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

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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.
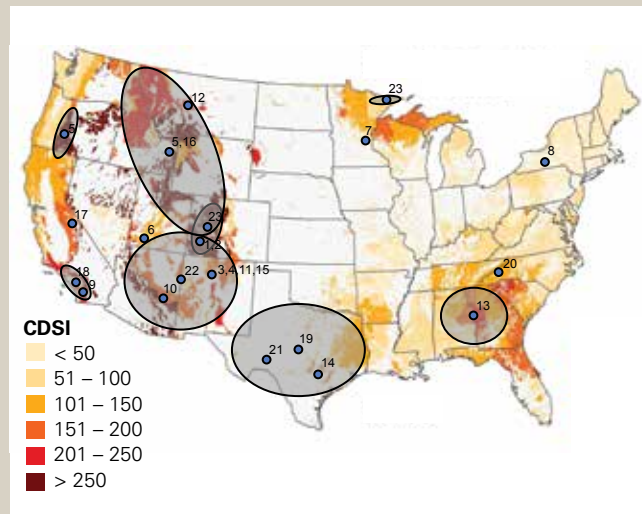

Figure 4.1—Cumulative drought severity index (CDSI) for forested lands from 1987–2013 with selected locations of drought- and heat-induced tree mortality indicated by blue circles and dots.
Numbers on map correspond to the following supporting references: 1–Anderegg and others (2012); 2–Anderegg and 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).
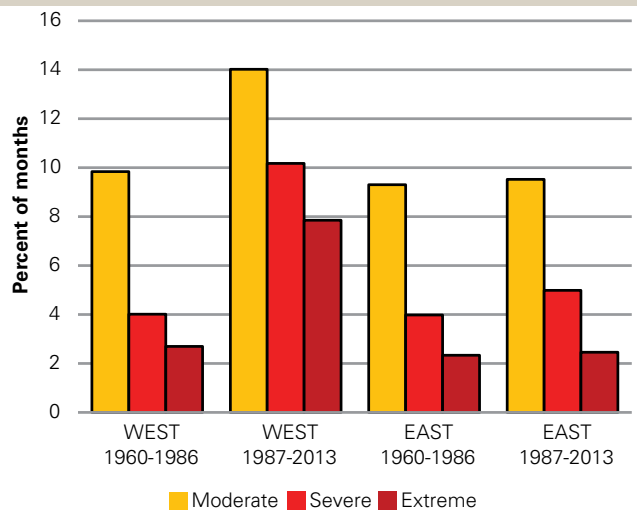

Figure 4.2—Drought for forested land of the conterminous United States for two 27–year periods from 1960 to 2013. For each forest type, drought conditions were summarized as the percentage of months during the 324–month period (27 years) among climate divisions that contained the forested land. (Peters 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,
