Tansley review

Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought?

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Summary

Severe droughts have been associated with regional-scale forest mortality worldwide. Climate change is expected to exacerbate regional mortality events; however, prediction remains difficult because the physiological mechanisms underlying drought survival and mortality are poorly understood. We developed a hydraulically based theory considering carbon balance and insect resistance that allowed development and examination of hypotheses regarding survival and mortality. Multiple mechanisms may cause mortality during drought. A common mechanism for plants with isohydric

regulation of water status results from avoidance of drought-induced hydraulic failure via stomatal closure, resulting in carbon starvation and a cascade of downstream effects such as reduced resistance to biotic agents. Mortality by hydraulic failure *per se* may occur for isohydric seedlings or trees near their maximum height. Although anisohydric plants are relatively drought-tolerant, they are predisposed to hydraulic failure because they operate with narrower hydraulic safety margins during drought. Elevated temperatures should exacerbate carbon starvation and hydraulic failure. Biotic agents may amplify and be amplified by drought-induced plant stress. Wet multidecadal climate oscillations may increase plant susceptibility to drought-induced mortality by stimulating shifts in hydraulic architecture, effectively predisposing plants to water stress. Climate warming and increased frequency of extreme events will probably cause increased regional mortality episodes. Isohydric and anisohydric water potential regulation may partition species between survival and mortality, and, as such, incorporating this hydraulic framework may be effective for modeling plant survival and mortality under future climate conditions.

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I. Introduction

Rapid and large-scale shifts in ecosystem structure and function can result from mortality of forest and woodland plants in response to extreme climate events (see Fig. 1; Condit *et al.*, 1995; Allen & Breshears, 1998; Hanson & Weltzin, 2000; Breshears *et al.*, 2005; Shaw *et al.*, 2005; Berg *et al.*, 2006; Gitlin *et al.*, 2006). Such widespread mortality events can have long-term impacts on community dynamics and species interactions, and may feed back upon atmospheric CO_2 and climate. Although many of the consequences of tree mortality are readily apparent, our current understanding of the causes of tree mortality is surprisingly limited, even though a rich literature exists on plant responses to stress. Essentially, we cannot address questions such as: how severe must a drought be to kill a tree; and during drought, which trees will die and which will survive? Consequently, our current ability to predict when regional-scale plant stress will exceed a threshold that results in widespread mortality is lacking, yet is fundamentally needed to assess potential climate-change impacts, including changes in vegetation and associated ecosystems and their feedbacks to the climate system (Keane *et al.*, 2001; Burkett *et al.*, 2005; Scholze *et al.*, 2006; IPCC, 2007).

Here we explore the seemingly simple questions of when and why some plants die during drought while others survive. This is a long-standing question (Bossel, 1986; Franklin *et al.*, 1987; Waring, 1987; Manion, 1991) relevant to both low rates of mortality that happen continuously and regional scale 'die-off' events that occur less frequently. Scientific focus on this question has increased in recent decades as evidence mounts that climate extremes such as severe drought have rapid, widespread and long-lasting impacts on the vegetation composition of landscapes (Condit *et al.*, 1995; Allen & Breshears, 1998; Hanson & Weltzin, 2000; Berg *et al.*, 2006). Numerous hypotheses to explain mechanisms of survival and mortality have been generated via theoretical, modeling, and experimental analyses. However, a broader framework that encompasses these different hypotheses is lacking, and most hypotheses remain untested. Here we address these issues by providing an overview of the key hypotheses of drought-related plant mortality; developing and employing a predictive hydraulic framework to make testable predictions of the mechanisms of plant mortality; and discussing the implications of the framework in the context of global climate change. This framework is consistent with prior theories (Bossel, 1986; Waring, 1987; Manion, 1991; Martínez-Vilalta *et al.*, 2002),

Fig. 1 Dead ponderosa pine (*Pinus ponderosa*) trees in Bandelier National Monument, New Mexico, USA. (Photograph courtesy of Craig Allen.)

