

Editorial

Improving our knowledge of drought-induced forest mortality through experiments, observations, and modeling

Regional and continental-scale forest and woodland mortality appears to be accelerating over recent decades (Allen *et al.*, 2010; Peng *et al.*, 2011). These contemporary increases in mortality are just the beginning, as temperature is rising rapidly and global models predict a large decline in the strength of the terrestrial carbon sink over the next century (Arora *et al.*, 2013). Even if precipitation variability remains similar to historical patterns, chronic warming (and warming-associated extremes (Reichstein *et al.*, 2013)) raise the likelihood of mortality through direct impacts on autotrophic respiration and on the growth of biotic agent populations, and indirect effects on stomatal conductance via rising vapor pressure deficit (VPD), thus impacting plant hydraulics and metabolism (Breshears *et al.*, 2013; Williams *et al.*, 2013). Although globally averaged Penman–Monteith estimates suggest little change in terrestrial water balance in recent decades, many regions have indeed experienced a substantial increase in drought (Sheffield *et al.*, 2012; Williams *et al.*, 2013). From a forest's perspective, drought may not be dictated via a strict Penman–Monteith framework due to nonlinear plant physiological interactions with meteorology, potentially explaining some disproportionately strong regional growth and mortality responses to rising VPD (Liu *et al.*, 2013; Williams *et al.*, 2013). The consequences of forest mortality include large climate feedbacks (Adams *et al.*, 2012; Maness *et al.*, 2012; Jiang *et al.*, 2013), impacts on community composition (Redmond & Barger, 2013), soil biochemistry (Cobb *et al.*, 2013) and the availability of fuel wood and food in developing nations (Anderegg *et al.*, 2012a).

The rapid growth in awareness of drought-induced forest mortality has substantially increased the magnitude of research on this topic. Between 2002 and 2012, the number of publications on 'drought-induced mortality' or 'drought mortality' and 'vegetation' and 'plant' (excluding the category 'medical') has risen by 355% (18 in 2002 to 82 in 2012), resulting in the diversification of our approaches and subsequent scientific breakthroughs. Because mortality processes scale across time and space, research has necessarily integrated scientific disciplines such as physiological ecology, remote sensing, and modeling, thereby generating greater understanding of the mechanisms of mortality and potential consequences for ecosystem function. In this piece introducing the *New Phytologist* 'Drought-induced Forest Mortality' Feature Issue, we present

some recent advances in forest mortality research. But first we highlight two notable challenges to this field: the dichotomy of drought vs pest- and pathogen-killed trees, and the trade-offs associated with doing laboratory studies on small plants vs field studies on mature trees.

The false dichotomy of drought vs biotic attack in mortality

Mortality causes are frequently lumped into two general categories: (1) climatological drought and subsequent physiological failure of metabolism in the absence of biotic attack agents; and (2) biotic-attack driven mortality, in which drought is not a required precursor. We suggest that this dichotomy is not useful, and that science will move more rapidly if we consider this as an interaction between (1) and (2). The *Pinus–Dendroctonus* beetle system that dominates much of the Rocky Mountains from New Mexico, USA to Yukon Territory, Canada exemplifies this challenge (see the cover image of *New Phytologist*, Volume 200, Issue 2, which accompanies this collection). These *Pinus* forests often succumb to beetles many years after climatological drought has ended; however, these outbreaks are dependent on drought-weakened hosts for initiation (Waring & Pitman, 1985; Raffa *et al.*, 2008). However, these beetle outbreaks are dependent on drought-weakened hosts for initiation (Raffa *et al.*, 2008; Powell & Bentz, 2009; McDowell *et al.*, 2011b). Determining whether *Pinus* forests were killed by 'drought' or by 'beetles' is difficult in these interdependent systems that operate over broad scales of space and time. We must somehow test the question 'if no drought had occurred within the past N decades, would biotic attacks have occurred?' Many forests and other vegetated ecosystems that die during or after drought are impacted by biotic attack agents that feed on stressed plants (Raffa *et al.*, 2008; Worrall *et al.*, 2008). Research across the continuum of (1) to (2) is essential to test hypotheses efficiently and in a manner amenable to model assimilation.

