



Research frontiers for improving our understanding of drought-induced tree and forest mortality

Henrik Hartmann, Catarina F. Moura, William R. L. Anderegg, Nadine K. Ruehr, Yann Salmon, Craig D. Allen, Stefan K. Arndt, David D. Breshears, Hendrik Davi, David Galbraith, et al.

► To cite this version:

Henrik Hartmann, Catarina F. Moura, William R. L. Anderegg, Nadine K. Ruehr, Yann Salmon, et al.. Research frontiers for improving our understanding of drought-induced tree and forest mortality. New Phytologist, 2018, 218 (1), pp.15 - 28. 10.1111/nph.15048 . hal-02626328

HAL Id: hal-02626328

<https://hal.inrae.fr/hal-02626328>

Submitted on 1 Jan 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



UNIVERSITY OF LEEDS

This is a repository copy of *Research frontiers for improving our understanding of drought-induced tree and forest mortality*.

White Rose Research Online URL for this paper:
<http://eprints.whiterose.ac.uk/127770/>

Version: Accepted Version

Article:

Hartmann, H, Moura, CF, Anderegg, WRL et al. (19 more authors) (2018) Research frontiers for improving our understanding of drought-induced tree and forest mortality. *New Phytologist*, 218 (1). pp. 15-28. ISSN 0028-646X

<https://doi.org/10.1111/nph.15048>

© 2018 The Authors. *New Phytologist* © 2018 New Phytologist. This is the peer reviewed version of the following article: Hartmann, H., et al., (2018), Research frontiers for improving our understanding of drought-induced tree and forest mortality. *New Phytol*, 218: 15–28.; which has been published in final form at <https://doi.org/10.1111/nph.15048>. This article may be used for non-commercial purposes in accordance with the Wiley Terms and Conditions for Self-Archiving.

Reuse

Unless indicated otherwise, fulltext items are protected by copyright with all rights reserved. The copyright exception in section 29 of the Copyright, Designs and Patents Act 1988 allows the making of a single copy solely for the purpose of non-commercial research or private study within the limits of fair dealing. The publisher or other rights-holder may allow further reproduction and re-use of this version - refer to the White Rose Research Online record for this item. Where records identify the publisher as the copyright holder, users can verify any specific terms of use on the publisher's website.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.



eprints@whiterose.ac.uk
<https://eprints.whiterose.ac.uk/>



Research frontiers for improving our understanding of drought-induced tree and forest mortality

Journal:	<i>New Phytologist</i>
Manuscript ID	NPH-V-2017-25407.R1
Manuscript Type:	V - Viewpoint
Date Submitted by the Author:	n/a
Complete List of Authors:	<p>Hartmann, Henrik; MPI for Biogeochemistry, Biogeochemical Processes Moura, Catarina; MPI for Biogeochemistry, Biogeochemical Integration; University of Coimbra, Centre for Functional Ecology, Department of Life Sciences; University of Lisbon, Forest Research Centre, School of Agriculture; University of California Berkeley, Department of Integrative Biology Anderegg, William; University of Utah, Department of Biology Ruehr, Nadine; Karlsruhe Institute of Technology, Institute of Meteorology and Climate Research - Atmospheric Environmental Research (IMK-IFU) Salmon, Yann; University of Helsinki, Department of Physics; University of Edinburgh, School of GeoSciences Allen, Craig; USGS, Fort Collins Science Center, Jemez Mountains Field Station Arndt, Stefan; The University of Melbourne, School of Ecosystem and Forest Sciences Breshears, David; The University of Arizona, School of Natural Resources and the Environment and Department of Ecology and Evolutionary Biology Davi, H; INRA URFM - UR629, Ecologie des Forest Méditerranéennes Galbraith, David; University of Leeds, School of Geography Ruthrof, Katinka; Murdoch University, Biological Sciences and Biotechnology Wunder, Jan; Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Insubric Ecosystems Research Group, Community Ecology; University of Auckland, Tree-Ring Laboratory, School of Environment Adams, Henry; Oklahoma State University, Dept. of Plant Biology, Ecology, and Evolution Bloemen, J; University of Innsbruck, Austria, Institute of Ecology Cailleret, Maxime; ETH Zürich, Forest Ecology, Department of Environmental Sciences; Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Research Unit Forest Dynamics Cobb, Richard; UC Davis, Plant Pathology Gessler, Arthur; Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Research Unit Forest Dynamics Grams, Thorsten; Technische Universität München, Ecophysiology of Plants Jansen, Steven; Ulm University, Institute for Systematic Botany and Ecology Kautz, Markus; Karlsruhe Institute of Technology, Institute of Meteorology and Climate Research - Atmospheric Environmental Research (IMK-IFU)</p>

	Lloret, F; Universitat Autònoma de Barcelona, Center for Ecological Research and Applied Forestry (CREAF); Universitat Autònoma de Barcelona, Unitat d'Ecologia, Department of Biologia Animal O'Brien, Michael; Consejo Superior de Investigaciones Científicas, Estacion Experimental de Zonas Aridas
Key Words:	tree death, carbon-water cycling, nutrients, dynamic vegetation models, monitoring network, insects and pathogens

SCHOLARONE™
Manuscripts

For Peer Review

Research frontiers for improving our understanding of drought-induced tree and forest mortality

Running head: **Frontiers in drought mortality research**

First authors*:

Hartmann¹, Henrik; **Moura**¹⁻⁴, Catarina F.; **Anderegg**⁵, William R. L.; **Ruehr**⁶, Nadine K.;
Salmon^{7,8}, Yann

Second authors:

Allen⁹, Craig; **Arndt**¹⁰, Stefan; **Breshears**¹¹, David D.; **Davi**¹², Hendrik; **Galbraith**¹³, David;
Ruthrof¹⁴, Katinka X.; **Wunder**^{15,16}, Jan

Third authors:

Adams¹⁷, Henry, **Bloemen**¹⁸, Jasper; **Cailleret**^{19, 20}, Maxime; **Cobb**²¹, Richard; **Gessler**²⁰,
Arthur; **Grams**²², Thorsten E. E.; **Jansen**²³, Steven; **Kautz**⁶, Markus; **Lloret**^{24, 25}, Francisco;
O'Brien²⁶, Michael

*corresponding author email: hhart@bgc-jena.mpg.de, phone: +49.3641.576294

¹ Max-Planck Institute for Biogeochemistry, Hans Knöll Str. 10, 07745 Jena, Germany

19 ² Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, Calçada
20 Martim de Freitas, 3000-456 Coimbra, Portugal

21 ³ Forest Research Centre, School of Agriculture, University of Lisbon, Tapada da Ajuda, 1349-
22 017 Lisboa, Portugal

23 ⁴ Department of Integrative Biology, University of California, Berkeley, CA 94720-3140, USA

24 ⁵ Department of Biology, University of Utah, Salt Lake City, UT 84112 USA

25 ⁶ Karlsruhe Institute of Technology (KIT), Institute of Meteorology and Climate Research -
26 Atmospheric Environmental Research (IMK-IFU), Kreuzeckbahnstr. 19, 82467 Garmisch-
27 Partenkirchen, Germany

28 ⁷ School of Geosciences, University of Edinburgh, Crew Building, The Kings Buildings,
29 Alexander Crum Brown Road, EH9 3FF Edinburgh, UK

30 ⁸ Department of Physics, University of Helsinki, P.O. Box 68, Gustaf Hållströmin katu 2b,
31 00014 University of Helsinki, Finland

32 ⁹ U.S. Geological Survey, Fort Collins Science Center, Jemez Mountains Field Station, Los
33 Alamos, New Mexico 87544 USA

34 ¹⁰ School of Ecosystem and Forest Sciences, The University of Melbourne, 500 Yarra
35 Boulevard, Richmond, 3121 VIC, Australia

36 ¹¹ School of Natural Resources and the Environment and Department of Ecology and
37 Evolutionary Biology, University of Arizona, Tucson, AZ 85721

38 ¹²INRA, URFM, Ecologie des Forest Méditerranéennes, Domaine Saint Paul, Site Agroparc,
39 84914 Avignon Cedex 9

40 ¹³School of Geography, University of Leeds, Leeds, LS2 9JT, UK

41 ¹⁴Murdoch University, South Street, Murdoch, 6150, Perth, Western Australia

42 ¹⁵Insubric Ecosystems Research Group, Community Ecology, Swiss Federal Institute for
43 Forest, Snow and Landscape Research WSL, a Ramèl 18, CH-6593 Cadenazzo

44 ¹⁶Tree-Ring Laboratory, School of Environment, University of Auckland, NZ-Auckland 1142,
45 New Zealand

46 ¹⁷Department of Plant Biology, Ecology, and Evolution, 301 Physical Sciences, Oklahoma
47 State University, Stillwater, OK 74074, USA

48 ¹⁸Institute of Ecology, University of Innsbruck, Sternwartestraße 15, 6020 Innsbruck

49 ¹⁹Forest Ecology, Department of Environmental Sciences, ETH Zürich. ETH-Zentrum, CHN
50 G77, Universitätstrasse 16, CH-8092 Zürich, Switzerland

51 ²⁰Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf,
52 Switzerland

53 ²¹Department of Natural Resources & Environmental Science, California Polytechnic State
54 University, San Luis Obispo, CA 93407, USA

55 ²²Technical University of Munich, Ecophysiology of Plants, Von-Carlowitz-Platz 2, 85354
56 Freising, Germany

57 ²³Ulm University, Institute of Systematic Botany and Ecology, Albert-Einstein-Allee 11,
58 89081 Ulm, Germany