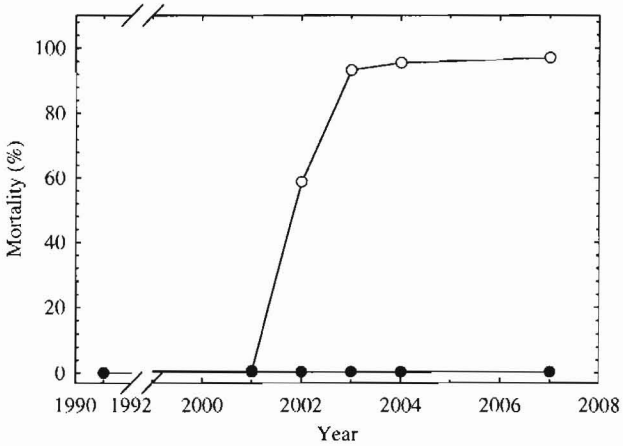

Fig. 2 Percentage mortality of piñon (open circles) and juniper (closed circles) trees at a 1.5 ha site, Mesita del Buey, near Los Alamos, New Mexico. For piñon, 16 of 484 trees survived (97% mortality), whereas for juniper, 559 out of 561 trees survived (< 1% mortality).

but provides an integrated perspective that recognizes the processes and mechanisms of survival and mortality as mutually inclusive.

We focus on the piñon–juniper woodlands (*Pinus edulis–Juniperus monosperma*) of southwestern USA as a model system, and examine additional evidence from a broader literature review. The piñon–juniper case study is useful because these species experienced different rates of mortality across the southwestern USA during the 2000–2002 drought (up to 95 and 25% mortality for piñon and juniper, respectively; Breshears *et al.*, 2005; Shaw *et al.*, 2005); piñon and juniper represent opposite ends of the spectrum in their hydraulic response to drought (Linton *et al.*, 1998); and sufficient physiological data exist for these two species to allow detailed examination of the hydraulic framework (Barnes, 1986; Lajtha & Barnes, 1991; Cobb *et al.*, 1997; Linton *et al.*, 1998; Pockman & Sperry, 2000; Williams & Ehleringer, 2000; West *et al.*, 2007a,b), including previously unpublished results from one particularly intensively studied site – Mesita del Buey in northern New Mexico (Barnes, 1986; Lajtha & Barnes, 1991; Breshears *et al.*, 2005; Breshears, 2008). At Mesita del Buey approx. 97% of the piñon trees died between 2000 and 2007, whereas only 0.4% of the junipers died during this period (Fig. 2). Although the piñon–juniper example represents an abrupt mortality event, the hypotheses we develop here should also apply, in theory, to the lower and more continuous mortality that occurs in the absence of drought.

II. Consequences of vegetation mortality

Drought-induced vegetation mortality has implications for ecosystem function, land–atmosphere interactions, and ecosystem services to humans (Dale *et al.*, 2000; NRC, 2007). Overstory mortality reduces photosynthetic uptake, potentially causing ecosystems to become a source of CO_2 to the atmosphere for some time period (Kurz & Apps, 1999; Law *et al.*, 2001; Breshears & Allen, 2002; Clark, 2004; Dore *et al.*, in press). Understory vegetation may respond with increased growth (Stone & Wolfe, 1996; Rich *et al.*, 2008), potentially altering successional pathways with feedbacks to surface hydrology and productivity. Reductions in total leaf area impact solar radiation input to the soil surface and subsequent soil processes such as nutrient cycling (Classen *et al.*, 2005; Hughes *et al.*, 2006), mycorrhizal activity (Swaty *et al.*, 2004), and erosion (Davenport *et al.*, 1998; Wilcox *et al.*, 2003). Transpiration (Bosch & Hewlett, 1982; Simonin *et al.*, 2007) and soil evaporation rates (Breshears *et al.*, 1998) are both altered, although the consequences of these changes on subsurface hydrology remain untested (Newman *et al.*, 2006). Vegetation mortality changes albedo and land–atmosphere exchanges of energy and latent heat at regional scales, and is thus likely to feedback on regional climate (Narisma *et al.*, 2003; Dirmeyer *et al.*, 2006). Widespread tree mortality can dramatically alter the availability of products of value to wildlife and humans, such as commodity production, biodiversity, aesthetics, and real estate values. Although climate change may cause migration of species on a decadal to millennial timescale, widespread mortality events have the capacity to radically transform regional scale landscapes on a subdecadal timescale with significant implications for ecosystem structure and function.

