Drought-induced tree mortality: ecological consequences, causes, and modeling

Weifeng Wang, Changhui Peng, Daniel D. Kneeshaw, Guy R. Larocque, and Zhibin Luo

Abstract: Drought-induced tree mortality, which rapidly alters forest ecosystem composition, structure, and function, as well as the feedbacks between the biosphere and climate, has occurred worldwide over the past few decades, and is expected to increase perversively as climate change progresses. The objectives of this review are to (1) highlight the likely ecological consequences of drought-induced tree mortality, (2) synthesize the hypotheses related to drought-induced tree mortality, (3) discuss the implications of current knowledge for modeling tree mortality processes under climate change, and (4) highlight future research needs. First, we emphasize the likely ecological consequences of tree mortality from ecosystem to biome to continental scales. We then document and criticize multiple non-exclusive tree mortality hypotheses (e.g., carbon starvation — carbon supply is less than carbon demand; and hydraulic failure — desiccation from failed water transport) from a more comprehensive ecological perspective. Next, we extend a forest decline concept model, Manion’s framework, by considering new emerging environmental conditions, for a more thorough understanding of the effects of climate change on forest decline. We find that an increase in drought frequency and (or) climate-change-type droughts may trigger increased background tree mortality rates and severe forest dieback events, accelerating species turnover and ecological regime shifts. The contribution of CO2 fertilization, rising temperature within the optimal growth range, and increased nitrogen deposition may defer or reduce this trend in tree mortality, but such contributions will vary between locations, species, and tree sizes. Multiple hypotheses proposed for drought-induced tree mortality are discussed, but coupling carbon and water cycles could help resolve the debate. The absence of a physiological understanding of tree mortality mechanisms limits the predictive ability of current models from stand-level process-based models to dynamic global vegetation models. We thus suggest that long-term observations, experiments, and models should be tightly interwoven during the research process to better forecast future climate changes and evaluate their impacts on forests.

Key words: biome shift, carbon starvation, mechanistic tree mortality modeling, forest die-off, global change, hydraulic failure.

Résumé : La mortalité des arbres induite par la sécheresse, altérant rapidement la composition, la structure et le fonctionnement des écosystèmes ainsi que des rétroactions entre biosphère et climat sont fréquemment survenus partout au monde, au cours des récentes décades. Et on s’attend à ce qu’elles augmentent de façon perversive, à mesure que le changement climatique progresse. Les objectifs de cette étude visent à (1) mettre en évidence les conséquences écologiques de la mortalité des arbres, induite par la sécheresse (2) synthétiser les hypothèses reliées à la mortalité des arbres, induite par la sécheresse (3) discuter l’implication des connaissances courantes pour la modélisation des processus de mortalité des arbres, sous l’influence du changement climatique, et (4) présenter les besoins futurs en recherche. D’abord, les auteurs mettent l’accent sur les conséquences écologiques probables de la mortalité des arbres aux échelles de l’écosystème, du biome et des continents. Ils documentent par la suite et critiquent les hypothèses multiples non exclusives de mortalité des arbres (p. ex. insuffisance d’apport en carbone; apport en carbone moindre que la demande; fracture hydraulique; dessiccation provenant d’un échec de transport de l’eau) dans une perspective écologique plus globale. Ensuite, ils étendent un modèle conceptuel du dépéris-

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sement forestier, le cadre de Manion, en considérant de nouvelles conditions environnementales émergentes, afin d’obtenir une compréhension plus complète des effets du changement climatique sur le dépérissement forestier. Les auteurs constatent qu’une augmentation de la fréquence des sécheresses et/ou des sécheresses de type « changement climatique » peut déclencher une augmentation des taux de mortalité des arbres et de sévères événements de dépérissement forestier, accélérant ainsi la succession des espèces et des modifications des régies écologiques. La contribution de la fertilisation par le CO₂, l’augmentation de la température dans l’écart optimal pour la croissance et l’augmentation du dépôt d’azote peuvent différer ou réduire cette tendance du dépérissement des arbres, mais ceci est appelé à varier entre les localités, les espèces et la dimension des arbres. Les auteurs discutent les multiples hypothèses proposées pour expliquer la mortalité des arbres induite par la sécheresse, mais le couplage avec le carbone et les cycles hydriques devrait résoudre le débat. L’absence d’une compréhension physiologique des mécanismes de mortalité limite le pouvoir prédictif des modèles courants, allant des modèles basés sur les processus à l’échelle du peuplement aux modèles de dynamique globale de la végétation. Les auteurs suggèrent que les observations, les expérimentations et les modèles à long terme devraient être étroitement interrélés au cours des processus de recherche, afin de mieux prédire le climat futur et évaluer ses impacts sur les forêts.