59 ²⁴CREAF - Center for Ecological Research and Applied Forestry, Cerdanyola del Vallès,
60 Barcelona, Spain

61 ²⁵Unitat d'Ecologia, Department of Biologia Animal, Biologia Vegetal i Ecologia, Universitat
62 Autònoma Barcelona, Edifici C, Campus UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain

63 ²⁶Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas,
64 Carretera de Sacramento s/n, E-04120 La Cañada, Almería, Spain

65

66 Summary

- 67 • Accumulating evidence highlights increased mortality risks for trees during severe
68 drought, particularly under warmer temperatures and increasing vapour pressure deficit
69 (VPD). Resulting forest die-off events have severe consequences for ecosystem services,
70 biophysical and biogeochemical land-atmosphere processes.
- 71 • Despite advances in monitoring, modelling and experimental studies of the causes and
72 consequences of tree death from individual tree to ecosystem and global scale, a
73 general mechanistic understanding and realistic predictions of drought mortality under
74 future climate conditions are still lacking.
- 75 • We update a global tree mortality map and present a roadmap to a more holistic
76 understanding of forest mortality across scales. We highlight priority research frontiers
77 that promote (1) new avenues for research on key tree ecophysiological responses to
78 drought, (2) scaling from the tree/plot level to the ecosystem and region, (3)
79 improvements of mortality risk predictions based on both empirical and mechanistic
80 insights, and (4) a global monitoring network of forest mortality.
- 81 • In light of recent and anticipated large forest die-off events such a research agenda is
82 timely and needed to achieve scientific understanding for realistic predictions for
83 drought-induced tree mortality. The implementation of a sustainable network will
84 require support by stakeholders and political authorities at the international level.

85

86 Keywords: tree death, carbon-water cycling, insects and pathogens, dynamic vegetation
87 models, monitoring network

88 1. Introduction

89 Forests cover about 30% of the terrestrial surface of the globe and annually sequester about
90 25% of the CO₂ emitted by human activities (Pan *et al.*, 2011). In forested regions, trees are
91 the dominating vegetation and structure ecosystem patterns and processes from the stand
92 level to entire landscapes. However, ongoing global warming, in concert with episodic
93 droughts, heat waves and associated increased VPD (Breshears *et al.*, 2013; Eamus *et al.*,
94 2013; Ruehr *et al.*, 2014), has been causing elevated levels of both chronic and acute stress
95 often leading to tree mortality across large forested regions of the globe (e.g., Dai, 2012). By
96 contrast, recent studies suggest that increasing specific humidity and elevated atmospheric
97 CO₂ concentration may partially offset mortality risk from drought and elevated
98 temperature (Liu *et al.*, 2017). Nevertheless, periods of drought and heat stress often
99 interact with other forest disturbances like fire and windthrow (Brando *et al.*, 2014) and can
100 significantly amplify the incidence and severity of biological disturbances such as outbreaks
101 of damaging insects and diseases (Williams *et al.*, 2013). Hence a better mechanistic
102 representation of the diverse processes that drive tree mortality under drought is needed to
103 improve predictions of forest responses to projected climate changes (McDowell *et al.*,
104 2015b) and to assess the fate of forests in coming decades.

105 Tree death is a challenging issue (see Box 1, Franklin *et al.*, 1987) and a major thrust of
106 research has investigated drought-induced tree mortality mechanisms, specifically testing
107 whether trees die from hydraulic failure (HF), carbon (C) starvation (CS), biotic attack or
108 from an interaction of those factors (McDowell *et al.*, 2008). However, despite many
109 investigations, it has become apparent that the current understanding of tree physiological
110 responses to drought and heat remains quite insufficient and further background

knowledge is clearly needed to generate realistic projections of forest mortality events under rapid climate change (Hartmann *et al.*, 2015). For example, we currently do not have a predictive framework to answer 1) which species will be more sensitive to a given drought at regional or global scales, 2) which individuals within a population will be more vulnerable, and 3) which quantitative thresholds of physiological parameters can be used to predict forest mortality under future climate scenarios. Simple physiological thresholds have been difficult to determine (Adams *et al.*, 2017) and lack of progress emphasizes that our current research agenda must be rethought. Furthermore, attempts to predict tree mortality at specific sites have been largely inconclusive and suggest major limitations in current models (McDowell *et al.*, 2013b), possibly due to a pauper understanding of mechanisms of mortality at scales larger than the individual tree (Clark *et al.*, 2016).

The complexity of tree mortality may greatly limit the generality and utility of physiological thresholds identified at the individual tree level for prediction at the population, landscape, regional or global levels. This implies, then, that physiological research at an individual scale might be most productive when identifying “risk factors” that predispose trees to die, analogous in the human mortality literature to lifestyle factors such as smoking cigarettes that greatly increase the odds of death from a given cause like cancer (Sijbrands *et al.*, 2009). The identification of key functional and physiological risk factor traits, informed by understanding of C and hydraulic dynamics during tree death, has strong promise to improve our prediction of probabilistic mortality risk at the population level (Fig. 1).

This synthesis is not intended as a reference for the ‘state of the art’ on drought-induced tree mortality understanding, as many recent reviews have already addressed challenges in predicting forest response to drought stress in detail (e.g., Allen *et al.*, 2015; Clark *et al.*,

2016). Here we identify key frontiers in drought-induced tree mortality research across different disciplines and scales, spanning physiological processes in individual tissues to assessments and predictions of local mortality events at regional to global scales (Fig. 2). In addition, we provide research recommendations that serve as guidelines for directing future work to the areas of greatest need. We conclude by setting out a multidisciplinary strategy including practical recommendations that aim to identify crucial physiological risk factors in tree and forest mortality. Such risk factors can provide mechanistic relationships for more realistic predictions of future forest conditions.

2. Mechanisms of tree mortality

The hydraulic framework of global-change drought-induced tree mortality (McDowell *et al.*, 2008) proposed two non-exclusive physiological mechanisms: CS and HF. The relative importance and potential interaction between these two mechanisms leading to tree death has structured most of the research since this scientific debate has been started (McDowell & Sevanto, 2010; Sala *et al.*, 2010). For this reason, we identify research frontiers mainly related to C and water relations as well as the role of biotic agents in tree mortality. In addition, the hydraulic framework emphasised ecological processes including plant resource acquisition, plant-biotic interactions and the ability of trees to recover from previous drought events. These topics, underrepresented in current research despite their potential significance in drought-induced tree mortality, are briefly discussed in Supporting Information (SI 1). Furthermore, some intrinsic factors known to influence tree responses to drought and heat, like tree functional type (Mitchell *et al.*, 2014; Ruehr *et al.*, 2016), developmental stage or age, are underrepresented in the current literature because most

experimental studies so far have been conducted mainly on evergreen species and on individual potted tree seedlings or saplings (Table 1). This lack of information highlights the overarching research frontier of expanding future research on mortality-relevant functional and physiological traits to a larger range of tree species, developmental stages and functional types.

Carbon

Support for CS is more ambiguous than for HF (O'Brien *et al.*, 2014; Sevanto *et al.*, 2014) and death from CS is still debated on (e.g., Körner, 2015) because complete depletion of C reserves is rarely observed. During water limitation, and in particular in combination with elevated temperatures and increasing VPD (Breshears *et al.*, 2013; Eamus *et al.*, 2013; Ruehr *et al.*, 2014), the net C balance of trees can become negative (Zhao *et al.*, 2013) and stored non-structural carbohydrates (NSC) must fuel respiration and several other vital processes, including osmoregulation (McDowell, 2011). Thus CS (defined here as the cessation of respiration) has to occur at non-zero NSC concentrations (Hartmann, 2015; Hoch, 2015). So far, however, many studies have addressed C dynamics during drought only partially, i.e. in individual tissues and/or organs. To systematically examine the role of tree C metabolism during drought mortality, we suggest investigating whole-tree C dynamics to identify the onset of a negative C balance during severe drought and in combination with high temperatures and high VPD. Such investigations must also address C storage mobilization and transport, regulation and remobilization of NSC or alternative reserve compounds such as lipids and proteins during drought (Zhao *et al.*, 2013; Fischer *et al.*, 2015).

While the responses of photosynthesis to drought have been extensively studied, less is known about changes in whole-plant allocation patterns to C sinks including respiration,

defence compounds, emissions of biogenic volatile organic compounds (VOC), root exudates and export to symbionts (e.g., mycorrhiza, rhizobia). VOC emissions (Loreto & Schnitzler, 2010) and respiration rates increase often with temperature (Adams *et al.*, 2009) but not always (Duan *et al.*, 2013) during drought. However, scarcity of data on these whole-tree processes currently limits our understanding of whole-tree C dynamics during drought-induced mortality. An important step forward would be to quantify the entire net C balance of trees to assess when C loss becomes larger than C uptake and available NSC reserves (see also interdependency section) and which minimum levels of NSC might become lethal (Weber *et al.*, in press).

Water

Hydraulic failure has been addressed in many mortality studies (see references in Table 1) but the point at which xylem embolism develops into fatal HF for a large number of tree species is still unresolved (Urli *et al.*, 2013; Li *et al.*, 2016), and little is known about the different plant hydraulic strategies related to drought resilience. Therefore, a key research need is to determine specific thresholds of recovery and fatal embolism across individual tissues and whole plants.

Key features derived from xylem vulnerability curves that are generated under controlled conditions in the lab, including water potential (Ψ) leading to 50% loss in hydraulic conductivity (Ψ_{50}) possibly lethal in gymnosperms (Brodribb & Cochard, 2009) or 88% (Ψ_{88}) possibly lethal in hydraulically more tolerant and dynamic angiosperms (Urli *et al.*, 2013; Li *et al.*, 2016), have been suggested as potential indicators of HF (Choat *et al.*, 2012).

