-associated changes in species composition could therefore negatively impact tribal subsistence-food production, health, culture, economic activities, and lifeways.

Specific impacts of drought on tribes in the United States

—Drought has varying effects according to the location of the tribe, which is connected to biophysical, cultural, and economic contexts. Drought in the Southwestern United States has effects on livestock, agriculture, water supply, water rights, soil quality, and aquatic species (Cozzetto and others 2013), requiring tribal peoples to use marginal resources and travel farther to haul water. Cozzetto and others (2013) identified five categories of tribal water resources impacts; these include impacts on: (1) water supply and management (including water sources and infrastructure); (2) aquatic species important for culture and subsistence; (3) ranching and agriculture, particularly from climate extremes (e.g., droughts, floods); (4) tribal sovereignty and rights associated with water resources, fishing, hunting, and gathering; and (5) soil quality (e.g., from coastal and riverine erosion prompting tribal relocation or from drought-related land degradation).

In a drought preparedness workshop in Flagstaff, AZ, in 2010 for tribes in the Four Corners Region, current drought effects and vulnerabilities were catalogued:

multiple impacts from seasonal dust storms; shifting plant ranges and absence of or reduction in ceremonial and medicinal plants; drying of springs and declines in surface water supplies; livestock reductions tied to poor range conditions; inadequate water infrastructure for the growing water demand in the region; bureaucratic and institutional conflict; and a rising degree of economic, social, and cultural vulnerability due to changing society and climate (Ferguson and others 2011). Workshop participants acknowledged impacts from complacency and a lack of respect for the precious nature of water and the threat of drought.

Many of the listed impacts of droughts on tribes in the United States are illustrated by specific experiences. For example, a multiyear drought in the early 2000s forced the Hualapai Tribe in Arizona to sell cattle because of high water and feed costs, resulting in increased wildfires, road closures associated with wildfires, increased invasive species and wildlife diseases, lost wetlands, wind erosion, and visibility problems (Cozzetto and others 2013). In the Pacific West, drought has reduced forage quantity (Bender and others 2011). Changes in ecosystem water status in the Midwest, Northeast, and South have reduced forest nut crop abundance and have stressed ecosystems used by tribes (McKenney-Easterling and others 2000, Speer and others 2009, Voggesser and others 2013).

The effects of drought are recognized to be greatest in locations of the United States where water is both scarce and key to tribal livelihoods. Reservoirs, hydropower facilities, irrigated agriculture, municipal water systems, tribal water rights, freshwater aquatic systems, and water-intensive recreation are all impacted by drought conditions (Dalton and others 2013). Solar and wind facilities, more common in the water-scarce Western United States, also require water for periodic cleaning of solar-collection and reflection surfaces and, for thermal power plants, turning steam turbines (Solar Energy Industries Association 2014); the water necessary to successfully support these alternative energy facilities may be lacking, especially during drought (Collins and others 2010).

But drought's effects, perhaps manageable for short-duration, low-severity, or moderate spatial-scale droughts, require addressing multiple trade-offs and longstanding water use allocation disputes when droughts increase in magnitude along these dimensions. Competition for limited water resources pits the interests and needs of hydropower, solar

power, irrigation, drinking water, aquatic systems, and water-intensive recreation. In the Northwest, for example, many water supplies are overallocated (more demand than water available), leading to conflicts among potential users and uses (Curry and others 2011). And in spite of the tribes' historical, treaty-based senior water-rights status, which gives them priority under normal (nondrought) conditions, when water is scarce, existing laws often mean that nontribe water consumers are given water allocation priority in order to provide water to livestock and for household (domestic) uses. Moreover, tribes' treaty-based seniority is often in legal dispute. Competition for water, the issue of treaty water rights, and how to interpret those rights in light of changing conditions, will become increasingly important and contentious (Lynn and others 2013).

Also, in the case of large-magnitude and persistent drought, fisheries disputes emerge between recreational fishers and native subsistence fishers. In the midst of drought and ongoing climate change, changes in streamflow and temperature threaten aquatic ecosystems, especially the spawning and migration of salmon and trout species. Cascading effects of limited water will impact recreational, commercial, and tribal fisherman. In Alaska, Alaska Natives and rural residents participate in a subsistence fishery that may experience catch limits and season reductions.

Just as for nontribal communities, indirect and direct effects of drought can result in health and economic losses. Because droughts increase wildfire activity, tribes in fire-prone landscapes may experience economic effects when wildfires force the closure of roads and recreation areas that they are dependent upon for their livelihood (Dalton and others 2013). Wildfire smoke and particulate matter is also a health concern in many tribal areas. In addition, drought is associated with food insecurity, especially for the poor and those living in rural communities, due to drought's direct effects on agricultural production. In some parts of the country, particularly the Colorado Plateau, drought impacts are compounded by warming temperatures that increase evapotranspiration rates, reduce soil moisture, and increase stress on vegetation and water resources, creating circumstances for increased soil erosion (Ferguson and others 2011). And, as highlighted in another section of this chapter, drought affects forest- and rangeland-based water production, which in extreme cases can limit access to clean and affordable drinking water (Ferguson and others 2011).

Conclusions

The U.S. economy and society more broadly is adapted to the rhythm of drought, in terms of its severity, duration, spatial extent, frequency, and seasonality. The effects of moderate, short-duration, and spatially limited droughts are easily handled by our economy through adjustments in inputs and outputs without altering our technologies, local economies, locations of human populations, or traditions. Intense, long-duration, and spatially expansive droughts that America has experienced, on the other hand, affect all of these components of society in sometimes profound ways, with impacts that can span decades.

While economists have a basic understanding of how drought affects forest and rangeland systems, we still know very little about how drought affects the economic and social systems of the United States (table 11.4). For example, although we have fairly precise measures of droughts' effects on Federal wildfire management expenditures, we know little about the scale of these impacts on State and local firefighting expenditures. Long-term or persistent droughts or indeed climate change related dryness, would further affect the required size of the overall firefighting capacity of all agencies of governments, for which we know very little.

Likewise, although we understand some of the benefits of trees in urban settings, we know less about how drought affects the production of those benefits in these same urban settings because effects are transmitted through loss of trees, and there is much to be learned about how drought affects mortality of the urban trees. Water effects of drought seem clearly quantified, yet less is understood about the long-term economic effects of water mining (the permanent draw-down of water supplies residing underground). While researchers have quantified some effects of drought on recreation-based goods and services, very little is known about how the various types of recreation activities substitute and complement each other across space and time, or how other modes of consumption outside of the recreation sector can mitigate some of the losses experienced by specific types of recreation.

In the timber products sector, silviculturists have a general understanding of the effects of drought on growth and yield. However, while the effects of drought on growth and yield in particular forest types in particular places might be acute, economies are

global: substitution possibilities for consumers of forest products and across producing regions reduce some of the negative impacts felt in the specific location of the drought, reducing net overall economic losses.

Finally, when describing the economic and social impacts of drought, all such effects need to be scaled by the size of the forest and rangeland based economy, the national economy, and the sizes of local and national human populations. Although smaller economies may be more greatly affected in terms of impacts on sectors, larger economies and more numerous populations are likely to experience greater overall impacts of drought due to potentially larger spatial coverage and because these economies are often less diverse economically (have fewer sectors), limiting substitution opportunities among labor, capital, and goods markets that can mitigate its most acute impacts.

Although this chapter describes some of the economic and social effects of drought in forest and rangelands (table 11.4), our examples did not address how a greater amount of sun (lower cloud cover), which is correlated with drought, can itself have separate effects on economies and societies and alter the suitability of habitats directly affected by sunshine. We also have sidestepped discussion of how forests and rangelands themselves might help to mitigate some of the negative effects of drought: trees provide shade that reduces energy use and water demands in urban settings; they provide shade for precipitation that is stored in the form of snow in high elevations; and they provide a refuge for hikers and campers seeking to escape high heat and sun associated with drought. With further study, these mitigating effects could be better quantified, and the missing pieces can be filled in. This additional study could help wildland managers and policymakers design new and adapt existing approaches to reducing the overall negative impacts of drought. The urgency of such policy and managerial responses could become greater as climate change alters the severity, duration, spatial extents, and frequencies of droughts in forests and rangelands, and as economies grow and populations grow into the future.

The research cited in this chapter also outlines many ways that the private sector, Government, and tribes can work to mitigate the overall effects of drought in society. Private-sector actors can respond to drought by pursuing innovative research and deploying new technology meant to improve water use efficiency; and governments can help by funding similar research and

Table 11.4—Measured effects of drought on the forest and rangeland sector, as reported in this chapter

Economic subsector or aspect	Mechanism	Ownership, spatial and temporal scope	Some effects identified
Timber products sector	Reduced net volume growth, leading to lower overall inventory quantities	National	Lower success in post-harvest and new planted forest seedling establishment success, reduced harvest volumes, lowered overall employment, increased fire-related timber salvage, timber production shifts to less drought-prone locations, altered timber procurement zones, changed locations of pulp and paper manufacturing facilities
Forest- and rangeland-based water	Reduced water quantity and quality	National Forests and Rangelands of the United States	<i>Home Use:</i> Drought encourages adoption of new municipal ordinances or graduated pricing that changes water-use by appliances in homes and outdoors on properties <i>Commercial:</i> lost output due to transfers of water use priorities away from agriculture and water-using manufacturing toward municipal users, to protect water-dependent wildlife and meet inelastic final consumer demand <i>Rangeland and Agriculture:</i> higher soil erosion rates and therefore long-run effects on productivity, planting of more drought-tolerant grasses, increased rates of tree-planting (including shelter belts), increased use of water-efficient irrigation technologies and techniques
Wildfire management	Higher wildfire activity	National Forests and Rangelands of the United States	Higher wildfire suppression and post-fire mitigation expenditures, 65 percent higher during drought compared to nondrought conditions
Recreation	Altered precipitation patterns, temperatures, and precipitation seasonality	National	Reduced snow-based recreation opportunities, reduced water-based recreation opportunities, enhanced equestrian and off-road vehicle activities, perhaps higher rates of visitation to nature interpretive centers
Urban and residential communities	Killing of valuable residential and street trees, due in particular to additional stresses from physical structures and infrastructure, higher vulnerability to other disturbances	Urban/residential areas; national	In the American Dust Bowl, 235 trees/block killed in Manhattan, KS; tree mortality reduced home values 1-10 percent; higher home energy costs due to lower shading, greater flooding risks and increased storm water management costs, deterioration in human health and welfare (including higher incidences of asthma, worsened human birth outcomes, higher human mortality)
Tribal values and lifeways	Altered provision of water-affected ecosystem goods and services valued by indigenous cultures, through effects on wildfire, insects, diseases, invasive species, altered production of nontimber forest and rangeland products	National	Increased epidemics of native and exotic pests, which reduces the supply of forest and rangeland-based ecosystem goods and services; bio-cultural losses due to worsened ecosystem health status; lost goods and services provided directly by water, including the spiritual value of water as a traditional “food,” water as a symbol for life, water as vehicle and instrument of purification and blessing rituals, water as a connection to wildlife; reduced availability of medicinal plants and traditional foods, adversely affecting human health; reduced productivity of, and income from, rangeland livestock managed by tribal peoples; increased marginalization of tribal peoples in the competition with the wider society for water supplies, fishing; reduced income and electricity provided by tribally owned hydroelectric facilities and other energy resources; lost income from recreation on tribal lands due to higher wildfire activity; increased use of local and traditional knowledge as a means of mitigating drought’s impacts

