

REVIEW

A synthesis of tree functional traits related to drought-induced mortality in forests across climatic zones

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Summary

1. Forest dieback caused by drought-induced tree mortality has been observed world-wide. Forecasting which trees in which locations are vulnerable to drought-induced mortality is important to predict the consequences of drought on forest structure, biodiversity and ecosystem function.

2. In this paper, our central aim was to compile a synthesis of tree traits and associated abiotic variables that can be used to predict drought-induced mortality.

3. We reviewed the literature that specifically links drought mortality to functional traits and site conditions (i.e. edaphic variables and biotic conditions), targeting studies that show clear use of tree traits in drought analysis. We separated the review into five climatic zones to determine global vs. regionally restricted relationships between traits and mortality.

4. Our synthesis identifies a number of traits that have clear relationships with drought-induced mortality (e.g. wood density at the species level and tree size and growth at the individual level). However, the lack of direct relationships between most traits and drought-induced mortality highlights areas where future research should focus to broaden our understanding.

5. *Synthesis and applications.* Our synthesis highlights established relationships between traits and drought-induced mortality, presents knowledge gaps for future research focus and suggests monitoring and research avenues for improving our understanding of drought-induced mortality. It is intended to assist ecologists and natural resource managers choose appropriate and measurable parameters for predicting local and regional scale tree mortality risk in different climatic zones within constraints of time and funding availability.

Key-words: climate change, drought-induced mortality, forest dieback, forested climatic zones, plant functional traits, plant–climate interactions, research gaps, water deficit

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Introduction

Tree mortality due to drought is a global phenomenon documented in a wide range of forest ecosystems (Allen *et al.* 2010). Globally, most tree species are highly vulnerable to death from hydraulic failure with slight increases in temperature or reductions in soil moisture (Choat *et al.* 2012; Anderegg *et al.* 2015a). Simultaneously, there is mounting evidence that many parts of the world will suffer increasing forest mortality from more severe and frequent droughts under future climates (Dai 2013). Recent evidence suggests that tree mortality during drought is already increasing, especially in dry parts of the world (van Mantgem *et al.* 2009; Steinkamp & Hickler 2015). Although our understanding of the mechanisms and processes that underlie drought-induced mortality continues to grow, our ability to identify vulnerable trees or stands of trees remains poor, which in turn inhibits our ability to model forest response to future climate scenarios. Predictions of which trees are most vulnerable and where, are urgently needed to project consequences of climate change and to inform mitigation strategies.

WHY FUNCTIONAL TRAITS

Measurements of comprehensive sets of traits and long-term monitoring of forest dynamics at informative scales are expensive and the availability of time and funds often constrains the number and type of traits and environmental parameters that can be measured. Forest ecologists and managers aiming to understand and predict drought vulnerability are therefore often faced with the problem of which traits to focus on. We provide information to aid decisions for development of research plans that maximize insights into local and regional scale differences in tree and forest vulnerability in the face of usually limited funding. Since trait expression varies across climatic zones (see Fig. 1 for differences in traits extracted from trait databases) and in turn the relative importance of traits and environmental parameters for drought mortality (summary in Table 1), we take a climatic zone-specific approach to evaluating the relative value of traits for their ability to predict drought-induced mortality. Therefore, we reviewed the state of knowledge on the relationships of traits for drought-induced mortality (at both the individual and species level) for each forested climatic zone. We appraised the informative value of traits shown or hypothesized to be important for tree differential vulnerability to drought-induced mortality, the effort, skill and cost involved in assessing them and the potential to archive samples for later analyses (when further evidence, urgency or funding sources arise). We specifically aimed to include traits that have been directly and mechanistically relevant to tree mortality.

Our review will assist researchers and managers in choosing the appropriate traits to measure in their given climatic zone while identifying knowledge gaps where

future research should be focused. This approach is aimed at addressing the following questions. (i) Can we identify (a set of) marker traits for differential tree vulnerability in each climatic zone? (ii) Which traits and environmental conditions should we prioritize as most informative and simple to measure in each climatic zone? and (iii) What are the knowledge gaps and what needs to be done to fill these?

OVERVIEW OF DROUGHT VULNERABILITY AND FUNCTIONAL TRAITS

Droughts are caused by rainfall deficits that reduce water availability significantly below the average annual conditions and often coincide with increases in temperature and evaporative demand, both of which have an important role in drought-induced mortality of trees (Eamus *et al.* 2013). At a global scale, predictable patterns of drought-induced tree mortality are limited, and even within climatic zones at regional and local scales, tree mortality is highly variable (McDowell *et al.* 2008; Choat *et al.* 2012; Camarero *et al.* 2015). However, there are three main factors that contribute to local and regional variation in mortality: (i) abiotic environmental conditions, (ii) competition or facilitation among trees and (iii) traits of the trees themselves. Pathogens and insects may also enhance mortality during drought (Anderegg *et al.* 2015b), but, for simplicity, we concentrate on direct drought-induced tree mortality only.

Assessment of key functional traits has the potential for projection of tree vulnerability to drought, detection of drought effects and prediction of forest composition and function under future climate scenarios. Functional traits are characteristics that determine the responses to environmental factors (i.e. response traits; Kattge *et al.* 2011). They can provide a bridge between ecophysiology, community composition and ecosystem function (Reich *et al.* 2003). Plant functional traits have received increasing attention because while they can be somewhat plastic, they allow extrapolation beyond the species level to understand and predict plant performance over larger phylogenetic and spatial scales (Kattge *et al.* 2011). A trait based approach is particularly valuable in diverse forests of temperate and tropical regions where measuring each tree species is difficult or impossible.

A wide range of tree traits have been shown, hypothesized or implied to be important in determining differential tree mortality in response to drought (Table 1). For most of these traits, their importance for determining differential tree vulnerability to drought within climatic zones has not been tested explicitly (Table 1). Rigorously testing the importance of various traits for predicting drought vulnerability of trees requires directly linking mortality, due to drought, with species traits. Experimental drought manipulation for trees is challenging because of the size and longevity of trees (but see examples Moser *et al.* 2014; Rowland *et al.* 2015). Furthermore, the