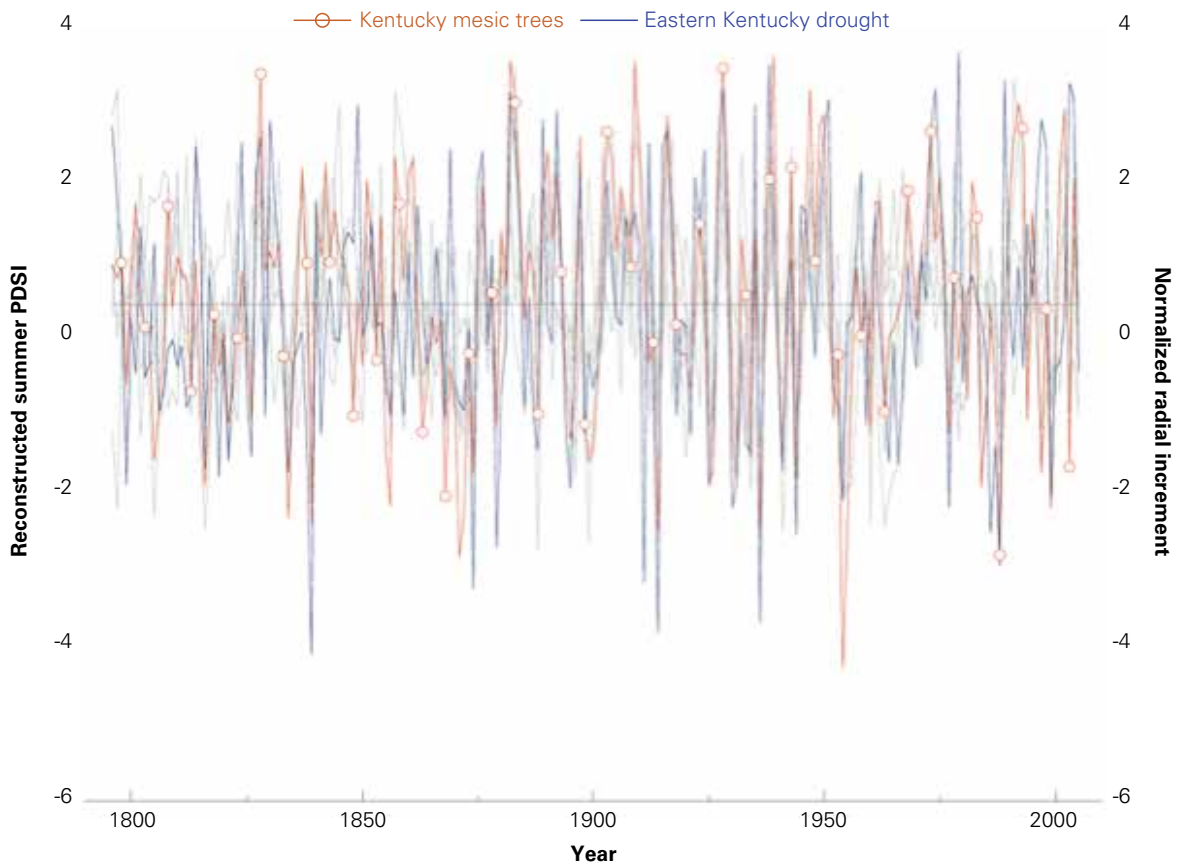
Figure 4.3—Growth responses to summer drought on mesic sites in Kentucky, 1796-2005. Average tree growth (orange line with circles) correlates with an independent reconstruction of summer Palmer Drought Severity Index (PDSI) (June, July, August) (r = 0.55, blue line). Chronologies plotted in light gray 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 (PDSI ≥ 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
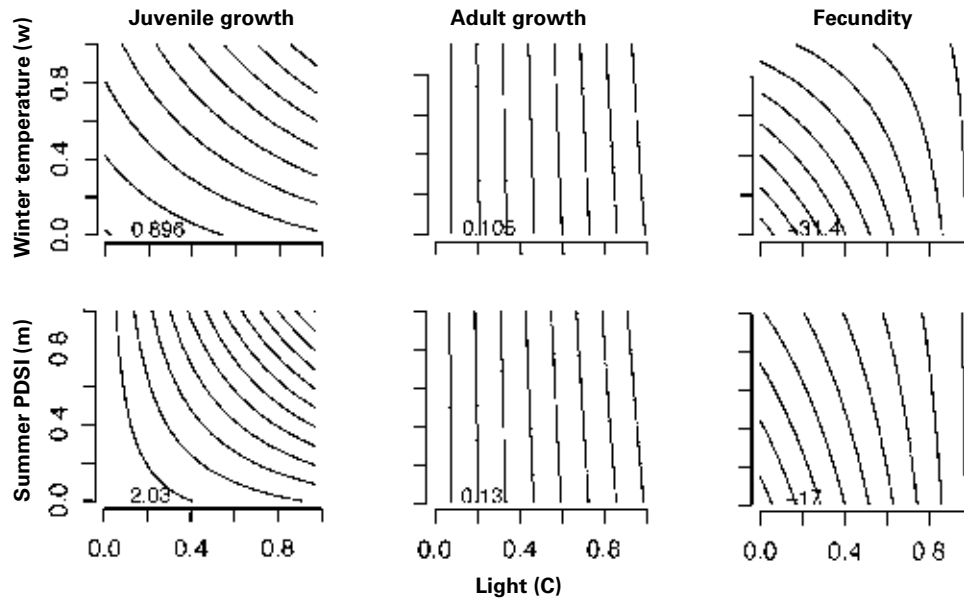
Figure 4.4—A joint distribution of three demographic responses is obtained when all responses are fitted simultaneously, as part of the same model. This example shows interactions that control responses of loblolly pine (*Pinus taeda*) to winter temperature (above) and summer Palmer Drought Severity 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