development (Miao and Popp 2014). Decisionmakers in the private and public sectors can act to reduce the negative effects of drought on wages, the cost of capital, income earned, and prices paid to consume water-intensive goods by investing in new technology that can reduce water input per unit of output. By investing in new water-storage technologies, for example, public and private organizations can reduce evaporation and water waste. Governments can also more directly collaborate with tribes to better monitor drought conditions and design interventions that can alleviate the special vulnerabilities that tribal societies face. This collaboration could include joint efforts to diversify tribal energy portfolios, protect traditional fishing and hunting rights when drought reduces animal populations, and create more effective mechanisms to respond to drought-related natural disturbances.

Literature Cited

- Abt, R.C.; Adams, T.O.; Houston, S.C.; Lupold, H.M. 2013. South Carolina's forest resource: A 20/15 program assessment. *South Carolina Forestry Magazine*: 36-39.
- Agthe, D.E.; Billings, R.B. 1987. Equity, price elasticity, and household income under increasing block rates for water. *American Journal of Economics and Sociology*. 46(3): 273-286.
- Akbari, H.; Kurn, D.M.; Bretz, S.E.; Hanford, J.W. 1997. Peak power and cooling energy savings of shade trees. *Energy and Buildings*. 25: 139-148.
- Allen C.D.; Macalady, A.K.; Chenchouni, K. [and others]. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*. 259(4): 660-684.
- Alley, W.M. 1984. The Palmer Drought Severity Index: limitations and assumptions. *Journal of Climate and Applied Meteorology*. 2: 1100-1109.
- Amateis, R.L.; Burkhart, H.E.; Waiswa, D. 2013. Estimating annual growth losses from drought in loblolly pine plantations. In: Guldin, J.M., ed. 2013. Proceedings of the 15th biennial southern silvicultural research conference. e-Gen. Tech. Rep. SRS-GTR-175. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 193-196.
- Anderson, L.; Cordell, H.K. 1988. Influence of trees on residential property values in Athens, Georgia (U.S.A.): a survey based on actual sales prices. *Landscape and Urban Planning*. 15: 153-164.
- Banerjee, O.; Bark, R.; Connor, J.; Crossman, N.D. 2013. An ecosystem services approach to estimating economic losses associated with drought. *Ecological Economics*. 91: 19-27.
- Barber, N.L.; Hutson, S.S.; Linsey, K.S. [and others]. 2009. Estimated use of water in the United States in 2005. Circular 1344. Reston, VA: US Geological Survey. 52 p. <http://pubs.usgs.gov/circ/1344/pdf/c1344.pdf>. [Date accessed: September 16, 2014].
- Bender, L.C.; Boren, J.C.; Halbritter, H. [and others]. 2011. Condition, survival, and productivity of mule deer in semiarid grassland-woodland in east-central New Mexico. *Human-Wildlife Interactions*. 5(2): 276-286.
- Benneer, L.S.; Lee, J.M.; Taylor, L.O. 2013. Municipal rebate programs for environmental retrofits: an evaluation of additionality and cost-effectiveness. *Journal of Policy Analysis and Management*. 32(2): 350-372.
- Boland, J.J.; Whittington, D. 2000. Water tariff design in developing countries: disadvantages of increasing block tariffs (IBTs) and advantages of uniform price with rebate (UPR) designs. IDRC Discussion Paper. Washington, DC: World Bank. 37 p. <http://www.researchgate.net/publication/228541240>. [Date accessed: March 10, 2015].
- Bowker, J.M.; Askew, A.E.; Cordell, H.K. [and others]. 2012. Outdoor recreation participation in the United States—projections to 2060: a technical document supporting the Forest Service 2010 RPA Assessment. Gen. Tech. Rep. SRS-160. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 34 p.
- Brennan, D.; Tapsuwan, S.; Ingram, G. 2007. The welfare costs of urban outdoor water restrictions. *Australian Journal of Agricultural and Resource Economics*. 51. 243-261.
- Brewer, J.; Glennon, R.; Ker, A. [and others]. 2007. Water markets in the west: prices, trading, and contractual forms. NBER Working Paper Number 13002. Washington, DC: National Bureau of Economic Research. 43 p. <http://www.nber.org/papers/w13002.pdf>. [Date accessed: September 16, 2014].
- Brown, T.C. 2004. The marginal economic value of streamflow from national forests. Discussion Paper DP-04-1, RMRS-4851. 97 p. http://www.fs.fed.us/rm/value/docs/marginal_economic_value_streamflow_forests.pdf. [Date accessed: September 16, 2014].
- Brown, T.C. 2006. Trends in water market activity and price in the Western United States. *Water Resources Research*. 42: W09402. 14 p. doi:10.1029/2005WR004180. [Published online: September 8, 2006].
- Brown, T.C.; Hobbins, M.T.; Ramirez, J.A. 2008. Spatial distribution of water supply in the coterminous United States. *Journal of the American Water Resources Association*. 44(6): 1474-1487.
- Butry, D.T.; Mercer, D.E.; Prestemon, J.P. [and others]. 2001. What is the price of catastrophic wildfire? *Journal of Forestry*. 99(11): 9-17.
- Calkin, D.E.; Gebert, K.M.; Jones, J.G.; Neilson, R.P. 2005. Forest Service large fire area burned and suppression expenditure trends, 1970–2002. *Journal of Forestry*. 103(4): 179-183.
- Carr, J.T. 1966. Texas droughts, causes classification and prediction. Report No. 30. Austin, TX: Texas Water Development Board. 58 p. https://www.twdb.texas.gov/publications/reports/numbered_reports/doc/R30/R30.pdf. [Date accessed: September 16, 2014].
- Carreiro, M.M.; Tripler, C.E. 2005. Forest remnants along urban-rural gradients: examining their potential for global change research. *Ecosystems*. 8: 568-582.
- City of San Diego. 2014. Rebate programs. <http://www.sandiego.gov/water/conservation/rebates/index.shtml>. [Date accessed: December 4, 2014].
- Clark J.R.; Kjelgren, R. 1990. Water as a limiting factor in the development of urban trees. *Journal of Arboriculture*. 16(8): 203-208.
- Colby, B.G. 1989. Estimating the value of water in alternative uses. *Natural Resources Journal*. 29: 511-527.
- Collinge, R.A. 1994. Transferable rate entitlements: the overlooked opportunity in municipal water pricing. *Public Finance Review*. 22(1): 46-64.

