Chapter 3
Approaches to Modeling Landscape-Scale Drought-Induced Forest Mortality

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Contents

3.1 Introduction

Global changes, including climate change, are rapidly creating new environmental conditions and stressors for forests around the world. Climate change may have modest direct effects, at least initially, but indirect effects and interactions with disturbances can produce important changes in forest composition and landscape

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pattern (Dale et al. 2001; Gustafson et al. 2010), with consequences for ecological function and ecosystem services. Global Circulation Models generate varied predictions of future climate in any given part of the globe, and precipitation projections are usually much more uncertain than those for temperature (IPCC 2007). Nevertheless, almost all forested regions are expected to be subject to warming trends throughout the current century, with warming already pronounced at high latitudes (IPCC 2007). While precipitation projections are variable and less certain, in very few locations do confidence intervals indicate that precipitation will increase sufficiently to compensate higher evapotranspiration rates caused by increased temperature and, in some locations, precipitation may actually decrease (IPCC 2007). Consequently, drought stress of vegetation is expected to become more common in many parts of the world and this will have consequences for tree establishment, survival, and growth. Because species differ in their ability to tolerate moisture deficits, long-term consequences will be significant for forest composition and landscape pattern through the processes of competition, succession, and altered disturbance regimes. In this chapter, we review how drought affects forest ecosystems and the different ways these effects have been modeled (both spatially and aspatially). Building on those efforts, we describe several approaches to modeling drought effects in Landscape Disturbance and Succession Models (LDSMs), discuss advantages and shortcomings of each, and include two case studies for illustration.

Researchers and forest managers often use LDSMs to project the interacting effects of succession and disturbance at broad spatial and temporal scales and to compare the outcomes of alternative scenarios or management options. These models are unique in that they explicitly account for spatial relationships and processes, and provide answers about ecosystem dynamics and function at ecological time scales. They provide exceptional power to explore the efficacy of proposed management actions to mitigate the negative consequences of global change on biodiversity and ecosystem services. Not surprisingly, they are becoming widely used to project the impacts of multiple global changes and their interactions with natural and anthropogenic disturbances.

Although in some LDSMs variability in precipitation is used to affect fire regimes and tree growth rates, surprisingly few include this approach to simulate drought as a disturbance that kills trees. Gustafson and Sturtevant (2013) developed a drought disturbance extension for the LANDIS-II LDSM, and their results suggested that drought-induced mortality alone can indeed change forest composition and affect carbon storage. However, in most LDSMs direct interactions between drought and other disturbance and succession processes (establishment, growth, and competition) are not yet explicitly simulated, although exploratory modeling exercises and other research suggest that such effects should be accounted for in studies of global change effects on forest ecosystems. For example, because tree species thrive in different climate envelopes a persistent change in climate should result in altered establishment and competitive relationships (Allen et al. 2010). Additionally, drought-induced changes in vegetation composition can lead to changes in disturbance regimes (e.g., fire), which in turn are also directly modified by climate. The generally weak capability of LDSMs to include these types of drought effects and their interactions is a significant gap that reduces our ability to accurately project forest dynamics under future climate conditions.

3.2 Effects of Drought on Forest Landscapes

The physiological mechanisms behind drought-associated tree mortality are generally attributed either to direct water stress or to contributing factors that are exacerbated by drought, such as insects and pathogens (Mattson and Haack 1987; Manion 1991). McDowell et al. (2008) described three primary interacting mechanisms that can lead to tree mortality under drought conditions: hydraulic failure, carbon starvation, and biological agents. Hydraulic failure results when soil water decreases and evaporative demand increases, leading to cavitation (formation of air pockets) in xylem conduits that prevents movement of water to plant tissue. Carbon starvation occurs when plants use stomatal closure to avoid hydraulic failure, and respiration subsequently depletes carbohydrate reserves. Biological disturbance agents (e.g., insects, fungal pathogens) often respond positively to the physiological stress of drought-affected trees through population irruptions and enhanced rates of attack, leading to further stress and damage to trees, and higher rates of mortality (Mattson and Haack 1987). The relative contribution of each mechanism depends on species physiological traits, environmental conditions, and the duration and magnitude of water stress (McDowell 2011).

Drought can affect forest ecosystems at multiple spatial scales. At the individual tree level, vulnerability to drought varies with factors such as age, species, environmental setting, and interactions with other disturbance agents. Isohydric tree species are more likely to maintain xylem water potential during drought via stomatal closure, avoiding hydraulic failure but risking eventual carbon starvation, while anisohydric species better tolerate drought by maintaining continued gas exchange, but risk hydraulic failure (Adams et al. 2009). Tree age is also a factor, with older individuals often more vulnerable to drought-induced disturbance agents (Mueller et al. 2005; Ganey and Vojta 2011), and younger trees susceptible to direct mortality due to moisture stress (Ogle et al. 2000; Suarez et al. 2004). Environmental settings that affect climatic water deficits also play a role, including influence of soil texture and depth on hydraulic conductivity and water storage, and influence of topographic position on incident solar radiation and air temperature (Stephenson 1998). However, the precise physiological mechanism behind drought-related mortality or survival of trees is not always clear (Sala et al. 2010; McDowell 2011). For instance, knowledge of the differential role of non-structural carbon reserves required to maintain hydraulic conductivity during periods of stress is lacking for many species (Sala et al. 2012).

Drought-induced mortality events can substantially change forest composition within stands, across landscapes, and at regional-scales. For instance, in forests of the Great Lakes region, historic declines in beech (*Fagus grandifolia*) populations were likely caused by multi-decadal droughts during the Medieval Climate Anomaly (Booth et al. 2012). In northern Patagonia, massive drought-induced overstory and sapling mortality in southern beech (*Nothofagus* spp.*)* forests during 1998–1999 favored advanced regeneration of Chilean cedar (*Austrocedrus chilensis*) over coigüe (*Nothofagus dombeyi*), potentially leading to long-term shifts in forest composition (Suarez et al. 2004). Severe and persistent droughts over the last several hundred years in the southwestern United States contributed to intermittent dominance of junipers (*Juniperus* spp.) over less drought-tolerant piñon pines (*Pinus* spp.), while periods of above-average moisture, including during the early A.D. 1900s, contributed to increased piñon pine populations (Shinneman and Baker 2009). The severe drought of the A.D. late 1990s to mid-2000s in the US southwest, and associated wildfire activity and bark beetle outbreaks, have since caused massive piñon pine die-off events (Mueller et al. 2005; Breshears et al. 2005).

Drought also alters forest structure across broad scales, including the distributions and densities of forest patches, tree size and age classes, and live and dead biomass (Hogg et al. 2008; Anderegg et al. 2013). Drought-induced changes in forest composition and structure in turn influence forest function, including nutrient cycling and carbon, water, and energy fluxes (Dale et al. 2001; McDowell et al. 2008; Anderegg et al. 2013). In the short-term, drought-induced losses of leaf area decrease gross primary productivity in a forest stand and recent droughts have been shown to reduce terrestrial net primary production at a global scale (Zhao and Running 2010). Drought-associated mortality can also potentially result in bioregional forest carbon sinks becoming carbon sources (Ma et al. 2012). Drought is a key driver of the occurrence and magnitude of other natural disturbance events such as wildfire. Drought increases fire weather indices, decreases fuel moisture, and increases fuel loads (through mortality), and in many forest landscapes the area burned by wildfire is highly correlated with spatial and temporal patterns of dry versus wet periods (Westerling and Swetnam 2003; Girardin et al. 2006; Heyerdahl et al. 2008). Depending on ecosystem resilience, extreme drought and associated disturbance may alter succession and as result convert ecosystems from one type to another, especially under climate regime shifts (Burkett et al. 2005).