However, variation in resistance to embolism may vary substantially within a single species over space and time (Anderegg, 2015) due to potential effects of plant development (young

vs. adult trees), seasonality (timing of drought), differences among tissues, life history (including air-seeding fatigue), hydraulic capacitance and – potentially – embolism repair. Finally, little is known about the levels of *in planta* xylem exposure to very low tensions and associated thresholds of massive HF, because measurements are typically conducted on excised branches or stem segments. Frequently applied vulnerability curves carry the risk of overestimating xylem embolism (McElrone *et al.*, 2012), therefore new non-destructive methods such as X-ray micro-tomography (Cochard *et al.*, 2015) or optical techniques (Brodribb *et al.*, 2016) may be promising avenues (Cochard *et al.*, 2015).

Plant traits linking wood anatomy to hydraulic properties such as wood density, pit membrane thickness between adjacent vessels and torus overlap in conifer tracheids may be useful proxies for embolism resistance (Li *et al.*, 2016). Given that some trees' hydraulic pathways may be highly segmented across organs (e.g., Tyree & Ewers, 1991; Bucci *et al.*, 2012; Johnson *et al.*, 2016), emerging research should identify critical levels of water potential related to embolism and organ loss. A better mechanistic understanding can then be gained by quantifying the range from recoverable to lethal xylem Ψ and its native embolism to provide a probabilistic base for mortality estimates. This should then be linked to hydraulic traits in different tree species/functional types across forested biomes.

Interdependencies

Carbon and water dynamics in plants are ultimately interrelated via stomatal regulation and vascular transport. The interdependency of CS and HF in drought-induced tree mortality has been conceptually well established (McDowell, 2011) but investigations have only recently addressed this formally (e.g., O'Brien *et al.*, 2014). Several urgent mortality-related frontiers emerge: 1) establish how disruption of xylem-phloem functioning relates to CS, and 2)

226 identify plant functional type-specific traits related to both CS and HF that can serve as risk
227 factors in mortality predictions.

228 A better knowledge of C transport processes, i.e. transport via living cells in xylem and
229 phloem, including the loss of interconnectivity between organs, represents a crucial step
230 towards mechanistic understanding of mortality. Measurements of phloem flow in trees are
231 challenging (Sevanto, 2014) and despite recent promising advances (Savage *et al.*, 2016)
232 phloem failure has rarely been experimentally investigated in studies on tree mortality
233 (Sevanto *et al.*, 2014). Modelling studies show that high xylem tensions may inhibit water
234 inflow into the phloem during drought, potentially leading to phloem transport failure of
235 NSC from sources to sink tissues (Mencuccini & Hölttä, 2010) due to elevated viscosity and
236 turgor collapse in the phloem (Sevanto, 2014). Investigations on real plants are needed to
237 assess the importance of phloem failure in tree mortality. Furthermore, remobilization of
238 stored carbohydrates, i.e. the hydrolysis of starch to sugars, during drought can be inhibited
239 by limited water availability (Sala *et al.*, 2010) and may contribute to C transport failure. We
240 thus emphasize the need to investigate the physiological limits of phloem transport and
241 remobilization of sugars.

242 NSC play an important role as osmolytes to maintain turgor and avoid desiccation as Ψ in
243 plant tissues decreases with drought (Sala *et al.*, 2012; Salmon *et al.*, 2015). As xylem
244 tension increases, sugars become an important component of xylem osmoregulation and for
245 maintaining xylem water flow (Secchi & Zwieniecki, 2011). These functions may limit NSC
246 availability for other critical metabolic processes (Sala *et al.*, 2012). To address this frontier,
247 the minimum threshold of NSC concentration required for osmoregulation should be
248 studied among different plant tissues, species/functional groups and environmental

conditions. Finally, the plasticity of hydraulic and C-related traits with life history (e.g., prior exposure to drought) and the gene-by-environment controls on these traits are relevant to consider.

Insects and Pathogens

Plant-damaging insects and pathogens can either kill trees directly as primary agents, or compound physiological stress as secondary agents of tree mortality. Outbreaks are often associated with drought and periods of higher-than-average temperatures (Desprez-Loustau *et al.*, 2006; Anderegg *et al.*, 2015b). These conditions can directly affect insect and pathogen fitness (e.g. reproduction, development, dispersal, mortality), as well as alter tree suitability and predisposition to attacks (e.g. substrate quality, defence capacity, attraction due to emitted VOC). Together, both mechanisms determine damage severity and likelihood of tree mortality triggered by biotic agents during drought. Understanding feedback loops and complex interactions between host trees, biotic agents and environmental conditions is thus crucial for predicting tree mortality. In this context we highlight the following research frontiers: 1) determine temperature-related changes in insect/pathogen phenology that dramatically increase outbreak risk, and 2) identify tree-intrinsic risk factors and critical values for drought-mediated predisposition to biotic attacks.

Higher temperatures have been reported to facilitate insect and pathogen phenology, finally resulting in an increased outbreak risk (Bentz *et al.*, 2010; Jönsson *et al.*, 2011). However, such positive relation is typically non-linear, species-specific, and constraint by distinct thermal upper and lower thresholds (Raffa *et al.*, 2015). Moreover, fitness effects of increased temperature are expected to be more pronounced at higher latitudes than in the tropics where species are typically closer to the edge of their thermal tolerance (Deutsch *et*

272 *al.*, 2008). Cooperation among plant ecophysiologists, phytopathologists and entomologists
273 have the potential to improve our empirical understanding of how gradual or extreme
274 temperature changes affect different insect/pathogen populations, and how altered
275 population dynamics can be linked to tree mortality across different ecosystems.

276 In parallel, drought stress can make host trees more susceptible to insect and pathogen
277 attacks due to temporally reduced tree defence mechanisms (Anderegg *et al.*, 2015b). In
278 conifers, decreasing carbohydrate availability and low Ψ during drought can limit the
279 production of defensive oleoresin and the generation of hydraulic pressure in resin ducts,
280 both needed to resist bark beetle attacks (Netherer *et al.*, 2015), and the emission of
281 specific VOC from trees attracting bark beetles is typically enhanced under drought and
282 elevated temperatures (Kautz *et al.*, 2013). Thus, drought clearly promotes tree mortality by
283 bark beetle attacks, while for defoliating and sap-feeding insects and pathogens this
284 relationship is less evident (Desprez-Loustau *et al.*, 2006). Pathogens often critically rely on
285 moisture, but could also benefit from reduced tree defence and the association with insects.
286 Foliage feeders are negatively affected by drought-induced alterations in leaf physiology
287 (e.g., toughness) and chemistry (e.g., C:N ratio). Adequately addressing the complex
288 interactions between positive and negative effects from different levels of drought stress
289 and/or elevated temperature on both hosts and agents and partitioning between causes of
290 mortality (drought vs. biotic agents) is challenging (Ryan *et al.*, 2015). A combination of
291 finely designed controlled experiments could provide information on risk factors including
292 tree C, water and nutrient balances that are critical for defense. Ideally, similarly designed
293 experiments should be conducted across different agent species, host types and levels of
294 drought severity to reveal tree defence strategies in relation to tree physiological status.

3. Process integration, scaling and modelling from tissues to the global vegetation

Predicting drought-induced tree mortality is especially challenging because it requires integrating processes that occur on temporal scales from seconds to decades and spatial scales from cells to continents (Fig. 2). Consequently, scaling physiological and ecological processes that influence the probability of mortality over large geographic areas is a major challenge that has to be addressed to predict future risks of regional and global die-off events. At larger spatial scales, mortality is inherently probabilistic and thus we focus here on how key physiological mechanisms and risk factors at the individual tree level can be scaled up to provide changes in the probability of mortality in a species, population, or region.

Process integration and scaling issues in predictions of mortality

Scaling from individual trees to ecosystems and regions requires determining key environmental factors that may change the probability of mortality in space: 1) lateral water flows and the role of groundwater or hydraulic lift in mitigating water stress (Barbeta *et al.*, 2015), 2) existing spatial variation in soils, microclimate, and stand structure, and 3) biotic interactions that include insects/pathogens, and plant-plant interactions such as competition for water (see also S1). For instance, landscape variability due to topography, soil characteristics, and management history likely promotes patchy patterns of mortality that are often observed across broad regions (Huang & Anderegg, 2012). The spatial pattern of tree mortality may be further affected by the interaction between drought and insect/pathogen outbreaks, due to the spatial nature of pest dispersal and infection

(Anderegg *et al.*, 2015b). The contribution of such interactions to mortality distribution in space remains a crucial research area to inform simulations of mortality events.

Furthermore, mortality events must be considered within the time scales of tree population dynamics and contingencies of climate variations. For example, the sequence of mortality events and high growth periods experienced by tree populations is likely critical to determine long-term vegetation community dynamics. Positive feedbacks will increase forest vulnerability to new episodes of drought, if successive droughts lead to cumulative physiological damage, exhaustion of resources, diminished defence capacity and/or non-reversible loss of regenerating structures and recruitment capacity. Alternatively, stabilizing feedbacks may operate if tree mortality increases survival of neighbours due to competition release and adaptation of the forest community to drier conditions (Lloret *et al.*, 2012). Consequently, we highlight the following frontiers: 1) Identify whether mortality probability of tree populations to drought increases or decreases with successive exposure to stress, 2) determine the extent to which genetic adaptation and phenotypic plasticity mediate population resilience to drought and probability of mortality within a population, and 3) understand the impact of drought on population regeneration including seed production and recruitment.