Mots-clés : déplacement des biomes, manque en carbone, dépérissement forestier, modélisation mécanistique de la mortalité des arbres, changement global, défaillance du circuit hydraulique.

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**Introduction**

Forests, the most important terrestrial ecosystems, play a crucial role in the global carbon cycle and affect regional hydrology and climatology through water balance and energy exchange (Bonan 2008; Chapin et al. 2008; Adams et al. 2010). Over recent decades, many forest mortality events around the world have been linked to drought and (or) heat (Allen et al. 2010). Recent drought occurrences have led to reductions in global terrestrial net primary productivity (Ciais et al. 2005; Zhao and Running 2010). Global-change-type droughts — the warming and drying impacts of global change — are gradually leading to increased background tree mortality rates (Clark 2004; Phillips et al. 2009, 2010; van Mantgem et al. 2009; Peng et al. 2011b) and triggering regional-scale forest dieback around forest transitions (Bre-shears et al. 2005; Hogg et al. 2008; Michaelian et al. 2011). Drought frequency and intensity have been predicted to increase under many climate change scenarios in the 21st century (Burke et al. 2006; IPCC 2007).

Our understanding of the impacts of the abnormal increases of tree mortality in forest ecosystems for periods during and (or) following a drought has improved over the last decade. Given that drought tolerance varies by species as well as tree size, drought-induced tree mortality can alter species richness and forest species composition, and thus forest functioning (Mueller et al. 2005). It can also both directly and indirectly influence the geographical distribution of tree species, leading to habitat shifts and subsequently, ecological regime shifts (Hansen et al. 2001). Large-scale forest dieback thus has a great potential to affect ecosystems and ecological functioning at multiple scales (Chapin et al. 2008; Adams et al. 2010). Although forests are able to adapt to new environmental conditions and absorb disturbances to some extent, abnormal tree mortality induced by droughts may still result in a variety of serious consequences, if they exceed the capacity of self-maintenance. We thus need to ask how increased background mortality rates alter intrinsic ecological processes, if and how broad-scale forest dieback leads to ecological regime shifts and affects earth system feedbacks.

Our understanding of tree mortality mechanisms and impact on ecosystem dynamics and earth system feedbacks still remains incomplete (Adams et al. 2010; Hartmann 2010; Sala et al. 2010). Furthermore, the lack of understanding of tree mortality mechanisms dramatically limits the ability of process-based models to predict tree mortality events and thus the creditability of process-based forecasting (Leuzinger and Quinn Thomas 2011; Zeppel et al. 2011). Currently, there is much debate on whether processes such as carbon starvation or hydraulic failure (McDowell et al. 2008; McDowell and Sevanto 2010; Sala et al. 2010) are the ultimate cause of tree death following droughts. The influence of these competing theories probably also varies between tree species. A better understanding of the causes and ecological consequences of drought-induced tree mortality is necessary to understand the structure and function of forest ecosystems, ecological regime shifts, as well as feedbacks between climate and the biosphere (Hanson and Weltzin 2000; Chapin et al. 2008; Adams et al. 2010; Hartmann 2010; Van der Mol len et al. 2011; Zeppel et al. 2011), as well as to decrease uncertainties in assessing global change impacts. Previous modeling efforts on tree mortality have been conducted using Manion’s framework (see reviews by Hawkes 2000; Keane et al. 2001; Seidl et al. 2011), an underlying and nonlinear theoretical framework of tree decline (Manion 1981). This framework, however, only considers negative influences that predispose, contribute to or incite tree death whereas the global change effects that we are currently experiencing (such as increased CO₂) have both positive and negative impacts.

This review synthesizes the likely ecological consequences from ecosystems to biomes to forests at a continental level and evaluates possible drought-induced tree mortality hypotheses. We then extend Manion’s tree mortality framework in the context of climate change and discuss the implications of current knowledge for modeling tree mortality processes under climate change. Next, we review the state of the art of mechanistically modeling drought-induced tree mortality among process-based models. Finally, we highlight future research needs.
Consequences for ecological processes

Droughts are a recurring natural disturbance and can be considered extreme events in forest ecosystems. More frequent droughts under global change may trigger severe tree mortality events, leading to serious ecological consequences. Although tree mortality might be mediated by population dynamics, such as recruitment and community processes such as species trade-offs to drought sensitivity, higher tree mortality than recruitment could still threaten the sustainability of forest ecosystem (e.g., van Mantgem et al. 2009; Peng et al. 2011b).