The value of small- vs large-tree studies

Here we highlight a challenge common throughout plant science: balancing the need for highly-controlled studies to unravel detailed mechanisms with the need for acquiring results relevant to the real world. Many observations of drought- and heat-related mortality have been described in large, mature trees (Allen *et al.*, 2010; Michaelian *et al.*, 2011; Matusick *et al.*, 2013). In contrast, substantial small tree research has focused on the process of death in controlled environments (Anderegg *et al.*, 2012a; Adams *et al.*, 2013; Mitchell *et al.*, 2013). This general focus on field-research on large trees and laboratory research on small trees has resulted in two challenges: (1) a lack of mechanistic research on drought-mortality in field-grown seedlings; and (2) indirectly, frequent criticism regarding the relevance of research on smaller trees in controlled environments to accurately predicting the impact of drought on larger trees growing in natural, field conditions.

Theory and evidence suggests vulnerability to drought-induced mortality should vary with tree size due to variation in both environmental and physiological differences (Table 1; Ryan *et al.*, 2006; McDowell *et al.*, 2008). Shallower rooting depth should make smaller trees more susceptible to the processes of hydraulic failure (progressive loss of water transport capacity) and carbon starvation (progressive loss of stored carbohydrates and subsequent failure to maintain turgor, metabolism, or defense efficacy). In large trees, the combination of greater belowground exploration, carbohydrate storage relative to demand (Piper & Fajardo 2011; Sala *et al.*, 2012), internal water stores, and lower transpiration per unit leaf area should be favorable during prolonged drought. However, these benefits partly reflect homeostatic adjustments in response to decreasing hydraulic conductance and photosynthesis with tree size (Ryan *et al.*, 2006). Therefore, plants attaining maximum height may have reached their capacity for these adjustments (Zhang *et al.*, 2009; McDowell *et al.*, 2011a), thereby limiting their ability to respond to further climate changes. These size-related physiological differences may explain the frequently observed parabolic (U-shaped) mortality pattern with plant size; highest mortality rates occur for the smallest and largest trees (McDowell *et al.*, 2008; Lines *et al.*, 2010; Phillips *et al.*, 2010). The interaction of drought with tree ontogeny and size is important because seedling mortality has large impacts on future ecosystem structure and function (Smith *et al.*, 2009; Bansal & Germino, 2010), while older trees contain the most carbon, and therefore their mortality generates the largest, longest lasting carbon losses (McKinley *et al.*, 2011).

Seedlings and saplings have long offered compelling study subjects because they are amenable to manipulation, thereby allowing investigation of physiological mechanisms. Small trees facilitate easier and more complete measurements, with extrapolation to whole individuals containing less error than for large trees. Small trees allow less costly and better controlled manipulations of environmental conditions and make multifactor manipulations

(e.g. irrigation, [CO₂], temperature) more feasible (Zeppel *et al.*, 2012; Duan *et al.*, 2013). Small trees offer a cost-effective model for molecular and physiological processes in larger trees, thus allowing hypothesis generation that can subsequently be tested on larger trees. Caveats exist regarding extrapolation and inferences. For example, thresholds and timing will likely differ with tree size (see Table 1 for details) and controlled environment studies with small trees must maximize the soil volume for roots to explore to avoid exacerbating or confounding drought symptoms (Poorter *et al.*, 2012). We conclude that studies with small plants in glasshouses are extremely valuable for making breakthrough tests of detailed physiological processes, and understanding the interaction of drought with tree ontogeny and size remains an essential research priority.

The New *Phytologist* Feature Issue on Drought and Forest Mortality

This issue contains a collection of papers that provide new insights into mortality processes, and myriad approaches and experimental systems. These include papers utilizing experimental manipulations in the field and laboratory, ground and space-based observational platforms, and multi-model-experiment examinations of mortality mechanisms.