III. Global patterns of mortality

Climate-related vegetation mortality has been observed on all six vegetated continents and all biomes and plant functional types (Auclair, 1993; Allen & Breshears, 2007). In the south Pacific, drought has been associated with mortality in Australian *Eucalyptus* (Fensham & Holman, 1999; Rice *et al.*, 2004; Jurskis, 2005) and *Nothofagus* in New Zealand (Wardle & Allen, 1983). The El-Niño Southern Oscillation has been associated with drought-associated mortality from the tropical moist forests of Borneo (Van Nieewstadt & Sheil, 2005), Central America (Clark, 2004) and the Amazon (Williamson *et al.*, 2000; Cox *et al.*, 2004), to temperate *Nothofagus* and *Austrocedrus* forests in Patagonia (Villalba & Veblen, 1998; Suarez *et al.*, 2004) and *Terminalia* forests in Venezuela (Dezzeo *et al.*, 1997). In the northern hemisphere, drought-associated mortality has been observed from subboreal China (*Picea meyeri*, Liang *et al.*, 2003) to tropical regions of Africa (Sahel species, and Ugandan *Uvairopsis*: Gonzalez, 2001 and Lwanga, 2003, respectively). In the temperate zone of Europe, drought reduced net primary productivity (Ciais *et al.*, 2005; Bréda *et al.*, 2006) and increased forest mortality (Martínez-Vilalta *et al.*, 2002; Lloret *et al.*, 2004; Bigler *et al.*, 2006). Likewise, regional-scale droughts in North America have recently been correlated with insect outbreaks and associated

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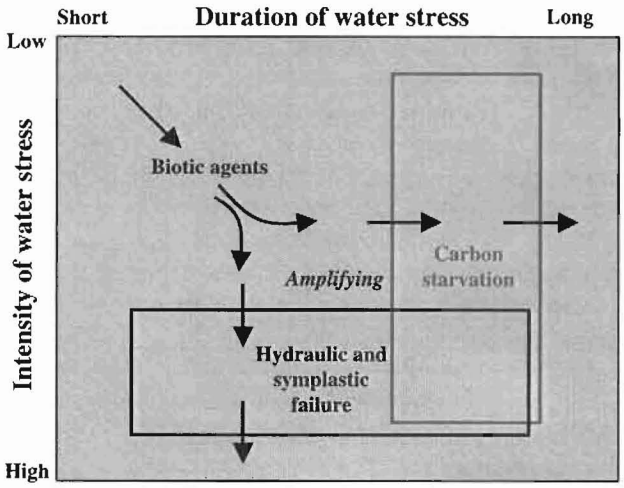

Fig. 3 Theoretical relationship, based on the hydraulic framework, between the temporal length of drought (duration), the relative decrease in water availability (intensity), and the three hypothesized mechanisms underlying mortality. Carbon starvation is hypothesized to occur when drought duration is long enough to curtail photosynthesis longer than the equivalent storage of carbon reserves for maintenance of metabolism. Hydraulic failure is hypothesized to occur if drought intensity is sufficient to push a plant past its threshold for irreversible desiccation before carbon starvation occurs. Biotic agents, such as insects and pathogens, can amplify or be amplified by both carbon starvation and hydraulic failure.

mortality of both deciduous and conifer species (Swetnam & Betancourt, 1998; Logan *et al.*, 2003; Breshears *et al.*, 2005; Frey *et al.*, 2004; Mueller *et al.*, 2005; Shaw *et al.*, 2005; Allen, 2007, C. Allen & N. Cobb, unpublished).

Examination of the global literature on vegetation mortality frequently points to water limitation being an important driver. Species adapted to dry environments tend to survive and grow better during drought than mesic-adapted species when grown together in common-garden experiments or in natural ecotones (VanSplunder *et al.*, 1996; Allen & Breshears, 1998; Volaire *et al.*, 1998; Sack, 2004; Adams & Kolb, 2005; Engelbrecht *et al.*, 2005). This indicates a role of genetic inheritance of drought survival traits. At the landscape scale, intraspecific mortality is typically highest in more arid locations, such as aspects facing the sun, well drained soils, or ridgetops (VanSplunder *et al.*, 1996; Allen & Breshears, 1998; Ogle *et al.*, 2000; Caspersen & Kobe, 2001; Slik, 2004; Gitlin *et al.*, 2006). Tree ring and long-term studies commonly report that mortality occurs only after exposure to prior droughts that initiate a growth decline (Pedersen, 1998; Demchik & Sharpe, 2000; Lloret *et al.*, 2004), or in response to a prolonged drought (Swetnam & Betancourt, 1998; Breshears *et al.*, 2005; Guarin & Taylor, 2005; Berg *et al.*, 2006; Bigler *et al.*, 2006). Likewise, most tree ring studies have observed that trees predisposed to die have lower mean growth rates or greater growth sensitivity to climate in the years proceeding mortality (Kolb & McCormick, 1993; Pedersen, 1998; Demchik & Sharpe, 2000; Ogle *et al.*, 2000; Wyckoff & Clark, 2002; Suarez *et al.*, 2004, but see Jenkins & Pallardy, 1995). Drought-associated tree mortality also appears to be more likely for plants at either end of size gradients – seedlings on one side and tall trees on the other (Condit *et al.*, 1995; Jenkins & Pallardy, 1995; Ogle *et al.*, 2000; Hanson *et al.*, 2001; Harrison, 2001; Clark, 2004; Lloret *et al.*, 2004; Rice *et al.*, 2004; Slik, 2004; Mueller *et al.*, 2005; Nepstad *et al.*, 2007). The tendency for conifers to maintain larger margins of safety from hydraulic failure than angiosperms may facilitate their survival during drought (Pittermann *et al.*, 2006). Below we show that many patterns discussed above are consistent with a hydraulic basis for mortality.