Modelling

Models are important tools for integrating process understanding and making future projections across a gamut of spatial scales, ranging from individual trees to the entire globe (Fig. 2). We focus here on the integration of mortality processes in dynamic vegetation models (DVMs), particularly dynamic global vegetation models (DGVMs), although similar approaches and algorithms will be useful also in other model classes. There is currently

considerable interest in improving the representation of tree mortality in DGVMs, given its importance on long-term forest dynamics (Bircher *et al.*, 2015), and in the regulation of ecosystem carbon storage (e.g., Friend *et al.*, 2014). However, tree mortality formulations in current DGVMs are generally simple, ranging from fixed carbon turnover rates (Galbraith *et al.*, 2013) to approaches where mortality is related to growth efficiency or negative carbon balance (McDowell *et al.*, 2011). Such approaches have been found to be insufficient to adequately capture observations of drought-induced tree mortality (e.g., Manusch *et al.*, 2012).

To address these problems, we identify the following research frontiers: 1) implement plant hydraulic representations in DVMs that allow for species- or plant functional type-specific drought strategies in dimensions of stomatal control, root distribution, allometry, and hydraulic properties such as vulnerability to embolism, 2) determine the key axes of drought trait trade-offs necessary to simulating different species' drought response strategies (Bartlett *et al.*, 2016) and how these are linked to probability of mortality (Anderegg *et al.*, 2016), and 3) test and validate probabilistic mortality functions at regional scales against extreme droughts in the observational record where probability of mortality can be estimated through forest inventories, other plot data, or remote-sensing estimates (Brienen *et al.*, 2015). We emphasize that if mortality projections are made at regional scales, model validation against independent mortality data should be performed at the same spatial scales to have confidence in model projections.

Among these three research areas, simulating plant hydraulics is a key frontier for several main reasons. First, loss of hydraulic conductivity has been observed in almost every mortality event or experiment (Adams *et al.*, 2017). Second, thresholds in hydraulic loss

have been documented in several species (e.g., Brodribb & Cochard, 2009) and hydraulic traits appear to predict which species in a community are at higher risk of mortality in a given drought (Anderegg *et al.*, 2016). Third, whole-tree hydraulic models exist and are relatively well-validated (e.g., Sperry & Love, 2015), suggesting they are suitable to incorporate into larger models,.

Testing and validating mortality algorithms in DVMs is challenging. Standard mortality benchmark datasets are greatly needed, but have not yet been proposed. Many DVMs include only woody biomass pools and do not have explicit representation of “trees” or at least tree cohorts that would be needed to calculate both drought hydraulic damage (e.g. embolism) and mortality rates to compare to plot-level data (McDowell *et al.*, 2013a). The non-linear and threshold-like nature of probability of mortality will make the determination and calibration of thresholds for plant functional types difficult, especially for coarse functional types that are implemented in DGVMs. However, recent advances in synthesizing large-scale plot networks (Crowther *et al.*, 2015; Liang *et al.*, 2016) and remote-sensing (e.g., Hansen *et al.*, 2013) may allow assessment of thresholds at regional and larger spatial scales and for coarse groups of plants. Models that can accurately capture processes across spatial and temporal scales – ecophysiological dynamics, such as seasonal and inter-annual changes in Ψ and hydraulic conductivity, plot-level mortality rates, and regional plot or satellite-estimated spatial and temporal patterns of mortality (Anderegg *et al.*, 2015a) – will be needed to improve confidence in mortality projections.

4. An integrative and multidisciplinary strategy for assessing, understanding and predicting future forest condition

In addition to the research frontiers and recommendations highlighted in the previous sections, we advocate here a comprehensive strategy towards a better understanding and forecasting of drought-induced tree mortality (Fig. 4, McDowell *et al.*, 2015a; Trumbore *et al.*, 2015) by including the following coordinated actions: 1) assess trends and hotspots in tree and forest mortality at the global scale via monitoring at multiple scales, 2) attribute mortality causes and drivers based on observations and manipulations in mortality-prone forest ecosystems and investigate the underlying physiological risk factors that may serve as mortality predictors that 3) allow then more realistic forecasting of forest responses to anticipated future climate such as changes in mortality probabilities with changing environmental conditions.

Assessing changes in forest condition via monitoring at multiple scales

Global forest health may be defined as “a mosaic of successional [forest] patches representing all stages of the natural range of disturbance and recovery” (Raffa *et al.*, 2009; p. 815, Trumbore *et al.*, 2015) and may be best assessed by changes in forest condition spanning scales from trees to the globe (McDowell *et al.*, 2015a) thereby providing early warning indicators of forest stress (Allen *et al.*, 2010). The most robust and likely the most easily detected proxy for changes in forest health may be mortality rates that are outside of the natural range of variability (Trumbore *et al.*, 2015). In fact, many countries have excellent existing networks of detailed forest inventory plots that allow assessment of changes in forest condition because they are measured and revisited on a regular basis – many of these also include measures of tree mortality (e.g., in the U.S., the Forest Inventory and Analysis Program; Shaw *et al.*, 2005). However, these monitoring data are not available in “real-time”, are often not openly accessible and synthesizing data from multiple plot

network sources (e.g., different countries) can be a complex task. In addition, historical inventory data typically have been field-collected on longer time intervals (commonly every 5 to 10 years), making it difficult to pinpoint mortality occurrences to specific climatic events and/or causes of tree death. By contrast, satellite data are becoming more easily available and may allow “close to real-time” assessments of changes in forest cover from disturbances over large regions (McDowell *et al.*, 2015a). Ground-based validation of satellite data may build on an already increasing number of inventory plot networks from both governmental agencies and/or multiple research institutions partnerships (like RAINFOR, FORESTPLOTS.NET or CTFS-ForestGEO) that cover different forest biomes. However, these plot-based monitoring networks were never designed to specifically address tree mortality, and we will need novel observation networks (or protocols) that allow a faster and more automated detection of mortality events.

Recent advances in remote sensing provide a new generation of tools that could enable global satellite monitoring of die-off and other broad-scale disturbances (McDowell *et al.*, 2015a). For example, the Global Forest Watch initiative (<http://www.globalforestwatch.org>) of the World Resources Institute is a good step forward to detecting temporal changes in forest cover from disturbance or mortality but the spatial resolution of the underlying data (30 m) is larger than the scale at which individual tree mortality occurs and precludes inferences on the underlying physiological processes. New technologies, like Lidar, now allow monitoring of individual trees over larger areas (e.g., Asner *et al.*, 2016) thereby closing the gap between tree-level information from inventory plots, and information at stand and regional scales derived from satellite data. The challenge now becomes to link these approaches in a coordinated manner, allowing (1) a direct flow of information

between the different layers of monitoring, (2) a continued improvement of remote sensing products and increases toward real-time mortality assessment and detection of mortality hotspots, and (3) a facilitated access to large international data sets to link ground-based and remotely sensed data (Trumbore *et al.*, 2015).

Although the Global Forest Watch provides “close to real-time” information on forest conditions, changes in forest cover are currently captured by identifying areas with well-defined boundary attributes, like forest management and land-use change, or large-scale severe disturbances (e.g., wild fires, windthrow, insect outbreaks). Climate change-driven mortality of individual trees would thus likely appear as remaining spatially-diffuse changes in forest cover and are currently not systematically assessed. Such mortality should become a focus for ground-proofing via existing inventory or research plot data. Additional assessment cruises or Lidar imaging will allow determining whether changes in forest cover are due to mortality or reduced vigour of trees. Such measurements can be supplemented by multi-spectral imagery installed on UAV (unmanned aerial vehicles, e.g., Dash *et al.*, 2017). Taken together such tools will open promising avenues to monitor forest health at scales relevant for detecting tree mortality (Hartmann *et al.*, in press).

Understanding mortality causes and identifying mechanisms for forecasting: the roles of observations and experiments

To forecast drought-induced tree mortality we need to understand mortality mechanisms at the tree level first and use this understanding to derive mortality-related risk factors that allow probabilistic mortality predictions at larger scales. Naturally-occurring lethal drought events (identified as hotspots of spatially-diffuse mortality) detected by remote-sensing, may become platforms for intensive long-term observations, mid-term field manipulations

455 and even close-up process studies of affected species under controlled environmental
456 conditions such as in greenhouses (Fig. 4). Drought properties (duration, severity and timing
457 of occurrence) that determine the physiological impact of water deficit on plants (Novák,
458 2009) have so far been almost completely neglected in drought mortality research and must
459 be addressed in both field observations and field/greenhouse studies. While observations
460 and experiments on drought progression are still limited and hampered by the underlying
461 complexity of defining drought (Paulo & Pereira, 2006), information gathered from
462 naturally-occurring droughts can help improve experimental designs by focusing on more
463 realistic combinations of drought characteristics (severity, duration, seasonality) along with
464 increases in temperatures and VPD (Ruehr *et al.*, 2016). These drought characteristics can
465 be manipulated in field and/or greenhouse or garden experiments to establish cross-species
466 risk factors for tree decline and robust parameters for mechanistic relationships between
467 changes in environmental conditions and tree physiological responses, especially if such
468 investigations cover a range of regions and biomes (Adams *et al.*, 2017).

