LA-UR-14-29321 (Accepted Manuscript)

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

Hartmann, Henrik
Adams, Henry David
Anderegg, William
Jansen, Steve
Zeppel, Melanie

Provided by the author(s) and the Los Alamos National Laboratory (2016-02-18).

To be published in: NEW PHYTOLOGIST ; Vol.205, iss.3, p.965-969, FEB 2015

DOI to publisher's version: 10.1111/nph.13246

Permalink to record: http://permalink.lanl.gov/object/view?what=info:lanl-repo/lareport/LA-UR-14-29321

Disclaimer:
Approved for public release. Los Alamos National Laboratory, an affirmative action/equal opportunity employer, is operated by the Los Alamos National Security, LLC for the National Nuclear Security Administration of the U.S. Department of Energy under contract DE-AC52-06NA25396. Los Alamos National Laboratory strongly supports academic freedom and a researcher's right to publish; as an institution, however, the Laboratory does not endorse the viewpoint of a publication or guarantee its technical correctness.

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

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

Word count: 1784

Tables: 1

Figures: 1

Keywords: interdisciplinary, stress, global warming, plant-water relations, carbon availability, desiccation, remote sensing, biotic agents

Drought-induced tree death mechanisms remain uncertain

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). 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.

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 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 6 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 dieback (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 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). In contrast, it was hypothesized that others 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 above- or below-ground 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.

Another major discussion revolved 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, including isohydry, rooting depth, hydraulic segmentation and the hydraulic fuse hypothesis (Bucci *et al.*, 2012; West *et al.*, 2012; Thomsen *et al.*, 2013), while others 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 above- or below-ground resprouting (Zeppel *et al.*, 2014) or embolism repair (Brodersen & McElrone, 2013).

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 lab 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 climatological consequences remain highly uncertain

The participants of the workshop recognized that four years 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 climatological 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. 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 Koerner (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 ageing 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.

Acknowledgements

The authors thank all participants of the workshop for valuable discussions and contributions. SJ acknowledges the German Research Foundation (DFG) for financial support. HDA was supported by the Los Alamos National Laboratory LDRD program, and the U.S. Department of Energy Office of Science, Biological and Environmental Research.

Henrik Hartmann[1*], Henry D. Adams[2], William R.L. Anderegg[3], Steven Jansen[4] and Melanie Zeppel[5]

[1]Department of Biogeochemical Processes, Max-Planck Institute for Biogeochemistry, Hans-Knoll Str. 10, 07745 Jena, Germany; [2]Earth and Environmental Sciences, Los Alamos National Laboratory, Los Alamos, NM 87545, USA; [3]Princeton Environmental Institute, Princeton University, Princeton NK 08544, USA; [4]Institute for Systematic Botany and Ecology, Ulm University, D-89081 Ulm, Germany; [5]Department of Biological Sciences, Macquarie University, NSW, Australia.

(*Author for correspondence: email hhart@bgc-jena.mpg.de; tel: +49 3641 576294)

References

Adams HD, Germino MJ, Breshears DD, Barron-Gafford GA, Guardiola-Claramonte M, Zou CB, Huxman TE. 2013. Nonstructural leaf carbohydrate dynamics of Pinus edulis during drought-induced tree mortality reveal role for carbon metabolism in mortality mechanism. *New Phytologist* **197**(4): 1142-1151.

Adams HD, Guardiola-Claramonte M, Barron-Gafford GA, Villegas JC, Breshears DD, Zou CB, Troch PA, Huxman TE. 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences* **106**(17): 7063-7066.

Adams HD, Luce CH, Breshears DD, Allen CD, Weiler M, Hale VC, Smith AMS, Huxman TE. 2012. Ecohydrological consequences of drought- and infestation- triggered tree die-off: insights and hypotheses. *Ecohydrology* **5**(2): 145-159.

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH, et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* **259**(4): 660-684.