IV. Hypotheses on mechanisms of drought-related mortality

Hypotheses regarding the causes of plant death were formulated through theoretical efforts of Manion (1991) and Bossel (1986). Briefly, Manion (1991) suggested the slow-decline hypothesis in which plants experience a three-stage decline over many years, driven initially by long-term stress, for example poor edaphic location, followed by a severe short-term stress, for example drought, and finally death occurring via a contributing factor, for example pathogen. Manion labeled these three factors the predisposing factors, inciting factors, and contributing factors, respectively. Bossel (1986) and Mueller-Dumbois (1987) hypothesized that longer-term stresses alone could result in rapid mortality, particularly through an imbalance between carbon uptake and loss that results in a negative carbon balance. Other efforts regarding mortality have built off these initial formulations, often with an emphasis towards the carbon balance hypothesis (Waring, 1987; Martínez-Vilalta *et al.*, 2002; Bréda *et al.*, 2006; Güneralp & Gertner, 2007). Here we draw on these perspectives to pose a more general framework in which we focus on three hypothetical mechanisms of mortality: biotic agent demographics, hydraulic failure, and carbon starvation (we use new terms for these hypotheses to avoid misconceptions or misunderstandings that may occur from use of older terms and because these terms most simply represent the current hypotheses). Within our framework, we hypothesize that the relevance of these different mechanisms relates to the intensity and duration of water stress (Fig. 3). The biotic agent demographics hypothesis suggests that drought drives changes in demographics of mortality agents (e.g. insects and pathogens) that subsequently drive forest mortality. Potential demographic changes include increased number of pathogen generations per year as a result of longer growing seasons, or decreased over-winter mortality because of warmer winter minimum temperatures. Biotic agents may amplify, or be amplified by, plant physiological stress (Fig. 3). The

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hydraulic-failure hypothesis predicts that reduced soil water supply coupled with high evaporative demand causes xylem conduits and the rhizosphere to cavitate (become air-filled), stopping the flow of water and desiccating plant tissues. The hydraulic-failure hypothesis is based on the tenet that complete desiccation leads to cellular death. Hydraulic failure may be particularly likely if drought is sufficiently intense that plants run out of water before they run out of carbon (Fig. 3). The carbon-starvation hypothesis predicts that stomatal closure to prevent hydraulic failure causes photosynthetic uptake of carbon to diminish and the plant starves as a result of continued metabolic demand for carbohydrates. This process may be exacerbated by photoinhibition or increased respiratory demands associated with elevated temperatures during drought. Therefore, carbon starvation is hydraulically driven but nonhydraulic mechanisms may also contribute. Carbon starvation may be particularly likely if drought is not intense enough to cause hydraulic failure, but lasts longer than the equivalent amount of plant carbon reserves (Fig. 3). Biotic agents can amplify either hydraulic failure, such as when beetles inoculate sapwood with xylem-occluding fungi that halts water transport (Larsson *et al.*, 1983; Waring & Pitman, 1985; Wullschleger *et al.*, 2004), or carbon starvation, such as by increasing carbon loss to resin production (Wallin *et al.*, 2003). Likewise, hydraulic failure or carbon starvation can amplify biotic attacks, for example, as a result of low production of carbon-based defensive compounds such as resin, increased emissions of volatiles such as ethanol that attract insects, and alteration of food quality for insects. Thus all three mechanisms may operate either inclusively or exclusively.