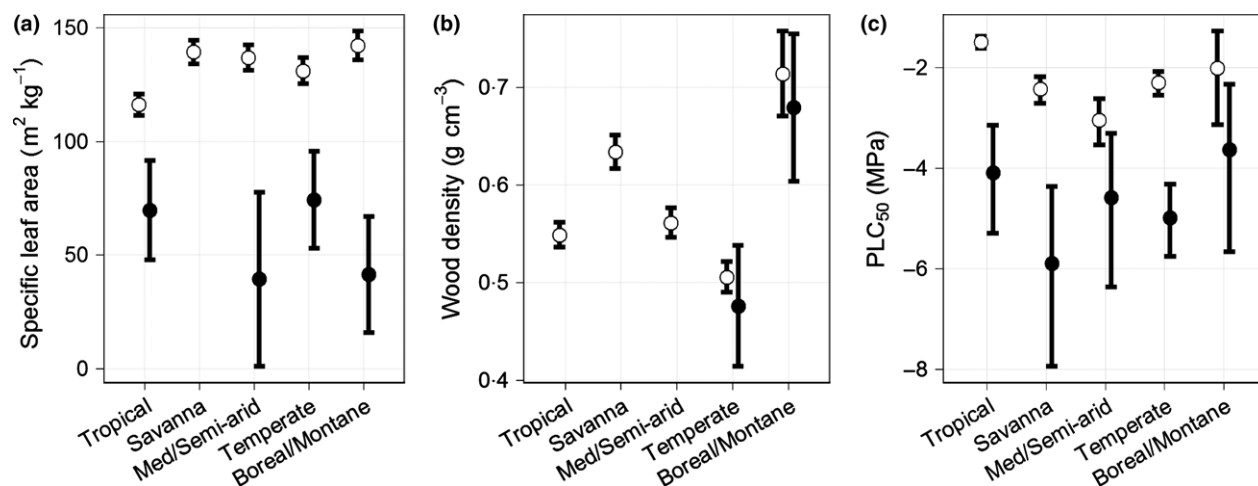


Fig. 1. Mean trait values (SE) by climatic zone for three traits. Data were collected from the TRY database for (a) specific leaf area and (b) wood density while (c) 50% loss of conductivity was taken from (Choat *et al.* 2012). Points represent model estimates of each trait for each plant functional type (○ = angiosperm and ● = gymnosperm; see Appendix S1, Supporting Information for analysis). It is important to note that angiosperm variation is much lower in all traits (a list of data sources used in the study are provided in the Data sources section).

methodologies, repeatability and theoretical assumptions underlying the use of physiological traits (e.g. cavitation resistance and non-structural carbohydrate storage) have been questioned (Rockwell, Wheeler & Holbrook 2014; Quentin *et al.* 2015). Specifically, the measurement of xylem cavitation and embolism has been criticized and suggest that plants may not be regularly acting at the brink of hydraulic failure (Rockwell, Wheeler & Holbrook 2014). However, we put aside these methodological uncertainties in this review as correlations among relative trait distributions and drought mortality have been found in spite of these measurement concerns (Choat *et al.* 2012; Anderegg *et al.* 2016).

Review of climatic zones

BOREAL AND MONTANE FORESTS

Boreal and montane climatic zones represent more than a third of forested landscapes (FAO 2001). Climatic variation is influenced by latitudinal and longitudinal gradients and topography, at large and local scales respectively. Drought-induced forest mortality in conjunction with elevated temperatures has already been reported in montane and boreal forests of Eurasia (Dobbertin & Rigling 2006; Kharuk *et al.* 2013b), the montane regions of the western USA (Anderegg *et al.* 2012) and the southern extent of the boreal forest in Canada (Hogg, Brandt & Michaelian 2008; Peng *et al.* 2011).

Under future global warming scenarios, seasonal droughts are likely to become more severe due to reduced snowpack and earlier snowmelt runoff (van Mantgem *et al.* 2009; Anderegg, Kane & Anderegg 2013). These altered precipitation patterns are projected to be exacerbated by fires (Bond-Lamberty *et al.* 2007; Mann *et al.* 2012) and insect outbreaks (Kurz *et al.* 2008). Overall,

drought is expected to play a greater role in the southern and lower elevation ecotones that transition into grass-dominated ecosystems (Peng *et al.* 2011), while areas that are dominated by more maritime climates will be less impacted by drought (Walsh *et al.* 2008). Drought effects in the northern extent of the boreal and montane zones will potentially be overshadowed or buffered by the positive effects of warmer conditions and the low evapotranspiration rates under a still relatively cool climate (Way & Oren 2010; Scheffer *et al.* 2012).

Relative to other forested climatic zones, the boreal climatic zone has low species diversity but high intraspecific diversity (Grulke 2010). Many of the dominant tree species have expansive ranges – for example, *Populus tremuloides* Michx. (Liefers, Landhauser & Hogg 2001) and *Pinus sylvestris* L. (Rehfeldt *et al.* 2002) – across both the boreal and montane climatic zones in North America and Eurasia. Therefore, intraspecific variation in traits that improve drought resistance is important to consider in these often monodominant forests within these climatic zones.

Seasonal drought, often during the summer growing season, is characteristic of these climatic zones. There is extensive research on the effect of drought on growth, carbon storage, hydraulic conductance and wood properties (Kavanagh *et al.* 1999; Anderegg *et al.* 2012; Adams *et al.* 2013) and the consequences of drought on stand dynamics and regeneration (Chapin *et al.* 2004; Soja *et al.* 2007; Moser *et al.* 2010; Michaelian *et al.* 2011). There is far less information on the role of traits in mediating mortality and promoting survival.

Drought survival–trait relationships

Two growth variables have been identified as indicative of susceptibility to drought of individual trees based on the

Table 1. Functional traits that potentially mediate drought-induced mortality (see Table S1 for references on how to measure these traits). The phrase 'No refs' indicate gaps in direct correlations within the literature. All traits could be measured at the individual level or averaged for a species level. For tree structure and growth traits, maximum values are considered species-level traits