- Collins, G.; Redsteer, M.H.; Hayes, M. [and others]. 2010. Climate change, drought and early warning on western native lands workshop report. National Integrated Drought Information System. http://www.drought.gov/workshops/tribal/NIDIS_Jackson_Hole_Report.pdf. [Date accessed: September 16, 2014].
- Cozzetto, K.; Chie, K.; Dittmer, K. [and others]. 2013. Climate change impacts on the water resources of American Indians and Alaska Natives in the U.S. *Climatic Change*. 120: 569-584.
- Creel, M.; Loomis, J. 1992. Recreation value of water to wetlands in the San Joaquin Valley: linked multinomial logit and count data trip frequency models. *Water Resources Research*. 28(10): 2597-2606.
- Curry, R.; Wichman, C.; Staudt, A. [and others]. 2011. Facing the storm: Indian tribes, climate-induced weather extremes, and the future for Indian Country. National Wildlife Federation. http://www.nwf.org/~media/PDFs/Global-Warming/Reports/TribalLands_ExtremeWeather_Report.ashx. [Date accessed: September 16, 2014].
- Dalhuisen, J.M.; Florax, R.J.G.M.; de Groot, H.L.F.; Nijkamp, P. [and others]. 2003. Price and income elasticities of residential water demand: a meta-analysis. *Land Economics*. 79(2): 292-308.
- Dalton, M.M.; Mote, P.W.; Snover, A.K. 2013. Climate change in the Northwest: implications for our landscapes, waters, and communities. Washington, DC: Island Press. 271 p.
- Dankwerts, J.E.; King, P.G. 1984. Conservative stocking or maximum profit: a grazing management dilemma. *Journal of Grassland Society of Southern Africa*. 1: 25-28.
- Diersen, M.A.; Taylor, G.; May, A. 2002. Direct and indirect effects of drought on South Dakota's economy. *Economics Commentator*. August 26. Brookings, SD: South Dakota State University. 432 p.
- Diersen, M.A.; Taylor, G. 2003. Examining economic impact and recovery in South Dakota from the 2002 drought. Economics Staff Paper 2003-8. Brookings, SD: Department of Economics, South Dakota State University. 20 p. <http://ageconsearch.umn.edu/bitstream/32028/1/sp03-08.pdf>. [Date accessed: September 16, 2014].
- Ding, Y.; Hayes, M.J.; Widhalm, M. 2010. Measuring economic impact of drought: a review and discussion, Paper 196. Papers in Natural Resources, School of Natural Resources. Lincoln, NE: University of Nebraska-Lincoln. 23 p. <http://digitalcommons.unl.edu/cgi/viewcontent.cgi?article=1198&context=natrespapers>. [Date accessed: September 16, 2014].
- Donovan, G.H.; Brown, T.C. 2005. An alternative incentive structure for wildfire management on national forest land. *Forest Science* 51(5): 387-395.
- Donovan, G.H.; Butry, D.T. 2009. The value of shade: estimating the effect of urban trees on summertime electricity use. *Energy and Buildings*. 41: 662-668.
- Donovan, G.H.; Michael, Y.L.; Butry, D.T. [and others]. 2011. Urban trees and the risk of poor birth outcomes. *Health and Place*. 17: 390-393.
- Donovan, G.H.; Butry, D.T. 2010. Trees in the city: valuing street trees in Portland, Oregon. *Landscape and Urban Planning*. 94(2): 77-83.
- Donovan, G.H.; Butry, D.T. 2011. The effect of urban trees on the rental price of single-family homes in Portland, Oregon. *Urban Forestry and Urban Greening*. 10(3): 163-168.
- Donovan, G.H.; Butry, D.T.; Michael, Y.L. [and others]. 2013. The relationship between trees and human health: evidence from the spread of the emerald ash borer. *American Journal of Preventive Medicine*. 44(2): 139-145.
- Donovan, G.H.; Prestemon, J.P. 2012. The effect of trees on crime in Portland, Oregon. *Environment and Behavior*. 44(1): 3-30.
- Elliott, K.J.; Swank, W.T. 1994. Impacts of drought on tree mortality and growth in a mixed hardwood forest. *Journal of Vegetation Science*. 5: 229-236.
- Englin, J.; Holmes, T.P.; Lutz, J. 2008. Wildfire and the economic value of wilderness recreation. In: Holmes, T.P.; Prestemon, J.P.; Abt, K.L., eds. *The economics of forest disturbances*. New York: Springer: 191-208.
- English, E. 2007. 110 in the shade: drought sears the Southeast. *Econ South*. 9(3): [unnumbered pages]. http://www.frbatlanta.org/pubs/econsouth/econsouth-vol_9_no_3-110_degrees_inshade_drought_searssoutheast.cfm?redirected=true. [Date accessed: September 16, 2014].
- Espey, M.; Espey, J.; Shaw, W.D. 1997. Price elasticity of residential demand for water: a meta-analysis. *Water Resources Research*. 33(6): 1369-1374.
- Executive Department, State of California. 2015. Executive Order B-29-15. https://www.gov.ca.gov/docs/4.1.15_Executive_Order.pdf. [Date accessed: October 19, 2015].
- Ferguson, D.B.; Alvord, C.; Crimmins, M. [and others]. 2011. Drought preparedness for tribes in the Four Corners Region. Workshop Report April 8-9, 2010, Tucson, AZ. <http://climas.arizona.edu/download/file/fid/423>. [Date accessed: September 16, 2014].
- Grafton, R.Q.; Ward, M. 2008. Prices versus rationing: marshallian surplus and mandatory water restrictions. *Economic Record*. 84: S57-S65. doi:10.1111/j.1475-4932.2008.00483.x. [Published online: August 28, 2008].
- Guan, H.; Munn, I.A. 2000. Harvest restrictions: an analysis of new capital expenditures in the Pacific Northwest and the South. *Journal of Forestry*. 98(4): 11-16.
- Hansen, L.T.; Hallam, A. 1991. National estimates of the recreational value of streamflow. *Water Resources Research*. 27(2): 167-175.
- Hanson, P.J.; Weltzin, J.F. 2000. Drought disturbance from climate change: response of United States forests. *The Science of the Total Environment*. 262: 205-220.
- Heim, R.R., Jr. 2002. A review of twentieth-century drought indices used in the United States. *Bulletin of the American Meteorological Society*. 83: 1149-1165.
- Holmes, T.P.; McNulty, S.; Vose, J.M. [and others]. 2014. A conceptual framework for adaptive forest management under climate change. In: Vose, J.M.; Klepzig, K.D., eds. *Climate change adaptation and mitigation management options—a guide for natural resource managers in southern forest ecosystems*. Boca Raton, FL: CRC Press: 45-59.
- Holmes, T.P.; Murphy, E.A.; Bell, K.P. [and others]. 2010. Property value impacts of hemlock woolly adelgid in residential forests. *Forest Science*. 56(6): 529-540.
- Hornbeck, R. 2012. The enduring impact of the American Dust Bowl: short- and long-run adjustments to environmental catastrophe. *American Economic Review*. 102(4): 1477-1507.
- Howe, C.W. 1997. Increasing efficiency in water markets: examples from the Western United States. In: Anderson, T.L.; Hill, P.J., eds. *Water marketing—the next generation*. Bozeman, MT: Property and Environment Research Center: 79-100.
- Just, R.E.; Hueth, D.L.; Schmitz, A.S. 1982. *Applied welfare economics and public policy*. Englewood Cliffs, NJ: Prentice-Hall. 491 p.

- Kjelgren, R.; Rupp, L.; Kilgren, D. 2000. Water conservation in urban landscapes. *HortScience*. 35(6): 1037-1040.
- Klos, R.J.; Wang, G.G.; Bauerle, W.L. [and others]. 2009. Drought impact on forest growth and mortality in the southeast USA: an analysis using Forest Health and Monitoring data. *Ecological Applications*. 19(3): 699-708.
- Knutson, C.L.; Hayes, M.J. 2001. South Carolina drought mitigation and response assessment: 1998-2000 drought. Quick Response Research Report #136. Boulder, CO: Natural Hazards Research and Applications Information Center. <http://www.colorado.edu/hazards/research/qr/q136/qr136.html>. [Date accessed: September 16, 2014].
- Kovacs, K.; Holmes, T.P.; Englin, J.E. [and others]. 2011. The dynamic response of housing values to a forest invasive disease: evidence from a sudden oak death infestation. *Environmental and Resource Economics*. 49: 445-471.
- Krause, K.; Chermak, J.M.; Brookshire, D.S. 2003. The demand for water: consumer response to scarcity. *Journal of Regulatory Economics*. 23(2): 167-191.
- Kuo, F.E.; Sullivan, W.C. 2001. Environment and crime in the inner city: does vegetation reduce crime? *Environment and Behavior*. 33(3): 343-367.
- Lee, K.H.; Isenhardt, T.M.; Schultz, R.C. 2003. Sediment and nutrient removal in an established multi-species riparian buffer. *Journal of Soil and Water Conservation*. 58(1): 1-8.
- Logar, I.; van den Bergh, J.C.J.M. 2013. Methods to assess costs of drought damages and policies for drought mitigation and adaptation: review and recommendations. *Water Resources Management*. 27: 1707-1720.
- Loomis, J.; Kent, P.; Strange, L. [and others]. 2000. Measuring the total economic value of restoring ecosystem services in an impaired river basin: results from a contingent valuation survey. *Ecological Economics*. 33(1): 103-117.
- Lovasi, G.S.; Quinn, J.W.; Neckerman, K.M. [and others]. 2008. Children living in areas with more street trees have lower prevalence of asthma. *Journal of Epidemiology and Community Health*. 62(7): 647-649.
- Lynn, K.; Daigle, J.; Hoffman, J. [and others]. 2013. The impacts of climate change on tribal traditional foods. *Climatic Change*. 120: 545-556.
- Mannering, J.V. 1981. The use of soil loss tolerances as a strategy for soil conservation. In: Morgan, R.P.C., ed. *Soil conservation: problems and prospects*. New York: John Wiley and Sons: 337-349.
- Mansur, E.T.; Olmstead, S.M. 2012. The value of scarce water: measuring the inefficiency of municipal regulations. *Journal of Urban Economics*. 71: 332-346.
- Marshall, J.K. 1973. Drought, land use and soil erosion. In: Lovett, J.V., ed. *The environmental, economic and social significance of drought*. Sydney, Australia: Angus and Robertson: 55-77.
- McKenney-Easterling, M.; DeWalle, D.R.; Iverson, L.R. [and others]. 2000. The potential impacts of climate change and variability on forests and forestry in the Mid-Atlantic Region. *Climate Research*. 14: 195-206.
- McLeman, R.A.; Dupre, J.; Ford, L.B. [and others]. 2014. What we learned from the Dust Bowl: lessons in science, policy, and adaptation. *Population and Environment*. 35(4): 417-440.
- McPherson, E.G.; Simpson, J.R. 2003. Potential energy savings in buildings by an urban tree planting programme in California. *Urban Forestry and Urban Greening*. 2: 73-86.
- Meyer, S.J.; Hubbard, K.G.; Wilhite, D.A. 1993. A crop-specific drought index for corn: I. Model development and validation. *Agronomy Journal*. 85(2): 388-395.
- Miao, Q.; Popp, D. 2014. Necessity as the mother of invention: innovative responses to natural disasters. *Journal of Environmental Economics and Management*. 68: 280-295.
- MIG. 2012. IMPLAN System, Version 3.0 and 2012 dataset. 16905 Northcross Dr., Suite 120, Huntsville, NC 28078: IMPLAN Group LLC.
- Munns, E.N.; Stoeckeler, J.H. 1946. How are the Great Plains shelterbelts? *Journal of Forestry*. 44(4): 237-257.
- National Oceanic and Atmospheric Administration (NOAA). 2014. Historical Palmer Drought Severity Indices by climate division. <http://www1.ncdc.noaa.gov/pub/data/cirs/>. [Date accessed: September 16, 2014].
- Nielsen-Pincus, M.; Moseley, C.; Gebert, K. 2014. Job growth and loss across sectors and time in the Western US: the impact of large wildfires. *Forest Policy and Economics*. 38: 199-206.
- Nowak D.J.; Hirabayashi S.; Bodine, A. [and others]. 2014. Tree and forest effects on air quality and human health in the United States. *Environmental Pollution*. 193: 119-129.
- Office of the White House. 2013a. Executive order—Preparing the United States for the impacts of climate change. <http://www.whitehouse.gov/the-press-office/2013/11/01/executive-order-preparing-united-states-impacts-climate-change>. [Date accessed: September 15, 2014].
- Office of the White House. 2013b. Introducing the National Drought Resilience Partnership. <http://www.whitehouse.gov/blog/2013/11/15/introducing-national-drought-resilience-partnership>. [Date accessed: September 15, 2014].
- Olmstead, S.M.; Hanemann, W.M.; Stavins, R.N. 2007. Water demand under alternative price structures. *Journal of Environmental Economics and Management*. 54(2): 181-198.
- Olmstead, S.M.; Stavins, R.N. 2009. Comparing price and nonprice approaches to urban water conservation. *Water Resources Research*. 45 (4): 10 p. W04301, doi:10.1029/2008WR007227. [Published online: April 25, 2009].
- Orwig, D.A.; Abrams, M.D. 1997. Variation in radial growth responses to drought among species, site, and canopy strata. *Trees*. 11: 474-484.
- Orwig, D.A.; Abrams, M.D. 1997. Variation in radial growth responses to drought among species, site, and canopy strata. *Trees*. 11: 474-484.
- Osborne, L.L.; Kovacic, D.A. 1993. Riparian vegetated buffer strips in water-quality restoration and stream management. *Freshwater Biology*. 29(2): 243-258.
- OZF-REX Foreign Exchange Services. 2014. AUD/USD average rate. <http://www.ozforex.com.au/forex-tools/historical-rate-tools/yearly-average-rates>. [Date accessed: July 25, 2014].
- Palmer, W.C. 1968. Keeping track of crop moisture conditions, nationwide: the new crop moisture index. *Weatherwise*. 21(4): 156-161.
- Pimental, D.; Harvey, C.; Resosudarmo, P. [and others]. 1995. Environmental and economic costs of soil erosion and conservation benefits. *Science*. 267: 1117-1122.
- Pimental, D.; Terhune, E.C.; Dyson-Hudson, R. [and others]. 1976. Land degradation: effects on food and energy resources. *Science*. 94: 149-155.