Dynamic global vegetation models (DGVMs) predict terrestrial vegetation changes and their impacts on climate forcing, typically having 5–16 plant functional types globally and in some cases, age- and size-structure (Medvigy *et al.*, 2009; Arora *et al.*, 2013). Information on thresholds and mechanisms leading to mortality is required in the major biomes for accurate mortality simulation within DGVMs (McDowell *et al.*, 2011b). Published research on mechanisms leading to drought-induced mortality is dominated by Northern Hemisphere temperate evergreen conifers and deciduous angiosperms (specifically, species in the *Pinus*, *Juniperus*, *Quercus*, and *Populus* genera) (Allen *et al.*, 2010). This Feature Issue is slightly more

Table 1 Key physiological and ecological differences between seedlings/saplings and mature plants. Carbon and water pools and fluxes are represented. Processes described reflect some representative processes; not all processes are presented nor is this an exhaustive review

Factor	Younger, smaller trees compared to older, larger trees	Example
Carbon		
Leaf area : sapwood area	Higher	McDowell <i>et al.</i> (2002)
Tree height	Lower	Ryan & Yoder (1997)
Bark thickness	Lower	Brando <i>et al.</i> (2012)
Carbohydrate storage	Lower relative to GPP and NPP	Piper & Farjado (2011), Sala <i>et al.</i> (2012) ¹
Photosynthetic capacity	Higher or Lower	Thomas & Winner (2002)
Respiration capacity (all tissues)	Higher	Ryan <i>et al.</i> (1994)
Partitioning to roots	Higher	Litton <i>et al.</i> (2007)
Partitioning to stem wood growth	Lower	Litton <i>et al.</i> (2007)
Partitioning to reproduction	None	Thomas (2011)
Water		
Root access to water	Lower	Christina <i>et al.</i> (2011)
Susceptibility to cavitation	Lower	Domec & Gartner (2001); Rice <i>et al.</i> (2004)
Water storage in xylem	Lower	Scholz <i>et al.</i> (2011)
Wood growth/leaf area	Higher	Ryan <i>et al.</i> (2006)
Transpiration/leaf area	Higher	Ryan <i>et al.</i> (2006)

¹In addition to Piper & Farjado (2011), sapwood volume increases with tree size (Ryan, 1989), while photosynthesis and growth decreases (Ryan *et al.*, 1997) allowing accumulation of carbohydrates.

balanced, with six papers on evergreen conifers, and four on deciduous angiosperms. The collection has 45% and 55% of papers on seedlings and mature trees, respectively, and 55%, 36%, and 9% of studies originated from North America, Europe, and Amazonia, respectively.

Rising vapor pressure deficit (VPD) accelerates mortality

High VPD has long been associated with stomatal closure (Schulze *et al.*, 1972). VPD is increasing exponentially with temperature and is just as important as precipitation in driving landscape disturbances (Clifford *et al.*, 2013; Williams *et al.*, 2013). In this collection, faster seedling and mature tree mortality was associated with rising VPD (Clifford *et al.*, 2013; Will *et al.*, 2013; Zhao *et al.*, 2013). Clifford *et al.*'s (2013) study provides a quantitative, regional-scale assessment of mortality thresholds for VPD and precipitation (see the Commentary by Hicke & Zeppel, 2013). Will *et al.* (2013) examine the impacts of VPD (with limited confounding of temperature) on 10 species of saplings, representing an important increase in our breadth of knowledge across species. Zhao *et al.* (2013) test how whole-plant carbon compensation points respond to temperature (and inherent VPD variation) during extended periods of dry soil, and unveils important components of mechanisms underlying the faster death of heated seedlings. Given forecasts of rising temperatures and continued inter-annual variability in precipitation, we recommend that the impact of rising VPD on mortality should be among our highest priorities for investigation.

Carbon starvation, hydraulic failure, and mortality

Manipulation of physiological function under controlled environments allows perturbation of physiology to test underlying mechanisms. Through sub-ambient (*c.* 75 ppm) [CO₂] and low irrigation manipulations, Hartmann *et al.* (2013) observe that water availability kills trees more quickly than outright carbon starvation despite severe carbohydrate depletion in low [CO₂] trees, thereby concluding that 'thirst beats hunger'. The results from this elegant test are consistent with recent studies that have induced carbon starvation through experimental termination of photosynthesis while maintaining abundant irrigation (Sevanto *et al.*, 2013; Quirk *et al.*, 2013; B. Chaszar *et al.*, unpublished data; see also the Commentary by O'Grady *et al.*, 2013).