| Functional trait | Abbrev | Unit | Climate zones with evidence | Boreal/Montane | Temperate | Mediterranean/ semi-arid | Savanna | Tropical |
|--------------------------------|------------|----------------------------------|---|--|---|--|--|--|
| <i>Tree structure</i> | | | | | | | | |
| Tree height | H_{\max} | m | Boreal, Temperate, Mediterranean, Savanna, Tropical | Worrall <i>et al.</i> (2008), Stahl <i>et al.</i> (2013) | Suarez, Ghermandi & Kitzberger (2004), van Mantgem & Stephenson (2007) | Valladares & Sánchez-Gómez (2006) | Viljoen (1995), O'Connor (1998), MacGregor & O'Connor (2002), Poorter & Markesteijn (2008), Phillips <i>et al.</i> (2010), Itoh <i>et al.</i> (2012) | Condit, Hubbell & Foster (1995), Nakagawa <i>et al.</i> (2000), Potts (2003), Phillips <i>et al.</i> (2010), Schuldt <i>et al.</i> (2011), Itoh <i>et al.</i> (2012) |
| Diameter at breast height | DBH | cm | Boreal, Temperate, Mediterranean, Savanna, Tropical | Ogle, Whitham & Cobb (2000), Bigler <i>et al.</i> (2007), Worrall <i>et al.</i> (2008), Stahl <i>et al.</i> (2013) | Suarez, Ghermandi & Kitzberger (2004), van Mantgem & Stephenson (2007), Camarero <i>et al.</i> (2015) | Ogle, Whitham & Cobb (2000), Lloret, Siscart & Dalmases (2004) | Viljoen (1995), MacGregor & O'Connor (2002), Phillips <i>et al.</i> (2010) | Condit, Hubbell & Foster (1995), Nakagawa <i>et al.</i> (2000), Potts (2003), Hole <i>et al.</i> (2007), Phillips <i>et al.</i> (2010), Itoh <i>et al.</i> (2012) |
| Above-ground biomass | AGB | kg | Mediterranean, Savanna | No refs | No refs | Valladares & Sánchez-Gómez (2006) | Fensham, Fairfax & Ward (2009) | No refs |
| Basal area increment | BAI | cm ² yr ⁻¹ | Boreal, Temperate, Mediterranean | Ogle, Whitham & Cobb (2000), Bigler <i>et al.</i> (2007) | Suarez, Ghermandi & Kitzberger (2004), Frank <i>et al.</i> (2015), Camarero <i>et al.</i> (2015) | Ogle, Whitham & Cobb (2000) | No refs | No refs |
| Above-ground biomass increment | ABI | kg yr ⁻¹ | Tropical | | | | | Moser <i>et al.</i> (2014) |
| Root biomass | BGB | g | Temperate, Savanna, Tropical | No refs | Bréda <i>et al.</i> (2006) | No refs | Fensham & Fairfax (2007) | Poorter & Markesteijn (2008), Markesteijn & Poorter (2009) |
| Below-ground biomass increment | BBI | kg yr ⁻¹ | | | | | | |
| Root-shoot ratio | RSR | kg kg ⁻¹ | Temperate, Mediterranean | No refs | Bréda <i>et al.</i> (2006) | Padilla & Pugnaire (2007) | No refs | No refs |
| <i>Leaf traits</i> | | | | | | | | |
| Specific leaf area | SLA | cm ² g ⁻¹ | Tropical | No refs | No refs | No refs | No refs | Poorter & Markesteijn (2008), Markesteijn & Poorter (2009) |

(continued)

Table 1. (continued)

| Functional trait | Abbrev | Unit | Climate zones with evidence | Boreal/Montane | Temperate | Mediterranean/semi-arid | Savanna | Tropical |
|-----------------------------------|--------------|--------------------------------|--|--|--|---|---|---|
| Leaf to sapwood area ratio | $A_L: A_X$ | | | | | | | |
| Non-structural carbohydrates leaf | NSC_{leaf} | % or $mg\ g^{-1}$ | Tropical | No refs | No refs | No refs | No refs | O'Brien <i>et al.</i> (2014, 2015) |
| Minimum leaf water potential | Ψ_{min} | MPa | Mediterranean, Tropical | No refs | No refs | Martínez-Vilalta & Piñol (2002), Villar-Salvador <i>et al.</i> (2004), Poyatos <i>et al.</i> (2008), McDowell <i>et al.</i> (2008), Breshears <i>et al.</i> (2009), Siam <i>et al.</i> (2009), Adams <i>et al.</i> (2013) | | Baltzer <i>et al.</i> (2008), Kursar <i>et al.</i> (2009) |
| Osmotic potential at full turgor | Ψ_p | MPa | Mediterranean | No refs | No refs | Siam <i>et al.</i> (2009) | No refs | No refs |
| Leaf turgor loss point | π_{lp} | MPa | Mediterranean | No refs | No refs | Robson <i>et al.</i> (2009), Siam <i>et al.</i> (2009) | No refs | No refs |
| Electrolyte leakage | PEL | % | | | | | | |
| <i>Stem wood</i> | | | | | | | | |
| Tree-ring width | TRW | mm | Boreal, Temperate, Mediterranean | Ogle, Whitham & Cobb (2000), Bigler <i>et al.</i> (2007) | Bigler & Bugmann (2004), Frank <i>et al.</i> (2015) | Ogle, Whitham & Cobb (2000) | No refs | No refs |
| Wood density | WD | $g\ cm^{-3}$ | Temperate, Mediterranean, Tropical | | Martínez-Meier <i>et al.</i> (2008), Hoffmann <i>et al.</i> (2011), Nardini, Battistuzzo & Savi (2013) | Jacobsen <i>et al.</i> (2007), Martínez-Vilalta <i>et al.</i> (2010) | No refs | Van Nieuwstadt & Sheil (2005), Phillips <i>et al.</i> (2009), Olson & Rosell (2013), O'Brien <i>et al.</i> (2014) |
| Vessel diameter | D | μm | Boreal, Temperate, Mediterranean, Tropical | Anderegg <i>et al.</i> (2012) | Lubbe <i>et al.</i> (2016), Schuldt <i>et al.</i> (2016) | No refs | Rice <i>et al.</i> (2004), Fensham & Fairfax (2007) | Schuldt <i>et al.</i> (2013) |
| Vessel density | V_D | $n\ mm^{-2}$ | Temperate | | Lubbe <i>et al.</i> (2016), Schuldt <i>et al.</i> (2016) | No refs | No refs | No refs |
| Potential conductivity | Kp | $kg\ m^{-1}\ MPa^{-1}\ s^{-1}$ | Boreal, Temperate, Savanna | McDowell <i>et al.</i> (2008) | Lubbe <i>et al.</i> (2016), Schuldt <i>et al.</i> (2016) | No refs | Fensham, Fairfax & Ward (2009) | No refs |

(continued)

Table 1. (continued)