3.2.1 Drought Dynamics

Drought has long been a significant source of natural disturbance in forest ecosystems worldwide (Allen et al. 2010) and in many regions drought events of the last 150 years far exceed the severity and duration of earlier droughts. In North America, reconstructions of the Palmer Drought Severity Index (PDSI), derived from tree rings as proxies for climate variability, reveal that severe droughts of the twentieth century, such as the 1930s Dust Bowl drought, were relatively minor compared to several, multi-decadal "mega-droughts" that occurred over the past 1200 years, typically centered over western North America (Cook et al. 2004;

Stahle et al. 2007). These extreme climate events likely caused substantial mortality of some tree species and altered forest composition (Grissino-Mayer and Swetnam 2000).

The frequency, extent, duration, and intensity of drought are primarily driven by global-scale interactions (teleconnections) between anomalous sea surface temperatures (SSTs) and atmospheric conditions, further modified by land surface conditions. The SST anomalies in the eastern tropical Pacific Ocean drive the El Nino-Southern Oscillation (ENSO), of which the cool (La Niña) phase has been recognized as a primary driver of severe droughts in southwestern and southeastern North America (Cook et al. 2011). Other SST anomalies, such as the warm phase of the Atlantic Multi-decadal Oscillation (AMO) and the cool phase of the Pacific Decadal Oscillation (PDO), may enhance ENSO events and are also considered major contributors of drought and pluvial events throughout North America (McCabe et al. 2004). Although drought events are less frequent in mesic forest regions compared to more arid regions, oceanic–atmospheric fluctuations have been linked to severe droughts that have occurred in eastern temperate forests (Seager et al. 2009), forests of the Pacific Northwest (Nelson et al. 2011), boreal forests (Fauria and Johnson 2008), and other forest regions worldwide (e.g., Hendon et al. 2007).

Anthropogenic global climate change will likely substantially alter the intensity, frequency, location, spatial extent, timing, and duration of future droughts, as well as associated effects on forest ecosystems. Recent assessments indicate that overall aridity, as well as the area affected by droughts, has increased during the twentieth century, at regional to global scales (Dai 2011). Based on projections from global climate models (GCMs), researchers predict that in the twenty-first century droughts will intensify in some regions, including southwestern North America (Seager et al. 2007) and southern Europe (Beniston 2009). A key challenge to forecasting drought under climate change is to reliably transform projected changes in atmospheric conditions into dynamic physical processes that account for interactions with ecological processes. Generating robust predictions of future drought trends and effects will therefore not only require downscaling GCM-projected climate variables to generate indices of drought (e.g., PDSI) applicable across temporal and spatial scales (Wehner et al. 2011), but also developing more effective models of the dynamic role of tropical SSTs to shape future regional drought patterns and behavior (Dai 2010). Moreover, to project future effects of drought, researchers must consider how climate variability affects vegetation conditions (e.g., mortality, fuel moisture) that drive drought-induced disturbance events such as wildfire (Westerling and Swetnam 2003) or that induce feedbacks to temperature and precipitation (Wang et al. 2012; Anderegg et al. 2013).

3.3 Approaches to Modeling Drought

Models that simulate forest landscape ecosystem processes can provide a comprehensive understanding of the many complex relationships among climate, vegetation, and biogeochemical dynamics, including how forest diversity, productivity, and mortality respond to drought under different environmental settings. In this section, we provide a brief overview of drought applications within four broadly defined ecosystem model categories: forest gap models, ecosystem process models, LDSMs, and dynamic global vegetation models (DGVMs). This is not an exhaustive review of such models and their functionality, nor do we attempt to address all varieties, hybrids, or similar models. Detailed classifications and assessments of forest ecosystem models and their uses have been provided in numerous comprehensive reviews (e.g., Mladenoff and Baker 1999; Bugmann 2001; Keane et al. 2004; Scheller and Mladenoff 2007; He et al. 2008; Medlyn et al. 2011). Here we provide a brief overview of the functionality of basic forest ecosystem models that can be used to simulate the effects of drought and associated disturbances, and how such models simulate spatial interactions among these dynamics at broad scales.

3.3.1 Past and Developing Approaches

Early forest gap models, such as JABOWA, were developed to simulate the effects of physiological drivers on the rates of establishment, growth, and mortality among competing species of trees within a relatively homogenous forest stand or patch (Botkin et al. 1972; Shugart 1984). Early gap models were not spatially explicit, but some later gap models were developed to simulate spatial interactions among trees at fine scales (Pacala et al. 1993: SORTIE; Miller and Urban 2000: FM), and to specifically address the influence of environmental gradients (e.g., Bugmann et al. 1996: FORCLIM). Gap models typically require input parameters for mean precipitation rates, temperature, soil attributes, and species tolerance to drought stress to calculate the effect of soil moisture deficits on tree productivity (e.g., Pastor and Post 1986: LINKAGES). Despite this, most early gap models did not simulate realistic disturbance-induced tree mortality (Keane et al. 2001), prompting researchers to design alternatives that could be used to simulate the effects of specific disturbance types, including drought, on forest ecosystems across a range of environmental conditions (Prentice et al. 1993: FORSKA; Bugmann and Cramer 1998: FORCLIM). These advancements have further evolved into spatially explicit applications of gap-based models that simulate mortality events and project forest composition, structure, and productivity at landscape scales (e.g., Busing et al. 2007: FORCLIM), though such models still do not account for interactions among landscape-scale processes.

Ecosystem process models are similar to forest gap models in that they simulate the effects of biogeochemical processes (e.g., fluxes of energy and mass) on ecological dynamics (e.g., forest growth rate, carbon accumulation). Unlike gap models, ecosystem process models emphasize biogeochemical dynamics for potential vegetation types rather than individual trees or species (Cushman et al. 2007). Ecosystem process models generally incorporate water availability, plant water use, and evapotranspiration at forest sites to calculate water balance and determine water stress, permitting investigations of drought influence on forest ecosystem productivity (Aber and Federer 1992: PnET; Running and Gower 1991: Forest-BGC). However, only a few such models have specifically included the effects of drought-induced mortality (e.g., Grant et al. 2006: Ecosys). Ecosystem process models have been applied at broad scales, typically using land cover data sets from remotely sensed imagery, with each pixel representing a site. For instance, Aber et al. (1995: PnET-II) estimated the effects of water stress on ecosystem productivity in the northeastern U.S., and Turner et al. (2007: BIOME-BGC) examined the influence of wildfire and logging disturbance on carbon dynamics in Oregon. However, similar to forest gap models, spatially explicit interactions among landscape-scale processes are not generally simulated in such models (Scheller and Mladenoff 2007).