Impacts of tree mortality on forest ecosystems

The following section details how tree death possibly impacts carbon and nitrogen cycles and develops the chains of responses to the increase of background tree mortality rates (Table 1). Drought-induced tree death notably decreases leaf area index (LAI) as would forest thinning, which results in decreasing the gross primary productivity (GPP) of forests in the short term. The growth response of residual trees to more growing space is often enhanced by relative increases in light, nitrogen availability, and water availability, leading to an offset of decreased LAI. Dead trees also substantially increase resource (e.g., nutrients and light) availability for residual organisms in drought-stressed ecosystems (Franklin et al. 1987). Resources may be made available instantly (e.g., light) or slowly (e.g., nutrients in dead organisms) (Franklin et al. 1987). Net primary productivity for each residual plant may increase due to increased resource availability. However, tree mortality also directly increases litterfall, which could release more carbon in the future due to decomposition processes (Michaelian et al. 2011).

Furthermore, severe tree mortality events might drive forest ecosystems beyond the ecological threshold of their current dynamic equilibrium and towards a new ecosystem trajectory (Hartmann 2010) where ecosystem structures, compositions, processes, and functions are fundamentally changed. Beyond the thresholds of climate drivers such as temperature and (or) precipitation, irreversible ecological processes such as tree mortality may lead to forest ecosystem retreat, resulting in ecological regime shifts (Fig. 1). Such ecological regime shifts can be considered to be a direct consequence of regional scale forest dieback, although tree species are expected to shift their geographical ranges polewards or to higher elevations as global warming occurs (Loarie et al. 2009; Doak and Morris 2010). In this way, ecosystems that are no longer acclimated to the new conditions may be succeeded by novel ecosystems comprised of pre-existing species, invading species, or their combination (Littell et al. 2010), consecutively changing ecosystem composition, structure, and functional diversity. For example, ponderosa pine (Pinus ponderosa)–dominated forests and pinyon pine (Pinus edulis), and juniper (Juniperus L. spp.)–dominated woodlands shifted to dominance by junipers and shrubs following the severe 2002 drought in northern Arizona, USA (Koepke et al. 2010). Biomes can shift when severe tree mortality occurs near the boundary of ecological regions or biomes due to droughts (Frelich and Reich 2010; Salazar and Nobre 2010). For instance, ecological regime shifts because of large areas of forest dieback have occurred in boreal and northern hardwood forests situated near the prairie–forest border of central North America (Michaelian et al. 2011), where the border shifted to the moister northeast during past decades and is expected to continue in the future (Frelich and Reich 2010).

Impacts of regional forest dieback on earth system

Forest mortality observations highlight the vulnerability of forests, which consequently could affect earth system processes (Adams et al. 2010). Such changes would not only alter the carbon balance but also change water and energy fluxes between the atmosphere and terrestrial ecosystems (Chapin et al. 2008) (Fig. 2). Thus, one direct consequence of sudden forest dieback is rapid loss of carbon back to the atmosphere. For instance, drought-induced water stress may be a cause of the reduction of 7.89 ± 3.22 Mt year⁻¹ in carbon biomass of Canadian boreal forests since 1963 (Ma et al. 2012). At the southern edge of the western Canadian boreal forest, droughts led to regional scale aspen (Populus tremuloides Michx.) forest dieback, and an estimated 29 Mt increase in dead biomass across an 11.5 Mha survey area, which corresponds to 14 Mt of potential future carbon emission to the atmosphere (Michaelian et al. 2011). Decomposition could switch forests from carbon sinks to sources for several decades following extensive tree mortality (Adams et al. 2010). In addition, large-scale forest cover loss because of forest dieback events will reduce CO₂ uptake from the atmosphere. Rising atmospheric CO₂ caused by these two pathways of carbon loss (decomposition and cover loss) might eventually lead to a warmer and drier climate, which can then intensify forest mortality (Fig. 2, right panel positive feedback loop). It would seem logical to infer that potential enrichment due to reductions of the forest carbon sink to rising CO₂ could enhance forest growth, which could decrease future forest mortality (Fig. 2, bottom right negative feedback loop). A more realistic understanding of the effects of forest mortality on feedbacks between the climate and biosphere system, however, requires the consideration of multiple feedbacks rather than the carbon cycle only (Chapin et al. 2008). Large areas of forest mortality are also expected to potentially change solar energy fluxes, increasing reflectance of short-wave radiation back to the atmosphere by increasing land surface albedo (Fig. 2, upper panel negative feedback loop) (Chapin et al. 2008). For example, in boreal forests, large increases in land surface albedo due to forest mortality events and the exposure of snow-covered ground could partially offset the radiative forcing of greenhouse gases (Chapin et al. 2008). Semiarid regions are probably most sensitive to albedo changes due to losses of forest cover (Adams et al. 2010; Rotenberg and Yakir 2010). Furthermore, changes in regional hydrology are also expected, since a loss of forest cover can alter water balance due to increased surface evaporation and decreased transpiration (Chapin et al. 2008), which could result in a drier climate (Fig. 2, left panel positive feedback loop).