| Functional trait | Abbrev | Unit | Climate zones with evidence | Boreal/Montane | Temperate | Mediterranean/semi-arid | Savanna | Tropical |
|--|-----------------------------------|--|---|---|---|---|---|------------------------------------|
| Non-structural carbohydrates stem wood | NSC _{stem} | % or mg g ⁻¹ | Boreal, Tropical | Rood <i>et al.</i> (2000), Landhäusser & Lieffers (2002), Galvez, Landhäusser & Tyree (2013) | No refs | No refs | No refs | O'Brien <i>et al.</i> (2014, 2015) |
| <i>Branch wood</i> | | | | | | | | |
| Non-structural carbohydrates branch wood | NSC _{branch} | % | Boreal | Rood <i>et al.</i> (2000), Landhäusser & Lieffers (2002), Galvez, Landhäusser & Tyree (2011, 2013) Hacke <i>et al.</i> (2001) | No refs | No refs | No refs | No refs |
| Sapwood area-specific hydraulic conductivity | K _S | kg m ⁻¹ MPa ⁻¹ s ⁻¹ | Boreal | | No refs | No refs | No refs | No refs |
| Leaf area-specific hydraulic conductivity | K _L | kg m ⁻¹ MPa ⁻¹ s ⁻¹ | Mediterranean, Tropical | No refs | No refs | Martínez-Vilalta & Piñol (2002), Mediavilla & Escudero (2004) | No refs | Markestijn <i>et al.</i> (2011b) |
| Embolism resistance | P ₅₀ , P ₈₈ | MPa | Boreal, Temperate, Mediterranean, Savanna | Anderegg <i>et al.</i> (2012, 2013), Anderegg, Kane & Anderegg (2013) | Brodrribb & Cochard (2009), Uri <i>et al.</i> (2013), Nardini, Battistuzzo & Savi (2013), Anderegg <i>et al.</i> (2016) | Martínez-Vilalta & Piñol (2002), Escudero (2004) | Rice <i>et al.</i> (2004), Fensham & Fairfax (2007) | |
| Hydraulic safety margin | HSM | MPa | Boreal, Temperate | Choat <i>et al.</i> (2012) | Anderegg <i>et al.</i> (2016) | No refs | No refs | No refs |
| <i>Roots traits</i> | | | | | | | | |
| Maximum rooting depth | MRD | m | Boreal, Temperate, Mediterranean, Savanna, Tropical | Yarie (2008), Chenlemuge <i>et al.</i> (2013), Kharuk <i>et al.</i> (2013a,b) | Bréda <i>et al.</i> (2006) | Padilla & Pugnaire (2007), Sarris, Siegwolf & Körner (2013), Padilla <i>et al.</i> (2015) | Rice <i>et al.</i> (2004), Fensham & Fairfax (2007) | Hertel <i>et al.</i> (2009) |
| Non-structural carbohydrates roots | NSC _{roots} | % or mg g ⁻¹ | Boreal, Tropical | Rood <i>et al.</i> (2000), Landhäusser & Lieffers (2002), Galvez, Landhäusser & Tyree (2011, 2013) | No refs | No refs | No refs | O'Brien <i>et al.</i> 2014 (2015) |

comparison of tree rings of dead and living trees after drought: high inter-annual growth variability and slow radial growth (Ogle, Whitham & Cobb 2000; Bigler *et al.* 2007). Large tree size – a potential proxy of old age – indicates mortality risk for trees (Stahl *et al.* 2013). For example, aspen stands with larger stems and more evaporative load on their leaves and had greater mortality during severe droughts in Colorado (Worrall *et al.* 2008).

Resistance to xylem embolism and hydraulic failure appears to be an important physiological trait based on both experimental tests and phenomenological observations (Anderegg *et al.* 2012). Furthermore, repeated drought events may lead to embolism fatigue due to numerous embolism events and the inability to repair embolized conduits (Anderegg *et al.* 2013), which may affect conifers considerably more than angiosperms (Choat *et al.* 2012). Therefore, properties such as wood density and conduit architecture, although untested in this climatic zone, will likely correlate with drought-induced mortality (Hacke *et al.* 2001). Rooting depth has been inferred to be important for drought survival in these forests, especially in areas with rocky, cold or frozen soils in boreal areas (Yarie 2008; Kharuk *et al.* 2013b).

Variables related to growth and regeneration strategies have been little explored for drought tolerance in these climatic zones. However, adaptations to fire such as vegetative sprouting may be applicable for drought resistance, especially in angiosperms as resprouting is less common in conifers (Zeppel *et al.* 2015). Resprouting could also be interpreted as a potentially intriguing mechanism to tolerate drought, whereby mortality of above-ground organs during drought results in the long-term survival of the tree (Worrall *et al.* 2010). For example, Hogg, Brandt & Michaelian (2008) observed large-scale above-ground mortality in the aspen parkland of Canada but often these stands recovered from their surviving root systems. In conjunction, NSC reserve status of the surviving tissues will likely play a role in the survival of these species (Landhäusser & Loeffers 2002; Galvez, Landhäusser & Tyree 2013).

Environmental and stand characteristics

Particularly in montane regions, topography (slope, aspect and elevation) are crucial variables for predicting tree mortality. Upper and mid slope positions on shallow or coarse textured soils will have rapid declines in water availability during drought. In montane forests in the Rocky Mountains, USA, south-facing slopes with more direct sun and higher evapotranspiration have had increased mortality during regional drought events (Worrall *et al.* 2008; Huang & Anderegg 2012). Furthermore, mesic sites in these zones will likely experience more droughts under future climate change scenarios, and tree species associated with wetter sites are often more vulnerable to embolism which would lead to higher mortality under drought (Kavanagh *et al.* 1999).

TEMPERATE FORESTS

Forests of the temperate climatic zone, including much of western Europe, eastern North America, north-eastern Asia, south-eastern Australia and New Zealand, can be separated into areas that experience regular late growing-season drought and areas that experience severe droughts on supra-annual intervals (Hanson & Weltzin 2000). Severe drought events are increasing in temperate areas of Europe and North America (Hanson & Weltzin 2000; Bréda *et al.* 2006) and shifts in precipitation are coupled with predicted increases in temperatures of 2–6 °C by 2100 relative to the end of the 20th century, which will be accompanied by increased evaporative demand (Forzieri *et al.* 2014). In Australasia, the intensification of El Niño Southern Oscillation (ENSO) is causing more frequent prolonged droughts (Dai 2013). The timing of drought is particularly important in the temperate climatic zone as an early growing-season drought can have substantial negative impacts on tree survival (Kramer, Leinonen & Loustau 2000) and a late growing-season drought can increase mortality in the following year (Solberg 2004).

Unlike other climatic zones, the temperate climatic zone benefits from many long-term forest-monitoring plots that provide *post-hoc* assessments of relationships between drought-induced mortality and traits. Also, tree response to drought has been relatively well studied in temperate forests of North America and Europe (Bréda *et al.* 2006; Allen *et al.* 2010) because many researchers are based in temperate areas. However, studying the morphological and physiological response often does not indicate traits with predictive power (see review in Bréda *et al.* 2006) and research is lacking in the other temperate regions, especially in Australasia.

Drought survival–trait relationships

Slow growth prior to the onset of drought is a good indicator of individual tree susceptibility to reduced soil water availability (Suarez, Ghermandi & Kitzberger 2004; Camarero *et al.* 2015; Cailleret *et al.* 2016). However, the strength of this relationship may be species specific (Camarero *et al.* 2015). Dendrochronological data are accordingly suited for predicting the time of tree death (Bigler & Bugmann 2004) as they record the trees' long-term response to declining water availability. Furthermore, individual tree size is important, with smaller trees and juveniles having higher mortality than larger trees (Suarez, Ghermandi & Kitzberger 2004; van Mantgem & Stephenson 2007). Russo *et al.* (2010) observed a negative correlation between mortality rate and maximum tree height – a species-level instead of individual-level trait – for woody species in New Zealand (Russo *et al.* 2010).

