Letters

Drought induced tree mortality – a tree-ring isotope based conceptual model to assess mechanisms and predispositions

Drought-induced tree mortality is likely to increase in future as climate models forecast increased frequency of drought events together with higher air temperatures (Dai, 2013; Allen *et al.*, 2015). Besides the presence of inciting (e.g. heat and drought events) and contributing (e.g. opportunistic biotic agents such as bark beetles) factors, predisposition of particular species or individuals of a given species is considered as central for understanding why some trees survive while others succumb to drought (Manion, 1981; McDowell *et al.*, 2008; Voltas *et al.*, 2013; Gessler *et al.*, 2016; Martin-StPaul *et al.*, 2017). This is also crucial for simulating tree mortality in dynamic vegetation models (Meir *et al.*, 2015). Predisposing factors are assumed to be related to long-term climatic stressors (Voltas *et al.*, 2013), prevailing long-term nutrient supply (Gessler *et al.*, 2016), water-use strategies (Hentschel *et al.*, 2014), tree height and interspecific and intraspecific competition (Grote *et al.*, 2016) and pests, pathogens or air pollution (Allen *et al.*, 2010).

Even though plants growing in dry environments may have the broadest hydraulic safety margins (Choat *et al.*, 2012; Martin-StPaul *et al.*, 2017), drought events force these and also the carbon safety margins to points where trees may be at risk of physiological failure or failure to defend against biotic attacks (McDowell, 2011). Hydraulic and symplastic failure, and strong reduction in carbon pools (also called 'carbon starvation') have been postulated as the two main, nonexclusive physiological mechanisms leading to tree mortality (Adams *et al.*, 2017), in strong interaction with biotic agents (Anderegg *et al.*, 2015). Hydraulic failure summarizes all aspects of cellular desiccation causing cessation of symplastic biochemical functioning, and disruption of water transport through xylem embolism (McDowell *et al.*, 2011). Carbon starvation describes the situation when the carbon demand for maintenance of cellular and defensive metabolism is not sufficiently met owing to low carbohydrate supply from photosynthesis and storage (McDowell *et al.*, 2008). Recently, Adams *et al.* (2017) showed that xylem hydraulic failure was ubiquitous across taxa, while carbon starvation was not universal but still common for gymnosperms (see also Martínez-Vilalta *et al.*, 2016) probably after long-term moderate drought stress (McDowell *et al.*, 2008). Moreover, hydraulic function and carbohydrate metabolism are strongly linked and thus there might be interdependencies between hydraulic failure and carbon starvation (McDowell, 2011; Sevanto *et al.*, 2014). Even though hydraulic failure might occur independently of carbon starvation, many cases have been observed where carbon balance and hydraulics were both impaired (Adams *et al.*, 2017). The carbon starvation–hydraulic failure concept as applied here is rather a continuum with relatively stronger influence of the one or the other process on mortality.

A tree's predisposition to carbon starvation or to hydraulic failure (Fig. 1a) may be indicated by specific syndromes of traits (Anderegg *et al.*, 2016) reflecting different strategies to face drought (Pivovaroff *et al.*, 2016), modified by differences in local resource availability. The main approach we have chosen for our conceptual model is a conspecific synchronic comparison of growth and tree ring isotopic signals between later dying and surviving trees over longer time periods from the same stand aiming to understand mortality mechanisms and the respective predisposition in a given environmental context. We do not claim our results to be generalizable for a given species as they will not only be affected by species specific traits but also by tree individual (intraspecific) trait differences and by local site conditions.

A key strategy for dealing with drought concerns the coupling between xylem resistance to embolism and stomatal response to drought (Martin-StPaul *et al.*, 2017). On the one side, conservative/stress resistant strategies through early stomatal closure during drought are often seen as predisposition to carbon deficiency. On the other side, acquisitive/competitive strategies with high tree-level hydraulic conductance and resource use are favourable for the development of individuals under normal conditions, but are assumed to increase the risk of xylem embolism and consequently mortality when water supply is restricted or atmospheric water demand is high (see Martínez-Vilalta & Garcia-Forner, 2017). Moreover, trait combinations that primarily allow acclimation to environmental factors other than drought might have distinct effects on the drought response. For instance, acclimation to high nutrient availability may increase tree sensitivity to hydraulic failure e.g. through a low ratio of root area to leaf area, while trait combinations favoured under low nutrient supply may facilitate the carbon starvation trajectory (Gessler *et al.*, 2016). While these trait differences mainly occur between species, more risky or more conservative resource-use strategies have also been observed within populations of a given species (Hentschel *et al.*, 2014).

