Meetings

Research frontiers in drought-induced tree mortality: crossing scales and disciplines

International Interdisciplinary Workshop on Tree Mortality, Jena, Germany, October 2014

Sudden and widespread forest die-back and die-off (e.g. Huang & Anderegg, 2012) and increased mortality rates (e.g. Peng *et al.*, 2011) in many forest ecosystems across the globe have been linked to drought and elevated temperatures (Allen *et al.*, 2010; Fig. 1). These observations have caused a focus on the physiological mechanisms of drought-induced tree mortality (e.g. McDowell *et al.*, 2008) and many studies, both observational and manipulative, have been carried out to explain tree death during drought from a physiological perspective (see Table 1 for examples). While it can be difficult to extract a common explanation for these recent papers, an emerging message appears to be that hydraulic failure almost always matters, while the role of carbon starvation and pest attack remain uncertain. Despite this recent wealth of research on the interplay of physiological mechanisms of drought-induced tree death (McDowell, 2011), there are still major knowledge gaps limiting understanding of widespread tree mortality and its prediction in a changing climate. For example, we still do not know answers to basic questions like: (1) whether mortality is increasing globally; (2) why some trees survive and others die in a given drought; (3) which components of tree physiology are critical to modeling tree mortality; and (4) what types and elements of drought are most important in predicting mortality.

'*. . . global trends in tree mortality and their potential to have ecological and climatalogical consequences remain highly uncertain . . .*'

Interdisciplinary approaches are required for maintaining research progress

While tree death is a phenomenon occurring at the organism level, forest mortality comprises processes that span across spatial, organizational and temporal scales. Because many different disciplines are involved across these scales, interdisciplinary approaches are required for maintaining research progress. To facilitate collaboration across disciplines, an International Interdisciplinary Workshop on Tree Mortality was recently held at the Max-Planck Institute (MPI) for Biogeochemistry in Jena, Germany. By bringing together scientists from a wide range of disciplines, the workshop aimed to: (1) brainstorm and identify research needs, in terms of conceptual and theoretical questions but also on methodological issues; (2) develop concrete research ideas; (3) establish networks for future collaborations; and (4) organize the writing of proposals and synthesis papers.

Burning questions on drought-induced tree mortality

More than 60 leading scientists from 18 different countries and from six continents gathered at the MPI in Jena. Participants brought a diversity of expertise in a wide range of disciplines, scales of observation/experimentation, and the geographical focus of study, providing an excellent basis for synthesizing the current state of knowledge but also for identifying knowledge gaps and research needs.

Several key areas of research received much discussion in the workshop and participants identified, during individual breakout sessions, the need to: (1) compile and analyze the ecological and societal consequences of drought-induced tree mortality; (2) define tree death from a functional perspective; (3) identify traits that allow drought avoidance or facilitate drought recovery; (4) define interdisciplinary future research avenues as a means to speed up progress; and (5) monitor global tree mortality and investigate mechanisms and processes in hot spot areas.

Consequences of tree mortality were addressed with a focus on post-disturbance ecological trajectories, as any consequences will ultimately depend on community and ecosystem processes that follow tree mortality (Adams *et al.*, 2012; Anderegg *et al.*, 2013a). The wide variety of research specialties and geographic expertise among members of this research group fostered a discussion comparing and contrasting variation in mortality agents (e.g. drought, temperature, insects, pathogens), ecological transitions following tree mortality, and post-mortality interactions with other disturbances (e.g. wildfire, harvesting), for multiple ecosystems from around the world. A lack of scientifically-informed guidance for land managers facing elevated or widespread tree die-off emerged as a key research gap from this discussion.

The definition of tree death, which greatly influences our conceptual framework for designing experiments and monitoring mortality, but is also essential to model forest die-back (Anderegg *et al.*, 2012a), was addressed in another breakout group meeting. While hydraulic failure and declining carbon availability are generally considered to be major mechanisms that may force a tree to the point of no recovery, our understanding of lethal levels of embolism (Urli *et al.*, 2013) and whether trees require a critical