469 Although often limited to small trees, controlled and replicated experiments can provide
470 insightful whole-tree perspectives on C dynamics including C flux measurements of gas
471 exchange (photosynthesis and respiration), C allocation, NSC and non-NSC storage and
472 remobilization (Ryan, 2011). An impressive attempt of studying tree C balance responses in
473 the field using whole-tree chambers has been recently demonstrated (Aspinwall *et al.*,
474 2016). Such studies combined with severe drought and heat treatments can provide
475 unprecedented insights in mature tree C dynamics on the verge of death and hence indicate
476 lethal NSC thresholds (Weber *et al.*, in press) or minimum NSC thresholds required for
477 osmoregulation. Studying such relationships in a large number of individuals and in several

species or combining research efforts across similar designed experiments will provide probabilistic mortality distributions to define the mortality risk zone (see Fig. 1).

Responses of a range of tree species and different functional types to different climate change scenarios, including elevated CO₂ and temperature with changes in VPD and specific humidity (Eamus *et al.*, 2013; Liu *et al.*, 2017), will provide information on the interplay of risk (e.g., high VPD) vs. “safety” (e.g., elevated CO₂) factors. Such studies are technically challenging and may be often limited to manipulation under controlled conditions (seedlings/saplings) in the greenhouse, but attempts have been made to carry research into natural setting in the field, and on larger trees (Aspinwall *et al.*, 2016).

In addition, observations and experiments along naturally-occurring drought and temperature gradients can be a valuable addition to drought experiments when studying tree responses to different climatic drivers (Stape *et al.*, 2006; Moore *et al.*, 2016; Binkley *et al.*, 2017) and interactions with nutrient limitations. Intensive field investigations will be most promising if common protocols for observations and measurements are developed and used across different projects (e.g., as in NutNet, DroughtNet and similar research networks). Impacts of insects and pathogens during drought must become part of protocols in field studies and observations, as they are crucial risk factors in tree mortality.

Forecasting forest responses to climatic change

Scaling physiological and ecological processes that influence mortality over large geographic areas and implementing them in models is challenging. We posit that there are critical, high-priority steps for improving vegetation models’ prediction of mortality: 1) model trees, and thus mortality, directly; incorporating individual-based representation of trees in DGVMs

(e.g., Purves & Pacala, 2008) will enable direct simulation of tree mortality probabilities, rather than changes in biomass pools. 2) model hydraulics; incorporate tree-level hydraulics into vegetation models and scaling responses to regional scales that account for diversity in species, stand structures, and other sources of variation is likely to improve mortality prediction. 3) Test mortality algorithms directly; more detailed and rigorous evaluation of mortality algorithms using plot networks and remote sensing products is greatly needed to test model simulations of mortality dynamics over large areas. Finally, 4), model NSC dynamics more realistically; like all sessile organisms, trees respond to environmental constraints by modifying resource (i.e. NSC) allocation to alleviate stress and compensate resource limitation. For example, plants are thought to increase root growth during drought to promote water uptake (*sensu* optimal partitioning, Poorter *et al.*, 2012). Although our knowledge of the regulation of NSC storage and remobilization in trees is still very limited (Hartmann & Trumbore, 2016) and accurate NSC measurements in plant tissues are still challenging (Quentin *et al.*, 2015) implementations of NSC dynamics in models that account for the perennial nature of trees will provide a more realistic predictions of tree responses to environmental change (Dietze *et al.*, 2014).

5. Conclusion

We provide a set of specific and crucial high-priority research frontiers that can help improving forecasting of forest conditions by promoting probabilistic mortality risk predictions. Similar to epidemiological research, mortality risk predictions for trees require also large data sets with substantial detail on the underlying physiological processes of the risk factors. This calls for international sharing of forest data and thus for a global monitoring network based on both governmental and academic support. Such a network

will combine field observations, manipulations, controlled experiments and modeling. Although the central theme of this network will be based on data sharing, knowledge transfer to effective policy-making and forest management will become increasingly important for forest conservation. As most governments and concerned NGOs have been acknowledging the central role of forests for human welfare and livelihood at the global scale, initiatives for forest monitoring should be ranked high up on the international political agenda.

Acknowledgments

We would like to thank all participants to the International Interdisciplinary Workshop on Tree Mortality at the Max-Planck for Biogeochemistry in Jena, Germany (October 2014) for fruitful discussions on this topic. We would also like to thank M. Mencuccini and three anonymous reviewers for useful comments on the manuscript, J. Atherton for insight in the emerging tools for remote sensing monitoring, and S. Schott for help designing figures 1 and 4.

List of financial support: C.F.M. was supported by the Portuguese Foundation for Science and Technology (FCT) and associated co-funding programs (fellowship SFRH/BPD/47131/2008 and travel funds from UID/BIA/04004/2013). Y.S. was supported by NERC (RA0929 to M. Mencuccini) and the Academy of Finland (1284701 to T. Vesala). N.K.R received support by the German Federal Ministry of Education and Research (BMBF) through the Helmholtz Association and its research programme ATMO and by the German Research Foundation through its Emmy Noether Program (RU 1657/2-1). W.R.L.A.

545 acknowledges support from the National Science Foundation NSF DEB EF-1340270. D.D.B.
546 acknowledges support from the National Science Foundation NSF EF-1340624, EF-1550756
547 and EAR-1331408. M.K. acknowledges support from the EU FP7 project LUC4C, grant
548 603542.

549

550 Authors' contribution statement:

551 HH, CM, WA, NKR and YS have contributed as first authors in equal parts to the coordination
552 and editing of the manuscript. CA, SA, DB, HD, DG, KR and JW have coordinated and edited
553 contributions of HA, JB, MC, RC, AG, TG, SJ, MK, FL and MO'B to individual sections of the
554 manuscript.

555

556 SUPPORTING INFORMATION

557 Additional supporting information may be found in the online version of this article:

558 **SI 1** Mechanisms interacting with tree mortality: proposition for new key research areas

559 **SI 2** References of published experimental studies on drought-induced tree mortality shown
560 in Table 1.

561 **SI 3** References documenting the most recent localities shown in Fig. 3.

562 References

- 563 **Adams HD, Guardiola-Claramonte M, Barron-Gafford GA, Villegas JC, Breshears DD, Zou CB, Troch PA,**
 564 **Huxman TE. 2009.** Temperature sensitivity of drought-induced tree mortality portends increased
 565 regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences*
 566 **106:** 7063-7066.
- 567 **Adams HD, Zeppel MJB, Anderegg WRL, Hartmann H, Landhausser SM, Tissue DT, Huxman TE, Hudson PJ,**
 568 **Franz TE, Allen CD, et al. 2017.** A multi-species synthesis of physiological mechanisms in drought-
 569 induced tree mortality. *Nature Ecology & Evolution* **1:** 1285-1291.
- 570 **Allen CD, Breshears DD, McDowell NG. 2015.** On underestimation of global vulnerability to tree mortality and
 571 forest die-off from hotter drought in the Anthropocene. *Ecosphere* **6:** art129.
- 572 **Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A,**
 573 **Breshears DD, Hogg EH, et al. 2010.** A global overview of drought and heat-induced tree mortality
 574 reveals emerging climate change risks for forests. *Forest Ecology and Management* **259:** 660-684.
- 575 **Anderegg WRL. 2015.** Spatial and temporal variation in plant hydraulic traits and their relevance for climate
 576 change impacts on vegetation. *New Phytologist* **205:** 1008-1014.
- 577 **Anderegg WRL, Berry JA, Field CB. 2012.** Linking definitions, mechanisms, and modeling of drought-induced
 578 tree death. *Trends in Plant Science* **17:** 693-700.
- 579 **Anderegg WRL, Flint A, Huang CY, Flint L, Berry JA, Davis FW, Sperry JS, Field CB. 2015a.** Tree mortality
 580 predicted from drought-induced vascular damage. *Nature Geoscience* **8:** 367-371.
- 581 **Anderegg WRL, Hicke JA, Fisher RA, Allen CD, Aukema J, Bentz B, Hood S, Lichstein JW, Macalady AK,**
 582 **McDowell N, et al. 2015b.** Tree mortality from drought, insects, and their interactions in a changing
 583 climate. *New Phytologist* **208:** 674-683.
- 584 **Anderegg WRL, Klein T, Bartlett M, Sack L, Pellegrini AFA, Choat B, Jansen S. 2016.** Meta-analysis reveals that
 585 hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe.
 586 *Proceedings of the National Academy of Sciences* **113:** 5024-5029.
- 587 **Asner GP, Brodrick PG, Anderson CB, Vaughn N, Knapp DE, Martin RE. 2016.** Progressive forest canopy water
 588 loss during the 2012-2015 California drought. *Proceedings of the National Academy of Sciences* **113:**
 589 249-255.
- 590 **Aspinwall MJ, Drake JE, Company C, Vårhammar A, Ghannoum O, Tissue DT, Reich PB, Tjoelker MG. 2016.**
 591 Convergent acclimation of leaf photosynthesis and respiration to prevailing ambient temperatures
 592 under current and warmer climates in *Eucalyptus tereticornis*. *New Phytologist* **212:** 354-367.
- 593 **Barbeta A, Mejía-Chang M, Ogaya R, Voltas J, Dawson TE, Peñuelas J. 2015.** The combined effects of a long-
 594 term experimental drought and an extreme drought on the use of plant-water sources in a
 595 Mediterranean forest. *Global Change Biology* **21:** 1213-1225.
- 596 **Bartlett MK, Klein T, Jansen S, Choat B, Sack L. 2016.** The correlations and sequence of plant stomatal,
 597 hydraulic, and wilting responses to drought. *Proceedings of the National Academy of Sciences* **113:**
 598 13098-13103.
- 599 **Binkley D, Campoe OC, Alvares C, Carneiro RL, Cegatta Í, Stape JL. 2017.** The interactions of climate, spacing
 600 and genetics on clonal *Eucalyptus* plantations across Brazil and Uruguay. *Forest Ecology and*
 601 *Management* **405:** 271-283.
- 602 **Bircher N, Cailleret M, Bugmann H. 2015.** The agony of choice: different empirical mortality models lead to
 603 sharply different future forest dynamics. *Ecological Applications* **25:** 1303-1318.
- 604 **Brando PM, Balch JK, Nepstad DC, Morton DC, Putz FE, Coe MT, Silvério D, Macedo MN, Davidson EA,**
 605 **Nóbrega CC, et al. 2014.** Abrupt increases in Amazonian tree mortality due to drought–fire
 606 interactions. *Proceedings of the National Academy of Sciences* **111:** 6347-6352.
- 607 **Breshears DD, Adams HD, Eamus D, McDowell NG, Law DJ, Will RE, Williams AP, Zou CB. 2013.** The critical
 608 amplifying role of increasing atmospheric moisture demand on tree mortality and associated regional
 609 die-off. *Frontiers in Plant Science* **4:** 266.
- 610 **Brienen RJW, Phillips OL, Feldpausch TR, Gloor E, Baker TR, Lloyd J, Lopez-Gonzalez G, Monteagudo-**
 611 **Mendoza A, Malhi Y, Lewis SL, et al. 2015.** Long-term decline of the Amazon carbon sink. *Nature* **519:**
 612 344-348.
- 613 **Brodrick TJ, Cochard H. 2009.** Hydraulic failure defines the recovery and point of death in water-stressed
 614 conifers. *Plant Physiology* **149:** 575-584.