Here, LDSMs are distinguished from gap and ecosystem process models in that they are primarily intended to simulate forest disturbance and successional processes, as well as their interactions, across broad spatial and temporal scales (He et al. 2008). These models also generally provide spatially continuous projections of disturbance and vegetation dynamics (Cushman et al. 2007) that are valuable for determining key drivers of landscape-level forest composition or structure (e.g., Shinneman et al. 2010: LANDIS-II) or disturbance behavior (e.g., Keane et al. 2011: Fire-BGCv2). Within this framework, the diverse LDSM family of models can be further classified based on whether they can be used to simulate multiple processes or operate at fine temporal resolutions (He et al. 2008), and whether community change is static or dynamic, with the former determined by a priori successional stages and the latter by the life history attributes, behavior (e.g., seed dispersal), and physiological requirements of individual species (Scheller and Mladenoff 2007). Some LDSMs directly or indirectly incorporate the influence of biogeochemical process on forest productivity (Scheller and Mladenoff 2004: LANDIS-II; Keane et al. 2011: Fire-BGCv2), and can be coupled with gap or ecosystem process models to derive inputs representing climate effects on species establishment probabilities or productivity (e.g., Xu et al. 2009: LANDIS-II and PnET-II). Unlike DGVMs (discussed below), LDSMs do not incorporate feedback loops with GCMs and they cannot yet be applied at continental to global scales.

Dynamic global vegetation models are similar to terrestrial biogeochemical models, but additionally simulate competition among vegetation types (but not individual species) and are coupled to GCMs, allowing feedbacks to climate at regional to global scales (Medlyn et al. 2011). Thus, DGVMs can be used to simulate climate change effects on tree establishment and mortality via mechanistic plant responses to biogeochemical and hydrological dynamics (e.g., Sato et al. 2007: SEIB–DGVM). Moreover, DGVMs are useful for simulating interactions among disturbance, vegetation conditions, and climatological processes. For instance, Lenihan et al. (2008: MC1) simulated interactions between climate, vegetation, and wildfire to predict altered patterns of plant community and biomass distribution due to increased area burned under warmer and drier climate projected for California, USA. However, specific drought mortality mechanisms for different vegetation types or species have generally not been incorporated in DVGMs (Wang et al. 2012).

The focus of this chapter is LDSMs. Though direct simulation of drought dynamics using LDSMs is reported in remarkably few published studies, these models have tremendous potential for effectively projecting drought impacts on forest composition, structure, and function at landscape scales, in part by including spatially and temporally explicit interactions with other disturbance agents, such as wildfire (Cushman et al. 2007). For example, LDSMs that include individual species response to climate variability are also well-suited for projecting the effects of future climate change (including increasing aridity) on forest ecosystem composition and productivity (Scheller and Mladenoff 2007; Gustafson 2013). Moreover, drought effects in process-based LDSMs can be derived using either empirical or mechanistic approaches. An empirical approach assumes that historical relationships between measures of drought and tree mortality of the past can be used to predict drought effects in the future. A mechanistic approach directly links climate drivers to mechanistic tree responses; for instance, projecting tree growth and productivity under variable soil water conditions. Alternatively, drought events and their effects can be simulated using relatively stochastic or deterministic modeling approaches. Below, we present case studies to illustrate how these various general approaches to ecosystem modeling can be incorporated in LDSMs, often in combination, to simulate drought effects through development of new model extensions, coupling of complimentary models, and integration of empirically derived relationships.

3.3.2 Empirical Approach

The empirical approach involves estimating statistical models to predict drought-induced tree mortality as a function of a measure of drought using long-term tree inventory records, which are then applied within an LDSM to simulate mortality at each time step. A recent example of this approach used the extensive US Forest Service Forest Inventory and Analysis (FIA) database to estimate empirical models for the upper Midwest (Gustafson and Sturtevant 2013) and northeast United States (Gustafson 2014). The major difficulty of this approach is detecting the drought-induced mortality signal in a data set amidst the mortality caused by all other factors. Drought is seldom noted as the cause of death in inventory records, yet drought stress often increases the susceptibility of trees to death by other factors. The approach also requires observations from a variety of wet and dry periods to provide a useful range of values of the predictor (drought) variable, which means that a fairly long (>40 years) inventory record may be required. The large number of observations in the FIA data set allows the drought signal to be detected.

Gustafson and Sturtevant (2013) implemented this empirical approach as an extension to LANDIS-II (Scheller et al. 2007), which is a grid-cell forest LDSM that simulates the forest development processes of establishment, growth, and competition, and the forest degenerative processes of senescence and disturbances such as wildfire, wind, insect outbreaks, and timber harvesting at large spatial

(>100,000 ha) and long temporal (centuries) scales. In the model, living and dead biomass (rather than stem density) are tracked within cohorts of species on each cell, and several parameters are included that represent aboveground productivity and mortality. LANDIS-II is a primarily process-based model that encapsulates distinct ecological or physical processes as independent extensions that act on the biomass of cohorts within cells on the landscape. The independent operation of each extension on the extant biomass of each species cohort on each landscape cell produces forest dynamics that are an emergent property of the interacting extensions. The drought extension as implemented by Gustafson and Sturtevant (2013) modeled drought using empirical relationships, while the other extensions (e.g., succession, timber harvest) used a process-based approach.

To estimate empirical drought models for the upper Midwest U.S., Gustafson and Sturtevant (2013) constructed a data set containing records of percent biomass lost to mortality (*pm*) by species on each FIA plot in each inventory and a measure of drought stress (PDSI) during each inventory period obtained from the National Climate Data Center (URL: http://www1.ncdc.noaa.gov/pub/data/cirs/). The FIA inventory records covered the period 1965 to 2010 (varied by state), with inventories at approximately 13 year intervals. Mixed linear models were estimated for four categories of species drought sensitivity and tested against a 30 % random sample of observations that were not used in developing the estimates. They found that, in the U.S. Midwest, drought length was a better predictor of mortality than drought severity.

A LANDIS-II drought extension was constructed to use the empirical models to simulate drought-induced biomass loss to mortality. At each time step, a measure of drought is drawn from a user-specified distribution and the regression coefficients are used to calculate the 95 % confidence interval (CI) of *pm*. For each cell on the landscape, and for each species in the cell, a value of *pm* is selected from the CI such that older cohorts will have a *pm* value found in the upper part of the CI and younger cohorts in the lower portions, consistent with other empirical observations (Allen et al. 2010; Ganey and Vojta 2011). Biomass is removed from species cohorts (beginning with oldest cohort) until the selected *pm* value has been reached. To simulate loss of seedlings to drought stress, the probability of establishment (P_{est}) for the species is modified (for the current time step only) to 0.0 if its seedlings are relatively sensitive to drought, and by half if seedlings are moderately sensitive to drought (Hanson and Weltzin 2000). For species relatively insensitive to drought P_{est} is unchanged. After simulating drought, normal establishment processes of sprouting and seed dispersal/germination are simulated using the succession extension. Additional details of the empirical models and the extension can be found in Gustafson and Sturtevant (2013).

