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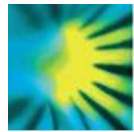
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Research frontiers for improving our understanding of drought-induced tree and forest mortality

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

3

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

5

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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

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

122 The complexity of tree mortality may greatly limit the generality and utility of physiological
123 thresholds identified at the individual tree level for prediction at the population, landscape,
124 regional or global levels. This implies, then, that physiological research at an individual scale
125 might be most productive when identifying “risk factors” that predispose trees to die,
126 analogous in the human mortality literature to lifestyle factors such as smoking cigarettes
127 that greatly increase the odds of death from a given cause like cancer (Sijbrands *et al.*,
128 2009). The identification of key functional and physiological risk factor traits, informed by
129 understanding of C and hydraulic dynamics during tree death, has strong promise to
130 improve our prediction of probabilistic mortality risk at the population level (Fig. 1).

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

134 2016). Here we identify key frontiers in drought-induced tree mortality research across
135 different disciplines and scales, spanning physiological processes in individual tissues to
136 assessments and predictions of local mortality events at regional to global scales (Fig. 2). In
137 addition, we provide research recommendations that serve as guidelines for directing future
138 work to the areas of greatest need. We conclude by setting out a multidisciplinary strategy
139 including practical recommendations that aim to identify crucial physiological risk factors in
140 tree and forest mortality. Such risk factors can provide mechanistic relationships for more
141 realistic predictions of future forest conditions.

142

143 2. Mechanisms of tree mortality

144 The hydraulic framework of global-change drought-induced tree mortality (McDowell *et al.*,
145 2008) proposed two non-exclusive physiological mechanisms: CS and HF. The relative
146 importance and potential interaction between these two mechanisms leading to tree death
147 has structured most of the research since this scientific debate has been started (McDowell
148 & Sevanto, 2010; Sala *et al.*, 2010). For this reason, we identify research frontiers mainly
149 related to C and water relations as well as the role of biotic agents in tree mortality. In
150 addition, the hydraulic framework emphasised ecological processes including plant resource
151 acquisition, plant-biotic interactions and the ability of trees to recover from previous
152 drought events. These topics, underrepresented in current research despite their potential
153 significance in drought-induced tree mortality, are briefly discussed in Supporting
154 Information (SI 1). Furthermore, some intrinsic factors known to influence tree responses to
155 drought and heat, like tree functional type (Mitchell *et al.*, 2014; Ruehr *et al.*, 2016),
156 developmental stage or age, are underrepresented in the current literature because most

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

162 *Carbon*

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

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

180 defence compounds, emissions of biogenic volatile organic compounds (VOC), root exudates
181 and export to symbionts (e.g., mycorrhiza, rhizobia). VOC emissions (Loreto & Schnitzler,
182 2010) and respiration rates increase often with temperature (Adams *et al.*, 2009) but not
183 always (Duan *et al.*, 2013) during drought. However, scarcity of data on these whole-tree
184 processes currently limits our understanding of whole-tree C dynamics during drought-
185 induced mortality. An important step forward would be to quantify the entire net C balance
186 of trees to assess when C loss becomes larger than C uptake and available NSC reserves (see
187 also interdependency section) and which minimum levels of NSC might become lethal
188 (Weber *et al.*, in press).

189 *Water*

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

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

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

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

211 Plant traits linking wood anatomy to hydraulic properties such as wood density, pit
212 membrane thickness between adjacent vessels and torus overlap in conifer tracheids may
213 be useful proxies for embolism resistance (Li *et al.*, 2016). Given that some trees' hydraulic
214 pathways may be highly segmented across organs (e.g., Tyree & Ewers, 1991; Bucci *et al.*,
215 2012; Johnson *et al.*, 2016), emerging research should identify critical levels of water
216 potential related to embolism and organ loss. A better mechanistic understanding can then
217 be gained by quantifying the range from recoverable to lethal xylem Ψ and its native
218 embolism to provide a probabilistic base for mortality estimates. This should then be linked
219 to hydraulic traits in different tree species/functional types across forested biomes.

220 *Interdependencies*

221 Carbon and water dynamics in plants are ultimately interrelated via stomatal regulation and
222 vascular transport. The interdependency of CS and HF in drought-induced tree mortality has
223 been conceptually well established (McDowell, 2011) but investigations have only recently
224 addressed this formally (e.g., O'Brien *et al.*, 2014). Several urgent mortality-related frontiers
225 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

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

252 *Insects and Pathogens*

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

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

272 *al.*, 2008). Cooperation among plant ecophysiologicals, 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.

295

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

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

306 *Process integration and scaling issues in predictions of mortality*

307 Scaling from individual trees to ecosystems and regions requires determining key
308 environmental factors that may change the probability of mortality in space: 1) lateral water
309 flows and the role of groundwater or hydraulic lift in mitigating water stress (Barbeta *et al.*,
310 2015), 2) existing spatial variation in soils, microclimate, and stand structure, and 3) biotic
311 interactions that include insects/pathogens, and plant-plant interactions such as
312 competition for water (see also S1). For instance, landscape variability due to topography,
313 soil characteristics, and management history likely promotes patchy patterns of mortality
314 that are often observed across broad regions (Huang & Anderegg, 2012). The spatial pattern
315 of tree mortality may be further affected by the interaction between drought and
316 insect/pathogen outbreaks, due to the spatial nature of pest dispersal and infection

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

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

334 *Modelling*

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

340 considerable interest in improving the representation of tree mortality in DGVMs, given its
341 importance on long-term forest dynamics (Bircher *et al.*, 2015), and in the regulation of
342 ecosystem carbon storage (e.g., Friend *et al.*, 2014). However, tree mortality formulations in
343 current DGVMs are generally simple, ranging from fixed carbon turnover rates (Galbraith *et*
344 *al.*, 2013) to approaches where mortality is related to growth efficiency or negative carbon
345 balance (McDowell *et al.*, 2011). Such approaches have been found to be insufficient to
346 adequately capture observations of drought-induced tree mortality (e.g., Manusch *et al.*,
347 2012).