- Prestemon, J.P.; Abt, K.L.; Gebert, K. 2008. Suppression cost forecasts in advance of wildfire seasons. *Forest Science*. 54(4): 381-396.
- Prestemon, J.P.; Holmes, T.P. 2008. Timber salvage economics. In Holmes, T.P.; Prestemon, J.P.; Abt, K.L., eds. *The economics of forest disturbances: wildfires, storms, and invasive species*. Dordrecht, The Netherlands: Springer: 167-190.
- Prestemon, J.P.; Wear, D.N.; Stewart, F. [and others]. 2006. Wildfire, timber salvage, and the economics of expediency. *Forest Policy and Economics*. 8(3): 312-322.
- Renwick, M.E.; Archibald, S.O. 1998. Demand side management policies for residential water use: who bears the conservation burden? *Land Economics*. 74(3): 343-359.
- Robinson, I.B. 1982. Drought relief schemes for the pastoral zone. *Australian Rangeland Journal*. 4: 67-77.
- Sanders, R.A. 1986. Urban vegetation impacts on the hydrology of Dayton, Ohio. *Urban Ecology*. 9(3-4): 361-376.
- Schaible, G.D.; Aillery, M.P. 2012. Water conservation in irrigated agriculture: trends and challenges in the face of emerging demands. *Economic Information Bulletin No. EIB-99*. Washington, DC: U.S. Department of Agriculture, Economic Research Service. 67 p. <http://www.ers.usda.gov/media/884158/eib99.pdf>. [Date accessed: September 16, 2014].
- Scheierling, S.M.; Loomis, J.B.; Young, R.A. 2006. Irrigation water demand: a meta-analysis of price elasticities. *Water Resources Research*. 42(1): 9 p. doi:10.1029/2005WR004009. [Published online: January 20, 2006].
- Sedell, J.; Sharpe, M.; Dravnieks Apple, D. [and others]. 2000. *Water and the Forest Service*. FS-660. Washington, DC: U.S. Forest Service. <http://www.fs.fed.us/publications/policy-analysis/water.pdf>. [Date accessed: September 16, 2014].
- Solar Energy Industries Association. 2014. *Water use management*. <http://www.seia.org/policy/power-plant-development/utility-scale-solar-power/water-use-management>. [Date accessed: December 5, 2014].
- Speer, J.H.; Grissino-Mayer, H.D.; Orvis, K.H. [and others]. 2009. Climate response of five oak species in the eastern deciduous forest of the southern Appalachian Mountains, USA. *Canadian Journal of Forest Research*. 39(3): 507-518.
- Stiles E.H.; Melchers L.E. 1935. The drought of 1934 and its effect on trees in Kansas. *Transactions of the Kansas Academy of Science*. 38: 107-127.
- Texas Commission on Environmental Quality. 2014. *Map of water systems under water use restriction*. <http://www.tceq.state.tx.us/drinkingwater/trot/location.html>. [Date accessed: September 15, 2014].
- Thomas, D.S.K.; Wilhelmi, O.V.; Finnessey, T.N. [and others]. 2013. A comprehensive framework for tourism and recreation drought vulnerability reduction. *Environmental Research Letters*. 8(4): 8 p. doi:10.1088/1748-9326/8/4/044004. [Published online: October 16, 2013].
- Thomas, D.; Wilhelmi, O. 2013. *Drought assessment for recreation and tourism: southwestern Colorado Report*. Denver, CO: The Colorado Water Conservation Board. <http://cwcbweblink.state.co.us/WebLink/ElectronicFile.aspx?docid=168866&searchid=e1f70-225d-4767-a0b8-335c00e084c8&dbid=0>. [Date accessed: September 15, 2014].
- Timmins, C. 2003. Demand-side technology standards under inefficient pricing regimes. *Environmental and Resource Economics*. 26(1): 107-124.
- Troy, A.; Grove, J.M.; O'Neil-Dunne, J. 2012. The relationship between tree canopy and crime rates across an urban-rural gradient in the greater Baltimore region. *Landscape and Urban Planning*. 106(3): 262-270.
- University of Oregon. 2015. *Tribal Climate Change Project*. [Homepage]. <http://tribalclimate.uoregon.edu/> [Date accessed: March 7, 2015].
- USDA Farm Service Agency. 2014. http://www.fsa.usda.gov/FSA/newsReleases?area=newsroom&subject=landing&topic=pfs&newstype=prfactsheet&type=detail&item=pf_20120720_insup_en_ed_desigp.html.%20 [Date accessed: %20 September%2015,%202014.]
- U.S. Department of Agriculture (USDA), Forest Service. 2000. *Protecting people and sustaining resources in fire-adapted ecosystems: a cohesive strategy*. Washington, DC: U.S. Department of Agriculture, Forest Service. <https://www.federalregister.gov/articles/2000/11/09/00-28509/protecting-people-and-sustaining-resources-in-fire-adapted-ecosystems-a-cohesive-strategy>. [Date accessed: October 16, 2015].
- U.S. Department of Agriculture (USDA), Forest Service. 2008. *Thorn fire salvage recovery project: record of decision and finding of non-significant Forest Plan Amendment #63*. Grant County, Oregon: USDA Forest Service. 917 p. https://scholarsbank.uoregon.edu/xmlui/bitstream/handle/1794/6646/Thorn_Fire_Salvage_Recovery_Project_FEIS_2008.pdf?sequence=1. [Date accessed: September 16, 2014].
- Voggesser, G.; Lynn, K.; Daigle, J. [and others]. 2013. Cultural impacts to tribes from climate change influences on forests. *Climatic Change*. 120: 615-626.
- Vose, J.M.; Swank, W.T. 1994. Effects of long-term drought on the hydrology and growth of a white pine plantation in the southern Appalachians. *Forest Ecology and Management*. 64: 25-39.
- Wallander, S.; Aillery, M.; Hellerstein, D. [and others]. 2013. *The role of conservation programs in drought risk adaptation*. Economic Research Report Number 148. Washington, DC: U.S. Department of Agriculture, Economic Research Service. 68 p.
- Wang, J.; Endreny, T.A.; Nowak, D.J. 2008. Mechanistic simulation of tree effects in an urban water balance model. *Journal of the American Water Resources Association*. 44 (1): 75-85.
- Ward, F.A.; Roach, B.A.; Henderson, J.E. 1996. The economic value of water in recreation: evidence from the California drought. *Water Resources Research*. 32(4): 1075-1081.
- Warziniack, T. 2014. A general equilibrium model of ecosystem services in a river basin. *Journal of the American Water Resources Association*. 50(3): 683-695.
- Waters, E.C.; Holland, D.W.; Weber, B.A. 1994. Interregional effects of reduced timber harvests: the impact of the northern spotted owl listing in rural and urban Oregon. *Journal of Agricultural and Resource Economics*. 19(1): 141-160.
- Wear, D.N.; Murray, B.C. 2004. Federal timber restrictions, interregional spillovers, and the impact on US softwood markets. *Journal of Environmental Economics and Management*. 47(2): 307-330.
- Weidner, E.; Todd, A. 2011. *From the forest to the faucet: drinking water and forests in the US*. Washington, DC: U.S. Department of Agriculture, Forest Service. 34 p. http://www.fs.fed.us/ecosystemservices/pdf/forests2faucets/F2F_Methods_Final.pdf. [Date accessed: September 16, 2014].
- Welsh, L.W.; Endter-Wada, J.; Downard, R.; Kettenring, K.M. 2013. Developing adaptive capacity to droughts: the rationality of locality. *Ecology and Society*. 18(2) Article 7: 10 p. <http://dx.doi.org/10.5751/ES-05484-180207>. [Date accessed: unknown].

Westerling, A.L.; Brown, T.J.; Gershunov, A. [and others]. 2003. Climate and wildfire in the Western United States. *Bulletin of the American Meteorological Society*. 84: 595–604.

Western Drought Coordination Council, USDA Farm Service Agency, and Federal Emergency Management Agency. 1999. *Catalog of Federal Drought Assistance Programs*. USDA Farm Service Agency. <http://drought.unl.edu/archive/wdcc/products/cat99.pdf>. [Date accessed: July 31, 2014].