Adams *et al.* (2017) synthesized the physiological mechanisms of drought induced tree mortality with a multi-species approach taking into account studies that assessed percentage loss of xylem hydraulic conductivity (PLC) and changes in nonstructural carbohydrates (NSCs) before mortality. Despite their potentially high ability to describe the mechanisms of tree mortality the determination of these physiological indicators is costly and labour intensive, and prone to methodological artefacts (e.g. Cochard *et al.*, 2013; Quentin *et al.*, 2015). These methods are not yet applicable to a large number of species and sites. Old grown trees
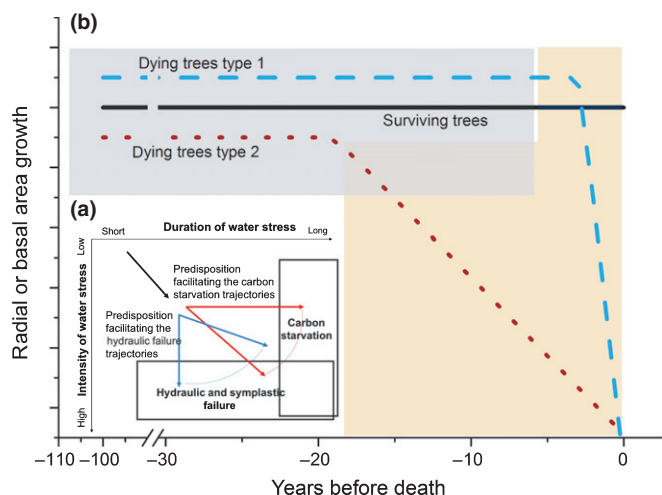
Fig. 1 Predisposition and trajectories leading to drought induced mortality. (a) Different trait combinations are assumed to predispose trees in a way that either the carbon starvation or hydraulic failure trajectory is facilitated during drought stress. However, due to the strong link between hydraulic function and carbohydrate metabolism various overlaps and ranges of trajectories might be possible. Carbon starvation only trajectories were not observed in the recent synthesis by Adams *et al.* (2017) but this might be due to the lack of data especially from old trees and dense forests. (b) Idealized types of long-term growth patterns and growth decline trajectories before drought induced mortality. Type 1 shows increased long-term growth compared to surviving trees and has only a short period of or even no growth decline directly before death suggesting hydraulic failure as the mortality mechanism. Type 2 shows a history of decreased long-term growth suggesting long-term carbon deficiency and thus carbon starvation. In order to obtain the physiological background such tree-ring derived growth patterns need to be combined with isotopic information. The grey shaded area indicates the long-term growth patterns, the yellow area the growth trajectories finally leading to death. For type 2, there is an overlap as continuous growth decline can be slow and last over long time periods. (a) Adapted from McDowell *et al.* (2008), with permission, and Gessler *et al.* (2016).

and dense stands are especially underrepresented in such studies, which may bias the interpretation of meta-analyses.

By contrast, tree-ring based measures are largely available now and can be applied for assessing mortality mechanisms. For instance, Cailleret *et al.* (2017) compared the annual radial growth of conspecific trees that died and that survived a specific event for a wide range of species and biomes focusing on both long-term growth and growth patterns before mortality. They especially observed strong and long-lasting growth declines before mortality (Fig. 1b, type 2) for gymnosperms but also for drought- and shade-tolerant angiosperms. They associated this pattern with a decrease in carbon reserves, which could also go along with a gradual decline in hydraulic performance. However, for some mortality events, dying trees showed a history of higher growth compared to surviving ones over the long term together with a fast growth decline before they actually died (Fig. 1b, type 1, e.g. Bigler & Veblen, 2009; Voltas *et al.*, 2013; Hentschel *et al.*, 2014).