1. A note on genetics

Genetic differences could potentially play an important role in all of these mechanisms (Gutschick & BassiriRad, 2003; Tuberosa *et al.*, 2003; Hamrick, 2004). However, genetic variation does not represent a mechanism of mortality or survival *per se*. Interspecific inheritance of phenotypic traits that facilitate drought resistance clearly occurs as shown in common-garden and ecotone experiments (VanSplunder *et al.*, 1996; Volaire *et al.*, 1998; Sack, 2004; Adams & Kolb, 2005; Engelbrecht *et al.*, 2005), although the evidence is less clear for intraspecific inheritance. Numerous common-garden studies on woody plants show intraspecific genetic variation in characteristics associated with drought resistance, such as vulnerability of xylem to cavitation (Kavanagh *et al.*, 1999), hydraulic conductance (Comstock, 2000) and water-use efficiency (Zhang *et al.*, 1995), stoma size and density (Mitton *et al.*, 1998), and insect attack (Christensen *et al.*, 1995). Long-lived trees, especially wind-pollinated species, have the highest degrees of genetic variation and thus could be expected to be the most resilient species to future droughts if genetic factors are important to survival (Mitton, 1995; Hamrick, 2004). Although genetic inheritance of drought survival mechanisms is clearly important, the mechanisms under selection are not yet clear.

V. Evidence for hypothesized mechanisms

Substantial evidence exists for the three mutually inclusive mechanisms of mortality: biotic agent demographics, hydraulic failure, and carbon starvation. As we explain below, a hydraulic framework is directly relevant to the latter two mechanisms and can be related to biotic agent demographics.

1. Biotic agent demographics

This hypothesis suggests that drought drives changes in demographics of mortality agents such as insects and pathogens, which subsequently drive forest mortality independently or in conjunction with drought-induced changes in host plant physiological condition. This hypothesis derives from the frequent observation that a temporal correlation exists between drought and outbreaks of insects (White, 1984; Mattson & Haack, 1987; Waring & Cobb, 1992; Clancy *et al.*, 1995; Shaw *et al.*, 2005; Fettig *et al.*, 2007) and pathogens (Houston, 1987; Manion, 1991). Predictions suggest population demographics such as growth rates and reproduction of biotic mortality agents will be exacerbated by climate change largely as a result of increased temperatures (Ayres & Lombardero, 2000; Logan *et al.*, 2003; Gan, 2004; Tran *et al.*, 2007). Empirical evidence and models suggest that drought associated with unusually warm weather will have an impact on many characteristics of insect population dynamics, including intrinsic population growth rate, the number of generations produced per year, synchrony of key developmental phases, winter mortality, and geographic range (Ungerer *et al.*, 1999; Logan & Bentz, 1999; Ayres & Lombardero, 2000; Simberloff, 2000; Logan & Powell, 2001; Logan *et al.*, 2003; Hicke *et al.*, 2006). Droughts may also affect insect and pathogen populations by influencing the abundance of key predators and mutualists (Ayres & Lombardero, 2000); the direction and magnitude of such effects are largely unknown. It is unlikely that drought will be beneficial to all insects that kill trees, or in all locations. For example, outbreaks of western spruce budworm in the southwestern USA are positively related to wet spring weather, negatively related to dry spring weather, and unrelated to temperature (Swetnam & Lynch, 1993). Likewise, the synchrony of insect emergence with temperature may have negative consequences for insect population growth at low elevations but positive impacts on population growth at higher elevations (Hicke *et al.*, 2006). Overall, warm droughts may increase the intensity of outbreaks of biotic mortality agents independent of concomitant changes in tree physiological condition related to drought, although the specific dynamics may vary by agent.

Drought-related mortality does not always include an obvious biotic mortality agent (Lloret *et al.*, 2004) and thus

