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Key words: carbon exchange, carbon storage, global change, modeling, multi-factor experiments, $Q_{10,}$ terrestrial ecosystems, terrestrial carbon cycle.

Mechanistic causes of tree drought mortality: recent results, unresolved questions and future research needs

96th Annual Meeting, Ecological Society of America in Austin, Texas, August 2011

There is evidence that drought is occurring more frequently (Huntington, 2006), with reports of forest productivity declines (Ciais *et al.*, 2005; Phillips *et al.*, 2009) and widespread forest mortality from drought (McDowell *et al.*, 2008; van Mantgem *et al.*, 2009; Allen *et al.*, 2010). Furthermore, drought frequency and severity will likely increase in many regions in the future (IPCC, 2007). Reports of tree mortality appear to be on the rise globally and may be related to increased temperatures elevating tree drought stress and the populations of tree pests and pathogens (Allen *et al.*, 2010). The consequences of tree mortality range from changes in community structure and species interactions to landscape effects on water, carbon, and energy budgets that could disrupt biosphere–atmosphere feedbacks which are important for climate regulation (Bonan, 2008; McDowell *et al.*, 2008).

'… causes of drought mortality may be interrelated for some species, but not related for others.'

In August 2011, at the Ecological Society of America meeting in Austin, Texas, researchers investigating drought mortality presented results from experimental, modelling, and observational studies. Research included investigations of physiological mechanisms, patterns of mortality across landscapes, potential contributions of tree stress and biotic agents, and how models could incorporate mortality mechanisms. Experimental results suggest that causes of drought mortality may be interrelated for some species, but not related for others.

Despite these potential ecological impacts, the causes and physiological mechanisms of drought-induced tree mortality remain unresolved (McDowell *et al.*, 2008; Adams *et al.*, 2009; Sala, 2009; McDowell, 2011). The absence of a mechanistic understanding means that most models of global change effects on climate and vegetation do not mechanistically model tree mortality in response to drought (McDowell *et al.*, 2011). Rather, they assume tree mortality can be captured through other modelled processes such as declines in productivity, which may not accurately model the thresholds leading to death, as well as consequences of forest mortality. Clearly, there is a need to include mortality processes in coupled vegetation–climate models to more accurately predict future global carbon and water budgets.

Multiple hypotheses for the mechanisms of drought-induced forest mortality have been proposed, yet the debate over mechanisms in current literature is ongoing. Hydraulic failure and carbon starvation have been the focus of early research, though additional mechanisms of carbon mobilization and transport failure, and carbon–hydraulic interactions, among others, could occur as well (Sala *et al.*, 2010; McDowell *et al.*, 2011). Tree death via hydraulic failure occurs from drought when xylem tension is sufficient to cause lethal levels of cavitation by air embolism (McDowell *et al.*, 2008). Carbon starvation would occur for trees that regulate stomatal conductance to prevent cavitation, but with closed stomata photosynthesis is curtailed. These trees would die by depleting stored carbohydrates during drought, or through a failure to move these resources among tissues (Sala *et al.*, 2010). Results presented at a recent meeting suggest that mortality involves a combination of mechanisms, including abiotic processes as well as biotic agents such as pests and diseases, which differ among species.

Drought experiments

Drought experiments killing piñon pine (*Pinus edulis*) were well-represented at the meeting. Sanna Sevanto (Los Alamos National Laboratory, NM, USA) described a glasshouse experiment where transplanted piñons were subjected to; shading while well-watered, drought, and control treatments while total nonstructural carbohydrates (NSC) were measured. This innovative experiment examined whether reduced photosynthesis through shading could lead to carbon starvation, allowing a comparison with drought stress. Henry Adams (University of Arizona, Tucson, AZ, USA) presented results from a glasshouse experiment where transplanted piñons were droughted under ambient and elevated temperatures, a treatment that was key to discerning links between physiological response and mortality mechanism (Fig. 1a, Adams *et al.*, 2009). Differences in survival time during drought were highly temperature sensitive and associated with cumulative respiration costs, but significant xylem cavitation also occurred. This suggested that hydraulic failure and carbon starvation were interrelated in this species. William Pockman (University of New Mexico, Albuquerque, NM, USA) described the differential responses of piñon and juniper to a field experiment where treatments include a control, 50% reduction, and 50% increase in ambient precipitation. This study uniquely demonstrated that insect and fungal pests were important causal agents in initial mortality of piñon. Trees treated with pesticide experienced greater drought stress without dying, than those trees killed initially.