In regard to thirsty trees, Nardini *et al.* (2013) demonstrated that the safety margin between xylem water potential and the water potential threshold for cavitation was correlated with canopy loss of six angiosperm trees during a severe regional drought, suggesting an opportunity to parameterize models for mechanistically-based hydraulic failure. In another field study on mature conifers, 5 yrs of a 47% reduction in precipitation generated reduced plant capacity to acquire and utilize water after rain events, eventually leading to mortality (Plaut *et al.*, 2013); reduced uptake capacity was moderated by species-specific variation in the xylem safety margin. These two studies hint to a consistent relationship between hydraulic safety margins and tissue/whole plant mortality, and they highlight the value of capturing observations during regional drought events and during multi-year experimental manipulations

in the field, allowing realistic imposition of drought and subsequent mortality processes to unfold.

We applaud all studies that provide novel insight into the processes of mortality; however, we emphasize the fundamental scientific principle that testing multiple competing hypotheses simultaneously is essential to disprove alternative hypotheses. In the case of the carbon–water interdependency hypotheses of mortality mechanisms, a combination of both hydraulic and carbon-related measurements is required. Poyatos *et al.* (2013) found drought induced a reduction in hydraulic conductance, a large constraint on photosynthesis, subsequent carbohydrate depletion, and eventual mortality of *Pinus sylvestris*. Mortality of these trees was not associated with biotic attack, thus providing novel insight into the process of 'drought' induced mortality *per se*, and a new insight into the carbon–water interdependency of purely metabolic mortality (no biotic attack).

Modeling mortality and process interdependencies

Interest in developing and evaluating dynamic global vegetation models (DGVMs) is rapidly growing. In this issue, two papers (McDowell *et al.*, 2013; Powell *et al.*, 2013) compared simulations from several models with data from three ecosystem-scale drought manipulations – two in Amazonia (Nepstad *et al.*, 2007; da Costa *et al.*, 2010) and the other in southwestern USA (Pangle *et al.*, 2012).

Both papers concluded that models cannot yet simulate drought-induced tree mortality satisfactorily, but critical ecosystem processes can still be revealed through model–experiment tests. Powell *et al.* (2013) show that our understanding and representation of mechanisms underlying drought-induced forest mortality in the tropics are inadequate for ecosystem modeling. Representation of stomatal conductance, the hydraulic system, respiration, and appropriate mortality thresholds emerged as the processes that were particularly influential on model predictions while also having the largest uncertainty (see the Commentary by Xu *et al.*, 2013). McDowell *et al.* (2013) found that physiologically advanced models all predicted interdependence of carbon starvation and hydraulic failure (including phloem failure) in mature trees that died in the experiment described by Plaut *et al.* (2013), but these models were also challenged in simulating the hydraulic system and in capturing the interaction between carbon, water, defense, and biotic attack. These two papers are representative of a large, international effort to reduce uncertainty in predictions of mortality, and are encouraging in their positive results and motivating in their challenging results.

Consequences of mortality

In addition to regional-scale carbon, water and energy budgets, forest mortality may alter species recruitment and soil biogeochemistry. Following 'sudden oak death' caused by *Phytophthora ramorum*, altered litterfall and soil nitrogen generated shifts in the dominant plant species (Cobb *et al.*, 2013). In southwestern Colorado, USA, the consequences of post-recruitment mortality were examined across 30 sites covering a gradient of 10–100% adult piñon pine mortality (Redmond & Barger, 2013). Recruitment was positively related to overstory cover, and negatively affected by

recent mortality. These studies point to mechanisms by which recruitment changes after forest mortality, and can provide insight for DGVM simulations of recovery after disturbances.

Conclusions

This Feature Issue presents some of the most recent advances in research on forest mortality during and after drought, including the mechanisms that drive mortality and subsequent consequences. As this field evolves, we will certainly continue to uncover both exciting breakthroughs, as well as new methodological challenges. Through a continued combination of approaches – from glasshouse to field studies, small plants to large ones, manipulations and observations, model tests, and broader assessment across many PFTs and climate regimes – we can quickly advance our understanding of rapid and widespread plant mortality in the future.

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