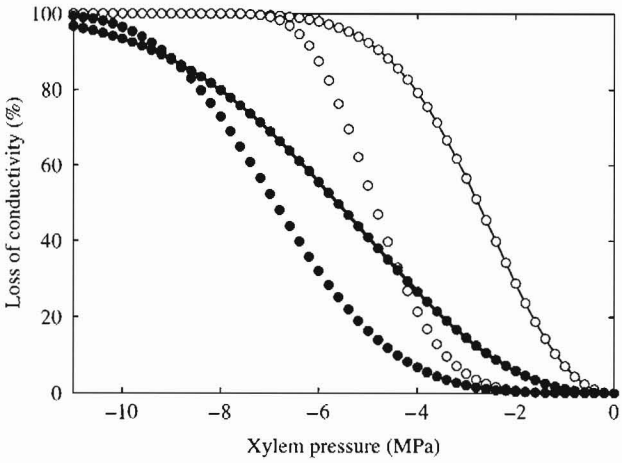

Fig. 4 The percentage loss of conductivity of excised root (connected circles) and stem (unconnected circles) segments of piñon (open circles) and juniper (closed circles) as a function of xylem pressure. These 'vulnerability curves' were obtained by the air-injection method (Linton *et al.*, 1998).

the biotic agents demographics hypothesis can explain, at most, only a portion of observed mortality. However, plants treated with insecticides often survive outbreaks of insects (Hastings *et al.*, 2001; Grosman & Upton, 2006; Romme *et al.*, 2006), indicating that biotic agents play a significant role in mortality. A prediction consistent with observations is that changes in demographics of biotic mortality agents must overlay changes in host plant physiological conditions to cause widespread mortality events (Berryman, 1976; Christiansen *et al.*, 1987).

2. Plant water relations

A review of plant regulation of water use is needed to consider the mechanisms of hydraulic failure and carbon starvation. In particular, it is critical to understand the structural and physiological mechanisms by which plants prevent evapotranspiration (E) from exceeding critical rates (E_{crit}) that result in xylem water potentials associated with hydraulic and symplastic failure (Ψ_{crit}). Furthermore, the impacts of E_{crit} avoidance on photosynthesis and subsequent dependency on stored carbohydrate reserves are critical to understanding carbon starvation (Cowan & Farquhar, 1977; Katul *et al.*, 2003). In this section we review plant water relations in the context of avoidance of E_{crit} and Ψ_{crit}, introduce a modeling framework for investigation of such regulation, and then investigate hypotheses regarding hydraulic failure and carbon starvation using the model and existing evidence from our piñon–juniper case study and the broader literature.

To maintain tissue hydration and photosynthesis, plants must replace water lost through E. As described by the cohesion tension theory, E generates tension that pulls water from the soil through the plant to the crown, where it diffuses to the atmosphere. Thus, E can be explicitly described via the steady-state formulation of the soil–plant–atmosphere hydraulic continuum (modified from Whitehead & Jarvis, 1981; Whitehead, 1998):

$$E = K_l (\Psi_s - \Psi_l - hp_w g) \qquad \text{Eqn 1}$$

In this corollary to Darcy's law, K_l is leaf-specific hydraulic conductance of the soil-plant continuum, Ψ_s and Ψ_l are soil and leaf water potentials, respectively, and $hp_w g$ is the gravitational pull on a water column of height h and density p_w. The tension difference across the plant ($\Psi_s - \Psi_l$) increases in proportion to E as long as K_l remains constant, for example no cavitation occurs. This mechanism is efficient because metabolic energy is not used to lift water to the crown. However, E has an upper limit (E_{crit}) because increasing tension causes decreased K_l as a result of air entry through pit pores into conduits, thereby initiating cavitation (nucleation of vaporization) and producing an embolized, or air-filled conduit (Fig. 4). In other words, hydraulic failure occurs when E exceeds the critical Ψ, K_l approaches zero, and the plant can no longer move water. The Ψ_{crit} value causing 100% cavitation varies widely among species (Pockman *et al.*, 1995; Pockman & Sperry, 2000; Maherali *et al.*, 2004) and is thought to be a function of interconduit pit structure (Pittermann *et al.*, 2005). An example of vulnerability to cavitation in stems and roots of piñon and juniper is presented in Fig. 4 (Linton *et al.*, 1998). Roots tend to be more vulnerable than stems, which may serve the advantage of protecting the more energetically costly stem tissues from cavitation (Sperry & Ikeda, 1997; Sperry *et al.*, 2002).