Xylem vulnerability to embolism has been shown to relate to drought-induced mortality (Anderegg *et al.* 2016). Lethal levels of hydraulic failure are assumed to be the water potential causing 50% loss of conductivity

(PLC₅₀) for conifers (Brodribb & Cochard 2009) but greater than or equal to the water potential causing 90% loss of conductivity (PLC₉₀) in angiosperms (Urli *et al.* 2013). Nardini, Battistuzzo & Savi (2013) found crown desiccation and shoot dieback to be more widespread in species with low embolism resistance.

Wood density positively correlated with tree survival during the severe drought of 2003 in European temperate forests (Martinez-Meier *et al.* 2008; Nardini, Battistuzzo & Savi 2013). Contrastingly, a study in the USA found low wood density species had higher survival after a severe drought because these species exhibited an avoidance strategy by stomatal closure and semi-deciduousness (Hoffmann *et al.* 2011) indicating the importance of drought deciduousness. Therefore, the ability to lose leaves and drought conditions may correlate with a different suite of traits for reducing drought mortality (see explanation in *Overview and Synthesis*). Additionally, angiosperms and gymnosperms showed different relationships between traits and drought-induced mortality, whereby wood density was important for angiosperms while hydraulic safety margins and PLC₅₀ were more important for gymnosperms (Anderegg *et al.* 2016).

Environmental and stand characteristics

Environmental and forest variables are also important for predicting tree mortality in temperate forests. In temperate angiosperm tree species, embolism resistance of the branch wood measured is closely related to climatic aridity (Wortemann *et al.* 2011; Schuldt *et al.* 2016) as well as soil water content (Awad *et al.* 2010). Klos *et al.* (2009) found more diverse forest stands had lower drought-induced mortality than less diverse stands. Although higher species diversity may not always improve drought resistance, it has a positive effect in drought-prone sites (Grossiord *et al.* 2014). Forests on steep rocky sites experienced higher mortality than lowland forests (Suarez, Ghermandi & Kitzberger 2004; Klos *et al.* 2009). Additionally, high tree density (i.e. increased competition) negatively correlated with survival (Klos *et al.* 2009).

MEDITERRANEAN AND SEMI-ARID CLIMATIC ZONES

Mediterranean and semi-arid climates are both characterized by dry summers alternating with cool and wet winters (Nahal 1981) and are the driest naturally forested regions. Since they are often spatially adjacent and share species, these two climatic zones are presented together (referred to as Mediterranean throughout). The recent increase in temperatures and decrease in precipitation have already led to drought-induced forest mortality in the Mediterranean climatic zone in Southwestern Europe, continental North America and Australia, (Peñuelas, Lloret & Montoya 2001; Lloret, Siscart & Dalmases 2004; Breshears *et al.* 2009; Matusick *et al.* 2013; Nardini,

Battistuzzo & Savi 2013). In the Mediterranean Basin yearly rainfall is expected to drop by up to 20% of current annual precipitation by 2050 and winter precipitation is expected to increase while temperatures are projected to increase approximately 4–5 °C in summer time and 2–3 °C in winter time (IPCC 2014) with similar patterns for other regions of this climatic zone. Changes in frequency, intensity and duration of extreme events are likely to result in more hot days, heat waves, heavy precipitation events and fewer cold days (Lloret, Siscart & Dalmases 2004). Mediterranean regions are especially sensitive to climatic changes causing desertification of these climatic zones and a resulting increase in the spatial cover of arid regions (Adeel *et al.* 2005; Klausmeyer & Shaw 2009).

Drought survival–trait relationships

Hydraulic properties seem to be connected to drought-induced mortality in Mediterranean climatic zones and have, therefore, been extensively studied (Martínez-Vilalta & Piñol 2002; Poyatos *et al.* 2008). Martínez-Vilalta & Piñol (2002) found that low leaf-specific hydraulic conductivity resulted in a higher level of embolism and mortality in Mediterranean pine species. Mediavilla & Escudero (2004) also indirectly suggested the importance of high leaf-specific conductivity for drought survival. Furthermore, wood density negatively correlated with mortality rate in a meta-analysis of species across Spain (Martínez-Vilalta *et al.* 2010), a result supported by studies on shrub species in other sites (Jacobsen *et al.* 2007). Osmotic adjustment (i.e. increasing osmotically active solutes) may be important for survival in the Mediterranean climatic zone in order to tolerate low water potentials (Siam *et al.* 2009). Seedling manipulations have shown the importance of this variable in Mediterranean *Quercus* spp. (Villar-Salvador *et al.* 2004). In montane areas where juniper (*Juniperus* spp.) and piñon pine (*Pinus edulis*) co-occur, mortality of piñon has been much higher, potentially due to its avoidance of hydraulic failure leading to carbon starvation, but alternatively, juniper has a high tolerance to low stem water potentials (McDowell *et al.* 2008; Breshears *et al.* 2009; Adams *et al.* 2013).

Tree size and morphological traits can directly affect survival at multiple ontogenetic stages. Direct experimental evidence from seedling manipulations in a nursery setting found that individuals with more biomass had higher mortality (Valladares & Sánchez-Gómez 2006). In observational studies of naturally occurring droughts, individuals of small diameter had higher mortality (Lloret, Siscart & Dalmases 2004). Rooting depth is important for survival for both seedlings (Padilla & Pugnaire 2007) and trees (Sarris, Siegwolf & Körner 2013) and is likely more important than biomass allocation traits such as shoot-to-root ratio (Padilla & Pugnaire 2007). Furthermore, highly variable and slow growth prior to a drought correlated with increased mortality (Ogle, Whitham & Cobb 2000).

Environmental and stand characteristics

Trees growing on ridges and steep slopes had higher mortality during drought than low-lying, flat areas (Lloret, Siscart & Dalmases 2004; Brouwers *et al.* 2013), and individuals on compact soils that had inhibited root growth had higher mortality than individuals on sites with fissured soils (Lloret, Siscart & Dalmases 2004). Dense stands of trees with more competition had consistently higher mortality in Mediterranean systems across the globe (Brouwers *et al.* 2013; Matusick *et al.* 2013).

SAVANNAS

The savanna climatic zone is characterized by the coexistence of woody and herbaceous life-forms and a distinct dry season (Scholes & Archer 1997). All savanna ecosystems are therefore water limited for at least part of the year, and a diverse range of life-history strategies has evolved to provide resistance to dry conditions.

Prolonged drought periods in recent decades have caused decreases in woody biomass across the savannas globally (Fensham, Fairfax & Ward 2009). Exploration of drought-induced tree death in nine different savanna systems indicated that mortality was triggered when less than two-thirds of expected rainfall was received over 3 years (Fensham, Fairfax & Ward 2009) and species became more vulnerable to mortality with increasing dominance (Fensham *et al.* 2015).

Of the trait studies exploring drought resistance in savannas (Stratton, Goldstein & Meinzer 2000; Bucci *et al.* 2003; Hao *et al.* 2008), few have linked traits to mortality. Both evergreen and deciduous species are afflicted by drought in the savannas around the globe (Fensham, Fairfax & Ward 2009), and most current insights have been gained from exploring patterns of mortality following multi-year drought events (e.g. Fensham *et al.* 2015).