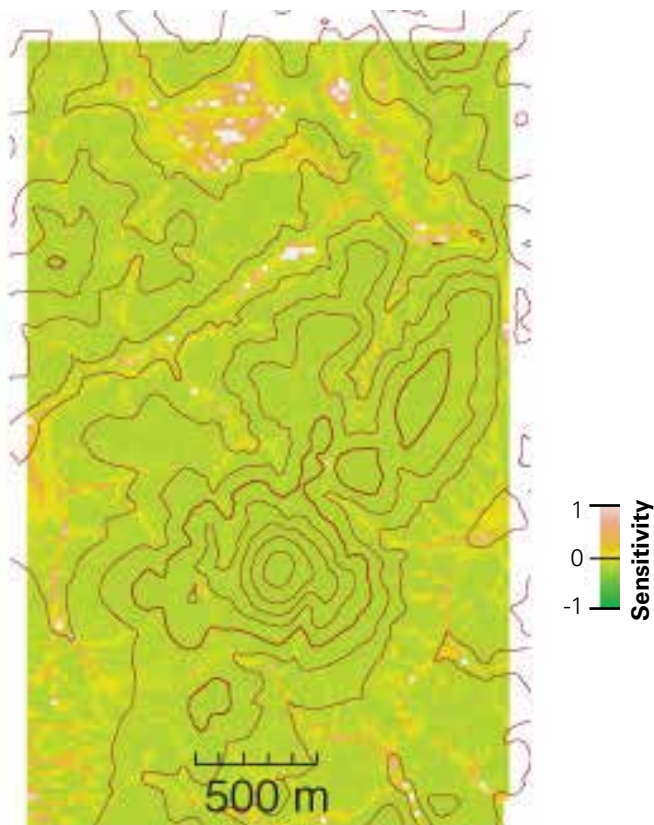
Figure 4.5—Drought effects on growth interact with soil moisture. For American elm (*Ulmus americana*) on the Piedmont Plateau in North Carolina, growth is most sensitive to drought on wet sites at low elevation (see contours), potentially contrary to the intuition that xeric stands are at greatest risk of drought. This is a positive moisture index/Palmer Drought Severity Index (PDSI) interaction, with the largest response to PDSI occuring on moist sites (Clark and others 2014b).

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), CO_2 (LaDeau and Clark 2001), and light availability (Clark and others

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

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.
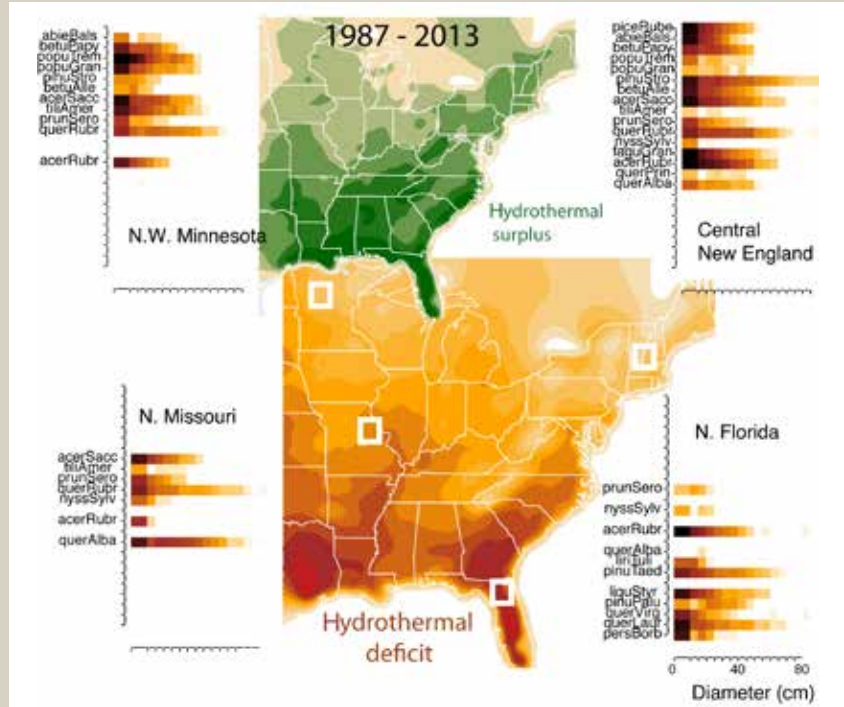
MOISTURE AND SIZE-SPECIES DISTRIBUTIONS

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).