Wildcat, D.R. 2013. Introduction: climate change and indigenous peoples of the USA. *Climatic Change*. 120: 509-515.

Worster, D. 1986. The dirty thirties: a study in agricultural capitalism. *Great Plains Quarterly*. 6: 107-116.

Wuebbles, D.; Meehl, G.; Hayhoe, K. [and others]. 2014. CMIP5 Climate Model Analyses: climate extremes in the United States. *Bulletin of the American Meteorological Society*. 95(4): 571-583.

Xiao, Q.; McPherson, E.G.; Simpson, J.R. [and others]. 1998. Rainfall interception by Sacramento's urban forest. *Journal of Arboriculture*. 24(4): 235-244.

Young, R.A. 2005. *Determining the economic value of water: concepts and methods*. Washington, DC: Resources for the Future. 357 p.

APPENDIX: Graphical Description of the Economic Effects of Drought on Production of a Good

Depending on its severity and persistence, one can view drought either as a transitory state or as a new “permanent” state, both of which have the potential to alter the distribution of inputs to productive economic activity. Figure 11.A1 describes how water scarcity (drought) would lead to a shift in resources used. It is a stylized model of one produced good (B) and two inputs, water (W) and another input (X) in the production of B. The vertical axis identifies the quantity of water used and the horizontal axis identifies the quantity of the other input in production in this two-input production technology. Two curves, labeled B_1 and B_2 , are shown. All along B_1 the output quantity is the same, but different quantities of W and X can be used to produce B_1 . The same is true for B_2 : output is constant along the entire curve, and the quantities of W and X can be varied to produce that output quantity. Assume that B_1 is the range of output quantities of B—a water-intensive good—that can be produced in normal (nondrought) conditions, while B_2 is the (lower) quantity produced under drought conditions. The angled straight lines identify the relative prices of the two inputs: the flatter the slope of these lines, the more expensive is water relative to the other input. Optimal production, in terms of minimizing costs of inputs, is defined where the straight lines are tangent to the curved lines of B. Assume that the two parallel-angled straight lines represent the relative price of W to X. Without a drought,

the production is at point *a*, using the quantity W_a of water X_a of the other input. Without a change in the relative prices of the inputs during drought, production would shift to the curve B_2 , implying lower levels of both inputs to production level defined at point *b*, with W_b units of water and X_b units of the other input. During a drought, however, water can become more expensive, flattening the sloped line to the single-angled one shown in figure 11.A1. In that case, the optimal combination of inputs would favor production at point *c*, implying a still lower quantity, W_c , of water but a higher quantity, X_c , of the other input. In this way, with higher relative prices for water, drought would increase demand for the other input and reduce the demand for water.

B_1 and B_2 in this example are produced by the same technology. In the face of persistent drought or changes in drought severity or frequencies or spatial extents, producers might invest in a technology that is more water efficient at producing the same good, to avoid persistently higher prices paid for the water as an input in production. New technology conceivably would use water less intensively and other inputs more intensively, yielding a comparable quantity of good produced but at lower cost.

Another way to view the effects of drought on an economy is to consider its effects on the supply and demand of goods and services that depend on water in their production and thereby affect the overall welfare or value produced by the production and consumption of goods whose production depends on water. [See Just and others (1982) for details of welfare analytical techniques.] Figure 11.A2 is an abstract expression of

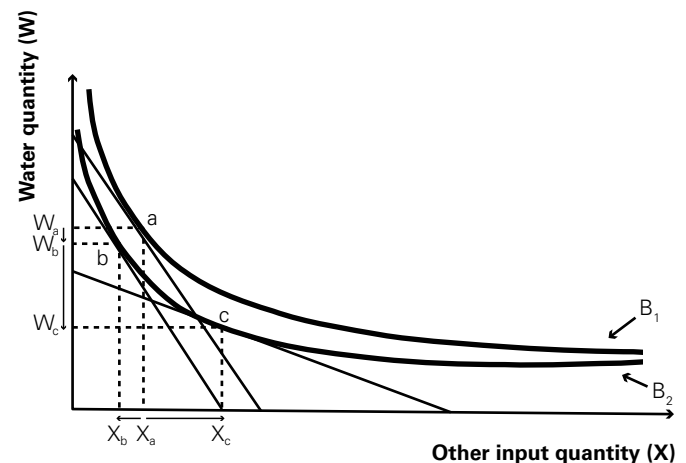


Figure 11.A1—Optimal quantities of water and other inputs in the production of a good, B.

the supply and demand for a good that depends on water for some of its production. The supply of this good is a function of the price per unit of capital (r), price per unit of labor (w), and the initial quantity of water provided by nature (N_0) available. The position of the supply function in price-quantity space is also a function of technology for producing the water-intensive good (z) (discussed later). Supply increases with the price of the good: a higher price of the good encourages more production as a rational response to greater potential profits earned by producers. Water provided by nature (N) affects the position of the supply curve (S_0) in price-quantity space; higher N would move supply outward (to the right). The prices of capital and labor also shift supply; if the price of either capital or labor is higher, then supply shifts back (to the left). Demand, D , is a function of total income of potential consumers (higher income shifts demand outward) and the quantity-demanded decreases with the price of the good. One way that income can change is if the prices of either capital or labor change. For example, if either the price of capital (also known as the return to capital or the interest rate) or the price of labor (the wage rate) decreases, then income would decrease. The area bounded by the vertical axis on the left, the supply curve on the bottom, and demand curve on the top is economic surplus, the sum of consumer

surplus and producer surplus, commonly referred to as welfare ($Welfare_0$)—the blue shaded portion in figure 11.A2. Consumer surplus is defined as the sum of what all demanders (consumers) of the good would be willing to pay minus what they would actually pay (the area above price and below the demand curve). Producer surplus is defined as the costs incurred in producing each good minus the prices received for those goods in the market, defined by the area above the supply curve and below the equilibrium market price. The price in equilibrium is P_0 and the quantity supplied is Q_0 .

Now, imagine a situation that reduces the provision of water, altering N_1 , as in the case of drought (figure 11.A3). This acts to shift supply back to S_1 . With demand fixed, welfare is reduced to a smaller area, to $Welfare_1$. The welfare lost is shaded in orange. Price increases to P_1 and quantity supplied decreases to Q_1 .

We note here that lower output would eventually lead to the freeing up of capital and labor from the water-intensive sector due to lower overall output, and this labor and capital would be available to the water-extensive sector of the economy. The price of capital and labor would decline as a result. The water-extensive sector, therefore, can gain as a result of the drought, mitigating some of the overall losses in the

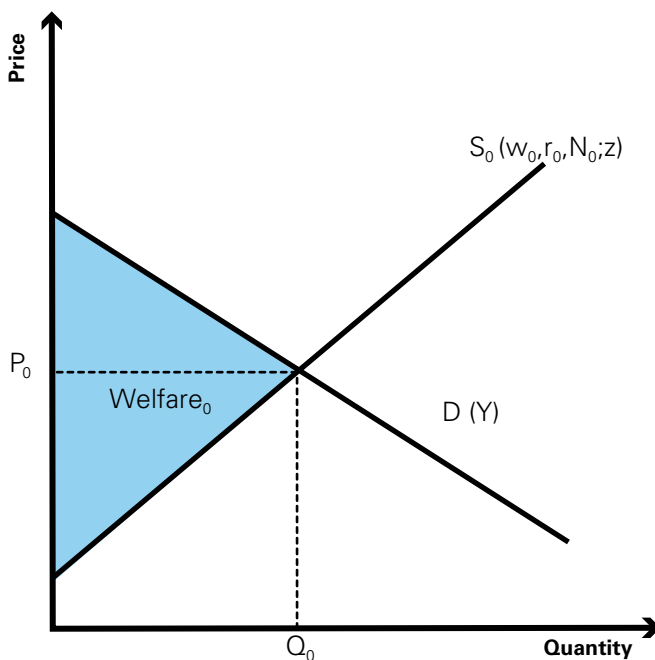


Figure 11.A2—A water-intensive goods market.

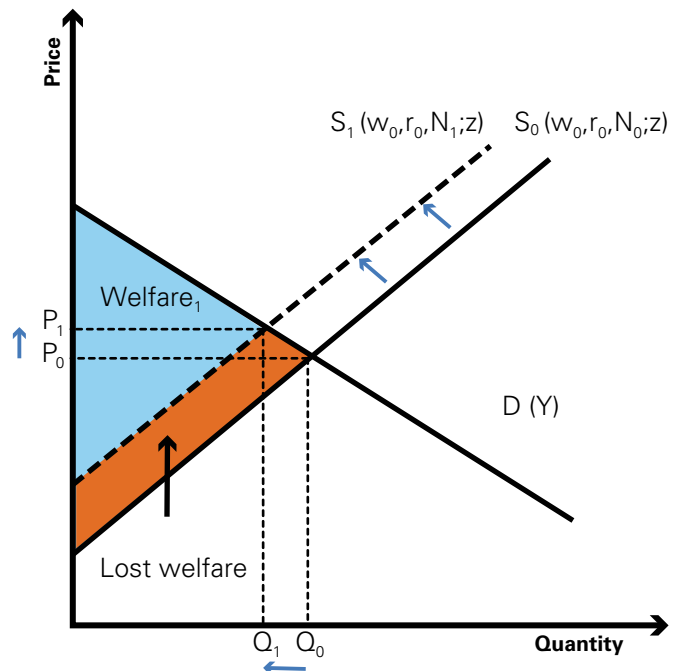


Figure 11.A3—A reduction in the quantity of water available in a water-intensive goods sector.

economy. Figure 11.A4 illustrates this scenario. For a good produced in the water-extensive economic sector, initial supply is SO_0 , expressed as a function of the initial price of capital (r_0) and labor (w_0). Demand for the good in that sector is DO , a function of total income (Y), as before. For the good in this water-extensive sector, PO_0 is the initial market price and OO_0 is the initial production quantity. Initial welfare in the market for this good is represented by the blue triangle and labeled $Welfare_0$. With drought, the prices of labor and capital drop to r_1 (and $r_1 < r_0$) and w_1 (and $w_1 < w_0$). Supply therefore shifts out to SO_1 , with a new and lower equilibrium price, PO_1 , and a higher equilibrium quantity, OO_1 . The effect for the market for this good is a gain in overall market welfare, adding the shaded tan area to the blue area. The above discussion is focused on particular goods, but it could apply to a whole basket (aggregate) of goods that are either water intensive (figs. 11.A1–11.A3) or not (fig. 11.A4) in their production.