Hydraulic failure also occurs within soils and is functionally similar to xylem cavitation. The hydraulic conductance of soils is a function of texture, water content, hydraulic conductivity, and water table depth. Greater tension is required to pull water through fine-textured soils because of their small pore sizes, and thus fine-textured soils have lower conductance than sandy soils when water is abundant. However, fine-textured soils retain hydraulic conductance longer and at more negative water potentials than coarse-textured soils because the low conductance of fine soils results in slower water loss to transpiration and drainage (Sperry *et al.*, 1998). Therefore, during drought we expect greater hydraulic failure in coarse-textured soil. Depth to water table also has an impact on plant hydraulics by limiting or allowing plants to obtain water during periods of drought (Dawson, 1996; Franks *et al.*, 2007). To compensate for coarse-textured soils or inaccessible water tables, plants may increase their soil-to-root, or rhizosphere conductance via adjusting fine root density (Ewers *et al.*, 2000; Hacke *et al.*, 2000), fine root hydraulic conductance (McElrone *et al.*, 2007) rooting depth, and other root characteristics (Stirzaker & Passioura, 1996).

Plant avoidance of hydraulic failure can be conceptualized using models of the soil–plant–atmosphere continuum.

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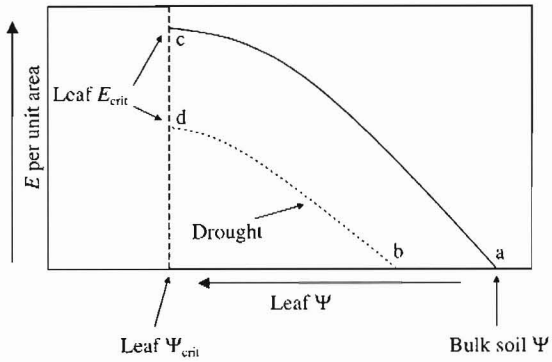

Fig. 5 Modeled transpiration per unit leaf area as a function of leaf water potential for a plant with relatively abundant soil moisture (solid line) and the same plant with reduced soil moisture availability (dashed line). Letters are referenced within the text.

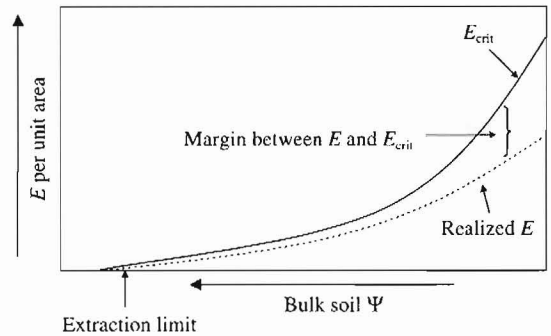

Fig. 6 Modeled transpiration per unit leaf area as a function of soil water potential. The solid line represents the transpiration threshold beyond which hydraulic failure occurs, and the dashed line represents realized transpiration, with the difference between the two lines representative of a hydraulic margin of safety.

Such models can then be used as the basis for predictions of mortality related to water stress. The relationship between E and Ψ_l can be modeled based on the hydraulic properties of soil and xylem, root distribution, and root-shoot allocation (Sperry *et al.*, 1998, 2002; Fig. 5). When E is zero, Ψ_l equilibrates with bulk soil water potential (Fig. 5a). As E increases, Ψ_l drops (Fig. 5, solid line a–c). For every unit increase in E, the drop in water potential becomes progressively greater because cavitation and rhizosphere drying reduce K_l of the flow path. If E increases past E_{crit}, and hence Ψ exceeds Ψ_{crit}, then hydraulic failure will occur (e.g. when the soil-plant K_l falls to zero, Fig. 5c). As drought decreases soil water potential within the rooting zone, hydraulic failure occurs at progressively lower values of E (Fig. 5, compare dashed drought trajectory b–d with a–c). If hydraulic failure is caused by xylem cavitation within stems, Ψ_{crit} corresponds to the pressure where 100% cavitation occurs (e.g. –6.9 MPa in piñon stems; Fig. 4). Drying of the rhizosphere may drive hydraulic failure at more positive Ψ_{crit} because roots and soils are typically more vulnerable than stems (Fig. 4). This does not mean that roots or soils will always be the location of hydraulic failure, however, because stems can reach much more negative water potentials as a result of their longer hydraulic path length (McDowell *et al.*, 2002a; Sperry *et al.*, 2002); hence trees that have reached their maximum height may be particularly vulnerable.

Using this hydraulic framework we can predict hydraulic failure during drought by plotting the decline in E_{crit} as a function of soil water potential (Fig. 6). When the soil water potential reaches Ψ_{crit}, E_{crit} is zero and no further water can be extracted (Fig. 6, 'extraction limit'). The actual water use must fall within this envelope (Fig. 6, 'realized transpiration'); if the transpiration threshold is exceeded, hydraulic failure results. Plants maintain E below E_{crit} over long time periods (e.g. years to centuries) via adjustment of structural features that allow maximum water uptake relative to demand by the plant crown, and over short time periods (e.g. diurnal cycles) via crown-level stomatal conductance (G_s) (Tyree & Sperry, 1988; Sperry *et al.*, 1998).