3.3.2.1 Case Study 1—Oconto County, Wisconsin

To provide a heuristic example of studying the effect of drought on forest composition, we used the LANDIS-II drought extension of Gustafson and Sturtevant

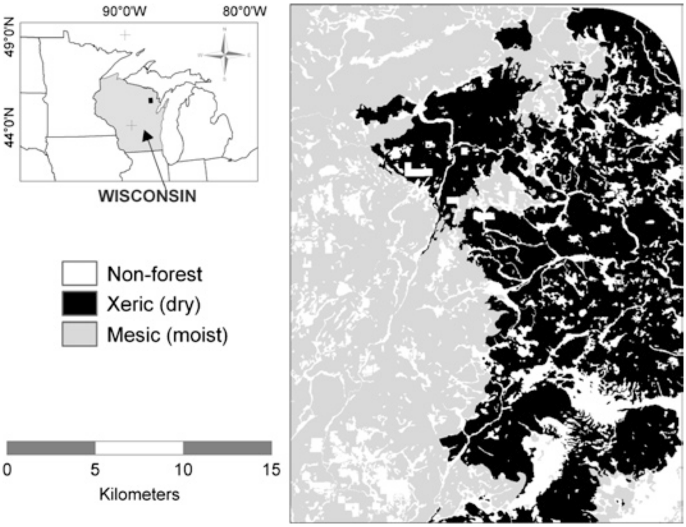

Fig. 3.1 Map of simulation study area in Oconto County, Wisconsin (USA)

(2013) to explore the effect of increasing drought length. We simulated three scenarios of mean drought length (years): no droughts, the current drought regime as simulated by Gustafson and Sturtevant (2013) (lognormal distribution of drought length with $\mu = 0.3$, $\sigma = 0.7$), and a drought regime with markedly longer droughts ($\mu = 1.2$, $\sigma = 0.7$). We conducted simulations on a 65,733 ha landscape on the Chequamegon-Nicolet National Forest in northeastern Wisconsin, USA (Fig. 3.1). We used the initial conditions map and LANDIS-II parameters described by Gustafson and Sturtevant (2013) that reflect current forest conditions and tree species vital attributes on each of the landforms. Because shade-intolerant species disappear without disturbance we also simulated each drought scenario with stand-replacing harvests on 5 % of the landscape per decade, with aspen (*Populus* spp.) and birch (*Betula* spp.) cut on an 80 year rotation and all other species on a 320 year rotation. We used version 6.0 (Scheller et al. 2007) of LANDIS-II with the Biomass Succession v3 (Scheller and Mladenoff 2004) and Biomass Harvest (Gustafson et al. 2000) extensions. Simulations were run for 300 years with three replicates and all extensions used a 10-year timestep. We evaluated the effect of increased drought on the amount of biomass killed by drought and on living biomass, by drought-susceptibility class (Table 3.1).

We found that, regardless of drought scenario, without harvesting the drought-susceptible pioneer species disappeared from the landscape by year 150 (Fig. 3.2a). As droughts lengthened, the total living biomass on the landscape declined modestly, and the relative abundance of somewhat drought-intolerant species decreased while that of the drought-tolerant class increased modestly

Table 3.1 Species assignments to the four drought sensitivity classes (reproduced from Gustafson and Sturtevant 2013)

Drought sensitivity class	Common name	Scientific name
Intolerant	Quaking aspen, big-toothed aspen, paper birch, black ash	*Populus tremuloides*, *P. grandidentata*, *Betula papyrifera*, *Fraxinus nigra*
Somewhat intolerant	Eastern hemlock, White spruce, Northern white cedar, yellow birch, balsam fir	*Tsuga canadensis*, *Picea glauca*, *Thuja occidentalis*, *Betula alleghaniensis*, *Abies balsamea*
Somewhat tolerant	Red maple, sugar maple, black cherry, white ash, basswood, American larch, black spruce	*Acer rubrum*, *A. saccharum*, *Prunus serotinus*, *Fraxinus americana*, *Tilia americana*, *Larix laricina*, *Picea mariana*
Tolerant	Red pine, white pine, jack pine, red oak, white oak	*Pinus rubra, P. strobus, P. banksiana, Quercus rubra, Q. alba*

(Fig. 3.2a). The amount of biomass lost to drought remained at equilibrium under the current drought regime, although the proportion lost by more drought-tolerant classes increased as the drought-intolerant class disappeared (Fig. 3.2b). Under the longer drought regime the total biomass lost to drought was higher than that under the current regime but also decreased over time as the drought-susceptible class disappeared.

When harvests were included, the drought-intolerant class actually increased through time (Fig. 3.3a) because that class is composed primarily of shade-intolerant species that require disturbance to persist (Table 3.1). As the length of droughts increased, the total living biomass decreased, with the somewhat drought-intolerant class losing relatively more biomass through time. The drought-intolerant class seemed to flourish under long droughts because with the addition of harvesting disturbance tolerant, single species stands were retained, resulting in vigorous regeneration and high rates of growth even after drought disturbance. This contrasts with observations in Alberta, Canada, where mature aspen dieback was related to drought severity and interactions with logging were not considered (Hogg et al. 2008). The amount of biomass lost to drought was higher when harvests occurred, with extremely high losses under the long drought scenario (note y-axis scaling in Fig. 3.3b). These losses were almost entirely from the drought-intolerant class, which became very abundant on the landscape because of harvesting and was especially susceptible to long droughts. It is interesting to note that this class maintained its presence on the landscape under both drought scenarios, and continued to increase in relative abundance through year 300. This example is quite simple, but it nonetheless provides insight into interactions between drought and harvest in the context of empirical studies (e.g., D'Amato et al. 2013).

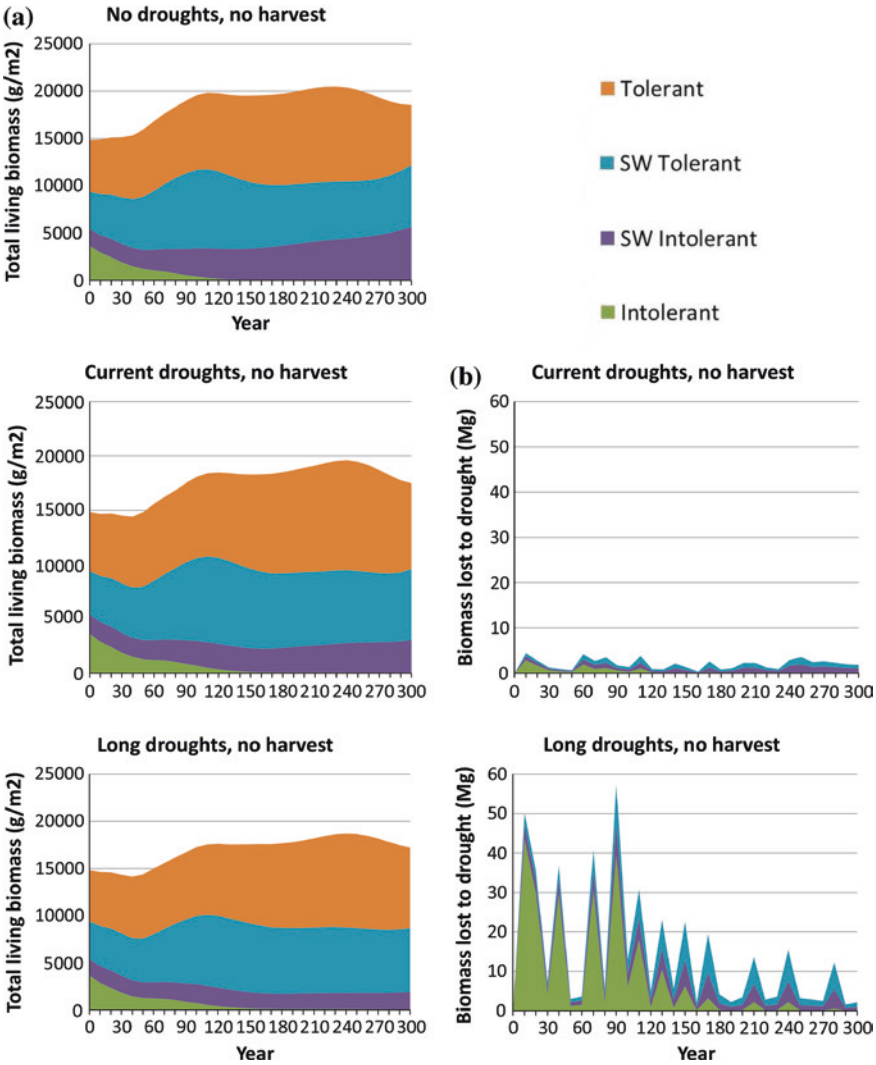

Fig. 3.2 Living (**a**) and killed (**b**) biomass by drought susceptibility class (Table 3.1) in simulated drought scenarios without timber harvesting for Oconto County, Wisconsin (USA)

3.3.2.2 Critique of the Empirical Approach

The empirical approach has two major advantages. First, empirical relationships are conceptually simple and are therefore relatively easy to build and test given an adequate data set. Second, relative to a mechanistic approach few parameters are needed to simulate drought mortality, reducing both the effort needed to estimate parameters and the cumulative error associated with additional parameters. Furthermore, the algorithms are simple, resulting in faster computation.