- 615 **Brodrribb TJ, Skelton RP, McAdam SAM, Bienaimé D, Lucani CJ, Marmottant P. 2016.** Visual quantification of
616 embolism reveals leaf vulnerability to hydraulic failure. *New Phytologist* **209**: 1403-1409.
- 617 **Bucci SJ, Scholz FG, Campanello PI, Montti L, Jimenez-Castillo M, Rockwell FA, Manna LL, Guerra P, Bernal PL,**
618 **Troncoso O, et al. 2012.** Hydraulic differences along the water transport system of South American
619 *Nothofagus* species: do leaves protect the stem functionality? *Tree Physiology* **32**: 880-893.
- 620 **Choat B, Jansen S, Brodrribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Feild TS, Gleason SM, Hacke UG, et**
621 **al. 2012.** Global convergence in the vulnerability of forests to drought. *Nature* **491**: 752-755.
- 622 **Clark JS, Iverson L, Woodall CW, Allen CD, Bell DM, Bragg DC, D'Amato AW, Davis FW, Hersh MH, Ibanez I, et**
623 **al. 2016.** The impacts of increasing drought on forest dynamics, structure, and biodiversity in the
624 United States. *Global Change Biology* **22**: 2329-2352.
- 625 **Cochard H, Delzon S, Badel E. 2015.** X-ray microtomography (micro-CT): a reference technology for high-
626 resolution quantification of xylem embolism in trees. *Plant, Cell & Environment* **38**: 201-206.
- 627 **Crowther TW, Glick HB, Covey KR, Bettigole C, Maynard DS, Thomas SM, Smith JR, Hintler G, Duguid MC,**
628 **Amatulli G, et al. 2015.** Mapping tree density at a global scale. *Nature* **525**: 201-205.
- 629 **Dai A. 2012.** Increasing drought under global warming in observations and models. *Nature Climate Change* **3**:
630 52-58.
- 631 **Dash JP, Watt MS, Pearse GD, Heaphy M, Dungey HS. 2017.** Assessing very high resolution UAV imagery for
632 monitoring forest health during a simulated disease outbreak. *ISPRS Journal of Photogrammetry and*
633 *Remote Sensing* **131**: 1-14.
- 634 **Desprez-Loustau M-L, Marçais B, Nageleisen L-M, Piou D, Vannini A. 2006.** Interactive effects of drought and
635 pathogens in forest trees. *Annals of Forest Science* **63**: 597-612.
- 636 **Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR. 2008.** Impacts of
637 climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of*
638 *Sciences* **105**: 6668-6672.
- 639 **Dietze MC, Sala A, Carbone MS, Czimczik CI, Mantooth JA, Richardson AD, Vargas R. 2014.** Nonstructural
640 carbon in woody plants. *Annual Review of Plant Biology* **65**: 667-687.
- 641 **Duan H, Amthor JS, Duursma RA, O'Grady AP, Choat B, Tissue DT. 2013.** Carbon dynamics of eucalypt
642 seedlings exposed to progressive drought in elevated [CO₂] and elevated temperature. *Tree*
643 *Physiology* **33**: 779-792.
- 644 **Eamus D, Boulain N, Cleverly J, Breshears DD. 2013.** Global change-type drought-induced tree mortality:
645 vapor pressure deficit is more important than temperature per se in causing decline in tree health.
646 *Ecology and Evolution* **3**: 2711-2729.
- 647 **FAO 2005.** Global forest resources assessment 2005—progress towards sustainable forest management. FAO
648 Forestry Paper 147. Rome.
- 649 **Fischer S, Hanf S, Frosch T, Gleixner G, Popp J, Trumbore S, Hartmann H. 2015.** *Pinus sylvestris* switches
650 respiration substrates under shading but not during drought. *New Phytologist* **207**: 542-550.
- 651 **Franklin JF, Shugart HH, Harmon ME. 1987.** Tree death as an ecological process. *Bioscience* **37**: 550-556.
- 652 **Friend AD, Lucht W, Rademacher TT, Keribin R, Betts R, Cadule P, Ciais P, Clark DB, Dankers R, Falloon PD, et**
653 **al. 2014.** Carbon residence time dominates uncertainty in terrestrial vegetation responses to future
654 climate and atmospheric CO₂. *Proceedings of the National Academy of Sciences* **111**: 3280-3285.
- 655 **Galbraith D, Malhi Y, Affum-Baffoe K, Castanho ADA, Doughty CE, Fisher RA, Lewis SL, Peh KSH, Phillips OL,**
656 **Quesada CA, et al. 2013.** Residence times of woody biomass in tropical forests. *Plant Ecology &*
657 *Diversity* **6**: 139-157.
- 658 **Galiano L, Martinez-Vilalta J, Lloret F. 2011.** Carbon reserves and canopy defoliation determine the recovery
659 of Scots pine 4 yr after a drought episode. *New Phytologist* **190**: 750-759.
- 660 **Guada G, Camarero JJ, Sanchez-Salguero R, Cerrillo RM. 2016.** Limited growth recovery after drought-induced
661 forest dieback in very defoliated trees of two pine species. *Frontiers in Plant Science* **7**: 1-12.
- 662 **Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ,**
663 **Loveland TR, et al. 2013.** High-resolution global maps of 21st-century forest cover change. *Science*
664 **342**: 850-853.
- 665 **Hartmann H. 2015.** Carbon starvation during drought-induced tree mortality – are we chasing a myth? *Journal*
666 *of Plant Hydraulics* **2**, e005: 1-5.
- 667 **Hartmann H, Adams HD, Anderegg WRL, Jansen S, Zeppel MJB. 2015.** Research frontiers in drought-induced
668 tree mortality: crossing scales and disciplines. *New Phytologist* **205**: 965-969.