Two experimental studies investigated drought mortality mechanisms in broad-leaved, angiosperm species. William Anderegg (Stanford University, Palo Alto, CA, USA) conducted field experiments with both transplanted and *in situ* clonal aspen (*Populus tremuloides*) trees in Colorado, the only angiosperm study to examine a widespread drought-induced mortality as it occurred in the field (Fig. 1b). Hydraulic failure, not carbon starvation was the cause of mortality; he observed increased NSC as aboveground tree stems died. Melanie Zeppel (Macquarie University, Sydney, Australia) presented results from a glasshouse study conducted at the University of Western Sydney, on the first study to compare mortality across a rising CO_2 gradient and ambient and elevated temperatures. The study investigated sensitivity of hydraulic failure and carbon starvation in *Eucalyptus sideroxylon* trees which were grown under treatment conditions from seedlings and droughted to mortality (Fig. 1c).

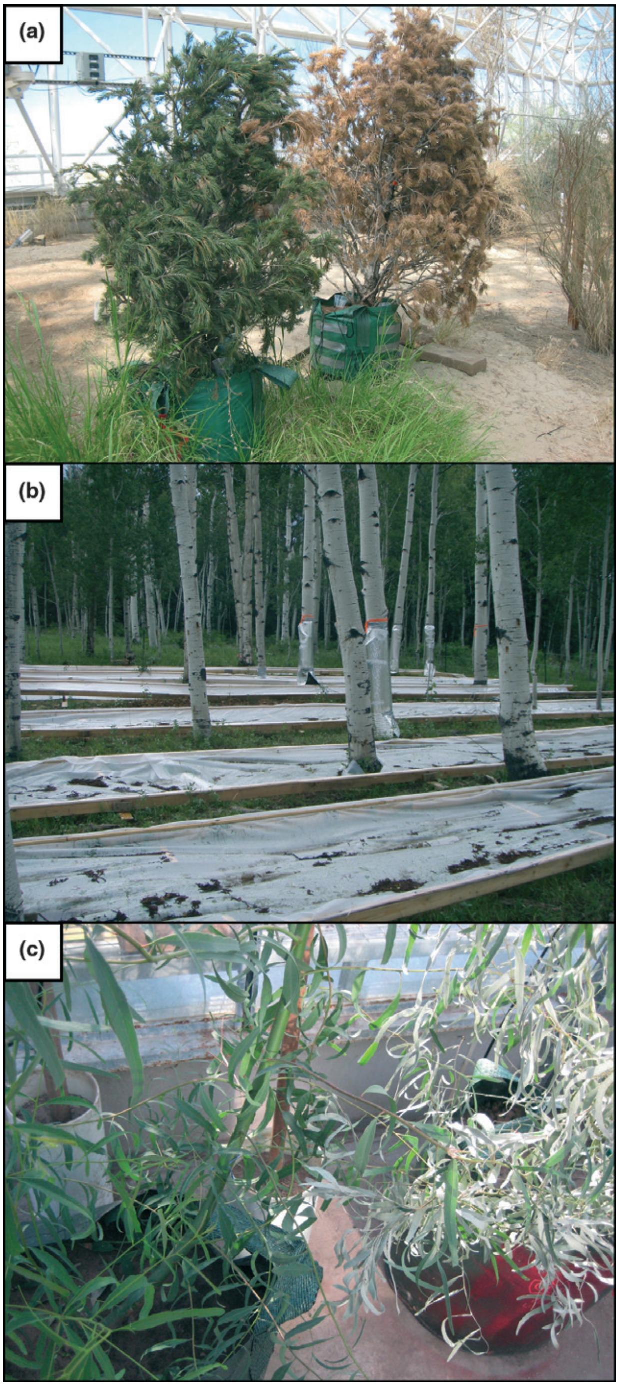

Fig. 1 Photographs of tree drought mortality research presented at the 2011 annual Ecological Society of America meeting. (a) Watered and unwatered piñon pine trees near the end of a drought experiment inside the biosphere 2 glasshouse. (b) A rain-out shelter field drought manipulation in an aspen forest in southwest Colorado. (c) Eucalyptus saplings in a glasshouse drought experiment at the University of Western Sydney, Australia.