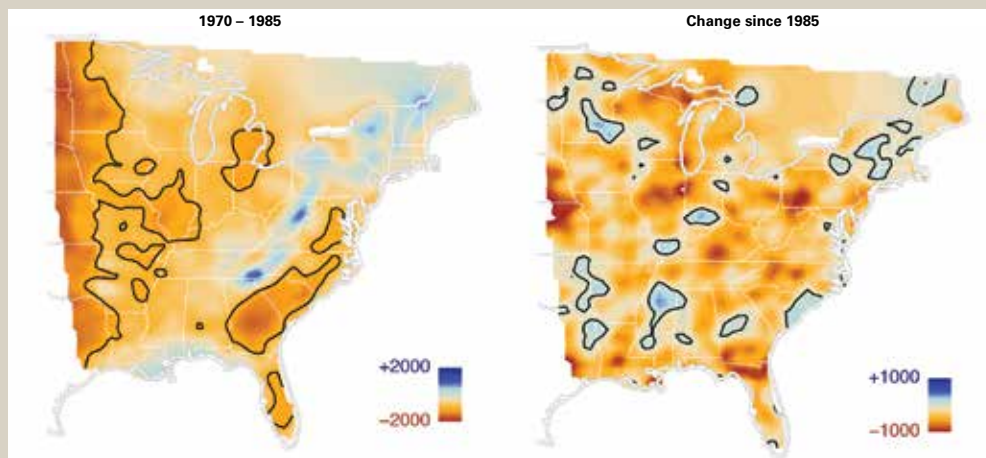

Figure. 4.7—Deficits commonly develop throughout the Eastern United States each growing season, particularly in the Midwest and Southeast. At left is the difference between surplus and deficit (black isohydrotherm is drawn at -1000 degree hours) from 1970 to 1985. The recent shift to larger deficits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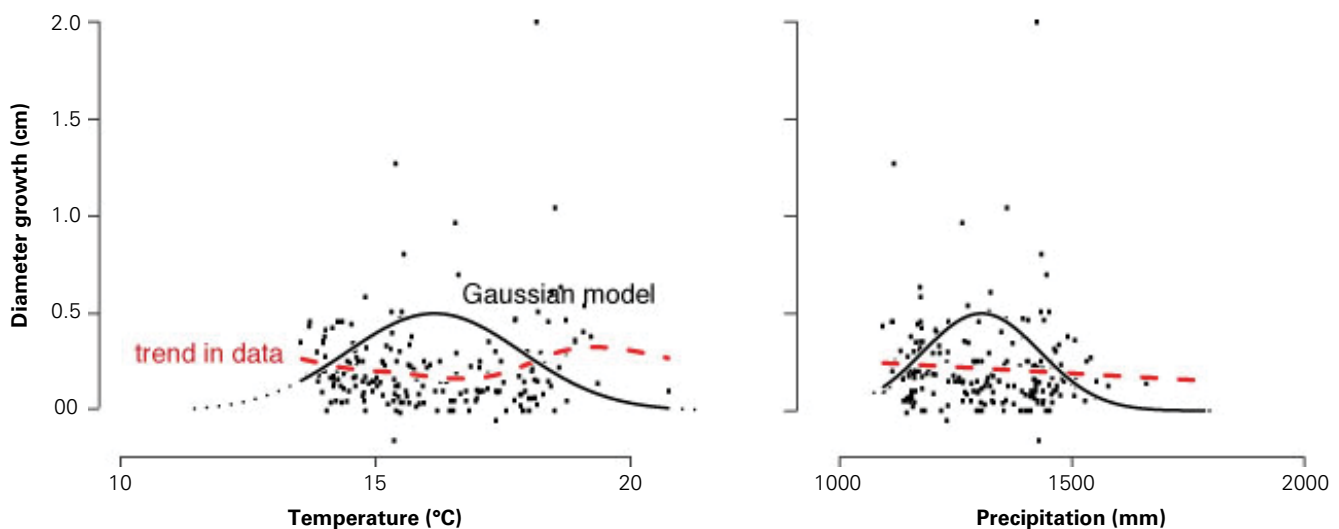

Figure 4.8—Models of distribution and abundance impose unrealistic relationships on Forest Inventory and Analysis data from the Eastern United States. The ubiquitous assumption that abundance and performance decline at range boundaries (e.g., a Gaussian model) contrasts with a spline smoothing (dashed 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 (*Querus 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 Hessl 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).