Mechanistic causes of drought-induced tree mortality

Due to the likely ecological consequences of abnormal tree
mortality events, the physiological causes of drought-induced tree mortality have recently attracted increasing interest (e.g., McDowell et al. 2008, 2011; Adams et al. 2009; Sala 2009; McDowell and Sevanto 2010; Sala et al. 2010; McDowell 2011; Zeppel et al. 2011; Anderegg et al. 2012). But, how much do we know about tree mortality mechanisms? Several hypotheses for the underlying mechanisms of drought-induced tree mortality have been proposed to shed light on the mystery. There is increasing evidence supporting hydraulic constraints within the soil–plant–atmosphere continuum as a limit for different plant species to cope with water-deficit stress (Bond et al. 2008). Based on the relationship between water potential and stomatal conductance, plants can be aggregated into two groups, i.e., isohydric and anisohydric species (Bréda et al. 2006; Tardieu and Simonneau 1998).

### Table 1

<table>
<thead>
<tr>
<th>No.</th>
<th>Time scale</th>
<th>Cause–effect chain</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Fast</td>
<td>Tree mortality ↑⇒ GPP ↓⇒ N demand ↓⇒ Soil N availability ↑⇒ GPP ↑</td>
</tr>
<tr>
<td>2</td>
<td>Fast</td>
<td>Tree mortality ↑⇒ Soil N availability ↑⇒ GPP ↑</td>
</tr>
<tr>
<td>3</td>
<td>Fast</td>
<td>Tree mortality ↑⇒ Soil water availability ↑⇒ GPP ↑</td>
</tr>
<tr>
<td>4</td>
<td>Slow</td>
<td>Tree mortality ↑⇒ Litterfall ↑⇒ Soil C stock ↑⇒ Decomposition ↑⇒ Soil C stock ↓</td>
</tr>
</tbody>
</table>

**Fig. 1.** Illustration of ecological regime shift resulting from drought stress in the forest-prairie ecotone. Black and hollow circles represent the current ecosystem state and the possible future ecosystem states, respectively, shifting with ecological drivers. Black arrows represent the possible movement directions of ecosystem state. Squares represent water availability (modified from Andersen et al. 2009).

**Fig. 2.** Causal loop diagram of how drought-induced forest mortality affects earth system feedbacks between ecosystems and the climate system in energy, carbon, and water cycles. Red arrows with plus marks and blue arrows with minus marks represent a cause-and-effect relationship in which the two variables change in the same and opposite directions, respectively. Symbols(+) and (−) represent positive and negative feedbacks, respectively.
anisms have been postulated to lead to tree mortality following droughts (Fig. 3).

Carbon starvation (carbon supply is less than carbon use) would occur for trees (isohydric species) that can regulate stomatal conductance and allow leaf water potential to drop as soil water potential declines to prevent possible cavitation during chronic drought, but photosynthesis also drops because of the regulated stomata (McDowell et al. 2008). Chronic drought could thus kill those trees because of negative carbon gain. An initial experimental study conducted by Adams et al. (2009) reported that warmer temperature (+4 °C) shortened the time to drought-induced mortality in pinyon pine trees (isohydric species) by nearly a third. It possibly supports the carbon starvation hypothesis as the primary mechanism of mortality. Hydraulic failure (desiccation from failed water transport) would occur when drought intensity passes the threshold for irreversible desiccation (McDowell et al. 2008; Sala et al. 2010). Extreme droughts kill trees (anisohydric species), which maintain a relatively constant leaf water potential regardless of drought conditions, through hydraulic failure (e.g., xylem cavitation) (Bond et al. 2008; McDowell et al. 2008). Either carbon starvation, hydraulic failure or both have been debated as causes in early research on drought-induced mortality (Adams et al. 2009; Sala 2009; McDowell and Sevanto 2010; Sala et al. 2010; Anderegg et al. 2012).