Landscape patterns and modelling

Jeff Kane (Northern Arizona University, Flagstaff, AZ, USA) compared mortality in northern Arizona mixed-conifer forest tree species, examining topographic information, diameter, and decay class within 85 plots. He reported that relationships between mortality and size strongly depended on species and site characteristics, which may be linked to mortality causes, such as pest–host relationships. Emergence timing of Mountain pine beetle (*Dendroctonus ponderosae*) was described by Barbara Bentz (Rocky Mountain Research Station, USDA Forest Service, Logan, UT, USA), who examined developmental timing of populations and associated phloem temperatures across a range of elevations and latitudes in the western United States. Preliminary results highlight the thermal flexibility of this insect that contributes to population success in multiple habitats.

Christine Tague (University of California, Santa Barbara, CA, USA) examined responses of ponderosa pine (*Pinus ponderosa*) to warming in a New Mexico watershed using a coupled hydrological and carbon cycle model (RHESSys). By modelling NSC, RHESSys reproduced observations of mortality across the watershed indicating carbon starvation was consistent with patterns of tree mortality. Although the model did not allow for hydraulic failure, it demonstrated how a mechanistic approach to tree mortality could be integrated into a descriptive model of forest change in response to climate.

Synthesis and discussion

Considering the results of these studies provides an early synthesis of the latest results in tree drought mortality research. It has been posited that isohydric species, those which close their stomata to minimize mid-day water stress in the xylem, are more likely to die from carbon starvation, and anisohydric species, which experience mid-day xylem stress while keeping stomata open, are more likely to die of hydraulic failure (McDowell *et al.*, 2008). Yet among the four studies on three species that investigated mortality mechanisms, the results were not so clear, suggesting that mechanisms were interrelated for isohydric piñon pine, while hydraulic failure operating alone was most consistent for the angiosperm species. However, experiments which included temperature treatments demonstrated a strong sensitivity of drought mortality to temperature, with earlier mortality under warmer conditions for isohydric and anisohydric species. The temperature response presented for mountain pine beetle also suggested that the interactions of temperature effects on host physiology and tree pests are important for predicting mortality across landscapes (Kane & Kolb, 2010). Additionally, observational and modelling studies presented at the meeting highlight that linking mortality patterns to causes are key to developing predictive capability.

This research field is largely still in its infancy, and there remain some key unresolved questions. Defining death in plants presents problems, although it is a critical need in tree mortality research. It is also emerging that determining the contribution of carbon starvation as a mechanism of tree drought mortality is not simple. Among meeting presentations and the published literature, no study has yet demonstrated carbon starvation in the absence of some hydraulic failure. Quantification of both carbon fluxes and NSC pools during drought through mortality are needed as pools and fluxes can be decoupled (Sala *et al.*, 2010; Ryan, 2011). Additionally we may need to consider how NSC is actively regulated for cryoprotection, desiccation resistance, growth, and tissue signalling to completely understand the contribution of interrelated mortality mechanisms. It also remains uncertain whether the categories of 'isohydric' or 'anisohydric' stomatal behaviour are useful predictors of tree mortality mechanisms.

The presenters at the Ecological Society of America meeting described a wide range of results on drought mortality mechanisms, biotic interactions, and linkages between these processes from this growing field of research. The meeting illuminated that trees from different ecosystems responded differently to drought. This combination of broad-leaved and conifer species allows a first comparison of results from different plant functional types. There remain many opportunities for research to expand our currently limited knowledge of drought mortality mechanisms. Future research should expand outward from hydraulic failure and carbon starvation to include less-understood but perhaps important processes, including phloem transport limitation, carbon mobilization and utilization limitations, and irreversible damage to photosynthetic pathways. Additional future challenges include experimental investigation of mechanisms in more species from different environments, determining the contribution of abiotic and biotic factors, understanding recovery from near-mortality, connecting mechanisms with landscape patterns, and integrating mechanisms into coupled vegetation–climate models. The potential consequences for ecosystems and biosphere–atmosphere interactions continue to drive interest in tree drought mortality and we look forward to future research.

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