The graphical representations in figures 11.A2–11.A4 ignore shifts in demand that would occur because of the lower prices of capital and labor, meaning overall lower income in the economy (Y). Losses in the water-intensive sector would tend to outweigh the gains in the water-extensive sector of the economy. In other words, the demand curves in figures 11.A3–11.A4 would also

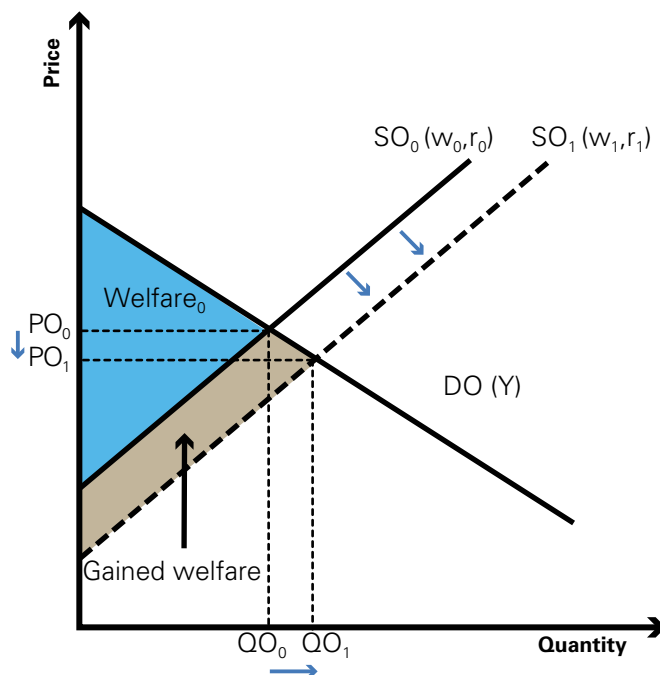


Figure 11.A4—Goods production in other sectors not directly affected by drought (water-extensive sectors).

shift back slightly, causing further adjustments in prices, quantities, and overall welfare in all markets. Other inputs to production could also be described beyond just labor, capital, and water. For example, land is an input common in the water-intensive sector—especially in agriculture. So if a drought affects the agricultural sector, just as for capital and labor, the market price of land would also drop.

One could also conceive of two kinds of labor: labor in the water-intensive sector and labor in the nonwater-intensive sector of the economy; in this case, the two kinds of labor might not be perfect substitutes for each other, due to specialized skills. If demand for labor in the water-intensive sector drops due to lower overall production possibilities, then some—but not all—labor could migrate to the nonwater-intensive sector of the economy; some labor, however, might remain idle until water returns (the drought ends) or the labor acquires new skills (e.g., through training) that makes it equivalent to the specialized labor of the nonwater-intensive sector.

Finally, not described in the figures, is a role for technology (z in figures 11.A2 and 11.A3) used in the water-intensive sector. New technology could be developed and used in the water-intensive sector that allows for more efficient use of water (smaller quantities used for each unit of output). This would cause the supply curve to shift outward, allowing for greater overall production levels at each price received for the water-intensive good in the market. This would serve to mitigate the overall negative consequences for the water-intensive sector, helping to support prices and keep wages and interest rates (and hence incomes) higher than they would be without the new technology. Producers of the water-intensive good could invest in research and development (Miao and Popp 2014) of new water-efficient technology, or governments can provide it or do research that makes its use feasible. An example of a water-efficient technology is a drip irrigation system, which uses less water than a sprinkler system in the agricultural sector.

Summary and Conclusions

Charles H. Luce
James S. Clark
James M. Vose
Toral Patel-Weynand

C.H. Luce is a Research Hydrologist, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station (RMRS), Boise, ID 83702.

J.S. Clark is the Nicholas Professor of Statistical Science at Duke University, Nicholas School of the Environment, Durham, NC 27708-0338.

J.M. Vose is a Research Ecologist, U.S. Department of Agriculture, Forest Service, Southern Research Station (SRS), Center for Integrated Forest Science (CIFS), North Carolina State University, Department of Forestry and Environmental Resources, Raleigh, NC 27695.

T. Patel-Weynand is Director of the Sustainable Forest Management Research (SFMR) staff, U.S. Department of Agriculture, Forest Service, Research and Development (R&D), Washington, DC 20024.

Introduction

Drought is a common disturbance force that drives many ecosystem processes (Dale and others 2001, Luce and others 2012). Forests and rangelands are inherently resilient to drought; however, recent droughts have had severe impacts on forests and rangelands in the United States (Breshears and others 2005, Westerling and others 2006), and there is a growing recognition that outcomes of drought in forests and rangelands in a warmer and drier future could be even more severe (Littell and others 2009, Vose and others 2012). Although most of the apparent changes thus far are in the West, all U.S. forests are vulnerable to drought. While projections of changes in drought regimes are uncertain, natural resource managers will be better prepared to manage for resiliency and adaptation to drought with an improved understanding of how drought affects forests and rangelands. To provide that understanding, the preceding syntheses focused on several key aspects of drought: characterizing drought in forests and rangelands, understanding drought impacts on ecosystem structure and function, and assessing the socioeconomic impacts. In the following sections, we summarize some of the key findings from our synthesis.

Characterizing Drought

Drought is characterized by the magnitude of the precipitation deficit (i.e., the difference from a reference condition such as a long-term mean) and its duration (chapter 2). Common metrics of drought incorporating these two factors include the Palmer Drought Severity Index (PDSI) (Palmer 1965) and the Standardized Precipitation Index (SPI) (McKee and others 1993). The SPI is strictly a function of precipitation and time, whereas the PDSI incorporates potential evapotranspiration. The question of whether precipitation droughts are becoming more severe as a consequence of climate change is open and being vigorously discussed (Luce and others 2013, Mann and Gleick 2015, Swain and others 2014, Trenberth and others 2014). Most forms of potential evapotranspiration-based drought indices implicitly include air temperature, consistently yielding increased drought severity, or even persistent drought, in future projections even where precipitation might be projected to increase or remain the same (e.g., Cook and others 2015, Dai 2011, Sheffield and others 2012). As a result, even unchanged drought characteristics in the future would likely yield increasing stress on plants because

of warmer temperatures at the very least (Adams and others 2009, Allen and others 2010, Breshears and others 2005, Diffenbaugh and others 2015).

Regardless of our capacity to project future drought with precision, it is increasingly important to detect its effects on forests and rangelands at large scales (chapter 9). Commonly used meteorological drought indices may not be appropriate for forests, so the ability to remotely sense drought symptoms in forests will become increasingly important. A number of spectral reflectance properties of forests change as trees become more water stressed, offering promise for the progress of drought to be monitored by remote sensing; but, the relationship between drought and spectral properties is not straightforward for forests due to factors such as lags in response and varying species sensitivities. Combining multiple data sources (e.g., remote sensing, climate, and plant data) will be required to determine the progress of the ecological consequences of drought.

Drought Effects on Wildlands

Drought affects forests in complex ways, ranging from reduced growth to mortality by starvation, desiccation, fire, or insects and pathogens. Drought also has an ecological role that shapes the structure and function of many forests. For example, fire-adapted ecosystems may also be thought of as “drought-adapted” because drought predisposes forest to wildfire. Similarly, some species that live in droughty conditions, such as bristlecone pine (*Pinus longaeva*), gain some resistance to spreading pathogens through a lack of nearby neighbors. Understanding some of these unique adaptations requires a broader understanding of the basic effects of drought on individual trees and forest communities.

The effects of drought on plants depend on the matric potential of soil water in the rooting zone (chapter 3). As leaves become drier due to a lack of available moisture in the soil to rewet them at night, stomata will close when the evaporative demand of the air (a function of warm temperatures and low humidity) becomes too great. When stomata close, plants are unable to fix carbon dioxide, leading to metabolic stress. If metabolic stress is severe, and the stomata are open, continued evaporation from leaves can lead to hydraulic failure, interrupting the flow of water up the stem to the leaves. Species differences in their allocation to roots, mycorrhizal associations, and xylem anatomy all contribute to species differences in drought tolerance.

Although elevated carbon dioxide (CO₂) can increase water use efficiency, the combined effects of rising CO₂ and drought are poorly understood. Translating impacts on trees to the stand and landscape scale is challenging; however, combined field evidence and models suggests that climate shifts are moving habitats faster than tree species can keep up (chapter 4). Hence, stand structure and species composition are expected to lag behind shifts in habitat caused by increasing drought and temperature change.

Increased drought tends to hinder nutrient uptake by plants, and it may reduce retranslocation of foliar nutrients if premature leaf senescence occurs (chapter 5). However, nutrients in the foliage tend to become more concentrated because carbon fixation and water uptake decrease. Microbial activity in soils may be reduced as soils dry out, but those portions of the soil with enough moisture may see more rapid metabolism if temperatures rise. Mortality associated with drought may increase carbon available to the soil in the short and medium term. Dieback can also severely limit carbon fixation by the biosphere. Recent, large diebacks have had global impacts on carbon cycles, including release of carbon from dead biomass and reduced vegetation uptake of carbon.

Natural enemies may capitalize on drought stress in trees, leading to large diebacks (Breshears and others 2005). Severe moisture stress reduces both chemical and physical defenses of trees to insects, and droughts are commonly precursors to severe outbreaks (Creeden and others 2014, Raffa and others 2008). Insects also benefit from the increased nutritional content of drought-stressed trees, making both defoliating and boring insect outbreaks more potent during drought conditions (chapter 6). Some fungal infections may be hampered by drier conditions, although many species may benefit from drought-related damage after moist conditions return. Insect attacks and fungal pathogens can further impair plant defenses against drought mortality. Prolonged and severe moisture stress can ultimately have negative feedbacks on insect populations simply through reduced production of food and food quality.