It is only recently that the consideration of tree mortality mechanisms through coupling carbon and water cycles has become more widely appreciated (McDowell 2011; McDowell et al. 2011). In Fig. 3, both cycles were coupled to better explain the nonexclusive mechanisms of hydraulic failure, carbon starvation, carbon mobilization, and transportation failure, as well as carbon–hydraulic interactions. During droughts, water shortage stress limits photosynthetic rate, respiration, and carbon mobilization. In particular, photosynthesis uses CO₂ and water to produce photosynthates. Thus, water shortage may reduce the amount of photosynthesize production. If too severe, water shortage may harm the biochemical processes associated with respiration and the amount of carbohydrate reserves. Insufficient carbohydrate reserves reduce the capacity of trees to survive under stress. Regarding the adaptive strategies of trees to droughts, such as foliage shedding, enhancing the allocation to roots, and the storage of reserves (Chaves et al. 2003), dysfunctions in any section of either the carbon cycle or the water cycle might directly induce tree mortality.

Extended Manion’s framework

Tree mortality is a complex and gradual process influenced by multiple and interacting factors such as life span, drought stress, insect pests, and diseases (Franklin et al. 1987; Waring 1987; Frey et al. 2004). Despite the fact that tree mortality is perhaps the least understood process in forest dynamics (Güneralp and Gertner 2007), an underlying and nonlinear theoretical framework (Manion’s framework) of tree decline has been proposed (Manion 1981). Manion’s tree decline concept addresses complex decline syndromes starting with a healthy tree that loses vigour and eventually dies. Based on the decline spiral model (Manion 1981), ecological agents were classified as predisposing, inciting, and contributing factors, respectively (Table 2). Predisposing factors, such as age, poor site conditions, and species vulnerability, represent chronic stresses that increase a tree’s vulnerability to inciting factors that can be considered as the first agents to stress tree
function and reduce vigour substantially (Archaux and Wolters 2006). In this way, inciting factors enhance opportunities for contributing factors (secondary agents) to establish and accelerate tree decline and death. Drought has often been considered to be an inciting factor and biotic agents (e.g., insect pests and diseases) as contributing factors (Hogg et al. 2002). However, to a certain degree, these factors are interchangeable. Drought may play a contributing role but not an inciting role in tree death; in turn, insect pests and diseases may act as factors inciting tree death. For example, in western Canada, a massive outbreak of mountain pine beetle (*Dendroctonus ponderosae* Hopkins, Coleoptera: Curculionidae, Scolytinae) has killed millions of trees weakened by droughts across 130000 km² of forest in multiple years (Kurz et al. 2008). The vigour of a tree will be determined by the effect of all three factors under Manion’s framework. In addition, some stress factors facilitate or enhance the significance of others (Smith 1970). No matter what factors first lead to a decrease in forest growth (or loss of vigour), other agents or factors (generally contributing factors) are the ones that directly cause tree death.

However, as useful as Manion’s pioneering theoretical framework is to understand the tree death process (Manion 1981), it needs to be extended in the context of environmental change. Elevated atmospheric CO₂, rising temperature, and elevated nitrogen deposition are often considered to have positive effects on forest carbon sequestration if other growth factors such as water are not limiting, which indicates an increase in tree vigour (see reviews by Boivinene and Running 2006; Luo et al. 2006; Huang et al. 2007; Hyvonen et al. 2007; Reay et al. 2008). These effects are defined here as stabilizing effects (Table 2). Tree mortality processes following the extended Manion’s framework under climate change are illustrated in Fig. 4.

An elevated atmospheric CO₂ concentration may increase the ratio of CO₂ to O₂ in the substomatal cavity, resulting in a decrease in carbon losses due to photosynthesis (see reviews by Luo et al. 2006; Huang et al. 2007). In terms of the exchange of water, elevated atmospheric CO₂ concentration could reduce stomatal conductance or induce longer periods of stomatal closure and hence increase the ratio of carbon gain to water loss (water use efficiency) in water-limited forest ecosystems (Wullschleger et al. 2002). Morgan et al. (2004) indicated that the effects of elevated CO₂ (e.g., higher water use efficiency and enhanced plant growth) could be particularly important in drier ecosystems. Wyckoff and Bowers (2010) reported that the impacts of droughts at the prairie–forest ecotone in the northern-central US might be diminished by rising CO₂ concentration. But recent studies have reported that the effects of CO₂ fertilization on forest productivity might still be constrained by limited nitrogen availability and (or) water limitation (Reich et al. 2006; Norby et al. 2010; Silva et al. 2010; Peñuelas et al. 2011). Elevated CO₂ concentrations do not necessarily increase the insensitivity to drought in trees, and its effects may vary across species and sizes of trees (Beerling et al. 1996; Warren et al. 2011; Way 2011). Nevertheless, the direct effects of elevated CO₂ concentration on photosynthetic efficiency and water use efficiency may at least partially offset the drought impacts for some species.

