Meetings

Forest mortality due to drought: latest insights, evidence and unresolved questions on physiological pathways and consequences of tree death

97th Annual Meeting, Ecological Society of America, in Portland, Oregon, August 2012

The intensity and severity of drought is increasing globally (Huntington, 2006) and will influence forest ecosystems alongside rising temperatures, heat waves, and changing interactions between pests/pathogens and hosts (Bonan, 2008; Allen *et al.*, 2010). Understanding the mechanisms underlying drought-induced forest mortality is important for modelling water and carbon fluxes, and predicting the impacts of forest die-off on ecosystem function, ecosystem services, biogeochemical cycles, and the climate system (Adams *et al.*, 2010; Anderegg *et al.*, 2012a). At the August 2012 Ecological Society of America (ESA) meeting in Portland, Oregon there was much interest in forest mortality due to drought, with a number of excellent presentations describing both the causes and consequences of drought-induced forest mortality, including experiments, observational studies and modelling results. Many of these presentations were part of a symposium on the mechanistic causes of forest mortality due to drought and an organized oral session discussing the ecological consequences of forest mortality. We present a summary of many, but not all, of these presentations.

> *'…More research is needed on micro-climatic, hydrological, mycorrhizal and biogeochemical consequences of and feedbacks to mortality'.*

Although much attention initially focused on three nonexclusive mechanisms of mortality – drought-driven changes in biotic agent dynamics, carbon starvation through declines in nonstructural carbohydrate reserves, and hydraulic failure through tension-induced cavitation of xylem elements (McDowell *et al.*, 2008) – a growing body of research has highlighted the need for a more expansive approach to physiological mechanisms (Sala *et al.*, 2010, 2012; McDowell *et al.*, 2011; Anderegg *et al.*, 2012b). This transformation of the discourse on physiological mechanisms frames the question in a broader context and involves recognition of: (1) fundamental interdependencies between water and carbon within plants; (2) broader consideration of taxonomic, geographic, and edaphic diversity in study species examined; and (3) definitions of death in a manner appropriate to a tree as a life form. A tree is a complex organism shaped by millions of years of evolutionary trade-offs. Thus, how a tree dies during drought is likely to be a complex process (Manion, 1991) – a cascade of multiple failures in multiple subsystems. Which processes act and the extent to which they influence mortality is likely to vary with drought type and sequence, soil and site characteristics, and tree ontogenetic stage, all of which need greater study. Finally, the interacting effects of drought with other global change effects – including CO_2 increases, temperature increases, changes in fire, nitrogen deposition, shifting biotic agent demographics, and nonnative species – are a key uncertainty in forest demographic and mortality dynamics.

The consequences of drought-induced forest die-off can be manifold for ecosystems, society, and the climate system. Tree mortality has effects that span the range of ecological organization across populations, communities, and ecosystems, and even biosphere–atmosphere feedbacks. Specifically, tree mortality can impact biodiversity, ecosystem function, such as nutrient and carbon cycling, ecosystem services provided to humans, and biophysical and biogeochemical climate feedbacks (Adams *et al.*, 2010; Anderegg *et al.*, 2012a). The ecological effects of forest die-off are not yet fully understood, often due to the contrasting changes wrought by tree mortality. For example, tree mortality can both relieve competition and reduce facilitation in plant communities, leading to counter-acting forces on understory plants. The consequences of forest die-off remain an active area of research which has received little attention outside of North America (Anderegg *et al.*, 2012a).

Physiological pathways of drought-induced mortality

At the annual ESA meeting, several speakers summarized the state of investigation into the physiology of tree drought mortality, and challenged the framework common to much recent research. Nate McDowell (Los Alamos National Laboratory, New Mexico, USA) provided an overview of many remaining questions regarding the processes and end-points of drought-induced mortality. He urged researchers to test multiple, rather than single hypotheses. Anna Sala (University of Montana, Missoula, USA) challenged the way we think about modelling tree growth, and reviewed the literature examining minimum thresholds of nonstructural carbohydrates (NSC) under multiple environmental stresses (Sala *et al.*, 2012). Michael Ryan (Colorado State University, Fort Collins, USA) discussed the roles of NSC in plant carbon balance and challenged interpretation of NSC concentrations without accounting for plant or tissue mass and NSC flux among tissues within a plant (Ryan, 2011).

Regarding experimental examination of mortality mechanisms, William Anderegg (Stanford University, California, USA) described a multi-year experiment, highlighting why it is important to consider extended periods, and time lags. Death 7-yr after a drought highlighted the complex cascade of interactions between hydraulic failure and carbon fluxes and pools. Henrik Hartmann (Max Plank Institute, Germany) described a conifer experiment from Germany which included three treatments: continuous drought, drought/irrigation cycles, and continuously irrigated control. He found that carbon metabolism in belowground tissues was related to mortality mechanism. Don White (CSIRO, Australia) presented the water relations of eucalypts and pines. He suggested that turgor loss point may be a key trait to measure in drought studies, and proposed thresholds of drought mortality for incorporation into models, specifically CABALA, a carbon balance model for predicting tree growth. Libby Pinkard (CSIRO, Australia) presented the results of an experiment combining defoliation and drought with *Eucalyptus globulus* and showed that responses to these two stresses were dynamically related. David Galvez (University of Alberta, Canada) placed *Populus tremuloides* and *P. balsamifora* seedlings under low temperature and drought stress and found physiological indication of mortality by mechanisms' interactions with seasonality of winter freezing. David Tissue (University of Western Sydney, Australia) described the interactive effects of elevated CO_2 temperatures and drought on mortality in *Eucalyptus sideroxylon* (Zeppel *et al.*, 2012) as well as the effect of heat waves on conifers and angiosperms. Todd Dawson (University of California, Berkley, USA) presented a risk matrix of mortality in Fynbos species based on rooting depth and degree of iso/anisohydry, which allowed a functional classification of drought response pathways in this flora (West *et al.*, 2012).