Fire commonly occurs in concert with drought, particularly more widespread fires (Heyerdahl and others 2008, Morgan and others 2008), and a range of meteorological drought indices offer some predictive capability for the amount of fire on the landscape (chapter 7). Drought can, inversely, limit the growth

of fuels, particularly in more arid locations, creating an interesting outcome where anomalously moist conditions preceding the dry season predict more fire (Abatzoglou and Kolden 2013, Littell and others 2009). Forest fires that occur in moist years tend to be less widespread (in part because they are easier to control), and severity patterns in these fires are controlled by topographic factors affecting soil moisture distributions (Dillon and others 2011). Conversely, fires are more likely to escape control during drought years, affecting more acreage. Although the fractional area of high severity is similar between drought and nondrought years, severity patterns show less discrimination in drought years. Land management and fire management choices that affect fuels can greatly affect the spread and severity of fires through their control on fuel availability.

When there is less water, there is less for trees and less for streams (chapter 10). Both evapotranspiration and streamflow react negatively to drought, and the sensitivity of streamflow to drought is not the same everywhere. Different soil, topography, vegetation types, and precipitation seasonality all affect changes in the partitioning of precipitation and energy inputs to the system to determine its response. Streams become generally warmer with lower flows, but water chemistry changes are substantially more complex, having some relation to changes in nitrogen fixing and uptake.

Rangelands are at the arid end of the spectrum of wildland ecosystems encompassing woodland, shrubland, and grassland ecosystems, and moisture deficits may be expressed on much shorter time scales than in forest ecosystems. Consequently, management and utilization of these systems is fairly responsive to drought indications as a result of historical experience (chapter 8). Native plant restoration is a strong focus of efforts to improve drought resilience in rangeland ecosystems.

Socioeconomic Impacts

Drought has direct consequences to forest and rangeland production that can translate into economic impacts. For example, droughts can negatively impact forest inventories and reduce forage and water available for livestock grazing in rangelands. Drought-related disturbance, such as wildfire, can have protracted effects. Wildfires can generate positive short-term impacts in local communities, including external resources to fight fire and economic activities in

post-fire timber salvage and burn area rehabilitation. However, long-term effects can include significant timber market losses. Reduced water yield from forests and rangelands during extended meteorological drought can have substantial impacts on domestic and agricultural water supplies. Drought can also have nonmarket effects on forests and rangelands, such as water-based outdoor recreation activities.

It is important to identify risk, potential impacts, and vulnerabilities related to water supply and water rights on tribal lands. Ongoing drought in the Western United States, where most tribal lands exist, is expected to continue to affect tribal health, culture, economies, and infrastructure. Competing demands for dwindling water resources challenge Federal trust responsibilities. Complicating factors, including warming streams and hydrologic cycle changes, affect fish populations important to tribal diets and ceremonies. Because of their natural resource dependence for income, employment, and cultural practices, many tribes are also vulnerable to higher rates of forest and rangeland disturbances, including invasive species spread, increased occurrences of epidemic pest populations and their associated damages, and wildfires.

Critical Research Needs

Despite the recognition of drought as a key driver of ecosystem processes and the impacts of drought on human well-being, there are significant uncertainties that limit our ability to predict the direct and indirect impacts of drought on our Nation's forests and rangelands. Examples of key areas of research needs identified by authors of this assessment include:

- **Improved Metrics for Quantifying, Detecting, and Predicting Drought in Forests and Rangelands**—

Unlike agricultural-based metrics, drought metrics for forests and rangelands may require a longer, multiyear “memory” of antecedent conditions. Adaptations might include reformulating drought measures to capture long-duration multiyear drought, targeting drought measures to the sensitive seasons of the year based on phenological insights, or embracing baselines that relate better to the nonequilibrium nature of forested and rangeland ecosystems. Empirically relating hydrologic drought measures (e.g., streamflow measures) and ecosystem outcomes at individual-to-stand levels may be one useful path toward advancing prediction, particularly given parallel

ecosystem values as encompassed in the terms “green water” and “blue water” (Falkenmark and Rockström 2006).

Ecohydrologic models that relate drought stress in plants and plant productivity as a function of available water and climate (e.g., Running and Hunt 1993, Tague and Band 2004) may yield useful insights with respect to which drought characteristics are likely most stressful in different kinds of plant communities depending on the basic climate in which they reside. Advances in understanding from such modeling, however, are contingent on improvements in plant physiology within these models.

- **Better Models for Predicting Drought Impacts on Ecosystem Processes and Population Dynamics**—

Existing biogeochemical cycling models perform poorly under drought conditions, stemming largely from the lack of root and stem hydraulic characteristics in those models. Scientists need to better understand the response of the belowground system, ecosystem interactions across multiple trophic scales, and the interaction of drought with elevated CO₂. These dynamics are critical areas for future research. We also need to better understand drought consequences at the stand-to-landscape scales. This challenge is related to the need for models to accommodate environmental change and forest response as a coherent joint distribution of species and sizes that responds to drought with feedbacks and interactions. Unlike some types of disturbance that might be treated as an extrinsic force, drought involves a feedback with water use by the stand and, thus, is more difficult to model. Understanding these feedback mechanisms requires a better understanding of species' differences in water use and sensitivity to drought, as well as the thresholds that determine species' physiological capacity to survive drought.

- **Improved Understanding of the Indirect Effects of Drought**—

Drought-productivity relationships related to physiological behaviors dominate the discussion of drought effects on forests, but the leveraging of drought by disturbance through insects, pathogens, and fire may be of greater influence in some places (Dale and others 2001). The stochastic nature of disturbance makes direct prediction through models difficult, but information about risk can be validated at landscape scales.

Despite bark beetle outbreaks impacting millions of forested acres in the United States, we still have a limited understanding of: (1) the relative role of temperature and precipitation deficit in drought-induced outbreaks of bark beetles; (2) identification of species which are capable of self-perpetuating outbreaks after drought subsides; (3) the level of drought-associated tree mortality that would occur without bark beetle attacks; (4) the effectiveness of manipulating forest composition and structure to reduce drought stress and bark beetle attacks in semi-arid forests; and (5) the level of drought intensity in pine forests of the Eastern United States that would shift the role of drought in beetle outbreaks from a negative to a positive driver. The impact of defoliators and fungal pathogens has been variable, underscoring the need for a greater understanding of the impacts of drought on defoliators' pathogens.

Drought and fire relationships show broadly a relationship between drier conditions and fire (e.g., flammability of fuels), but there is a growing recognition and examples demonstrating that the relationship of drought to development and accumulation of fuels is important as well. The principle area of uncertainty in drought-fire relationships is in understanding the relative roles of precipitation and temperature as controls on risk. From the observational point of view related to fire occurrence and size, the window of opportunity is an important quantity in its own right, but if that window occurs in warm period, it exacerbates the drying of vegetation as well; separating these influences would be important in exploring climate change impacts, which affect timing and drying intensity through different mechanisms.

- **Improved Understanding of Genetic Contributions to Resilience in Native Rangeland Plants**—Drought adaptation in rangelands is arguably well developed with respect to balancing range utilization, simply out of the long-term lessons about recovery of rangelands with respect to herbivory. Important areas of learning, however, are occurring in the area of native plant restoration in the context of strong invasive species presence and changing climate. Finding seed sources with strong resilience to drought is an example of how research can help with assisted migration of important genetic diversity within the native plant communities.

- **Improved Quantification of Socioeconomic Impacts**—Although we have fairly precise measures of droughts' effects on Federal wildfire management expenditures, we know little about the scale of these impacts on State and local firefighting expenditures. Long-term or persistent droughts or indeed climate-change-related dryness, would further affect the required size of the overall firefighting capacity of all agencies of governments. Water effects of drought are quantifiable, yet less is understood about the long-term economic effects of water mining (the permanent draw-down of water supplies residing underground). While researchers have quantified some effects of drought on recreation-based goods and services, very little is known about how the various types of recreation activities substitute and complement each other across space and time, or how other modes of consumption outside of the recreation sector can mitigate some of the losses experienced by specific types of recreation. We need an improved understanding of the effects of scale on economic impacts. For example, the effects of drought on growth and yield in particular forest types in particular places might be acute; however, economies are global and substitution possibilities for consumers of forest products and across producing regions reduce some of the negative impacts felt in the specific location of the drought, reducing net overall economic losses.

Management Responses

How can forest and rangeland practices adapt to changing drought regimes? Frequent, low-severity drought may selectively favor more drought-tolerant species and create forests and rangelands better adapted to future conditions without the need for management intervention. By contrast, severe drought (especially in combination with insect outbreaks or fire) may threaten large-scale changes that warrant substantial management responses. Actions could range from reducing vulnerability, facilitating post-drought recovery, or facilitating a transition to a new condition.

Management actions can either mitigate or exacerbate the effects of drought. A first principal for increasing resilience and adaptation would be to avoid management actions that exacerbate the effects of current or future drought. Options can include altering structural or functional components of vegetation. Structural changes can be implemented by thinning

or density management of planted forests. Thinned stands require less water and can be less vulnerable to water stress and insect outbreaks. Reduced fuel loads in thinned stands can also reduce wildfire risk. Increasing species and age-class diversity within stands can reduce insect attack intensity as well. Functional changes can be implemented by favoring or planting more drought- and disturbance-adapted species. Management for a diversity of species can reduce stand vulnerability to drought, as uncertainty in future climate can motivate management for a mix of drought-tolerant species and genotypes. In some regions of the United States, planting or favoring more drought-tolerant species may conflict with management objectives that favor rapid accumulation of biomass, as fast-growing woody species often use more water and can exacerbate drought impacts.