Table 2. Factors influencing drought-induced tree mortality under the extended Manion’s framework.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Predisposing factor</strong></td>
<td></td>
</tr>
<tr>
<td>Old age, senescence</td>
<td>Frey et al. 2004</td>
</tr>
<tr>
<td>Ecotone</td>
<td>Frey et al. 2004</td>
</tr>
<tr>
<td>Species vulnerability (e.g., shade-intolerant, drought-intolerant, susceptibility to fire, insect and disease)</td>
<td>Archaux and Wolters 2006</td>
</tr>
<tr>
<td><strong>Inciting or contributing factor</strong></td>
<td></td>
</tr>
<tr>
<td>Insect pests and disease</td>
<td>Frey et al. 2004</td>
</tr>
<tr>
<td>Environmental stresses (flooding, drought, cold)</td>
<td>Frey et al. 2004</td>
</tr>
<tr>
<td><strong>Stabilizing effect</strong></td>
<td></td>
</tr>
<tr>
<td>Elevated CO₂ concentration</td>
<td>Luo et al. 2006; Huang et al. 2007</td>
</tr>
<tr>
<td>Increased nitrogen deposition</td>
<td>Hyvonen et al. 2007; Reay et al. 2008</td>
</tr>
<tr>
<td>Modest warming</td>
<td>Hyvonen et al. 2007; Luo 2007</td>
</tr>
</tbody>
</table>

*Stabilizing effects represent the potential positive effects on forest growth of new emerging global environmental conditions.

Future increases in nitrogen deposition could increase nitrogen availability, thus enhancing forest growth in nitrogen-limited forest ecosystems (Hyvonen et al. 2007; Reay et al. 2008). Rising temperature also accelerates the soil mineralization rate and hence enhances nitrogen availability (Luo 2007). As suggested by Way (2011), nitrogen-saturated forest ecosystems may be less vulnerable to drought impacts since high CO₂ may continuously stimulate photosynthesis due to increased water use efficiency. However, a key uncertainty for nitrogen deposition is to what degree annual rates of nitrogen deposition can approach nitrogen saturation in the context of climate change (e.g., rising temperature and elevated CO₂ concentration), and hence stimulate forest productivity (Aber et al. 1998; Yang et al. 2011).

The synergistic effects of recent changes in environmental
conditions, including elevated atmospheric CO₂ concentrations, rising temperature, and elevated nitrogen deposition, are expected to further stimulate forest production, enhance tree survival, and reduce drought impacts. Rising atmospheric CO₂ levels and nitrogen deposition during the past century have resulted in consistent increases in water use efficiency, although this may not prevent growth decline and forest mortality induced by recent frequent temperature droughts (Silva et al. 2010; Peñuelas et al. 2011). To some extent, these positive factors (potentially stimulating growth) still offset the impacts of drought on forest growth and determine the survivability and success of tree species, retarding or reducing mortality events. The trade-off of the four factors (predisposing, inciting, contributing factors, and stabilizing effect) will determine the physiological thresholds of individual tree growth decline and mortality under changing climate (Fig. 4). Most cases that reported a pervasive increase in drought-induced tree mortality have focused on either individual drought events (e.g., Phillips et al. 2009; Michaelian et al. 2011) or occurred in traditionally drier regions (e.g., van Mantgem et al. 2009; Michaelian et al. 2011; Peng et al. 2011b). For example, Peng et al. (2011b) reported a smaller increase of tree mortality rates in natural old growth boreal forests in western Canada than in eastern Canada. In the western US, a xeric region, the background mortality rates for all western forest types increased by a four-fold factor compared with the 1950s mortality rate (van Mantgem et al. 2009), whereas drought may not be the principle factor of tree mortality in central and eastern US (Dietze and Moor-croft 2011). Therefore, the effects of the four factors under the extended Manion’s framework will likely influence survival, growth, and tree mortality, but in different ways, locations, species, and tree sizes.