- Hartmann H, Schuldt B, Saners TGM, Macinnis-Ng C, Boehmer HJ, Allen CD, Bolte A, Crowther TW, Hansen MC, Medlyn B, et al. in press. Monitoring global tree mortality patterns and trends. *New Phytologist* xx: xx-xx.
- Hartmann H, Trumbore S. 2016. Understanding the roles of nonstructural carbohydrates in forest trees – from what we can measure to what we want to know. *New Phytologist* **211**: 386-403.
- Hartmann H, Ziegler W, Trumbore S. 2013. Lethal drought leads to reduction in nonstructural carbohydrates in Norway spruce tree roots but not in the canopy. *Functional Ecology* **27**: 413-427.
- Hoch G. 2015. Carbon reserves as indicators for carbon limitation in trees. In: Lüttge U, Beyschlag W eds. *Progress in Botany*. Cham, Switzerland: Springer International Publishing, 321-346.
- Huang C-Y, Anderegg WRL. 2012. Large drought-induced aboveground live biomass losses in southern Rocky Mountain aspen forests. *Global Change Biology* **18**: 1016-1027.
- IPCC. 2014. *Climate Change 2014: Impacts, Adaptation and Vulnerability: Regional Aspects*. Cambridge, UK: Cambridge University Press.
- Johnson DM, Wortemann R, McCulloh KA, Jordan-Meille L, Ward E, Warren JM, Palmroth S, Domec J-C. 2016. A test of the hydraulic vulnerability segmentation hypothesis in angiosperm and conifer tree species. *Tree Physiology* **36**: 983-993.
- Kautz M, Schopf R, Ohser J. 2013. The sun-effect: microclimatic alterations predispose forest edges to bark beetle infestations. *European Journal of Forest Research* **132**: 453-465.
- Klimešová J, Nobis MP, Herben T. 2015. Senescence, ageing and death of the whole plant: morphological prerequisites and constraints of plant immortality. *New Phytologist* **206**: 14-18.
- Körner C. 2015. Paradigm shift in plant growth control. *Current Opinion in Plant Biology* **25**: 107-114.
- Larson DW. 2001. The paradox of great longevity in a short-lived tree species. *Experimental Gerontology* **36**: 651-673.
- Li S, Feifel M, Karimi Z, Schuldt B, Choat B, Jansen S. 2016. Leaf gas exchange performance and the lethal water potential of five European species during drought. *Tree Physiology* **36**: 179-192.
- Liang J, Crowther TW, Picard N, Wiser S, Zhou M, Alberti G, Schulze E-D, McGuire AD, Bozzato F, Pretzsch H, et al. 2016. Positive biodiversity-productivity relationship predominant in global forests. *Science* **354**.
- Liu Y, Parolari AJ, Kumar M, Huang C-W, Katul GG, Porporato A. 2017. Increasing atmospheric humidity and CO₂ concentration alleviate forest mortality risk. *Proceedings of the National Academy of Sciences* **114**: 9918-9923.
- Lloret F, Escudero A, Iriondo JM, Martínez-Vilalta J, Valladares F. 2012. Extreme climatic events and vegetation: the role of stabilizing processes. *Global Change Biology* **18**: 797-805.
- Loreto F, Schnitzler J-P. 2010. Abiotic stresses and induced BVOCs. *Trends in Plant Science* **15**: 154-166.
- Manusch C, Bugmann H, Heiri C, Wolf A. 2012. Tree mortality in dynamic vegetation models—a key feature for accurately simulating forest properties. *Ecological Modelling* **243**: 101-111.
- McDowell NG. 2011. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiology* **155**: 1051-1059.
- McDowell NG, Beerling DJ, Breshears DD, Fisher RA, Raffa KF, Stitt M. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology & Evolution* **26**: 523-532.
- McDowell NG, Coops NC, Beck PSA, Chambers JQ, Gangodagamage C, Hicke JA, Huang CY, Kennedy R, Krofcheck DJ, Litvak M, et al. 2015a. Global satellite monitoring of climate-induced vegetation disturbances. *Trends in Plant Science* **20**: 114-123.
- McDowell NG, Fisher RA, Xu C, Domec JC, Hölttä T, Mackay DS, Sperry JS, Boutz A, Dickman L, Gehres N, et al. 2013a. Evaluating theories of drought-induced vegetation mortality using a multimodel–experiment framework. *New Phytologist* **200**: 304-321.
- McDowell NG, 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**: 719-739.
- McDowell NG, Ryan MG, Zeppel MJB, Tissue DT. 2013b. Feature: Improving our knowledge of drought-induced forest mortality through experiments, observations, and modeling. *New Phytologist* **200**: 289-293.
- McDowell NG, Sevanto S. 2010. The mechanisms of carbon starvation: how, when, or does it even occur at all? *New Phytologist* **186**: 264-266.

- McDowell NG, Williams AP, Xu C, Pockman WT, Dickman LT, Sevanto S, Pangle R, Limousin J, Plaut J, Mackay DS, et al. 2015b. Multi-scale predictions of massive conifer mortality due to chronic temperature rise. *Nature Climate Change* 6: 295-300.
- McElrone AJ, Brodersen CR, Alsina MM, Drayton WM, Matthews MA, Shackel KA, Wada H, Zufferey V, Choat B. 2012. Centrifuge technique consistently overestimates vulnerability to water stress-induced cavitation in grapevines as confirmed with high-resolution computed tomography. *New Phytologist* 196: 661-665.
- Mencuccini M, Hölttä T. 2010. The significance of phloem transport for the speed with which canopy photosynthesis and belowground respiration are linked. *New Phytologist* 185: 189-203.
- Mitchell PJ, O'Grady AP, Tissue DT, Worledge D, Pinkard EA. 2014. Co-ordination of growth, gas exchange and hydraulics define the carbon safety margin in tree species with contrasting drought strategies. *Tree Physiology* 34: 443-458.
- Moore GW, Edgar CB, Vogel JG, Washington-Allen RA, March Rosaleen G, Zehnder R. 2016. Tree mortality from an exceptional drought spanning mesic to semiarid ecoregions. *Ecological Applications* 26: 602-611.
- Netherer S, Matthews B, Katzensteiner K, Blackwell E, Henschke P, Hietz P, Pennerstorfer J, Rosner S, Kikuta S, Schume H, et al. 2015. Do water-limiting conditions predispose Norway spruce to bark beetle attack? *New Phytologist* 205: 1128-1141.
- Novák V 2009. Physiological Drought – How to Quantify it? In: Střelcová K, Mátyás C, Kleidon A, Lapin M, Matejka F, Blaženec M, Škvarenina J, Holécý J eds. *Bioclimatology and Natural Hazards*. Dordrecht: Springer Netherlands, 89-95.
- O'Brien MJ, Leuzinger S, Philipson CD, Tay J, Hector A. 2014. Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. *Nature Climate Change* 4: 710-714.
- Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG, et al. 2011. A large and persistent carbon sink in the world's forests. *Science* 333: 988-993.
- Paulo AA, Pereira LS. 2006. Drought Concepts and Characterization. *Water International* 31: 37-49.
- Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L. 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytologist* 193: 30-50.
- Purves D, Pacala S. 2008. Predictive models of forest dynamics. *Science* 320: 1452-1453.
- Quentin AG, Pinkard EA, Ryan MG, Tissue DT, Baggett LS, Adams HD, Maillard P, Marchand J, Landhausser SM, Lacomte A, et al. 2015. Non-structural carbohydrates in woody plants compared among laboratories. *Tree Physiology* 35: 1146-1165.
- Raffa KF, Aukema B, Bentz BJ, Carroll A, Erbilgin N, Herms DA, Hicke JA, Hofstetter RW, Katovich S, Lindgren BS. 2009. A literal use of "forest health" safeguards against misuse and misapplication. *Journal of Forestry* 5: 276-277.
- Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Kolb TE. 2015. Responses of tree-killing bark beetles to a changing climate. *Climate Change and Insect Pests*. Wallingford, Oxfordshire, United Kingdom: Centre for Agriculture and Biosciences International (CABI): 173-201.
- Ruehr NK, Gast A, Weber C, Daub B, Arneth A. 2016. Water availability as dominant control of heat stress responses in two contrasting tree species. *Tree Physiology* 36: 164--178.
- Ruehr NK, Law BE, Quandt D, Williams M. 2014. Effects of heat and drought on carbon and water dynamics in a regenerating semi-arid pine forest: a combined experimental and modeling approach. *Biogeosciences* 11: 4139-4156.
- Ryan MG. 2011. Tree responses to drought. *Tree Physiology* 31: 237-239.
- Ryan MG, Sapes G, Sala A, Hood SM. 2015. Tree physiology and bark beetles. *New Phytologist* 205: 955-957.
- Sala A, Piper F, Hoch G. 2010. Physiological mechanisms of drought-induced tree mortality are far from being resolved. *New Phytologist* 186: 274-281.
- Sala A, Woodruff DR, Meinzer FC. 2012. Carbon dynamics in trees: feast or famine? *Tree Physiology* 32: 764-775.
- Salmon Y, Torres-Ruiz JM, Poyatos R, Martinez-Vilalta J, Meir P, Cochard H, Mencuccini M. 2015. Balancing the risks of hydraulic failure and carbon starvation: a twig scale analysis in declining Scots pine. *Plant Cell Environment* 38: 2575-2588.
- Savage JA, Clearwater MJ, Haines DF, Klein T, Mencuccini M, Sevanto S, Turgeon R, Zhang C. 2016. Allocation, stress tolerance and carbon transport in plants: how does phloem physiology affect plant ecology? *Plant, Cell & Environment* 39: 709-725.

- 779 **Secchi F, Zwieniecki MA. 2011.** Sensing embolism in xylem vessels: the role of sucrose as a trigger for refilling.
 780 *Plant, Cell & Environment* **34**: 514-524.
- 781 **Sevanto S. 2014.** Phloem transport and drought. *Journal of Experimental Botany* **65**: 1751-1759.
- 782 **Sevanto S, McDowell NG, Dickman LT, Pangle R, Pockman WT. 2014.** How do trees die? A test of the hydraulic
 783 failure and carbon starvation hypotheses. *Plant, Cell & Environment* **37**: 153-161.
- 784 **Shaw JD, Steed BE, DeBlander LT. 2005.** Forest Inventory and Analysis (FIA) annual inventory answers the
 785 question: What is happening to pinyon-juniper woodlands? *Journal of Forestry* **103**: 280-285.
- 786 **Sijbrands EJG, Tornij E, Homsma SJ. 2009.** Mortality risk prediction by an insurance company and long-term
 787 follow-up of 62,000 men. *PLoS One* **4**: e5457.
- 788 **Sperry JS, Love DM. 2015.** What plant hydraulics can tell us about responses to climate-change droughts. *New*
 789 *Phytologist* **207**: 14-27.
- 790 **Stape JL, Binkley D, Jacob WS, Takahashi EN. 2006.** A twin-plot approach to determine nutrient limitation and
 791 potential productivity in Eucalyptus plantations at landscape scales in Brazil. *Forest Ecology and*
 792 *Management* **223**: 358-362.
- 793 **Taiz L, Zeiger E. 2002.** *Plant physiology*. Sunderland, Massachusetts: Sinauer.
- 794 **Trumbore S, Brando P, Hartmann H. 2015.** Forest health and global change. *Science* **349**: 814-818.
- 795 **Tyree MT, Ewers FW. 1991.** The hydraulic architecture of trees and other woody plants. *New Phytologist* **119**:
 796 345-360.
- 797 **Urli M, Porté AJ, Cochard H, Guengant Y, Burlett R, Delzon S. 2013.** Xylem embolism threshold for
 798 catastrophic hydraulic failure in angiosperm trees. *Tree Physiology* **33**: 672-683.
- 799 **Weber R, Schwendener A, Schmid S, Lambert S, Wiley E, Landhäuser S, Hartmann H, Hoch G. in press.** Living
 800 on next to nothing: Tree seedlings can survive weeks with very low carbohydrate concentrations. *New*
 801 *Phytologist* **XXX**: xx-xx.
- 802 **Williams AP, Allen CD, Macalady AK, Griffin D, Woodhouse CA, Meko DM, Swetnam TW, Rauscher SA,**
 803 **Seager R, Grissino-Mayer HD. 2013.** Temperature as a potent driver of regional forest drought stress
 804 and tree mortality. *Nature Climate Change* **3**: 292-297.
- 805 **Zhao J, Hartmann H, Trumbore S, Ziegler W, Zhang Y. 2013.** High temperature causes negative whole-plant
 806 carbon balance under mild drought. *New Phytologist* **200**: 330-339.