A number of talks described an ongoing 5-yr experimental manipulation at Sevilleta LTER in New Mexico in a piñon pine–juniper woodland that includes drought and precipitation addition treatments. Jenn Plaut (University of New Mexico, Albuquerque, USA) showed that species differences in drought response, specifically stomatal conductance, were related to differences in survival during drought. Patrick Hudson (University of New Mexico, Albuquerque, USA) presented research examining changes in the hydraulic vulnerability curves for these two species. Monica Gaylord (Northern Arizona University, Flagstaff, USA) demonstrated that tree pests, including bark beetles were nearly always associated with mortality. Turin Dickman (University of New Mexico, Albuquerque, USA) compared NSC responses from the Sevilleta experiment to a glasshouse experiment also conducted with piñon pine. She related time-to-mortality during drought to NSC dynamics, indicating that a role for carbon metabolism in mortality of some trees but not others, regardless of species.

Several talks examined models of physiological pathways leading to mortality. Maurizio Mencuccini (University of Edinburgh, UK) presented preliminary results from a xylem-phloem model based on the work of Hölttä *et al.* (2009) to examine the potential for hydraulic failure, carbon starvation, and phloem transport failure in steady state. Brent Ewers (University of Wyoming, Laramie, USA) presented on plant hydraulic theory in the model TREEScav to predict changes in plant hydraulics, evapotranspiration, and net ecosystem exchange across soils, elevation and level of mountain pine beetle-induced mortality.

Consequences of tree mortality

A broad array of talks examined various aspects of the consequences of tree mortality. A number of presentations described Alaskan forests, discussing the growth rate collapse and mortality resulting from drought, insect attack (Rosemary Sherriff, Humboldt State University, Arcata, CA USA) and high temperatures (Glenn Juday, University of Alaska Fairbanks, USA). Amy Whipple (Northern Arizona University, Flagstaff, USA) described links between drought related mortality, genetics, herbivory and mycorrhizal fungi in a piñon pine–juniper woodland.

Finally, speakers discussed the hydrological consequences of forest mortality in different ecosystems. Paul Brooks (University of Arizona, Tucson, USA) detailed the effects of forest mortality on ecohydrology, including implications for water budgets and biogeochemical changes across multiple spatial scales, while John Frank (United States Forest Service, USA) detailed the effects of spruce/fir mortality on transpiration. David Clow (United States Geological Survey, USA) presented on changes to soil and water chemistry in response to pine beetle induced mortality.

Brian Harvey (University of Wisconsin-Madison, USA) showed that despite looking for a relationship, in Douglas fir trees in the Greater Yellowstone region, between percentage of dead trees and fire severity, no relationship was apparent, an important and unexpected conclusion. Jeff Kane (Northern Arizona University, Flagstaff, USA) described the effects of juniper mortality on plant community composition and diversity, including increased invasion by nonnative grasses (Kane *et al.*, 2011).

Outstanding issues and research gaps

A number of key outstanding issues ran through many of the presentations during the meeting. First, clear and quantitative descriptions of how drought was defined, implemented, and measured during experimental and observational studies would greatly facilitate comparison across species and regions. Second, a clear and concrete definition of tree mortality remains an important challenge in the field, as it both influences experimental results and allows for comparison of multiple studies (Anderegg *et al.*, 2012b). Third, care must be taken to define and separate proximate causes of mortality from other feedbacks and more distal causes, distinguishing among processes within a relevant framework (Manion, 1991; McDowell *et al.*, 2011; Anderegg *et al.*, 2012b) while avoiding false dichotomies among interrelated hypothesized mechanisms (i.e. the incorrect interpretation of McDowell *et al.*, 2008 as carbon starvation vs hydraulic failure, McDowell *et al.*, 2011). Fourth, we need a broader consideration of the carbon dynamics of plants and their relation to mortality for carbohydrate pools in multiple tissues and at the whole plant level, and for the carbon demands of growth, maintenance and growth respiration, defence compounds, embolism refilling, including nonmetabolic functions of phloem loading, signalling, and osmoregulation. More research is also needed on micro-climatic, hydrological, mycorrhizal and biogeochemical consequences of and feedbacks to mortality. Finally, as much of the presented research focused on western North America, more research is needed in a broader variety and scope of systems with greater geographic, taxonomic, and edaphic diversity.

Future collaborative projects

Two organizational meetings related to tree mortality occurred at the annual ESA conference, aiming to facilitate future collaborative work. An National Science Foundation (NSF) funded, international project called the Drought Open Source Ecology project, involving collaborators across the United States, Europe and Australia, is underway examining the impact of the 2012 drought season across a global scale, using, simple easily measured data collected before and during drought (contact anderegg@standford.edu for details). A group interested in a multi-species comparison and synthesis of tree drought mortality physiology research met to initiate their collaboration at the recent meeting (contact adamshd@lanl.gov for details).

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Key words: biosphere–atmosphere interactions, carbon cycling, carbon starvation, climate change, forest die-off, hydraulic failure, plant hydraulics.