Yet, growth patterns alone might not provide sufficient information to clearly differentiate between predisposing factors that promote trajectories towards carbon starvation, hydraulic failure or both, which is also due to the fact that at least part of the growth activity is not source driven and thus not related to

carbon availability (Körner, 2015). However, stable isotope ratios in tree-rings allow us to obtain additional retrospective insights into ecophysiological processes. Due to the relationship between photosynthetic carbon isotope fractionation and the ratio of leaf internal and ambient CO_2 concentration (c_i/c_a) or – to be more precise – of chloroplastic CO_2 concentration (c_c) and c_i (Farquhar *et al.*, 1982), the $\delta^{13}C$ of organic matter can be used to assess diffusional vs biochemical controls over photosynthesis (*A*) at the leaf level and allows us to quantify intrinsic water-use efficiency (WUE$_i$), equivalent to the ratio between *A* and stomatal conductance (g_s). Moreover, due to its relationship to g_s either via a joint influence of water vapour pressure deficit (VPD) (Scheidegger *et al.*, 2000) or via transpirational dilution of evaporatively enriched leaf water (Gessler *et al.*, 2009), $\delta^{18}O$ in tree-rings can be used to disentangle effects of g_s and *A*, when the caveats put forward by Roden & Siegwolf (2012) are considered for the interpretation. One of the major challenges for the interpretation of tree ring $\delta^{18}O$ values are variations in $\delta^{18}O$ of the source water (Gessler *et al.*, 2014) related to changes in soil water uptake depths. In fact, it has been observed that with increasing drought, trees can take up water from deeper soil layers (e.g. Barbeta & Peñuelas, 2017; Grossiord *et al.*, 2017). To avoid any effect of temporal changes in source water $\delta^{18}O$ we compared later dying and surviving trees in a synchronic approach (i.e. without considering temporal trends). Long-term synchronic assessments of growth pattern and dual isotope ($\delta^{13}C$ and $\delta^{18}O$) information combined with the analysis of changes in growth directly before death (see Fig. 1b, yellow shaded area; diachronic approach) might thus provide a conceptual framework for analysing and categorizing potential mechanisms of mortality.

We hypothesize the presence of four combinations of long-term growth rate and isotopic patterns in tree-rings, which can indicate stronger predisposition to hydraulic failure or to carbon starvation. It needs to be considered that we compare individuals from the same species at the same stand thus mainly focusing on intraspecific trait variability that might be caused either by genetic or local environmental differences. As a consequence, the following four combinations might well be affected by species-specific traits but also strongly reflect the local population genetic and environmental context of the local population. (1) Trees showing high growth rates associated with low water-use efficiency, i.e. high g_s, and thus high water consumption per unit of leaf area (type 1 in Fig. 1b, water use inefficient). We assume that such individuals within a community follow a prodigal strategy as defined by Hentschel *et al.* (2014), investing in water transport and maximizing carbon assimilation during periods with high water supply. However, this strategy can be detrimental for the safety of their hydraulic system during drought events (high risk of hydraulic failure), which can finally lead to rapid growth decline and mortality. (2) Higher growth related to high water-use efficiency (type 1, water use efficient). In this case, dying trees are not assumed to have lower g_s but higher *A* than surviving trees. Higher photosynthesis would in this case lead to higher aboveground biomass and also the need for supporting a larger crown area with water under drought, which would favour hydraulic failure (Gessler *et al.*, 2016). (3) Trees with low growth

rates over long time periods combined with high WUE_i as a consequence of reduced g_s (type 2, water use efficient). This strategy may be efficient to save water and sustain hydraulic functions, but may cause deficient carbon supply in the long run (high risk of carbon starvation). (4) Lower growth related to low WUE_i as a consequence of long term reduced A being also a predisposition for carbon starvation (type 2, water use inefficient). Combinations (1) and (2) are assumed to be associated with only a very short or even no growth decline directly before death (Fig. 1b, type 1).

To test our hypothesis, and to develop a substantiated conceptual framework, we screened the literature for combined annual assessments of radial growth and $\delta^{13}C$ in tree-rings for conspecific dying and surviving individuals growing in the same stands (Supporting Information Table S1; Levanič *et al.*, 2011; Voltas *et al.*, 2013; Hentschel *et al.*, 2014; Csank *et al.*, 2016; Colangelo *et al.*, 2017; Timofeeva *et al.*, 2017) without claiming complete coverage of all studies published. In four of these publications additional $\delta^{18}O$ data were available at least for a part of the tree-ring series (Voltas *et al.*, 2013; Hentschel *et al.*, 2014; Csank *et al.*, 2016; Colangelo *et al.*, 2017). The common inciting factor for mortality or the occurrence of strong dieback symptoms was drought, sometimes together with bark beetles (Csank *et al.*, 2016) or winter frost (Voltas *et al.*, 2013). All trees were defined as dominant and the species covered were *Picea abies, Picea glauca, Pinus sylvestris, Quercus robur* and *Quercus frainetto*. We omitted the last 5 years before death (or the occurrence of severe dieback symptoms, when trees were not yet dead when samples were taken; Hentschel *et al.*, 2014; Colangelo *et al.*, 2017), to obtain only the longer-term growth and isotope signals (i.e. the grey area in Fig. 1b), and calculated for the remaining years (6–100 years) the average yearly growth ratio between later dying and surviving trees and their difference in carbon isotope composition ($\Delta\delta^{13}C$). When applying our concept to large data sets a more standardized approach for selecting the time periods for the synchronic approach with comparable time windows might need to be chosen. Based on an assessment of the growth trajectories directly before death, also a period > 5 years might be omitted to calculate long-term trends not affected by the growth or isotopic changes directly related to the mortality event. As a result of our synchronic analysis (comparing later dying and surviving trees without considering the temporal trends), we found that the four theoretical cases mentioned earlier can occur (i.e. all four quadrants of Fig. 2a were populated with data).