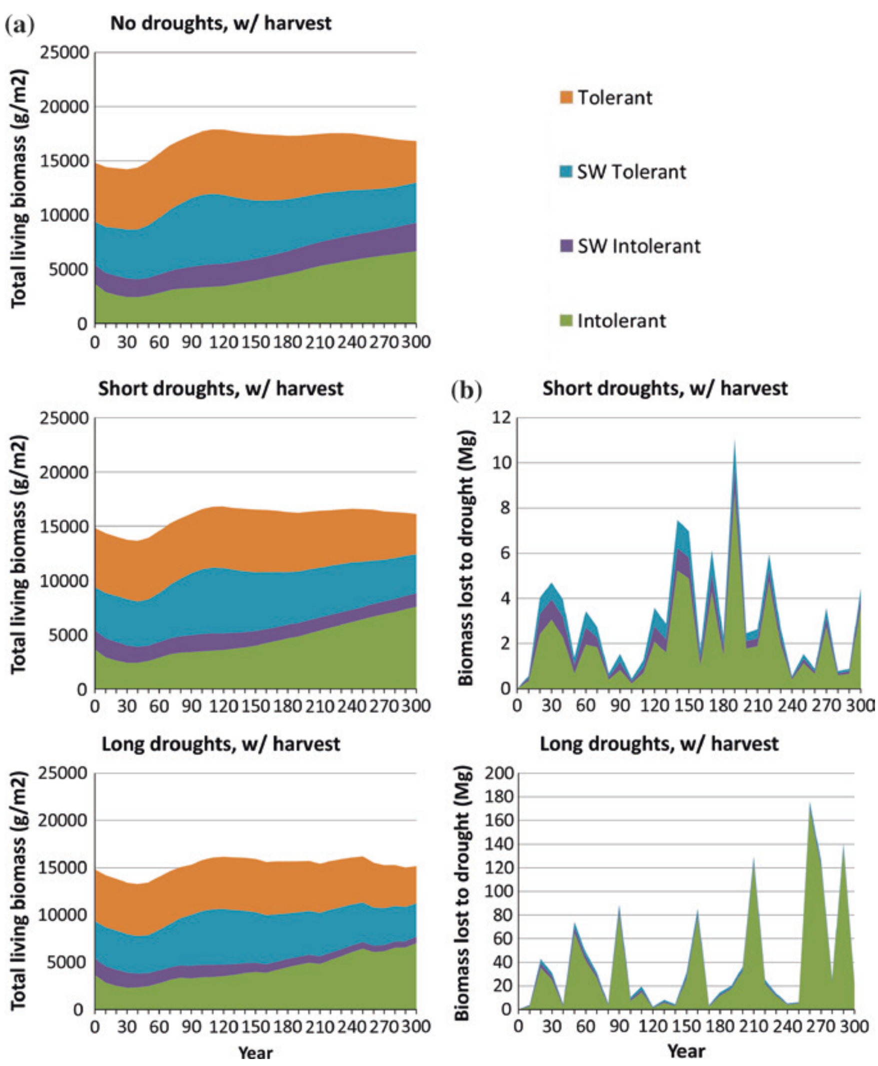

Fig. 3.3 Living (**a**) and killed (**b**) biomass by drought susceptibility class (Table 3.1) in simulated drought scenarios with timber harvesting for Oconto County, Wisconsin (USA). Note y-axis scaling differences in the right-hand plots

On the other hand, the empirical approach has several shortcomings. The most important is the increasing evidence that the known (past) relationships between drought and mortality are very unlikely to be valid into the future. If only the distribution of measures of drought varied under climate change, then the empirical approach might remain valid. But the increased evapotranspirative demand caused by concomitant higher temperatures indicates that moisture stress will increase in a way that is not linearly related to precipitation (Dale et al. 2001). And even when a drought index is used that better accounts for both temperature and precipitation (e.g., the moisture index of Thornthwaite (1948) that calculates moisture stress as a function of potential evapotranspiration and precipitation), the potential shuffling of community assemblies will likely change competitive dynamics. We expect that species will not shift their ranges in unison and therefore communities will re-assemble (Iverson et al. 2008). This change in competitive interactions coupled with increasing drought stress may alter species susceptibility to mortality.

There are also other disadvantages: (1) Because the estimation of empirical models usually requires records that span long time periods, few suitable data sets are available for estimating the statistical models. Even the long-term FIA database may not always be adequate for building empirical models (e.g., Gustafson 2014). (2) Relationships between measures of drought and tree mortality may be only weakly significant, likely because of statistical noise (Gustafson and Sturtevant 2013). This results in uncertainty that may be unacceptably high, especially when coupled with the uncertainty inherent in other components of the LDSM (Xu et al. 2009). (3) The general applicability of empirical models has yet to be established. Gustafson (2014) attempted to use empirical models constructed in the U.S. Midwest in the U.S. northeast. However, it was difficult to verify that their validity, because droughts were rare in that region during the period for which records were available. Moreover, empirical models for northeast species not found in the Midwest did not exist. (4) Moisture stress reduces growth rates and can ultimately lead to mortality by several associated causes (Bréda et al. 2006), but growth rates and mortality are not coupled in the empirical approach. Thus, the LDSM will simulate normal growth during a drought, even though some portion of cohort biomass is lost to mortality. In reality, the effects of drought on growth varies among species (Bréda et al. 2006), which may affect competition and ultimately successional outcomes, apart from the mortality effects of drought.

3.3.3 Deterministic Approach

Ideally, projections of future drought frequency, severity, and extent should incorporate the influence of enhanced evaporative demand under climate change using GCM-derived projections and temperature-sensitive drought indices (Dai 2010; Wehner et al. 2011). However, such climate variables are not typically incorporated directly into process-based LDSMs, and thus drought projections may need to be deterministically integrated, such that simulations of future drought effects on forest ecosystems can include temporally and spatially synchronized interactions with climate change effects on species establishment and productivity, as well as other disturbance events (e.g., wildfire).