Anderegg WRL, Anderegg LDL. 2013. Hydraulic and carbohydrate changes in experimental drought-induced mortality of saplings in two conifer species. *Tree Physiology* **33**(3): 252-260.

Anderegg WRL, Berry JA, Field CB. 2012a. Linking definitions, mechanisms, and modeling of drought-induced tree death. *Trends in Plant Science* **17**(12): 693-700.

Anderegg WRL, Berry JA, Smith DD, Sperry JS, Anderegg LDL, Field CB. 2012b. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *Proceedings of the National Academy of Sciences* **109**(1): 233-237.

Anderegg WRL, Kane JM, Anderegg LDL. 2013a. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Clim. Change* **3**(1): 30-36.

Anderegg WRL, Plavcová L, Anderegg LDL, Hacke UG, Berry JA, Field CB. 2013b. Drought's legacy: multiyear hydraulic deterioration underlies widespread aspen forest die-off and portends increased future risk. *Global Change Biology* **19**(4): 1188-1196.

Breshears DD, Myers OB, Meyer CW, Barnes FJ, Zou CB, Allen CD, McDowell NG, Pockman WT. 2009. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Frontiers in Ecology and the Environment* **7**(4): 185-189.

Brodersen CR, McElrone AJ. 2013. Maintenance of xylem network transport capacity: a review of embolism repair in vascular plants. *Front Plant Sci* **4**.

Bucci SJ, Scholz FG, Campanello PI, Montti L, Jimenez-Castillo M, Rockwell FA, Manna LL, Guerra P, Bernal PL, Troncoso O, et al. 2012. Hydraulic differences along the water transport system of South American Nothofagus species: do leaves protect the stem functionality? *Tree Physiology*.

Dickman LT, McDowell NG, Sevanto S, Pangle RE, Pockman WT. 2014. Carbohydrate dynamics and mortality in a piñon-juniper woodland under three future precipitation scenarios. *Plant, Cell & Environment*: n/a-n/a.

Duan H, Amthor JS, Duursma RA, O'Grady AP, Choat B, Tissue DT. 2013. Carbon dynamics of eucalypt seedlings exposed to progressive drought in elevated [CO2] and elevated temperature. *Tree Physiology* **33**(8): 779-792.

FAO 2005. Global forest resources assessment 2005—progress towards sustainable forest management. FAO Forestry Paper 147. Rome.

Fisher RA, Williams M, Da Costa AL, Malhi Y, Da Costa RF, Almeida S, Meir P. 2007. The response of an Eastern Amazonian rain forest to drought stress: results and modelling analyses from a throughfall exclusion experiment. *Global Change Biology* **13**(11): 2361-2378.

Galiano L, Martínez-Vilalta J, Lloret F. 2011. Carbon reserves and canopy defoliation determine the recovery of Scots pine 4 yr after a drought episode. *New Phytologist* **190**(3): 750-759.

Galvez DA, Landhäusser SM, Tyree MT. 2013. Low root reserve accumulation during drought may lead to winter mortality in poplar seedlings. *New Phytologist*: n/a-n/a.

Gaylord ML, Kolb TE, Pockman WT, Plaut JA, Yepez EA, Macalady AK, Pangle RE, McDowell NG. 2013. Drought predisposes piñon–juniper woodlands to insect attacks and mortality. *New Phytologist* **198**(2): 567-578.

Hartmann H, Ziegler W, Kolle O, Trumbore S. 2013a. Thirst beats hunger – declining hydration during drought prevents carbon starvation in Norway spruce saplings. *New Phytologist* **200**(2): 340-349.

Hartmann H, Ziegler W, Trumbore S. 2013b. Lethal drought leads to reduction in nonstructural carbohydrates in Norway spruce tree roots but not in the canopy. *Functional Ecology* **27**(2): 413-427.

Huang C-Y, Anderegg WRL. 2012. Large drought-induced aboveground live biomass losses in southern Rocky Mountain aspen forests. *Global Change Biology* **18**(3): 1016-1027.

McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG, et al. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* **178**(4): 719-739.