809 Box 1 Death is a complex issue in plants

810 A fundamental question in research on tree mortality concerns the underlying concept of
811 tree death. While apparently intuitive, the concept of tree death is quite different from the
812 concept of death in animals. In contrast to animals, plants lack a nervous system serving as a
813 control organ and indicator of vital functions. In plants, meristematic cells maintain their
814 capacity to differentiate throughout the life time of the plant and many plant cell types,
815 even after their maturation, can re-differentiate, reinitiate cell division and, in some
816 instances, reproduce whole organisms (Taiz & Zeiger, 2002). Meristematic tissues which can
817 be found in stem and root apices and in the vascular cambium, allow trees to potentially
818 grow indeterminately and to produce a modular body where organs/tissues may die off
819 without causing mortality of the entire tree (Klimešová *et al.*, 2015). Some tree species can
820 survive thousands of years by creating hydraulically independent units that allow large tree
821 parts to die back, while the organism itself survives (Larson, 2001).

822 A universal definition of tree death might thus be impossible to achieve. Instead, death
823 indicators must be operationally defined at processes and scales meaningful to the scientific
824 field, type of trees and research goals. Vegetation modelers may consider sustained periods
825 of zero growth or the absence of aboveground living biomass (e.g. branches and stems) as
826 mortality; while ecosystem ecologists may accept a high degree of defoliation at the canopy
827 level in evergreen species (Galiano *et al.*, 2011; Guada *et al.*, 2016), and physiologists the
828 absence of dark respiration (Hartmann *et al.*, 2013) or mortality of cambial cells (Li *et al.*,
829 2016) as indicator of tree death. An alternative, potentially useful concept is the “point of
830 no return”, when the organism is irreversibly prone to death although some tissues may still
831 be alive. Several whole-plant metrics of the point of no return have been proposed,

including loss of living aboveground tissue (quantified via leaf wilting and/or application of vital dyes to branch/stem tissues), cessation of water transport and hydraulic conductivity/water potential gradients that do not recover when conditions get wetter (Anderegg *et al.*, 2012).

Given the interdisciplinary character of tree mortality research, we must accept that an operational definition of tree death of a particular discipline will remain ambiguous to other disciplines. While being aware of the difficulty in translating this concept across disciplines, we urge here the need to clearly define and report criteria of tree death in individual studies while thriving for more uniform definitions within each discipline and plant functional group (e.g., evergreens vs. deciduous trees).

843 Tables

For Peer Review

844 Table 1 Summary of published experimental studies on drought-induced tree mortality
 845 (Adams *et al.*, 2017) showing plant functional type (PFT), study type (field, greenhouse [GH],
 846 growth chamber [Cham] or outdoor potted [Out-pot]) and developmental stage of the trees
 847 used in each study. Please see details for PFT below the table. References can be found in SI
 848 2.

Species	PFT		Study type	Develop. stage	Reference
	mai n	alternat e			
<i>Acer pseudoplatanus</i>	TBD		Out-pot	Seedling	Piper and Fajardo 2016
<i>Populus balsamifera</i>	TBD	BBD	GH/Out-pot	Seedling	Galvez et al. 2013
<i>Populus tremuloides</i>	TBD	BBD	Field	Mature	Anderegg et al. 2012
<i>Populus tremuloides</i>	TBD	BBD	GH/Out-pot	Seedling	Galvez et al. 2013
<i>Eucalyptus globulus</i>	TBE		GH	Seedling	Mitchell et al. 2013, 2014
<i>Eucalyptus radiata</i>	TBE		GH	Seedling	Duan et al. 2014
<i>Eucalyptus smithii</i>	TBE		GH	Seedling	Mitchell et al. 2013, 2014
<i>Nothofagus dombeyi</i>	TBE		GH	Sapling	Piper 2011
<i>Nothofagus nitida</i>	TBE		GH	Sapling	Piper 2011
<i>Callitris rhomboidea</i>	TNE		GH	Seedling	Duan et al. 2015
<i>Juniperus osteosperma</i>	TNE		Out-pot	Sapling	Anderegg and Anderegg 2013
<i>Picea abies</i>	TNE	BNE	Out-pot	Sapling	Hartmann et al. 2013a
<i>Picea abies</i>	TNE	BNE	Cham	Sapling	Hartmann et al. 2013b
<i>Pinus sylvestris</i>	TNE	BNE	GH	Sapling	Garcia Forner et al. 2016
<i>Pinus edulis</i>	TNE		GH	Sapling	Adams et al. 2009, 2013
<i>Pinus edulis</i>	TNE		Out-pot	Sapling	Anderegg and Anderegg 2013
<i>Pinus edulis</i>	TNE		Field	Mature	Plaut et al. 2012
<i>Pinus edulis</i>	TNE		GH	Sapling	Sevanto et al. 2014
<i>Pinus radiata</i>	TNE		GH	Seedling	Duan et al. 2015

<i>Pinus radiata</i>	TNE		GH	Seedling	Mitchell et al. 2013, 2014
<i>Pinus sylvestris</i>	TNE	BNE	Field	Mature	Galiano et al. 2011
<i>Dryobalanops lanceolata</i>	TrBE		GH	Seedling	O'Brien et al. 2015
<i>Durio oxleyanus</i>	TrBE		GH	Seedling	O'Brien et al. 2015
<i>Hopea nervosa</i>	TrBE		GH	Seedling	O'Brien et al. 2015
<i>Koompassia excelsa</i>	TrBE		GH	Seedling	O'Brien et al. 2015
<i>Parashorea malaanonan</i>	TrBE		GH	Seedling	O'Brien et al. 2015
<i>Parashorea tomentella</i>	TrBE		GH	Seedling	O'Brien et al. 2015
<i>Shorea argentifolia</i>	TrBE		GH	Seedling	O'Brien et al. 2015
<i>Shorea beccariana</i>	TrBE		GH	Seedling	O'Brien et al. 2015
<i>Shorea macrophylla</i>	TrBE		GH	Seedling	O'Brien et al. 2015
<i>Shorea parvifolia</i>	TrBE		GH	Seedling	O'Brien et al. 2015

849 TBD - temperate broadleaf deciduous, TBE - temperate broadleaf evergreen, TNE-temperate
850 needleleaf evergreen, TrBE - tropical broadleaf evergreen, BBD - boreal broadleaf
851 deciduous, BNE - boreal needleleaf evergreen

852

853

854 Figure captions

855 Figure 1 Conceptual representation of a probabilistic framework for predicting mortality of a
856 tree population (e.g., species, plant functional type) based on risk factors. Ecophysiological
857 research must determine thresholds for “risk factors”, e.g. like xylem traits that are relevant
858 for drought vulnerability/tolerance, and beyond which the probability of mortality
859 increases. The spread of the “mortality risk zone” represents the variability of the risk factor
860 with respect to occurring mortality. Different risk factors can interact, as when vulnerability
861 to biotic attack increases with depletion of carbohydrates (McDowell *et al.*, 2011).

862 Figure 2 Spatial and temporal scales of tree and forest mortality. Ecophysiological processes
863 integrate over time and from tissue to tree level. These are further influenced by biotic and
864 abiotic interactions at the ecosystem level and scale up to landscapes and longer time
865 scales. A wide range of tools are needed for detecting, understanding and predicting tree
866 death occurrences: while ground-based assessments provide data for process integration at
867 smaller spatial scales, remote-sensing and large-scale monitoring are increasingly important
868 for model-based global simulations and projections of forest mortality in future climate
869 conditions.

870 Figure 3 Locations of substantial drought- and heat-induced tree mortality around the globe
871 since 1970, documented by peer-reviewed studies, updated from Allen *et al.* (2015). Global
872 forest cover (dark green) and other wooded regions (light green) based on FAO (2005).
873 Studies compiled through 2009 (red dots) are summarized and listed in Allen *et al.* (2010);
874 additional localities include the white dots and oval shapes derived from Figure 4-7 and its
875 associated caption in IPCC (2014), the black dots from Fig. 2 in Allen *et al.* (2015), and
876 additional localities (blue) from other recent publications listed in SI 3

Figure 4 Conceptual framework for focused research on drought-induced tree and forest mortality. A coordinated monitoring network that combines inventory plot data and satellite-based remote sensing can provide information on changes in forest cover and identify potential hotspots of mortality. Mortality occurrences in these hotspots can be validated using aerial-based remote sensing technologies like Lidar. In these hotspots, investigations on the underlying physiological processes and ecological interactions through a combination of experimental manipulations and intensive field observations will provide mechanistic relationships allowing more realistic forecasting of forest conditions under anticipated future climate.

Mortality probability (%)

100

50

0

Manuscript submitted to New Phytologist for review

Risk factor value