Drought survival–trait relationships

Larger trees have been found to be more prone to drought-induced death than smaller ones in a variety of savanna ecosystems (Viljoen 1995; MacGregor & O'Connor 2002; Phillips *et al.* 2010). Investigations following extensive tree death in Australian savannas indicate that stem hydraulics, resistance to embolism and rooting strategies are important factors governing susceptibility to drought (Fensham & Fairfax 2007).

Root density, particularly for vertical roots, was greater in resistant species than in susceptible species (Fensham & Fairfax 2007). Species prone to mortality tend to have a vascular system adapted for rapid above-ground growth but susceptible to embolism and a limited investment in roots. Drought-resistant species feature a more conservative physiology, with reduced hydraulic conductivity and substantial root systems (Fensham, Fairfax & Ward

2009). Resprouting from underground systems of geoxyles is another strategy that may allow recovery from partial dieback in the savannas (Zeppel *et al.* 2015).

Environmental and stand characteristics

Spatial and temporal environmental context was a strong determinant of susceptibility to drought in a severe drought in the savannas of South Africa (1991–1992). Three key patterns emerged from this event: (i) historically drier regions were less impacted than historically wetter regions; (ii) the spatial distribution of mortality was very heterogeneous; and (iii) the intensity of damage to the same species in the same general area was highly variable (Viljoen 1995). Vegetation in drier regions is better adapted to drought conditions, so mortality is lower than in areas that have evolved with higher rainfall. On a finer spatial scale, micro-topography and variation in soil texture regulate the availability of soil moisture to roots, and cases of whole patch die-back can often be traced to run-off hydrological conditions with high inter-tree competition for moisture (MacGregor & O'Connor 2002). Some of these findings mirrored droughts of the 1990s in northeastern Australia, whereby there were no apparent physiological differences between trees within a single species that were recently killed by drought and those that remained relatively healthy (Fensham & Fairfax 2007). Rather, tree death increased as surface soil moisture became less available – places where tree densities were high and where the clay content of the sub-soils increased (Fensham & Fairfax 2007) – and where species become more vulnerable to mortality with increasing dominance (Fensham *et al.* 2015).

TROPICAL FORESTS

A spectrum of drought regimes occurs throughout the tropical climatic zone with one or 2 yearly dry seasons of different intensity overlain by irregular inter-annual drought periods in parts of Southeast Asia and the Amazon Basin. Climate change is altering the severity and frequency of drought periods in the tropical climatic zone (Hulme & Viner 1998). These alterations in precipitation patterns are largely driven by changes to ENSO cycles (Huang & Xie 2015; Chadwick *et al.* 2016). Large-scale mortality events were associated with intense ENSO events in the Amazon Basin (Lewis *et al.* 2011), Central America (Condit, Hubbell & Foster 1995) and Southeast Asia (Potts 2003; Itoh *et al.* 2012).

Tropical forests are the most diverse forests on earth, and a diverse range of tree strategies has evolved to promote resistance to drought. Disentangling the relative importance of which traits contribute to drought resistance is difficult in such highly diverse forests. The majority of evidence exists in the form of correlations after severe drought events (Potts 2003; Phillips *et al.* 2009), large experimental manipulations (Rowland *et al.* 2015),

observations of strategies along rainfall and topographic gradients (Hao *et al.* 2008; Itoh *et al.* 2012) and from seedlings (reviewed in Comita & Engelbrecht 2014).

Drought mortality–trait relationships

Tree size is consistently correlated with increased mortality both in direct experimental manipulations and observational studies across forest type, topography and geographic location (Condit, Hubbell & Foster 1995; Nakagawa *et al.* 2000; Potts 2003; Itoh *et al.* 2012). Large trees have higher mortality rates during drought than smaller trees, both in seasonally dry and in perhumid tropical environments (Phillips *et al.* 2010). This might be caused by high radial growth rates and leaf transpiration and thus a high demand for water (Moser *et al.* 2014).

Many studies have measured sapwood and leaf-specific conductivity in forests across the tropical climatic zone but with little evidence that this relates to drought survival (Choat, Sack & Holbrook 2007; Hao *et al.* 2008; Markesteijn *et al.* 2011a). Contrastingly, wood anatomy traits such as vessel diameter, density and maximum length have been far less studied (Markesteijn *et al.* 2011a) but may be important based on their correlation with growth rate and tree size. High wood density improves survival during drought (Phillips *et al.* 2009; Olson & Rosell 2013) while tree successional status or growth strategy is associated with tree drought survival with shade-tolerant species surviving better than fast-growing pioneer species (Becker, Lye & Goh 1998; Ouedraogo *et al.* 2013).

Experimental studies of seedlings have shown more direct relationships between traits and survival (reviewed in Comita & Engelbrecht 2014). In both Panama and the Malay-Thai Peninsula, across a wet to dry forest gradient, maintenance of living tissue at low lethal leaf water potentials directly correlated with seedling survival under drought in the field (Baltzer *et al.* 2008; Kursar *et al.* 2009). In perhumid lowland forests of Borneo, non-structural carbohydrate concentrations and wood density positively correlated with time to death of seedlings (O'Brien *et al.* 2014).

Environmental and stand characteristics

Habitat associations and topography play a role, whereby species associated with wet conditions have higher mortality than dry site species (Nakagawa *et al.* 2000; Engelbrecht *et al.* 2007; Itoh *et al.* 2012) and individuals on ridges do worse than individuals in valleys (Nakagawa *et al.* 2000; Potts 2003).

OVERVIEW AND SYNTHESIS

Size and growth variables – easy and cheap

Although maximum tree height and maximum growth rate are species-level traits, tree size, growth rate and

growth variability are measured at the individual level and are important for predicting mortality in every climatic zone (except Mediterranean where results are inconsistent). These variables – likely because they are often easily and directly measured from diameter measurements – consistently showed clear relationships with mortality, whereby increasing tree size and growth variation positively correlate with mortality and growth rate negatively correlates with mortality (Fig. 2).

Similarly, rooting depth is important for Mediterranean and savanna climatic zones, which experience severe annual drought. However, this variable is more difficult to measure and likely negatively impacts the tree in the measurement process (Fig. 2).

Wood properties – easy and cheap

Wood density was the most consistently measured trait and showed a negative correlation with mortality in every climatic zone except the savanna where no evidence for a relationship with mortality has been presented (Figs 2 and 3). This trait is relatively easy to measure and is useful because of its correlation with fibre wall thickness (Ziemińska *et al.* 2013) and potentially other vessel/xylem anatomy traits that influence tolerance to low stem water potentials. It is also an indirect indicator of resistance to embolism. A couple of caveats should be considered when using this trait. (i) Wood density is a derivative of other traits and therefore does not provide a mechanistic understanding of drought-induced mortality. (2) Patterns of hydraulic attributes with mortality are associations and their impacts at the leaf level are not well studied. Regardless, wood density is a trait for predicting mortality.