McDowell NG. 2011. Mechanisms Linking Drought, Hydraulics, Carbon Metabolism, and Vegetation Mortality. *Plant Physiology* **155**(3): 1051-1059.

Metcalfe DB, Meir P, Aragão LEOC, Lobo-do-Vale R, Galbraith D, Fisher RA, Chaves MM, Maroco JP, da Costa ACL, de Almeida SS, et al. 2010. Shifts in plant respiration and carbon use efficiency at a large-scale drought experiment in the eastern Amazon. *New Phytologist* **187**(3): 608-621.

Mitchell PJ, O'Grady AP, Tissue DT, White DA, Ottenschlaeger ML, Pinkard EA. 2013. Drought response strategies define the relative contributions of hydraulic dysfunction and carbohydrate depletion during tree mortality. *New Phytologist* **197**(3): 862-872.

O'Brien MJ, Burslem DFRP, Caduff A, Tay J, Hector A. 2014a. Contrasting nonstructural carbohydrate dynamics of tropical tree seedlings under water deficit and variability. *New Phytologist*: n/a-n/a.

O'Brien MJ, Leuzinger S, Philipson CD, Tay J, Hector A. 2014b. Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. *Nature Clim. Change* **advance online publication**.

Peng C, Ma Z, Lei X, Zhu Q, Chen H, Wang W, Liu S, Li W, Fang X, Zhou X. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Clim. Change* **1**(9): 467-471.

Piper F. 2011. Drought induces opposite changes in the concentration of non-structural carbohydrates of two evergreen Nothofagus species of differential drought resistance. *Annals of Forest Science* **68**(2): 415-424.

Plaut JA, Yepez EA, Hill J, Pangle R, Sperry JS, Pockman WT, McDowell NG. 2012. Hydraulic limits preceding mortality in a piñon–juniper woodland under experimental drought. *Plant, Cell & Environment* **35**(9): 1601-1617.

Quirk J, McDowell NG, Leake JR, Hudson PJ, Beerling DJ. 2013. Increased susceptibility to drought-induced mortality in Sequoia sempervirens (Cupressaceae) trees under Cenozoic atmospheric carbon dioxide starvation. *American Journal of Botany* **100**(3): 582-591.

Schenk HJ, Espino S, Goedhart CM, Nordenstahl M, Cabrera HIM, Jones CS. 2008. Hydraulic integration and shrub growth form linked across continental aridity gradients. *Proceedings of the National Academy of Sciences* **105**(32): 11248-11253.

Settele J, Scholes R, Betts R, Bunn SE, Leadley P, Nepstad D, Overpeck JT, Taboada MA 2014. Terrestrial and inland water systems. In: Field CB, Barros VR, Dokken DJ, Mach KJ, Mastrandrea MD, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES, Levy AN, MacCracken S, Mastrandrea PR, White LL eds. *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel of Climate Change*. Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press, 271-359.

Sevanto S, McDowell NG, Dickman LT, Pangle R, Pockman WT. 2013. How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. *Plant, Cell & Environment*: n/a-n/a.

Thomsen JE, Bohrer G, Matheny AM, Ivanov VY, He L, Renninger HJ, Schäfer KVR. 2013. Contrasting hydraulic strategies during dry soil conditions in Quercus rubra and Acer rubrum in a sandy site in Michigan. *Forests* **4**(4): 1106-1120.

Urli M, Porté AJ, Cochard H, Guengant Y, Burlett R, Delzon S. 2013. Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. *Tree Physiology*.

West AG, Dawson TE, February EC, Midgley GF, Bond WJ, Aston TL. 2012. Diverse functional responses to drought in a Mediterranean-type shrubland in South Africa. *New Phytologist* **195**(2): 396-407.

Zeppel MJB, Harrison S, Adams HD, Li G, Kelley DI, West A, Dawson TE, R. F, Medlyn B, Palmer AR, et al. 2014. Drought and resprouting plants. *New Phytologist* **In Press**.