348 To address these problems, we identify the following research frontiers: 1) implement plant
349 hydraulic representations in DVMs that allow for species- or plant functional type-specific
350 drought strategies in dimensions of stomatal control, root distribution, allometry, and
351 hydraulic properties such as vulnerability to embolism, 2) determine the key axes of drought
352 trait trade-offs necessary to simulating different species' drought response strategies
353 (Bartlett *et al.*, 2016) and how these are linked to probability of mortality (Anderegg *et al.*,
354 2016), and 3) test and validate probabilistic mortality functions at regional scales against
355 extreme droughts in the observational record where probability of mortality can be
356 estimated through forest inventories, other plot data, or remote-sensing estimates (Brienen
357 *et al.*, 2015). We emphasize that if mortality projections are made at regional scales, model
358 validation against independent mortality data should be performed at the same spatial
359 scales to have confidence in model projections.

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

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

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

383

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

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

396 *Assessing changes in forest condition via monitoring at multiple scales*

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

409 network sources (e.g., different countries) can be a complex task. In addition, historical
410 inventory data typically have been field-collected on longer time intervals (commonly every
411 5 to 10 years), making it difficult to pinpoint mortality occurrences to specific climatic events
412 and/or causes of tree death. By contrast, satellite data are becoming more easily available
413 and may allow “close to real-time” assessments of changes in forest cover from
414 disturbances over large regions (McDowell *et al.*, 2015a). Ground-based validation of
415 satellite data may build on an already increasing number of inventory plot networks from
416 both governmental agencies and/or multiple research institutions partnerships (like
417 RAINFOR, FORESTPLOTS.NET or CTFS-ForestGEO) that cover different forest biomes.
418 However, these plot-based monitoring networks were never designed to specifically address
419 tree mortality, and we will need novel observation networks (or protocols) that allow a
420 faster and more automated detection of mortality events.

421 Recent advances in remote sensing provide a new generation of tools that could enable
422 global satellite monitoring of die-off and other broad-scale disturbances (McDowell *et al.*,
423 2015a). For example, the Global Forest Watch initiative (<http://www.globalforestwatch.org>)
424 of the World Resources Institute is a good step forward to detecting temporal changes in
425 forest cover from disturbance or mortality but the spatial resolution of the underlying data
426 (30 m) is larger than the scale at which individual tree mortality occurs and precludes
427 inferences on the underlying physiological processes. New technologies, like Lidar, now
428 allow monitoring of individual trees over larger areas (e.g., Asner *et al.*, 2016) thereby
429 closing the gap between tree-level information from inventory plots, and information at
430 stand and regional scales derived from satellite data. The challenge now becomes to link
431 these approaches in a coordinated manner, allowing (1) a direct flow of information

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

436 Although the Global Forest Watch provides “close to real-time” information on forest
437 conditions, changes in forest cover are currently captured by identifying areas with well-
438 defined boundary attributes, like forest management and land-use change, or large-scale
439 severe disturbances (e.g., wild fires, windthrow, insect outbreaks). Climate change-driven
440 mortality of individual trees would thus likely appear as remaining spatially-diffuse changes
441 in forest cover and are currently not systematically assessed. Such mortality should become
442 a focus for ground-proofing via existing inventory or research plot data. Additional
443 assessment cruises or Lidar imaging will allow determining whether changes in forest cover
444 are due to mortality or reduced vigour of trees. Such measurements can be supplemented
445 by multi-spectral imagery installed on UAV (unmanned aerial vehicles, e.g., Dash *et al.*,
446 2017). Taken together such tools will open promising avenues to monitor forest health at
447 scales relevant for detecting tree mortality (Hartmann *et al.*, in press).

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

450 To forecast drought-induced tree mortality we need to understand mortality mechanisms at
451 the tree level first and use this understanding to derive mortality-related risk factors that
452 allow probabilistic mortality predictions at larger scales. Naturally-occurring lethal drought
453 events (identified as hotspots of spatially-diffuse mortality) detected by remote-sensing,
454 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

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

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

487 In addition, observations and experiments along naturally-occurring drought and
488 temperature gradients can be a valuable addition to drought experiments when studying
489 tree responses to different climatic drivers (Stape *et al.*, 2006; Moore *et al.*, 2016; Binkley *et al.*,
490 2017) and interactions with nutrient limitations. Intensive field investigations will be
491 most promising if common protocols for observations and measurements are developed
492 and used across different projects (e.g., as in NutNet, DroughtNet and similar research
493 networks). Impacts of insects and pathogens during drought must become part of protocols
494 in field studies and observations, as they are crucial risk factors in tree mortality.

495 *Forecasting forest responses to climatic change*

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

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

516 5. Conclusion

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

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

530

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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.

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806 carbon balance under mild drought. *New Phytologist* **200**: 330-339.

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808

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,

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

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

842

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
	main	alternate			
<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

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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

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

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