**State of the art modeling of drought-induced tree mortality**

Under Manion’s framework, efforts in modeling tree mortality have been made over past decades (see reviews by Hawkes 2000; Keane et al. 2001; Seidl et al. 2011). Current process-based models have the capacity to simulate carbon, nitrogen, and water cycles, energy balance and vegetation dynamics. Thus, the transient drought response of trees (e.g., declines in productivity) can be readily modeled by physiological models. However, these models may not accurately capture the physiological mechanisms of tree mortality and well predict long-term ecological consequences. Due to the complexity of tree mortality, in the context of climate change, the extended Manion’s framework should be considered in process-based models for predicting climate change effects on tree mortality. Here, we limit our review to modeling studies that mechanistically simulate drought-induced tree mortality.

Tree mortality modeling based on carbon balance (respiration demand > GPP) has started to be used to represent carbon starvation. A forest dieback model (Bossel 1986) included a mechanistic mortality algorithm developed from a perspective of carbon balance. Since then, there has been an
increase in the number of modeling studies based on carbon balance as a mortality mechanism. For instance, a European study used a process-based model to simulate drought-induced mortality based on negative carbon balance and drought-related leaf area loss (Sabaté et al. 2002). Güneralp and Gertner (2007) also suggested that carbon imbalances play a crucial role in the onset of tree mortality under Manion’s framework. In such models, drought-induced tree mortality ($\mu$) is generally given by

$$
\mu = \begin{cases} 
0 & \frac{GPP + C_S}{C_{Demand}} \geq 1 \\
\frac{GPP + C_S}{C_{Demand}} & < 1
\end{cases}
$$

where $a$ is a constant value ranging from 0 to 1; GPP is gross primary productivity; $C_S$ is stored nonstructural carbohydrate pool; $C_{Demand}$ is the need of necessary metabolism (e.g., respiration). The stored non-structural carbohydrate pool might only be defined in some models, where tree mortality may occur when stored carbon severely depleted.

Alternatively, tree mortality due to xylem cavitation has also been explored. For example, Martínez-Vilalta et al. (2002) used hydraulic loss in xylem conductivity and its feedback to leaf area as a proxy for death from drought in their plant water balance model. Zavala (2004) integrated two drought tolerance mechanisms (avoidance of soil and leaf water potential reaching the wilting point, respectively) into a process-based model through regulating stomatal conductance. The algorithm was then used in a stand-level model that accounts for drought stress and subsequent drought-induced tree mortality, with leaf water potential approaching the cavitation threshold as a key driver (Zavala and Bravo de la Parra 2005). Tree mortality related to hydraulic failure could be defined as

$$
\mu = \begin{cases} 
0 & K_{st} \geq K_{st, safe} \\
\frac{1}{a} & K_{st} < K_{st, safe}
\end{cases}
$$

where $K_{st}$ is stem hydraulic conductivity; $K_{st, safe}$ is a critical threshold of stem hydraulic conductivity to avoid xylem cavitation (Fig. 3).

Although stand-level process-based models have begun to mechanically model drought-induced tree mortality, dynamic global vegetation models (DGVMs) are the models that need to consider drought-induced tree mortality to better predict the ecological consequences of climate change and climate–biosphere feedbacks at the regional or global level. DGVMs were designed to represent the biogeochemical and hydrological processes of vegetation dynamics as a response to a changing climate for large spatial and temporal scales and do not take into account the behaviour of individual species (Quillet et al. 2010). Recent meetings and studies have begun to mention the importance of modeling drought-induced tree mortality (Delbart et al. 2010; Galbraith et al. 2010; Leuzinger and Quinn Thomas 2011; Zeppel et al. 2011). For example, Delbart et al. (2010) found that huge errors (overestimated aboveground net primary productivity on average by 63% determined by comparison to a set of ground measurements) in simulations of the DGVM ORCHIDEE across Amazonian forests originated from the misrepresenta-

**Challenges and the future**

From our synthesis of drought-induced tree mortality causes, ecological consequences, and modeling, we identify the following major gaps between long-term observations, experiments, and process-based tree mortality modeling:

1. Long-term observations will improve our understanding of the ecological consequences of tree mortality, and are expected to improve our modeling ability. But current records or calculations of mortality rates are diverse (e.g., accumulated mortality, basal area reduction, and timber loss) and hard to uniformly quantify. Observations need to be consistent for statistically integrating results from individual studies. We proposed that at least three variables, including stand density change, basal area reduction, and biomass reduction, should be quantified for investigating
changes in background tree mortality. Both gross forest cover loss and estimated biomass reduction should be accounted for when examining regional forest dieback events. To do so, models could be calibrated and validated using the long-term observational data.