Table 1. A summary of recent experimental and observational research on the physiology of drought-induced tree mortality. This list is not comprehensive and comprises mainly studies focused on carbon starvation or hydraulic failure causes mortality.

Study	Type of Study	Species	Location
(Adams *et al.*, 2009; Adams *et al.*, 2013)	Experiment	*Pinus edulis*	Arizona, USA
(Anderegg *et al.*, 2012b; Anderegg *et al.*, 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, Austalia
(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; Hartmann *et al.*, 2013b)	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.*, 2014a; O'Brien *et al.*, 2014b)	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.*, 2013)	Experiment	*Pinus edulis*	New Mexico, USA

Fig. 1

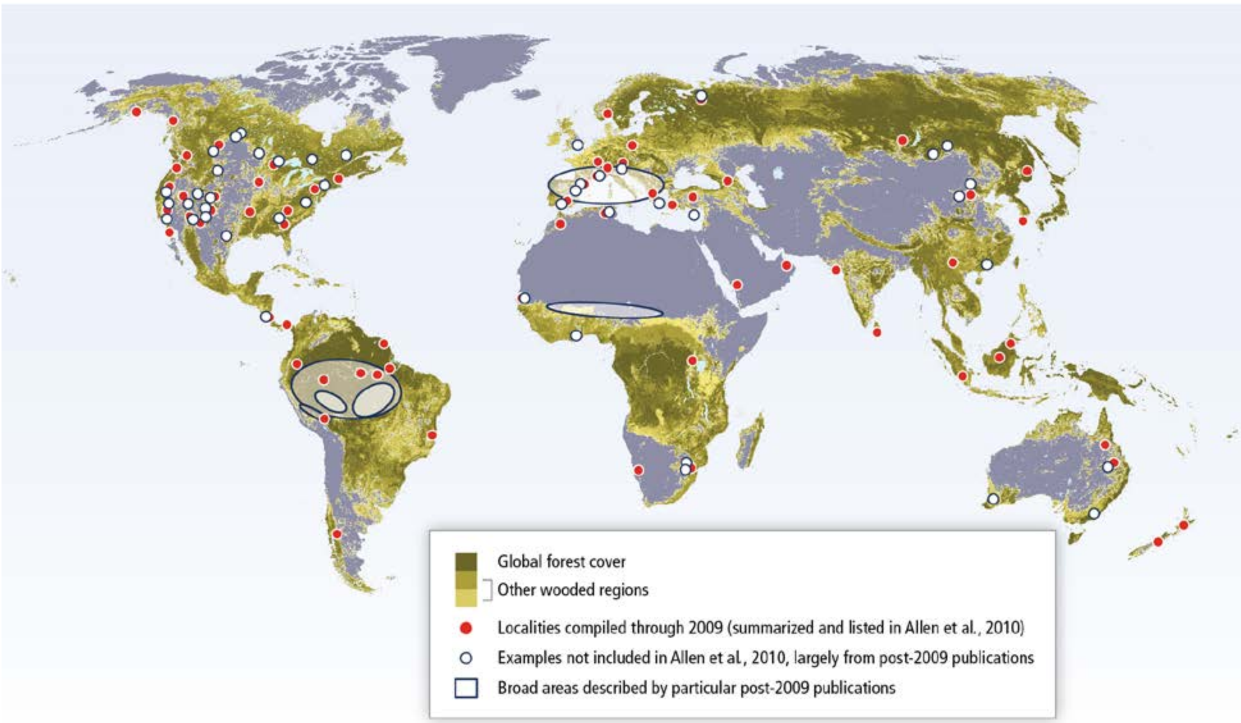

Fig. 1 Locations of substantial drought- and heat-induced tree mortality around the globe since 1970 (global forest cover and other wooded regions based on FAO, 2005). Studies compiled through 2009 (red dots) are summarized and listed in Allen, C.D. et al. (2010). Localities and measurement networks not included in Allen, C.D. 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).