For a closer examination of the drivers for the observed WUE_i patterns (i.e. to disentangle the respective effects of A and g_s), we analysed the difference in oxygen isotope composition between dying and surviving trees ($\Delta\delta^{18}O$) together with $\Delta\delta^{13}C$ (Fig. 2b). Even though $\delta^{18}O$ values were only available for a subset of the studies, there was at least one report with both isotope information for each quadrant in Fig. 2(a). With the dual isotope approach based on Scheidegger *et al.* (2000), we could confirm that the long-term reduced WUE_i of later dying trees that co-occurred with increased growth was due to higher g_s (blue arrows in Fig. 2b). Such a $\Delta\delta^{18}O$ vs $\Delta\delta^{13}C$ pattern was also observed for *Q. frainetto* at the site SP, where growth of later dying trees was only marginally higher. Connected with long-term growth reduction, increased
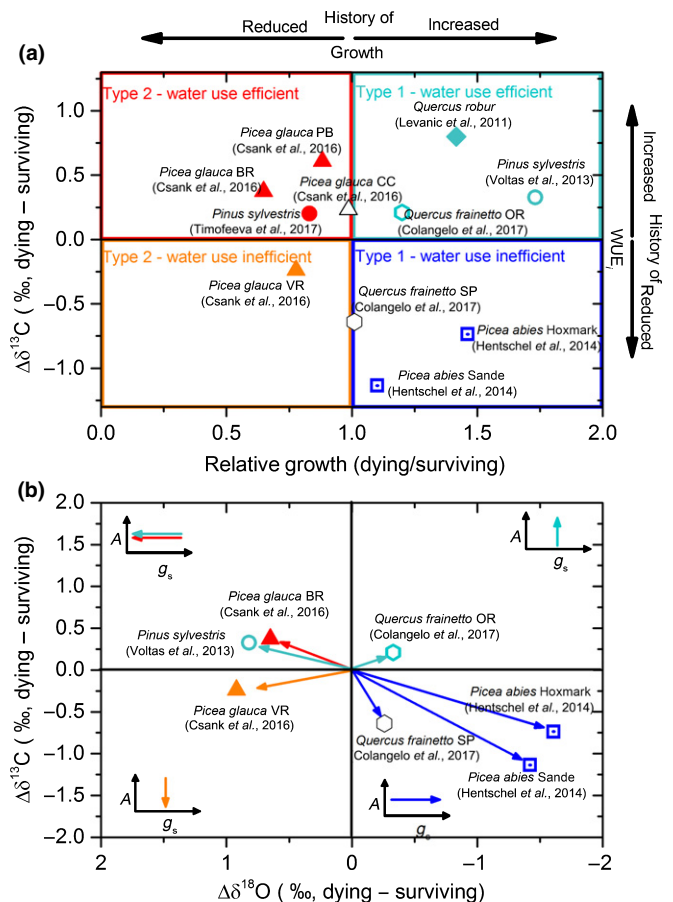

Fig. 2 Long-term growth ratios and differences in isotope composition between later dying and surviving trees. In (a) the growth ratios are plotted against the differences in $\delta^{13}C$ ($\Delta\delta^{13}C$) resulting in four quadrants indicating a history of reduced growth and increased intrinsic water-use efficiency (WUE_i; red square), reduced growth and decreased WUE_i (orange square), increased growth and increased WUE_i (turquoise square) and increased growth and decreased WUE_i (blue square). Type 1 and 2 correspond to the types of long-term growth patterns of dying vs surviving trees in Fig. 1(b). In (b) the $\Delta\delta^{13}C$ is plotted against the difference in $\delta^{18}O$ ($\Delta\delta^{18}O$) and the small inserts indicate the interpretation of the $\Delta\delta^{13}C$–$\Delta\delta^{18}O$ relationship according to Scheidegger *et al.* (2000). In (a) and (b) the same symbol shapes indicate data from the same study but from different sites (sites are indicated after the species name). The symbol colour has been chosen according to the four quadrants in (a).