Furthermore, it is important to couple wood density with drought response strategy of the species (i.e. avoid or tolerate and isohydric or anisohydric). Species that tolerate drought will show a positive relationship between wood density and survival while this relationship will become uncoupled for drought avoiders (Hoffmann *et al.* 2011). The drought response strategies are especially important for predicting drought mortality in temperate, Mediterranean and tropical climatic zones, which have species that span a continuum between these dichotomous responses (Klein 2014). Therefore, stomatal sensitivity is another important trait in order to clearly identify the level of a species isohydric versus anisohydric response (Tardieu & Simonneau 1998).

Wood density and other wood anatomy traits such as vessel size can be analysed from archived wood samples (Fig. 3). Samples can be collected and stored for future measurements. For example, a plot across a landscape that was designed to assess forest carbon could collect branch samples as well. If a mortality-inducing drought were to happen after the survey, the archived samples would provide essential information for understanding the mortality patterns after the drought.

| | | Direct traits | Indirect traits | Environmental factors | Life-history strategies |
|---------------|------------------|---|--|---|---|
| Boreal | Higher mortality | - Slow growth - Larger trees - More inter-annual variability | - Wood density - Vessel architecture Because hydraulic failure is main mechanism | - Shallow soils - Individuals on wet sites - Upper slopes and southern aspects | |
| | Lower mortality | - Tolerance to low stem water potential | - Deeper roots | | - Sprouting - Belowground resources and biomass storage |
| Temperate | Higher mortality | - Smaller trees - Slow growth (some spp. only interacts with other traits) | - Wood density - Vessel architecture Because hydraulic failure is main mechanism | - Lower plant density - Higher tree density - Steep, rocky and upslope sites | |
| | Lower mortality | - Larger hydraulics safety margins - Higher wood density (interacts with ontogeny) | - Stomatal response indicates avoidance vs. tolerance strategy | - Lowland sites | - Drought avoidance may prevent importance of resistance traits |
| Mediterranean | Higher mortality | - Inter-annual variability - Slow growth (drought) - Low specific leaf conductivity | | - High stand density - Compacted and shallow soils - Steep, rocky and upslope sites | |
| | Lower mortality | - Deep roots - High wood density | - Solutes - Nonstructural carbohydrates - Leaf water potential at high VPD | - Lowland sites | |
| Savanna | Higher mortality | - Larger trees | - Slow growth - Larger trees - More inter-annual variability | - Wetter sites - High stand density - High clay content in subsoil | |
| | Lower mortality | - Deep and extensive roots - Root basal area in vertical roots | - Embolism resistance is important so wood architecture traits are key | | |
| Tropical | Higher mortality | - Larger trees - Lack of tolerance to low stem water potential | - Wood density - Vessel architecture Because hydraulic failure is main mechanism | - Individuals on wet sites - Individuals on ridges | - Fast growing pioneers - Evergreen |
| | Lower mortality | High: - nonstructural carbohydrates - root mass fraction - wood density | | | - Shade tolerant - Drought deciduous - Slow growing trees |

Fig. 2. Overview of functional plant traits, environmental factors and life-history strategies that indicate vulnerability to drought-induced mortality across the five main forested climatic zones (summarized from our literature review, for references see text). Traits and individual variables where a direct correlation with mortality was found are defined as direct while traits and variables that have been inferred without showing a direct correlation are defined as indirect.

Physiological traits – more difficult and costly

Physiological traits such as hydraulic safety margin, water potential at P_{50} or P_{88} and minimum leaf water potential were directly related to mortality in most climatic zones (Fig. 2; Anderegg *et al.* 2016). Furthermore, leaf-specific conductivity, solute concentrations and leaf water potential at high vapour pressure deficit or low soil water availability were traits that correlated with mortality in the

temperate and Mediterranean climatic zones. These traits are rather important but can be time consuming and complex to measure. Wood density is the cheaper and easier option that appears to correlate well with PLC values (Nardini, Battistuzzo & Savi 2013). Non-structural carbohydrates were also important for resprouting in boreal ecosystems and hydraulic integrity in tropical regions but are time consuming, complex and costly to measure (Figs 2 and 3; Quentin *et al.* 2015).

| | Simple | Complex | Archive potential | Knowledge-gaps |
|---------------|---|---|--|--|
| Boreal | <ul style="list-style-type: none"> - Wood density - Size (Height or DBH) - Vegetative resprouting - Growth (repeated DBH) - Angio- or gymnosperm - Topography | <ul style="list-style-type: none"> - Root NSC - Rooting depth - Vessel architecture - Growth (wood cores) | <ul style="list-style-type: none"> - Wood cores for: wood density, growth rates, xylem architecture - Branches for: NSC content, xylem architecture | <ul style="list-style-type: none"> - Xylem traits (e.g. vessel lumen area, vessel density) - Loss of hydraulic conductivity values |
| Temperate | <ul style="list-style-type: none"> - Topography - Wood density - Site water content - Size (Height or DBH) - Drought deciduousness - Tree and stem density - Growth (repeated DBH) - Angio- or gymnosperm | <ul style="list-style-type: none"> - Growth (wood cores) - Point at 50% loss of hydraulic conductivity | <ul style="list-style-type: none"> - Leaf specific hydraulic conductivity - Wood cores for: wood density, growth rates, xylem architecture - Branches for: NSC content, xylem architecture | <ul style="list-style-type: none"> - Xylem traits (e.g. vessel lumen area, vessel density) |
| Mediterranean | <ul style="list-style-type: none"> - Topography - Wood density - Soil compaction - Size (Height or DBH) - Tree and stem density - Growth (repeated DBH) | <ul style="list-style-type: none"> - Rooting depth - Osmotic adjustment - Growth (wood cores) - Leaf specific hydraulic conductivity - Loss of hydraulic conductivity values | <ul style="list-style-type: none"> - Leaf specific hydraulic conductivity - Wood cores for: wood density, growth rates, xylem architecture - Branches for: NSC content, xylem architecture | <ul style="list-style-type: none"> - Xylem traits (e.g. vessel lumen area, vessel density) |
| Savanna | <ul style="list-style-type: none"> - Soil texture - Topography - Wood density - Size (Height or DBH) - Tree and stem density - Vegetative resprouting - Growth (repeated DBH) | <ul style="list-style-type: none"> - Rooting depth - Vertical root density - Growth (wood cores) - Loss of hydraulic conductivity values | <ul style="list-style-type: none"> - Leaf specific hydraulic conductivity - Wood cores for: wood density, growth rates, xylem architecture - Branches for: NSC content, xylem architecture | <ul style="list-style-type: none"> - Xylem traits (e.g. vessel lumen area, vessel density) |
| Tropical | <ul style="list-style-type: none"> - Topography - Wood density - Habitat association - Size (Height or DBH) - Growth (repeated DBH) - Tree successional status | <ul style="list-style-type: none"> - NSC content - Leaf water potential at desiccation | <ul style="list-style-type: none"> - Leaf specific hydraulic conductivity - Wood cores for: wood density, growth rates, xylem architecture - Branches for: NSC content, xylem architecture | <ul style="list-style-type: none"> - Xylem traits (e.g. vessel lumen area, vessel density) |
| Global | <ul style="list-style-type: none"> - Tree size - Wood density - Topography - Growth (DBH) | <ul style="list-style-type: none"> - Growth (wood cores) - Loss of hydraulic conductivity | <ul style="list-style-type: none"> - Leaf, wood cores and branches are useful for archiving in all climate zones | <ul style="list-style-type: none"> - Data on xylem traits are limited in most systems |