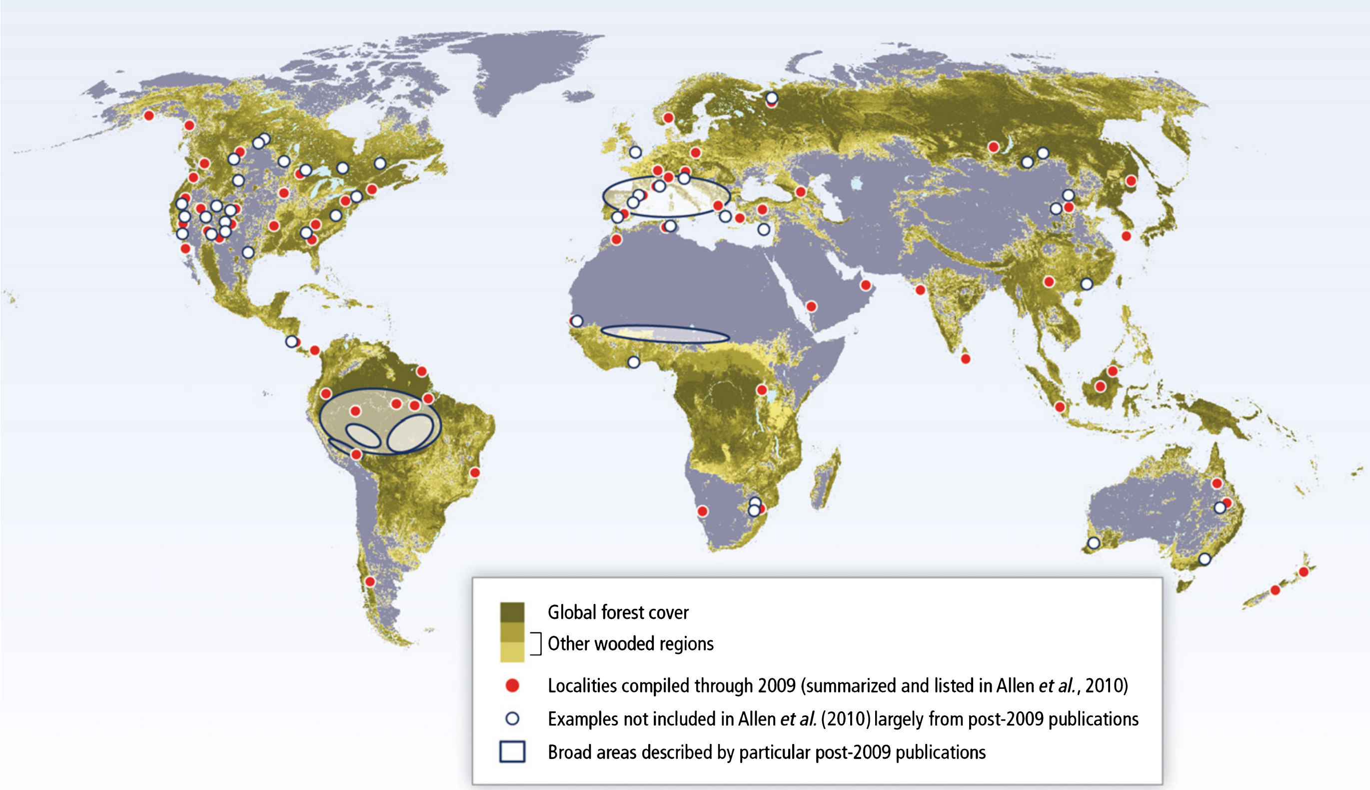

Fig. 1 Locations of substantial drought- and heat-induced tree mortality around the globe since 1970 (global forest cover and other wooded regions based on FAO, 2005). Studies compiled through 2009 (red dots) are summarized and listed in Allen *et al.* (2010). Localities and measurement networks not included in Allen *et al.* (2010), which are largely from post-2009 publications, have been added to this map (white dots and shapes) © IPCC. Fig. 4-7 from Settele *et al.* (2014 and references within).

Table 1 A summary of recent experimental and observational research on the physiology of drought-induced tree mortality

Study	Type of study	Species	Location
Adams *et al.* (2009, 2013)	Experiment	*Pinus edulis*	Arizona, USA
Anderegg *et al.* (2012b, 2013b)	Observational	*Populus tremuloides*	Colorado, USA
Anderegg & Anderegg (2013)	Experiment	*Juniperus osteosperma, Pinus edulis*	Colorado, USA
Breshears *et al.* (2009)	Observational	*Pinus edulis*	New Mexico, USA
Duan *et al.* (2013)	Experiment	*Eucalyptus radiata*	New South Wales, Australia
Fisher *et al.* (2007)	Experiment	Multiple tropical tree species	Brazil
Galiano *et al.* (2011)	Observational	*Pinus sylvestris*	Spain
Galvez *et al.* (2013)	Experiment	*Populus balsamea, Populus tremuloides*	Alberta, Canada
Gaylord *et al.* (2013)	Experiment	*Pinus edulis*	New Mexico, USA
Hartmann *et al.* (2013a,b)	Experiment	*Picea abies*	Germany
Metcalfe *et al.* (2010)	Experiment	Multiple tropical tree species	Brazil
Mitchell *et al.* (2013)	Experiment	*Eucalyptus globulus, Eucalyptus smithii, Pinus radiata*	Tasmania, Australia
O'Brien *et al.* (2014, 2015)	Experiment	Multiple tropical tree species	Malaysia
Piper (2011)	Experiment	*Nothofagus dombeyi, Nothofagus nitida*	Chile
Plaut *et al.* (2012), Dickman *et al.* (2014)	Experiment	*Pinus edulis*	New Mexico, USA
Quirk *et al.* (2013)	Experiment	*Sequoia sempervirens*	UK
Sevanto *et al.* (2014)	Experiment	*Pinus edulis*	New Mexico, USA