Since forest harvest has been shown to increase annual water yield, some have proposed that the effects of drought on water supply could be mitigated by cutting forests, but there are concerns that such an approach could be maladaptive (Brown and others 2005, Troendle and others 2010). A major challenge in managing forests to enhance water supply is the large reduction of forest cover that might be needed to create an appreciable effect on water yield. Hence, potential increases in streamflow through forest cutting are limited by the amount of land that can be harvested or maintained in early seral stages at a given time. In addition, streamflow responses are often short term due to rapid forest regrowth, and the aggrading post-harvest forest may actually transpire water more rapidly than the uncut forest. Because drought is unpredictable, it may not be possible to time harvesting precisely when needed to offset the effects of drought. Furthermore, in contrast to management actions that are intended to augment streamflow, increasing drought stress in some forest ecosystems may warrant management strategies that retain water on the landscape (and hence reduce streamflow) in order to keep trees alive. Management efforts should focus on minimizing inputs of sediments and nutrients into the stream. It may be beneficial to plan the timing of management activities so they do not disturb streams during low-flow periods and to avoid vulnerable areas during droughts. Since removal and alteration of riparian vegetation increases stream temperatures, maintaining or increasing shading from solar radiation through riparian buffer conservation and restoration may help protect streams against high temperatures during drought.

Literature Cited

- Abatzoglou, J.T.; Kolden, C.A. 2013. Relationships between climate and macroscale area burned in the Western United States. *International Journal of Wildland Fire*. 22(7): 1003-1020.
- Adams, H.D.; Guardiola-Claramonte, M.; Barron-Gafford, G.A. [and others]. 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences*. 106(17): 7063-7066.
- Allen, C.D.; Macalady, A.K.; Chenchouni, H. [and others]. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*. 259(4): 660-684.
- Breshears, D.D.; Cobb, N.S.; Rich, P.M. [and others]. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences*. 102: 15,144-15,148.
- Brown, A.; Zhang, L.; McMahon, T. [and others]. 2005. A review of paired catchment studies for determining changes in water yield resulting from alterations in vegetation. *Journal of Hydrology*. 310(1-4): 28-61.
- Cook, B.I.; Ault, T.R.; Smerdon, J.E. 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. *Science Advances*. 1(1): e1400082. doi: 10.1126/sciadv.1400082. [Published online: February 12, 2015].
- Creeden, E.P.; Hicke, J.A.; Buotte, P.C. 2014. Climate, weather, and recent mountain pine beetle outbreaks in the Western United States. *Forest Ecology and Management*. 312: 239-251.
- Dai, A. 2011. Drought under global warming: a review. *Wiley Interdisciplinary Reviews: Climate Change*. 2(1): 45-65. doi: 10.1002/wcc.81. [Published online: October 19, 2010].
- Dale, V.H.; Joyce, L.A.; McNulty, S. [and others]. 2001. Climate change and forest disturbances. *BioScience*. 51(9): 723-734.
- Diffenbaugh, N.S.; Swain, D.L.; Touma, D. 2015. Anthropogenic warming has increased drought risk in California. *Proceedings of the National Academy of Sciences*. 112(13): 3931-3936.
- Dillon, G.K.; Holden, Z.A.; Morgan, P. [and others]. 2011. Both topography and climate affected forest and woodland burn severity in two regions of the Western U.S., 1984 to 2006. *Ecosphere*. 2(12): 130. 33 p. doi: 10.1890/ES11-00271.1. [Published online: December 12, 2011].
- Falkenmark, M.; Rockström, J. 2006. The new blue and green water paradigm: breaking new ground for water resources planning and management. *Journal of Water Resources Planning and Management*. 132(3): 129-132.
- Heyerdahl, E.K.; Morgan, P.; Riser II, J.P. 2008. Multi-season climate synchronized historical fires in dry forests (1650–1900), Northern Rockies, USA. *Ecology*. 89(3): 705–716.
- Littell, J.S.; McKenzie, D.; Peterson, D.L.; Westerling, A.L. 2009. Climate and wildfire area burned in western U.S. ecoregions, 1916-2003. *Ecological Applications*. 19(4): 1003-1021.
- Luce, C.; Morgan, P.; Dwire, K. [and others]. 2012. Climate change, forests, fire, water, and fish: building resilient landscapes, streams, and managers. Gen. Tech. Rep. RMRS-GTR-290. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 207 p.

- Luce, C.H.; Abatzoglou, J.T.; Holden, Z.A. 2013. The missing mountain water: slower westerlies decrease orographic enhancement in the Pacific Northwest USA. *Science*. 342(6164): 1360-1364. doi: 10.1126/science.1242335. [Published online: November 29, 2013].
- Mann, M.E.; Gleick, P.H. 2015. Climate change and California drought in the 21st century. *Proceedings of the National Academy of Sciences*. 112(13): 3858-3859.
- McKee, T.B.; Doesken, N.J.; Kleist, J. 1993. The relationship of drought frequency and duration to time scales. In: *Proceedings of the 8th Conference on Applied Climatology*. 17-22 January, Anaheim, CA. Boston: American Meteorological Society: 179-184.
- Morgan, P.; Heyerdahl, E.K.; Gibson, C.E. 2008. Multi-season climate synchronized widespread forest fires throughout the 20th century, Northern Rocky Mountains. USA. *Ecology*. 89(3): 717-728.
- Palmer, W.C. 1965. Meteorological drought. Res. Pap. No. 45. Washington, DC: U.S. Department of Commerce, Weather Bureau. 58 p.
- Raffa, K.F.; Aukema, B.H.; Bentz, B.J. [and others]. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience*. 58(6): 501-517.
- Running, S.W.; Hunt, E.R. 1993. Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global-scale models. In: Ehleringer, J.R.; Field, C., eds. *Scaling physiological processes: leaf to globe*. San Diego: Academic Press: 141-158.
- Sheffield, J.; Wood, E.F.; Roderick, M.L. 2012. Little change in global drought over the past 60 years. *Nature*. 491(7424): 435-438.
- Swain, D.L.; Tsiang, M.; Haugen, M. [and others]. 2014. The extraordinary California drought of 2013/2014: character, context, and the role of climate change. *Bulletin of the American Meteorological Society*. 95(9): S3-S7.
- Tague, C.; Band, L. 2004. RHESys: regional hydro-ecologic simulation system—an object-oriented approach to spatially distributed modeling of carbon, water, and nutrient cycling. *Earth Interactions*. 8(19): 1-42.
- Trenberth, K.E.; Dai, A.; van der Schrier, G. [and others]. 2014. Global warming and changes in drought. *Nature Climate Change*. 4(1): 17-22.
- Troendle, C.A.; MacDonald, L.; Luce, C.H.; Larsen, I.J. 2010. Fuel management and water yield. In: Elliot, W.J.; Miller, I.S.; Audin, L., eds. *Cumulative watershed effects of fuel management in the Western United States*. Gen. Tech. Rep. RMRS-GTR-231. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 124-148.
- Vose, J.M.; Peterson, D.L.; Patel-Weynand, T., eds. 2012. *Effects of climatic variability and change on forest ecosystems: a comprehensive science synthesis for the U.S. forest sectors*. Gen. Tech. Rep. PNW-GTR-870. Corvallis, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 265 p.
- Westerling, A.L.; Hidalgo, H.G.; Cayan, D.R.; Swetnam, T.W. 2006. Warming and earlier spring increases western U.S. forest wildfire activity. *Science*. 313(5789): 940-943. doi: 10.1126/science.1128834. [Published online: July 6, 2006].

Vose, J.M.; Clark, J.S.; Luce, C.H.; Patel-Weynand, T., eds. 2016. Effects of drought on forests and rangelands in the United States: a comprehensive science synthesis. Gen. Tech. Rep. WO-93b. Washington, DC: U.S. Department of Agriculture, Forest Service, Washington Office. 289 p.

This assessment provides input to the reauthorized National Integrated Drought Information System (NIDIS) and the National Climate Assessment (NCA), and it establishes the scientific foundation needed to manage for drought resilience and adaptation. Focal areas include drought characterization; drought impacts on forest processes and disturbances such as insect outbreaks and wildfire; and consequences on forest and rangeland values. Drought can be a severe natural disaster with substantial social and economic consequences. Drought becomes most obvious when large-scale changes are observed; however, even moderate drought can have long-lasting impacts on the structure and function of forests and rangelands without these obvious large-scale changes. Large, stand-level impacts of drought are already underway in the West, but all U.S. forests are vulnerable to drought. Drought-associated forest disturbances are expected to increase with climatic change. Management actions can either mitigate or exacerbate the effects of drought. A first principal for increasing resilience and adaptation is to avoid management actions that exacerbate the effects of current or future drought. Options to mitigate drought include altering structural or functional components of vegetation, minimizing drought-mediated disturbance such as wildfire or insect outbreaks, and managing for reliable flow of water.

Keywords: Climate change, drought, forest disturbances, natural disasters, water quantity and quality.



In accordance with Federal civil rights law and U.S. Department of Agriculture (USDA) civil rights regulations and policies, the USDA, its Agencies, offices, and employees, and institutions participating in or administering USDA programs are prohibited from discriminating based on race, color, national origin, religion, sex, gender identity (including gender expression), sexual orientation, disability, age, marital status, family/parental status, income derived from a public assistance program, political beliefs, or reprisal or retaliation for prior civil rights activity, in any program or activity conducted or funded by USDA (not all bases apply to all programs). Remedies and complaint filing deadlines vary by program or incident.

Persons with disabilities who require alternative means of communication for program information (e.g., Braille, large print, audiotape, American Sign Language, etc.) should contact the responsible Agency or USDA's TARGET Center at (202) 720-2600 (voice and TTY) or contact USDA through the Federal Relay Service at (800) 877-8339. Additionally, program information may be made available in languages other than English.

To file a program discrimination complaint, complete the USDA Program Discrimination Complaint Form, AD-3027, found online at http://www.ascr.usda.gov/complaint_filing_cust.html and at any USDA office or write a letter addressed to USDA and provide in the letter all of the information requested in the form. To request a copy of the complaint form, call (866) 632-9992. Submit your completed form or letter to USDA by: (1) mail: U.S. Department of Agriculture, Office of the Assistant Secretary for Civil Rights, 1400 Independence Avenue, SW, Washington, D.C. 20250-9410; (2) fax: (202) 690-7442; or (3) email: program.intake@usda.gov.

USDA is an equal opportunity provider, employer, and lender.