WUE_i was shown to be a result of reduced g_s (red arrow in Fig. 2b). High WUE_i in fast growing trees might as a first guess be most likely related to higher maximum A, potentially due to better long-term nutrient supply (e.g. Evans, 1989). Such a pattern in A was, in fact, observed for *Q. frainetto* at the OR site. Our result for *P. sylvestris* (turquoise arrow to the upper right), however, indicates that also stomatal conductance per leaf area could be reduced probably because of high individual tree leaf area (Mencuccini & Comstock, 1999; Levanič *et al.*, 2011). Our assumption cannot be directly proven based on tree-ring information but there is good evidence to assume that a reduction of g_s at leaf level (which is what $\delta^{13}C$ and $\delta^{18}O$ indicate) can only support more intensive radial stem growth with a larger leaf area. Similar to higher g_s at unchanged leaf area, a larger leaf area is an advantage during periods of high moisture

availability allowing for high carbon acquisition. Jump *et al.* (2017) showed that favourable climatic and management conditions can indeed lead to structural overshoots of aboveground tree biomass. Large crowns, however, can predispose trees to severe drought stress and cavitation when transpirational demand is high and soil water availability low. For the case where reduced long-term growth was accompanied by low WUE$_i$, δ^{18}O data highlight the potential cause of reduced maximum *A* (orange arrow). Even though the individual trees were deemed to be dominant (see Table S1), dying trees may have experienced lower light and nutrient availability (e.g. through high competition), or may have shown high crown defoliation, which might generally explain lower growth. Restriction of plant nutrient availability during drought might not only impair growth but is also assumed to enhance the risk of carbon starvation (Gessler *et al.*, 2016). It needs to be mentioned that there is the possibility that not only differences in the evaporative enrichment of leaf water between later dying and surviving trees might occur, but also differences in the soil water uptake depth and thus in δ^{18}O of source water, which could compromise the interpretation of the dual isotope approach. This is the main reason why we carried out conspecific comparisons as we assume that the trees of the same species with the same age and dominance class, growing under comparable soil and atmospheric conditions took up water from sources not too different in their δ^{18}O signature over the long term. Still, this cannot be fully excluded as local differences in resource availability might also cause water with different isotopic signatures being taken up and we need a wider application of novel approaches (e.g. Waterhouse *et al.*, 2013) that allow separation of source water and evaporative effects on the tree ring δ^{18}O signals.

In most cases with higher growth (*P. sylvestris, Q. robur;* increased growth with increased WUE$_i$; *P. abies* increased growth with decreased WUE$_i$), later dying trees also showed larger vessels or higher xylem conductivity than surviving ones (Levanič *et al.*, 2011; Voltas *et al.*, 2013; Hentschel *et al.*, 2014) supporting the association between higher water conductance with higher risk of xylem cavitation during drought. Cavitation or other decreases in hydraulic performance as mortality mechanisms are also supported by the fact that in all conifers and *Q. frainetto* (site OR) that showed a long-term history of clearly higher growth, there was either no growth reduction until immediately before death or the occurrence of severe dieback symptoms (compared to surviving trees) or the time span of growth decline was between 2 and 5 years only (Table S1; for the assessment of these trajectories the last 5 years before death were not omitted). In *Q. robur*, the growth decline lasted longer (11 years) but we need to assume that the lowering of the ground water table, that was the mortality inciting event in this study, caused a rather gradual increase of drought stress over several years.

In cases in which later dying trees showed lower long-term growth, there was, by contrast, no clear short-term trajectory of a sudden substantial growth reduction immediately before death. This points to a slow mortality process that is explainable with the carbon starvation trajectory that might, however, go along with long-term deterioration of the hydraulic system (cf. Pellizzari *et al.*, 2016; Cailleret *et al.*, 2017).