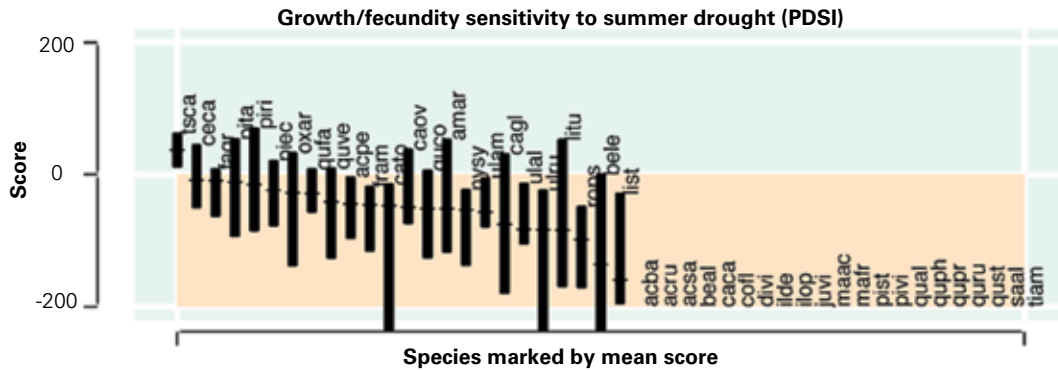
Figure 4.9—The joint distribution of growth and fecundity provides a sensitivity estimate to drought for southeastern tree species. High prediction scores on the vertical axis indicate high sensitivity (relative rather than absolute scores are meaningful). Species without bars at right are off the scale 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).
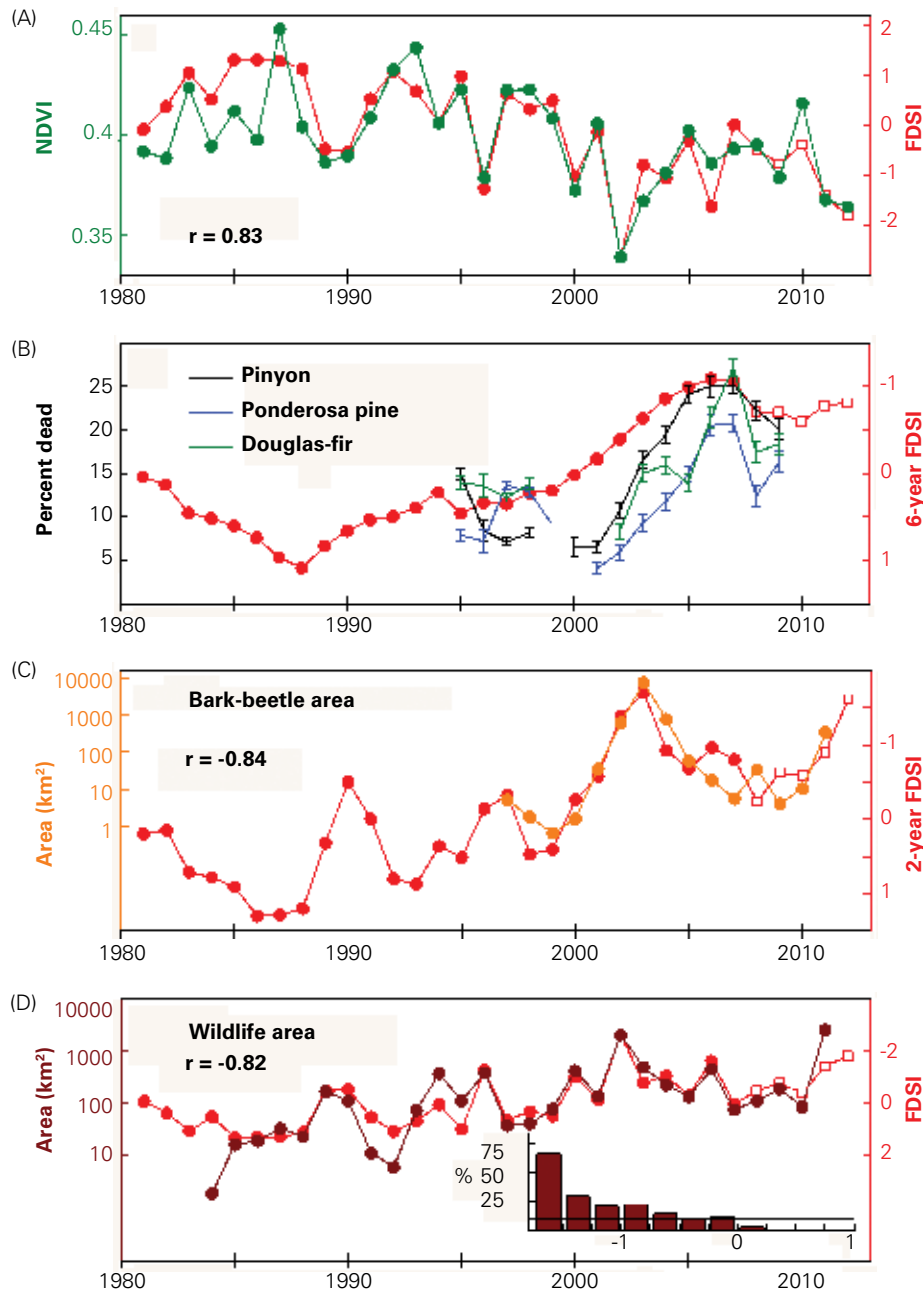
Figure 4.10—Forest productivity and mortality and the Forest Drought Severity Index (FDSI) (see text). (A) Annual average late-June to early-August Normalized Difference Vegetation Index (NDVI). (B) Percent standing