3.3.3.1 Case Study 2—Voyageurs National Park

To illustrate, we projected future drought occurrences using GCM outputs for the period 2000–2099 and simulated potential drought effects on a 157,000 ha southern boreal forest landscape (52 % forested, 48 % lakes/wetlands) in Voyageurs National Park (VNP) and vicinity in northern Minnesota, USA (Fig. 3.4). We used an established model to generate a self-calibrating drought index (SC-PDSI) compatible with climatological regions (Wells et al. 2004), that requires inputs for monthly average temperature, monthly total precipitation, normal mean temperature and precipitation, latitude, and available soil water holding capacity (AWHC). We derived future monthly climate values from the Canadian Centre for Climate Modelling and Analysis (CCCma) Coupled Global Climate Model (www.cccsn.ec.gc.ca) under the SRES-A2 emissions scenario (IPCC 2007), used 1961–1990 climate means as normals, and derived AWHC values from the State Soil Geographic (STATSGO2) database (http://websoilsurvey.nrcs.usda.gov/). Compared to the normal period, the A2 climate scenario predicts a nearly 6°C increase in mean annual temperature and a ≈90 mm increase in annual precipitation (and with greater variability) by the end of the twenty-first century.

Species establishment, growth, and mortality were simulated using LANDIS-II with the biomass succession, base fire, and wind disturbance extensions (Scheller et al. 2007; and as described in the case study in Sect. 3.3.2.1). Species life history traits and disturbance parameterization largely followed Shinneman et al. (2010). Species probability of establishment (P_{est}) and maximum aboveground net primary productivity (ANPP) inputs for the biomass succession extension (Scheller and Mladenoff 2004) were calculated under contemporary and future climate scenarios using PnET for LANDIS (Xu et al. 2009). The PnET extension for LANDIS uses equations from the PnET-II (Aber et al. 1995) ecosystem process model to generate estimates of maximum ANPP, and equations from the LINKAGES (Pastor and Post 1986) forest gap model to estimate species establishment probabilities, under different climate conditions. Input values for species ecophysiological parameters were obtained from relevant sources (e.g., Reich et al. 1999; Peters et al. 2013), and key site and climate parameters (and sources) are nearly identical to those for the drought model described above. Thus, P_{est} and maximum ANPP values for each tree species in the VNP landscape were estimated annually using climate parameters that temporally and spatially correspond to those used for annual drought projections. Inputs were calculated for three primary ecoregion types (two upland types, one wet forest type), delineated using soil (STATSGO2) and recent forest classification maps (http://www1.usgs.gov/vip/voya/voya.zip).

Drought effects were simulated in LANDIS-II using a recently developed empirical stress-mortality extension that simulates the effects of stress events on tree mortality and biomass at predetermined time steps (Shinneman et al. in prep). Specifically, future drought events were simulated via the extension for each year in which projected growing-season (March–August) cumulative PDSI values sum to −12 or lower (capturing moderate to extreme droughts). Each occurrence of a

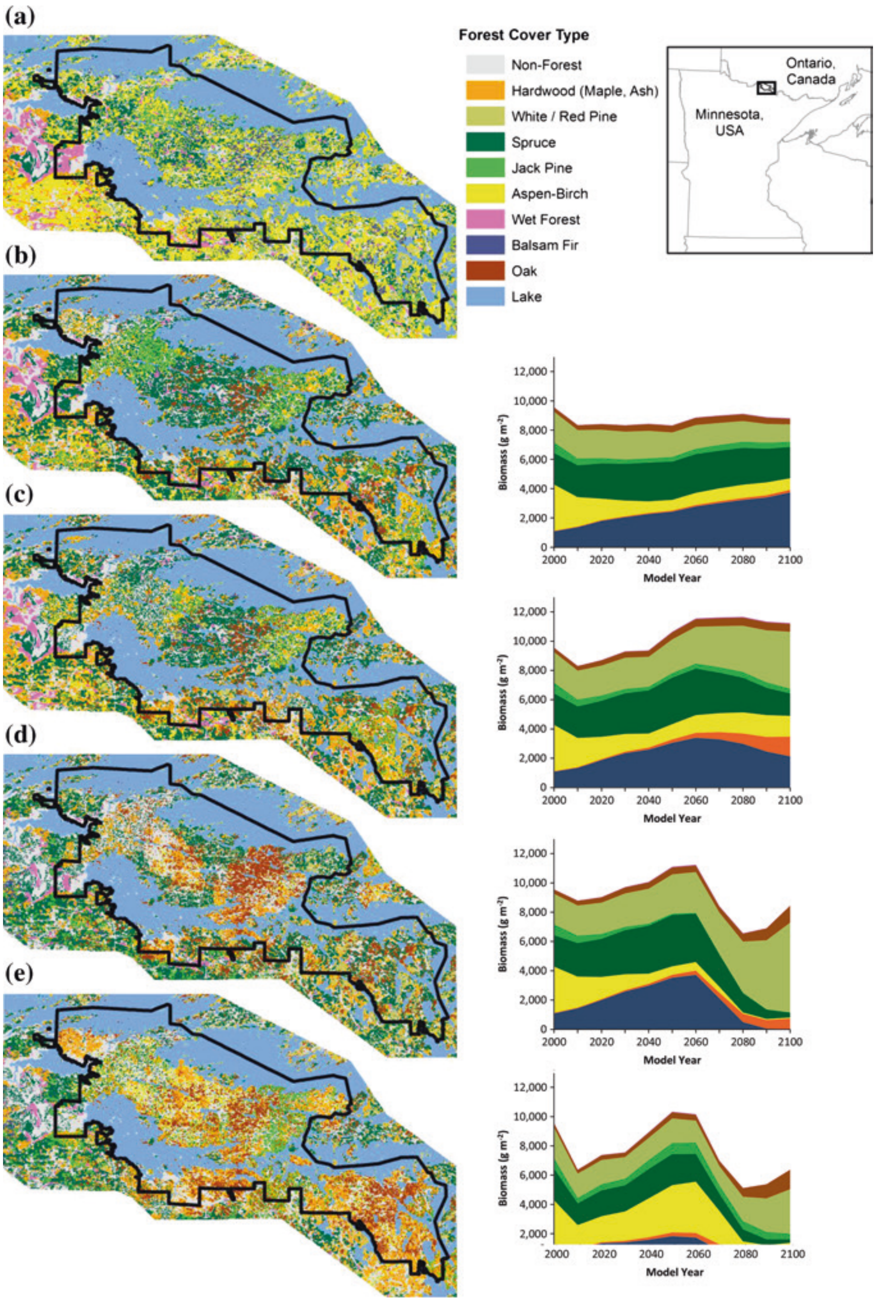

Fig. 3.4 Forest composition and aboveground biomass over time for Voyageurs National Park and vicinity, relative to the contemporary (i.e., recently mapped and classified, not modeled) landscape (**a**) and four modeled future scenarios: contemporary climate, contemporary fire regime, and no drought (**b**); future climate, contemporary fire regime, and no drought (**c**); future climate, contemporary fire regime, and climate change-induced drought (**d**); and future climate, future fire regime, and climate change-induced drought (**e**)

drought event triggered predetermined amounts of biomass reduction from mortality for selected species-age cohorts, ranging from 5 to 33 % for older cohorts across the drought-intolerant to tolerant species groups (refer to Table 3.1), respectively, and with generally lower mortality rates for younger cohorts (Gustafson and Sturtevant 2013). Although drought mortality rates associated with each species were not available for the study area, a simulated maximum rate of 33 % for oldest cohorts of drought-sensitive species is comparable to extensive drought-induced mortality documented for similar forests nearby (e.g., Jones et al. 1993; Michaelian et al. 2011). Finally, if consecutive drought years resulted in >90 % biomass reduction for any species-age cohort, complete cohort mortality was triggered.