The cases of dying *P. sylvestris* show that both long-term increased or decreased growth can occur within one species (Voltas *et al.*, 2013; Timofeeva *et al.*, 2017). High variability of growth patterns preceding mortality have already been observed in this species, with either fast declines (Herguido *et al.*, 2016) or with
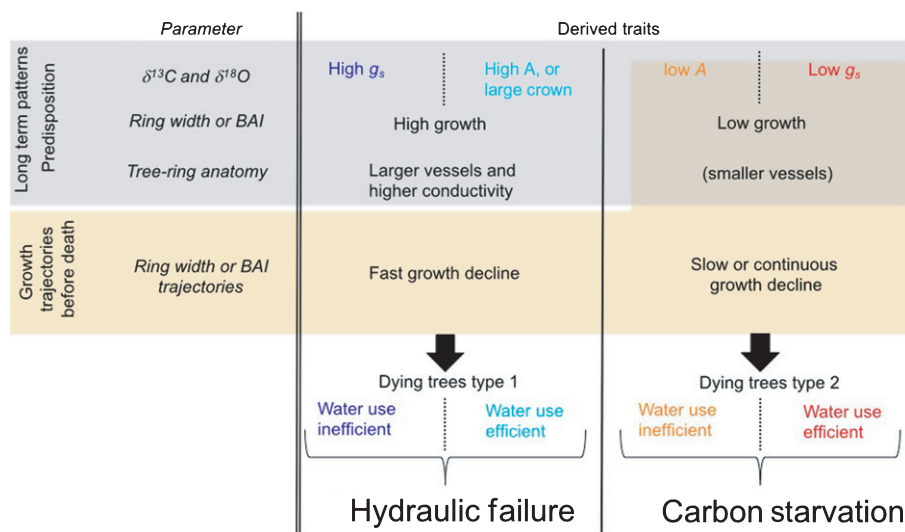

Fig. 3 Conceptual framework to identify mortality mechanisms from tree-ring information. Long-term patterns of δ^{13}C, δ^{18}O, growth and tree-ring anatomy inform about trait combinations predisposing trees to either hydraulic failure or to carbon starvation taking into account that both mechanisms are interrelated. The terms 'high' and 'low' need always to be seen relative to surviving trees as assessed in a synchronic approach. The growth trajectories (assessed in a diachronic approach) during or after the inciting stress period provide additional information. The joint analysis of long-term growth and gas exchange physiology together with growth decline trajectories leading to death provide comprehensive and complementary information on likely mortality mechanisms. For type 2, there is an overlap between long-term patterns and the patterns during stress periods as continuous growth decline can be slow and last over long time periods. All traits with the exception of smaller vessels (tree-ring anatomy was not assessed in the studies with reduced growth) have been observed in at least some of the studies analysed here. Additional measurements of loss of conductance and nonstructural carbohydrates (NSCs) at tree death might help to corroborate the classification into mortality mechanisms. BAI, basal area increment.

slow and long-lasting growth reductions (Rigling *et al.*, 2004; Bigler *et al.*, 2006; Hereş *et al.*, 2012). *Pinus sylvestris* is assumed to react to water deficit following a conservative water-use strategy (Irvine *et al.*, 1998) that is assumed to make it susceptible to carbon starvation under drought (Adams *et al.*, 2017). Our findings point to the fact that tree species' responses to drought stress might be highly plastic, and strongly dependent on site- and individual-specific context, i.e. on the type (e.g. drought vs bark beetle attack), duration, frequency, and intensity of stress factors that predisposed and triggered mortality (Lévesque *et al.*, 2013; Cailleret *et al.*, 2017).

Whilst long-term growth patterns of later dying vs surviving trees as well as the short-term growth trajectories directly before tree death (cf. Cailleret *et al.*, 2017) might be affected by various different abiotic and biotic drivers and thus might not be directly indicative for particular mortality mechanisms, we argue that a tree-ring multi-parameter approach permits deeper and more reliable insights into the predisposition for, and the mechanisms of, tree mortality.

Long-term growth and isotope-based gas exchange physiological patterns analysed together allow the classification of trait combinations (Fig. 3) leading to susceptibility of the hydraulic system to drought and/or indicating long-term carbon starvation. Additional information on xylem anatomical and tree biochemical traits (e.g. NSC analyses), as well as short-term growth trajectories directly before death, will allow corroboration of the physiological classification.

We acknowledge that our framework has to be confirmed by considering a larger number of species from different biomes (e.g. tropical zone) and with different functional traits (especially deciduous trees), and a larger number of sites with different drought intensities and durations and with a wide variety of predisposing mortality factors. However, we strongly believe that combining long-term growth and isotope-based gas exchange data is a promising tool to retrospectively detect physiological mechanisms involved in drought-induced tree mortality and to identify trait combinations that allow the prediction of vulnerability or resistance to future drought conditions.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Table S1 Characterization of the trees in the studies analysed

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