dead trees from FIA plot data for the three most common southwestern conifer species. (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
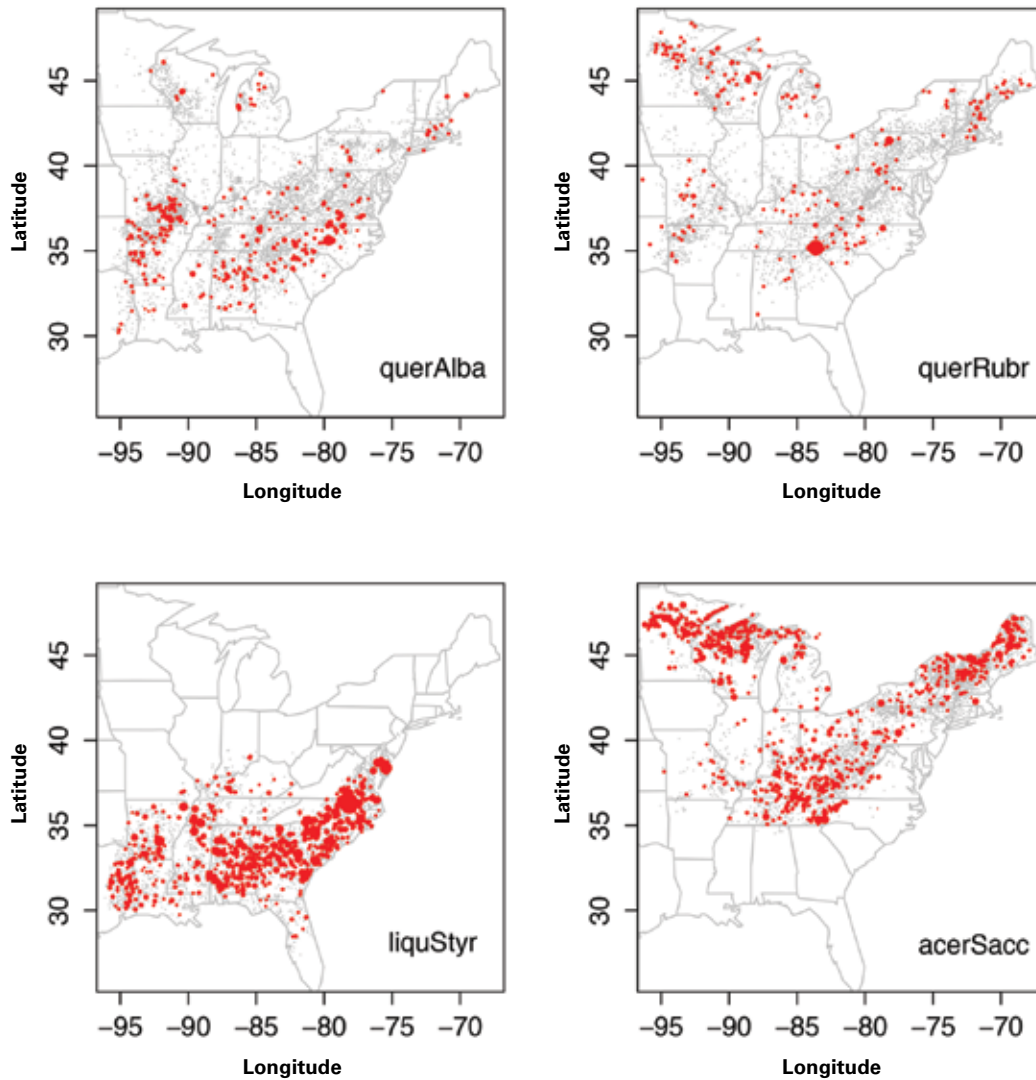
Figure 4.11—New recruits to FIA plots are relatively rare for oaks (upper panels) in comparison to other species having similar abundances in adult size classes (below). This comes at a time when moisture deficits are becoming more severe throughout the East (fig. 4.7) and despite the fact that many 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 CO_2-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 CO_2 (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).