Here we present model output for the VNP landscape, as a prototype for a regional model currently in development (Shinneman et al. in prep.) that demonstrates potential interactions among drought mortality, wildfire, and climate change effects on species establishment, growth, and productivity. Spatial resolution for forest conditions was 1 ha, and temporal resolution varied depending on the process simulated, but drought inputs were at annual resolution, while most output was reported for 10-year time steps. We present results at the end of a 100-year period (2000–2100) under four successively altered scenarios: (1) contemporary climate, contemporary fire regime, and no drought, (2) future climate, contemporary fire regime, and no drought; (3) future climate, contemporary fire regime, and climate change-induced drought; and (4) future climate, future fire regime, and climate change-induced drought. Thus, in all scenarios, forest composition and biomass were affected by both fire and climate-driven species establishment probabilities, and two scenarios additionally simulated mortality from drought. All scenarios also included modest amounts of wind disturbance (Shinneman et al. 2010). Contemporary fire regimes for VNP were simulated to achieve an approximately 400 year mean fire rotation, based on recent fire records for the region, while future fire rotation was reduced to about 200 years, based on fire rotations projected under climate change (Flannigan et al. 2005). Biomass output results are limited here to the dominant upland forest ecoregion type in VNP, which is characterized by generally shallow, nutrient-poor, coarse-textured soils with low water holding capacity. Projected SC-PDSI values derived from the CGCM-A2 climate scenario indicate that moderate to severe drought will be common across the three land types in the latter half of the twenty-first century, occurring in 35 to 65 % of the growing seasons between 2060 and 2099, with the upland forest ecoregion type most vulnerable.

Results show that under the current climate scenario, with a contemporary fire regime and no drought mortality (Scenario 1), regional forest composition transitioned from primarily aspen-dominated (due to past timber harvest and wildfire) in the contemporary landscape (Fig. 3.4a) to large expanses of late-successional boreal conifers, especially shade-tolerant, fire-sensitive balsam fir (*Abies balsamea*) (Fig. 3.4b). Similar projections have been made for the region using other models (Shinneman et al. 2010). Accordingly, biomass of shade-tolerant and fire-intolerant species increased over time, while biomass decreased for most early successional and fire-dependent species, especially white pine (*Pinus strobus*)/red pine (*Pinus resinosa*), and aspen (Fig. 3.4b). With warmer temperatures and no drought (Scenario 2), the shift in composition toward boreal conifers was less pronounced, as spruce (*Picea* spp.)-fir biomass declined substantially after 2060 under less favorable climate, while white pine and hardwood species biomass increased (Fig. 3.4c), similar to other LDSM projections for the region (Ravenscroft et al. 2010). However, when drought effects were simulated under climate change (Scenario 3), oak (*Quercus* spp.) and white pine biomass and cover increased more substantially, while boreal species biomass declined more precipitously after 2060 (Fig. 3.4d). Under drought, climate change and more frequent wildfire (Scenario 4), forest composition was similar to Scenario 3, but with more even proportions of forest cover types at the landscape scale, and a substantial decline in mean forest biomass (75 % of the mean forest biomass of Scenario 3 at year 2100; 57 % of that in Scenario 2).

Thus, scenarios in which the effects of warmer temperatures and associated drought were simulated shifted the landscape away from dominance by boreal forest species—spruce, jack pine (*Pinus banksiana*), and aspen—which declined from about 78 % of the forest landscape area at model year 2000 to less than 50 % at model year 2100, and from 75 % of mean upland forest biomass at year 2000 to only about 5 % in 2100. In contrast, temperate forest species increased under these scenarios, with more oak, white pine, maple (*Acer* spp.), and ash (*Fraxinus* spp.). When fire frequency increased under warmer, drought-filled climate conditions, the forest landscape shifted further toward temperate species and overall upland forest biomass declined substantially, suggesting a shift toward open forest structures dominated by early successional, drought-tolerant, and fire-tolerant (or resprouting) species, and representing the effects of recently burned forest (about 10 % of the initial forest area). Boreal spruce-fir cover types mostly remained dominant in ecoregions with higher soil water content (e.g., wetland-forest and clay soil ecoregions, Fig. 3.4a-e maps; biomass output not shown). Warmer temperatures without drought (Scenario 2) did not have these dramatic effects, as more of the upland forest area and biomass was represented by boreal species, although the area covered by these species still diminished steadily after 2060.

3.3.3.2 Critique of the Deterministic Approach

The primary advantage of incorporating a relatively deterministic approach within an otherwise stochastic LDSM is that climate effects on species establishment/growth and drought-induced mortality are more directly linked in time and space. Although the fire events simulated in the above example were not directly linked to climate-induced drought events, advanced fire and fuel extensions have been developed that do allow climate to directly influence fuel conditions and fire occurrence (Sturtevant et al. 2009). However, a more seamless approach would be to develop the ability to directly integrate user-provided climate inputs among all relevant processes and their extensions in LANDIS-II (and similar LDSMs), further unifying the influence of climate on ecological processes and disturbance interactions across time and space. Indeed, if such climate-input functionality used a random weather generator approach (e.g., LARS-WG), stochasticity inherent in many LDSMs (providing estimates of variation in future forest conditions) would be preserved. A climate library extension for LANDIS-II that will provide much of this capability is nearing completion (Robert Scheller, pers. comm.)

A potential disadvantage to modeling drought using a deterministic approach is that predetermined drought events of a minimum intensity trigger a uniform rate of mortality for each species-age cohort. Moreover, the data and empirically derived relationships needed to parameterize drought-induced mortality for species-age cohorts in many forest ecosystems are likely to be insufficient, primarily due to a lack of long-term, tree mortality data that can be directly attributable to the effects of drought (Gustafson and Sturtevant 2013), but also due to uncertainty about changing ecosystem responses under future climate conditions. Thus, further development of the stress-mortality extension used in the above example might include the ability to represent a continuum of drought intensity, with mortality rates determined by integration with mechanistic, process-based models (discussed below).

Finally, when projecting future drought under climate change, careful consideration should be given to selecting appropriate drought indices, GCMs, and downscaling methods. Precipitation projections in particular can vary substantially among GCMs and may be more difficult to effectively downscale from global to landscape scales (IPCC 2007). Although use of a multi-model ensemble approach could reduce the uncertainty among models, ensemble climate models may also unrealistically reduce the variability of drought intensity predicted by the more reliable individual GCMs (Wehner et al. 2011).

3.3.4 Process-Based (Mechanistic) Approach

In many cases using a direct, mechanistic approach to model drought effects on forests may be advantageous as it allows explicit simulation of the physiological processes that induce drought stress and lead to altered rates of cohort establishment, growth, and mortality in response to changes in water and light availability. Although LDSMs can be externally coupled with ecosystem process models (e.g., to define species growth and establishment input parameters, as in our case studies), such an approach limits the direct response of key processes to drought stress. Incorporating changing water and light availability directly into an LDSM not only permits ready simulations of drought-enhanced rates of biomass loss and mortality among species as a stochastic and spatially explicit process, but the effects of specific drought events can be incorporated into the model, affecting future competitive interactions and disturbance events, including the effect of future drought.

Such a mechanistic approach may become feasible with the development of a new LANDIS-II succession extension that includes moisture and light as limited resources to simulate competition among tree cohorts. The new extension (PnET-Succession) incorporates elements of the PnET-II biogeochemical model (Aber et al. 1995; Ollinger et al. 1998) into an extension based on the Biomass Succession extension (Scheller and Mladenoff 2004) to calculate growth as a function of limited light and soil water resources. This new capability allows growth rates to vary at each time step in response to competition for light, and more importantly for this discussion, for water.