Fig. 3. A synthesis of important variables (i.e. traits, individual variables and environmental conditions) for predicting drought-induced mortality that are either simple (cheap and time efficient) or complex (expensive, difficult or time consuming) to measure for each or the five climatic zones. Additionally, we highlight that stem and branch material could be archived for analysis after mortality from drought, and traits that lack direct evidence in relation to drought-induced mortality.

Wood anatomy variables may be particularly valuable for predicting drought-induced mortality but accounting for differences between angiosperms and gymnosperms is important for clearly distinguishing their value (Fig. 1; Russo *et al.* 2010; Choat *et al.* 2012; Anderegg *et al.* 2016). A meta-analysis by Anderegg *et al.* (2016) found that PLC was a better correlate of mortality for gymnosperms while wood density was better for angiosperms. However, these relationships may be related to the differences in wood anatomy, especially since wood density in angiosperms is an aggregate of multiple vessel traits (Preston, Cornwell & Denoyer 2006; Zanne *et al.* 2010). Therefore, controlling for angiosperms and gymnosperms in analysis of trait–mortality relationships is important for predicting the impacts of drought.

Life-history variables – categorical

The review showed that the magnitude and direction of relationships between traits and drought-induced mortality varies with plant phylogeny (e.g. angiosperms and gymnosperms), life-history strategy (e.g. *r* and *K* selection or successional stage) and drought response (e.g. drought deciduous and evergreen). Therefore, simple categorical measures of these will explain much of the variability in plant mortality (Figs 2 and 3). Furthermore, these classifications can often be simply obtained from plant biology literature.

Site characteristics – important to explain intraspecific variability

Soil depth and texture are important environmental variables for predicting drought mortality in every climatic zone (Fig. 2). Topographic variables such as slope and aspect or site classifications such as riparian, lowland and ridgetop are essential for understanding drought-induced mortality in all climatic zones as well. In boreal, temperate, Mediterranean and savanna climatic zones, tree density metrics such as stand stocking, density and size class distributions are useful indicators of drought-induced mortality with high stocking and single age class stands being more vulnerable. Wet sites provide an interesting variable because they not only increase susceptibility of trees but also are less likely to reach severely low soil water availabilities.

Knowledge gaps

Our capacity to predict and understand underlying physiological mechanisms of drought mortality would be considerably enhanced with better data directly linking physiological and functional traits to mortality in single climatic zones and across climatic zones. To fill these knowledge gaps, we need experimental evidence of trait–drought relationships, which requires measurements before and during imposed drought until mortality is

reached. Alternatively, monitoring functional traits in long-term plots in which mortality can be assessed during future (or past) drought events will improve the predictive power of trait analysis. Archiving samples could provide an option for assessing trait–drought relationships after drought, whereby samples could be stored and analysis of xylem architecture, non-structural carbohydrates or other traits could be carried out after drought and then correlated with mortality. These approaches are costly and time consuming but if consistent methods and analysis are used, they would yield informative and valuable results.

Use for managers

This synthesis can be used by forest managers in three ways. (i) Managers can select appropriate traits to measure in their forests based on time and cost constraints (simple vs. complex traits; Fig. 3) to begin assessing the vulnerability of their forest to drought scenarios. (ii) The traits summarized in Figs 2 and 3 can be included in forest stand assessments to begin monitoring shifts in functional trait distributions under a changing climate, which will be an indicator of alterations in biodiversity and ecosystem function. For example, van der Sande *et al.* (2016) showed significant shifts in the trait composition of a Neotropical forest after only a decade and concluded a drier climate was a key driver of those shifts. (iii) Archiving stem and branch samples for *post-hoc* analysis of traits related to drought mortality in the event of a severe drought. Archived samples can lead to new insights on the mechanisms of mortality and directly fill knowledge gaps regarding the direct relationship between wood anatomy traits and drought-induced mortality without *a priori* cost and effort.

Conclusion

Our aim was to refer to a selection of the most informative studies in which direct relationships between traits and mortality were observed. From our literature search, it is clear that there is already a strong global support for the importance of simple traits such as tree size and wood density for mediating drought-induced mortality. Furthermore, the role of environmental variables for accelerating or decelerating drought-induced mortality seem to show universal patterns across climatic zones with higher mortality on wet sites, densely stocked forests and shallow, rocky soils. However, the predictive power of these traits and environmental conditions remains relatively limited. More research directly linking traits and drought mortality is necessary, especially for physiological traits. Our review highlights the need for linking forest inventory assessments with drought events and trait surveys for building our predictions of the effects of drought on the future of forest communities.

Authors' contributions

M.O.B., C.M.N., B.M.J.E., B.S. and G.P. conceived the initial concept for this manuscript. M.O.B. wrote or compiled drafts for each climatic zone review, summarized the climatic zone content, wrote the synthesis and made Figs 1 and 3. C.M.N. wrote the original draft of the introduction, compiled Fig. 2 and contributed to the synthesis and revising process throughout. M.O.B. and C.M.N. led the revisions process. B.S. and G.P. compiled Table 1. J.K. and J.J. organized, sorted and cleaned the TRY data. S.M.L., P.V., Y.P. and S.R.L. contributed to the climatic zone review. S.M.L. and B.M.J.E. contributed comments to the outline, tables and manuscript at an early stage. S.J. and B.M.J.E. contributed feedback and revisions.

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Data accessibility

All data are from previously published articles, see 'Data sources'. Data from these articles are stored in the TRY Database (Kattge *et al.* 2011; <https://www.try-db.org>; accessed 3 November 2015) including the 'Xylem Functional Traits (XFT) Database'. These data are made available upon reasonable request (e.g. replication of analysis) from the original data owners. See Appendix S1 for how data were compiled and analysed.

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Supporting Information

Details of electronic Supporting Information are provided below.

Table S1. Table with references to methods for measuring traits.

Appendix S1. Description of data compilation and analysis for Fig. 1.