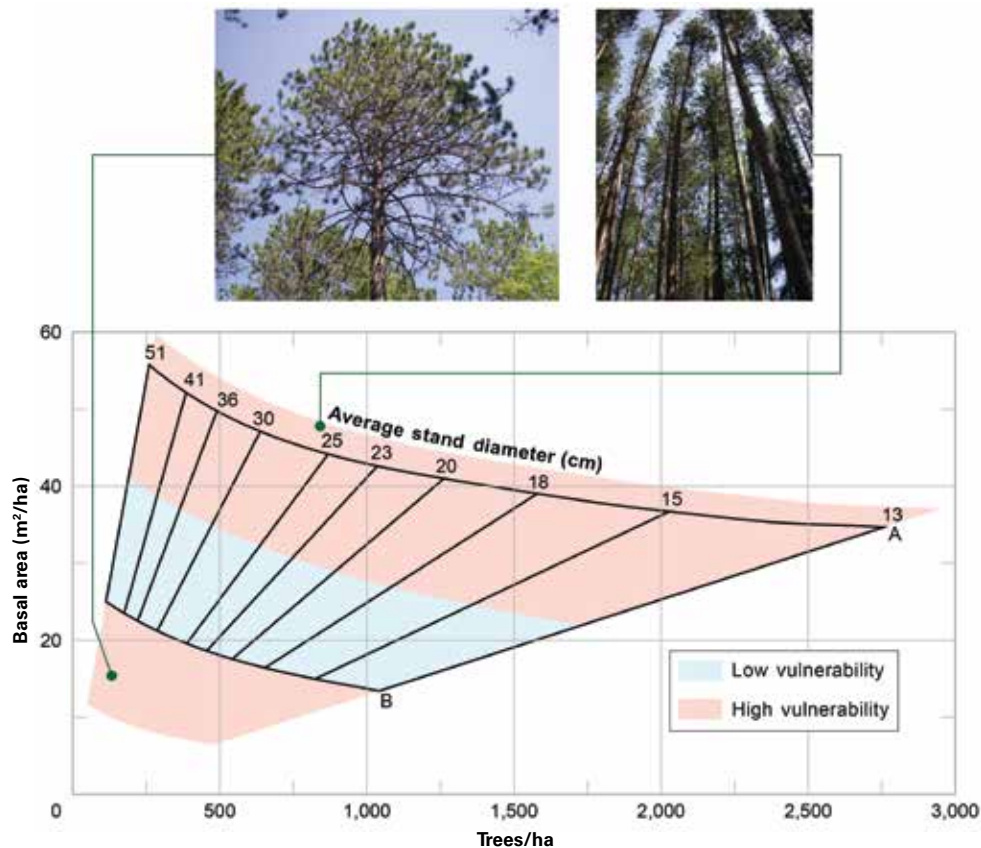

Figure 4.12—Hypothetical zones of drought susceptibility within a size/density management diagram for red pine. Trees may be susceptible to drought in two size/density situations: (1) at high density of large trees, with intense competition, and (2) at low density and high leaf-area to sapwood-area ratios,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

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