2. There is an apparent gap in understanding ecological thresholds causing regime shifts in response to extreme droughts. For example, key environmental thresholds that occur when the buffering capacity for individual tree species are exceeded need to be identified as well as when and which thresholds of tree mortality rates will be exceeded causing an acceleration in species turnover and landscape evolution (e.g., Frelich and Reich 2010; Koepke et al. 2010). To forecast long-term ecosystem response to future climate change, relative information about ecological thresholds might be needed by process-based models to assess the impacts of global change.

3. Currently, there is surprisingly little species-specific knowledge on the regulation of xylem water potentials and on the patterns of carbohydrates stored in response to abrupt events such as droughts (Allen et al. 2010). Drought experiments could be used to better develop our understanding of tree responses to drought, if a whole tree approach and coupled measurements of water and carbon are considered (Ryan 2011). Therefore, linking multiple physiological pathways (carbon and water) to mortality through drought experiments would help to understand tree mortality mechanisms.

4. Future modeling effort will be needed to establish algorithms corresponding to the aforementioned hypotheses of drought-induced mortality and test these hypotheses through linking monitoring data and experimental data. Even if the aforementioned modeling studies attempted to simulate drought-induced tree mortality, they still may not accurately represent the thresholds of tree suppression and mortality response to drought due to our incomplete understanding of physiological mortality mechanisms (Zeppel et al. 2011). Interweaving both data (monitoring and experimental) and models will be important to improve the forecasting capability of process-based models (Leuzinger and Quinn Thomas 2011; Zeppel et al. 2011). So called model-data fusion techniques (see reviews by Wang et al. 2009; Peng et al. 2011a) could provide a novel quantitative approach that permits process-based models to test hypotheses based on multiple observational data sources (data assimilation) and optimization techniques such as Monte Carlo and Kalman filter. In this way, quantifying the relationships between tree mortality and carbon starvation, carbon transportation failure, hydraulic failure, as well as their combinations would improve our understanding of drought-induced tree mortality.

5. Effectively implementing the interconnected drivers under the extended Manion’s framework remains a big challenge for current process-based modeling. Research is required to understand how and when other factors, such as insects and diseases, start to destroy and kill trees or buffer the drought impacts since tree mortality is usually a multi-factorial process (Table 2). Under the extended Manion’s framework that we proposed, drought is considered to be an important “predisposing” factor for many other disturbances, such as insects and disease. However, interactions between droughts and insects have been little investigated and poorly understood, but may be quite important (Seidl et al. 2011). The challenge of modeling insect population dynamics requires integration over processes and scales, combining information about host and insect sensitivity to climate (e.g., Régnière et al. 2012), timing of life cycle processes, reproductive success and mortality (see review by Raffa et al. 2008; Seidl et al. 2011). More comprehensive understanding of drought-induced forest mortality across landscapes will require the judicious incorporation and interactions of forest physiological models and climate-driven insect population models. On the other hand, the simultaneous global change drivers, such as rising CO2 concentration and rising nitrogen deposition, might buffer drought impacts. For example, tree response to drought may change substantially when considered under concurrent modest warming and elevated CO2 concentration. Therefore, responding to threats of climate change requires, as stated by Williams et al. (2008), “a concerted, multi-disciplinary, multi-scale, multi-taxon research effort that improves our predictive capacity to identify and prioritise vulnerable species in order to inform governments of the seriousness of the threat and to facilitate conservation adaptation and management”.

The warming and drying effects of global climate change may lead to tree growth decline, and subsequent increases in background tree mortality rates under changing environmental conditions. These impacts may reach ecological thresholds, subsequently, leading to ecological regime shifts within forest ecosystems, or even forest biome shifts (Fig. 1). Broad-scale forest dieback probably enhances the climate warming trend, although the cooler effect of an increase in albedo may at least partially offset this effect (Fig. 2). Our extended Manion’s framework by adding a set of stimulating growth effects could help to draw a more complete picture of tree mortality processes under a warming and drying world (Fig. 4). Developing mechanistic-based tree mortality algorithms in stand-level process-based models and DGVMs is challenging, but necessary to improve our predictive capacity to understand carbon budgets and vegetation dynamics under climate change and to support long-term climate forecasts. In summary, assessing the impacts of climate change on forest ecosystems requires a more quantitative understanding of the response (resistance and elasticity) of forests, the mortality mechanisms, the interactions among biotic and abiotic factors, the effects of concurrent climate drivers, and their consequences at different spatial and temporal scales.

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