A full description of the PnET-Succession extension is well beyond the scope of this chapter, but can be found in De Bruijn et al. (2014). However, a few key elements will illuminate how the extension can facilitate the simulation of drought mortality as a process. First, species cohort growth rates are calculated as a function of photosynthesis, which depends fundamentally on soil water availability, defined as the ratio of transpiration and potential transpiration. Soil water is tracked at the grid-cell level using a bulk hydrology model based on precipitation, air temperature, and consumption by species cohorts. Cohorts compete for water and light in each cell, and cohort biomass determines the priority of access to radiation and soil moisture, with the largest cohorts having first access to both resources. When water is adequate, the rate of photosynthesis (leaf area index) for a given species cohort increases with light that is available to the cohort (dependent on canopy position and leaf area), atmospheric carbon dioxide (CO_2) concentration and foliar nitrogen (N), and decreases with age and departure from optimal temperature. As soil water availability decreases, photosynthesis also decreases. The PnET-Succession extension accounts for reductions in photosynthesis by respiration such that foliar respiration rate depends on temperature and moisture, while maintenance respiration depends only on temperature.

Thus, in the PnET-Succession extension, photosynthetic rates (and therefore growth rates) vary by species and cohorts monthly as a function of precipitation and temperature (among other factors), which directly affects competition and ultimately successional outcomes. Capitalizing on this approach of simulating growth via the process of photosynthesis, drought-induced mortality would result when carbon reserves are depleted by respiration. Such mortality may further depend on the length of time that water limitations occur, based on the drought-tolerance of species. For studies of the effects of climate change on forest successional dynamics, a “weather stream” of temperature, precipitation, and radiation from downscaled global circulation models would allow growth and establishment rates to vary at each time step in response to temperature and precipitation, and drought-induced mortality would be simulated when moisture stress depresses growth rates below respiration levels for a prolonged period. An initial test of the ability of PnET-Succession to simulate drought effects compared empirical physiological measurements from a precipitation manipulation experiment in a piñon-juniper ecosystem (Pangle et al. 2012) with values predicted by PnET-Succession. For the purposes of landscape modeling of forest growth and succession over long time periods, net photosynthesis is the key output of the model, and it responded similar to the empirical measures under both precipitation diversion and irrigation treatments (Gustafson et al. 2015). Modeled carbon reserves also varied consistently with empirical measures under drought and wet conditions, and modeled carbon reserves for experimental plots were well correlated with observed mortality rates. These results suggest that this simple physiological approach holds promise to mechanistically simulate drought effects under climate change at broad temporal and spatial scales. Additional testing is ongoing.

3.3.4.1 Critique of the Mechanistic Approach

The primary advantage of the mechanistic approach is that it is built on first principles. The physiology of tree water use in response to availability is well studied and relationships between water availability and growth rates are well established. Mortality becomes deterministic as a consequence of physiological moisture stress and carbon balance, rather than the outcome of a probability density function. The sophistication of the modeling of those processes can be small or great, depending on the research or management question. De Bruijn et al. (2014) added elements of the PnET-II model into LANDIS-II, but other physiology models could be used instead. Additionally, mechanistic approaches to simulate direct drought-induced mortality are almost certainly more robust under climate change scenarios than empirical approaches (Keane et al. 2001), but indirect mortality (e.g., by insects) may also need to be explicitly simulated. Robustness under novel conditions is one of the key criteria for assessing the utility of models to forecast forest dynamics as a consequence of global changes (Gustafson 2013). Another advantage is that the mechanistic approach is general and can be applied in any system for which the physiological relationships of water stress and photosynthesis are known. Finally, a mechanistic, process-based approach overcomes the decoupling of moisture stress and growth rates that is inherent in the empirical approach.

One important disadvantage is that process-based models are more complex, requiring more parameters that increase uncertainty and potentially requiring more time for computation. Validation of performance under future conditions that do not yet exist (e.g., increased atmospheric CO_2 concentrations) also remains a challenge. Model users must rely on validation of the process model under the range of historical conditions or from experimental studies, and assume that the physiological processes of growth and death will not fundamentally change in the future.

3.4 Future Prospects

Modeling drought effects in LDSMs is still in its infancy, and no current approach is clearly robust. In part, this is related to the newness of the modeling attempts, but is also the result of lingering ambiguity about the physiology of tree mortality from moisture stress (Sala et al. 2010), as well as challenges inherent in projecting future drought events under climate change (Dai 2010). It is very likely that new and innovative techniques will be developed, perhaps involving a combination of empirical and process-based approaches. In the face of climate change, the key to achieving robust capabilities is to model the links between the important factors that determine moisture stress (e.g., precipitation, temperature, and other biotic and abiotic factors) and tree mortality. Somewhat robust tree- and site-scale models already exist, but innovations are needed to successfully implement such approaches at broader temporal and spatial scales.

Although many aspects of the physiology of photosynthesis, growth, water use, and carbon allocation within trees are well known, the fundamental mechanisms determining tree survival or mortality during drought remain poorly understood despite decades of research (Bréda et al. 2006; Allen et al. 2010; Sala et al. 2010). Manion's (1991) decline spiral model posits that drought triggers mortality of trees that are already under stress by factors such as old age, poor site conditions, and air pollution, allowing them to be killed by tissue damage or biotic agents such as wood-boring insects and fungal pathogens. McDowell et al. (2008) suggest three mutually non-exclusive mechanisms by which drought could lead to forest mortality: (1) extreme drought kills trees through cavitation of water columns within the xylem, (2) long-term water stress produces plant carbon deficits that lead to death or reduced ability to defend against biotic agents such as insects or pathogens, and (3) extended warmth during droughts can result in increased populations of biotic agents, allowing them to overwhelm their already stressed tree hosts. Although these hypotheses have growing support, the physiology of tree death by moisture stress is not unambiguous (Bréda et al. 2006; Sala et al. 2010), and the process is to some extent still simulated by proxy. Moreover, drought effects may be offset or vary unpredictably among species due to increasing atmospheric CO_2 concentrations and N deposition, which affect plant water use and photosynthetic efficiency (Wang et al. 2012).

We have alluded to several knowledge gaps that hinder our ability to model drought effects on forested landscapes, not the least of which includes critical uncertainties related to the physiology of drought-induced mortality for most tree species. Although long-term empirical and experimental climate change studies are few, their findings should be incorporated into LDSMs, as should remote sensing data that provide additional information about the relationships between drought and tree response (e.g., Breshears et al. 2005). There may also be value in combining existing models that use different approaches and operate at different scales, as demonstrated by the joining of the LANDIS-II and PnET-II models (as described in Sect. 3.3). Ultimately, advances are needed to allow modelers to link changes in fundamental environmental drivers to their differential effects on tree species as well as their interactions with growth, competition, mortality, and various natural and anthropogenic disturbances.

3.5 Conclusions

Based on our review of the literature and experience, as well as results from the relatively heuristic case studies provided here, we can draw some general conclusions: (1) Because of changing climate, drought stress will increasingly affect the dynamics of forested landscapes, resulting in altered ecosystem composition, structure, and function. (2) Because climate change will produce new environmental conditions and stressors (including drought) that will interact in complex ways with forest growth, succession, and disturbance, to reliably project future forest dynamics LDSMs must better link the variability in climate with that inherent in the fundamental drivers of ecosystems. (3) Inclusion of drought as a process that alters forests in LDSMs is in its infancy but, because of the increasing importance of drought, these capabilities must be rapidly advanced.

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