This list is not comprehensive and comprises mainly studies focused on carbon starvation or hydraulic failure causes of mortality.

amount of carbon availability, needs more research and consideration of a larger taxonomic range of species. It was also emphasized that more research is needed to quantify cellular death. A cellular focus on plant death tied to whole-plant physiology also challenges our understanding of vascular transport, xylem–phloem interactions, and connectivity between aboveground and belowground tissues. In fact, plants may be highly segmented with an independently redundant modular design at different anatomical and developmental scales (Schenk *et al.*, 2008), which means that various organs or tissues may fatally desiccate while other tissues such as apical, cambial and/or root meristems may survive and will keep a plant alive. Finally, chlorophyll fluorescence was suggested as one promising parameter to predict mortality for evergreen and non-resprouting plant species, especially if remote sensing data for large forest areas will become available (e.g. NASA's carbon mapping satellite OCO-2).

Unresolved questions remain around costs, trade-offs and life history strategies that allow mortality avoidance and recovery from severe drought stress. It was hypothesized that some plants use different structures, processes and life-history strategies to *avoid* stress. These strategies may include isohydry, rooting depth, hydraulic segmentation and the hydraulic fuse hypothesis (Bucci *et al.*, 2012; West *et al.*, 2012; Thomsen *et al.*, 2013). By contrast, it was hypothesized that other plants *tolerate* high levels of stress, or percent loss of conductivity in the xylem and subsequently *recover* from this drought-stress using the strategies of aboveground or belowground resprouting (Zeppel *et al.*, 2014) or embolism repair (Brodersen & McElrone, 2013). However, the costs, trade-offs and life history strategies involved in recovery remain a key research gap but also a prerequisite for developing better models of tree mortality.

Detailed physiological knowledge gaps and research needs at larger organizational and spatial scales have been identified elsewhere already (e.g. Allen *et al.*, 2010; McDowell, 2011). However, there has been very little progress in filling these gaps or in directing research efforts in these directions. Past research may have been focusing too much on specific processes (carbon starvation vs hydraulic failure) and a more holistic approach of research may be required for both developing mitigating strategies and for improving our understanding of the underlying processes. Focusing on hot spots of drought-induced tree mortality as study systems, a combination of field assessments and manipulative experiments both in the field and in the laboratory will provide empirical data on thresholds of drought tolerance as a management tool but will also yield mechanistic insights into tree mortality useful for modeling.

Global trends in tree mortality and its potential to have ecological and climatalogical consequences remain highly uncertain

The participants of the workshop recognized that 4 yr following an assessment documenting the global extent of widespread tree mortality (Allen *et al.*, 2010), there is yet no forest health assessment to determine whether tree mortality is increasing globally, or whether it can be attributed to increasing drought or temperatures. Therefore, global trends in tree mortality and their potential to have ecological and climatalogical consequences remain highly uncertain. To determine the patterns and trends of forest mortality, researchers urged the development of a global-scale monitoring network on forest conditions. Such data are considered not only critical to motivate action from governments, policy-makers and forest managers but also to devise specific action strategies to mitigate the problem. Challenges to be considered here include: (1) access to large inventory networks from both the public and the private sector; and (2) obtaining data for forested areas not regularly or not at all inventoried. For such forests, remote sensing data may be the only feasible strategy, but ground validation of satellite data is difficult in many regions. Securing access to inventory data requires collaboration among forest managers, policy-makers and scientists which must be initiated at high administrative or even political levels. Participants at the workshop acknowledged the amplitude of such an initiative and the need for further discussions on these issues. A working group has been charged with the funding and organization of a follow-up workshop focusing on the coordination of a global monitoring network. Please visit https://www.bgc-jena.mpg.de/bgp/index.php/Main/MortalityWorkshop for information on further developments.

Setting a final keynote to the workshop, Christian Körner (University of Basel, Switzerland) gave an insightful closing lecture on the unlikelihood of general carbon limitation in trees and hence of carbon starvation as a causal mechanism in drought-induced mortality. Although the evidence he presented was not interpreted as a refutation of carbon starvation by all participants, his thoughts surely highlighted the need for future research to consider a much broader range of processes than carbon starvation vs hydraulic failure (Table 1). Major challenges ahead that researchers working on tree mortality will need to address over the next years include xylem–phloem (hydraulic–carbon) interactions, lethal embolism stress thresholds, potential recovery of xylem, genetic and epigenetic mechanisms associated with tree aging and fitness, morphological constraints or adaptations to senescence and death at the whole plant level (e.g. resprouting capacity, production of durable organs vs organ replacement), pests and pathogens, species interactions as well as ecological and societal consequences of mortality.

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