The long-term structural adjustments that maintain homeostasis between water supply, water demand, and plant metabolism (Whitehead & Jarvis, 1981; Cinnirella *et al.*, 2002; Katul *et al.*, 2003; Bréda *et al.*, 2006) may all play a role in the survival or mortality of plants during drought. These adjustments are influenced over decadal time scales in response to climate, plant size, edaphic properties such as soil texture and depth, and stand density (Maherali & DeLucia, 2001; McDowell *et al.*, 2002a, 2006; Sperry *et al.*, 2002; Mencuccini, 2003). Long-term homeostasis was originally defined mathematically by Whitehead & Jarvis (1981) as a steady-state derivation of Darcy's law similar to Eqn 1:

$$E = \frac{k_s A_s}{h \eta A_l} \times \Delta\Psi \qquad \text{Eqn 2}$$

where k_s is saturated permeability of the conducting path, A_s is sapwood area, A_l is leaf area, h is height, η is the viscosity of water, and $\Delta\Psi$ is $\Psi_s - \Psi_l - hp_w g$ (Eqn 1). Although Eqn 2 is a simplification of the plant hydraulic system (Domec *et al.*, 2007), it has proven remarkably accurate (Whitehead, 1998; Oren *et al.*, 1999; Schäfer *et al.*, 2000; McDowell *et al.*, 2002a, 2005; Phillips *et al.*, 2002; Barnard & Ryan, 2003). Furthermore, the structural adjustments included in Eqn 2 are consistent with the Sperry *et al.* (1998) model (Addington *et al.*, 2006). Taken together, homeostatic factors from Eqns 1 and 2 that have been empirically documented include: (i) vulnerability of xylem conductance to low water potentials (see Fig. 4) (Pockman & Sperry, 2000; Ogle & Reynolds, 2002; Maherali *et al.*, 2004); (ii) xylem permeability (Pothier *et al.*, 1989; McElrone *et al.*, 2004); (iii) refilling of cavitated elements (Sperry *et al.*, 1987; Borghetti *et al.*, 1991; Holbrook & Zwieniecki, 1999; Tyree *et al.*, 1999; Salleo *et al.*, 2004; West *et al.*, 2007a); (iv) the soil-to-leaf water potential gradient

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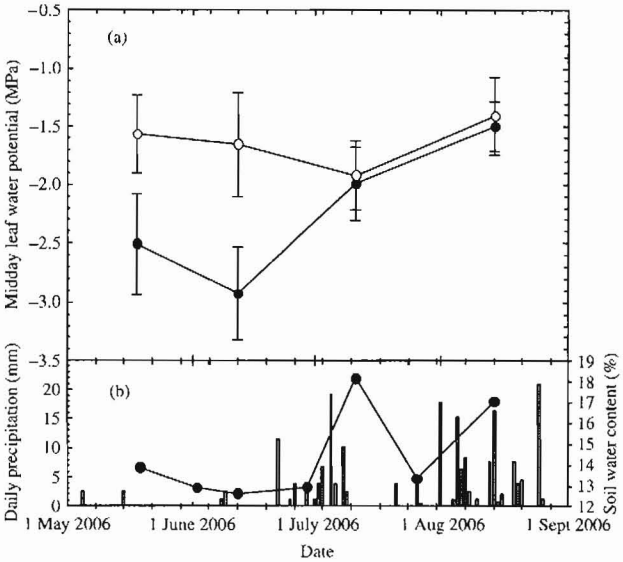

Fig. 7 (a) Midday (11 : 00–13 : 00 h) leaf water potential for piñon (open circles) and juniper (closed circles); and (b) daily precipitation (left axis, bars) and soil water content at 20 cm (right axis, filled symbols) at Mesita del Buey near Los Alamos, New Mexico. Bars in (a) are standard errors. Water potential was measured via pressure chamber within 5 min of twig collection, and consisted of two twigs per individual and five individuals per species per time period. Soil water content was measured via neutron probe.

(Hacke *et al.*, 2000; McDowell *et al.*, 2002a; Barnard & Ryan, 2003); (v) vertical distribution of root density as a function of soil water availability (VanSplunder *et al.*, 1996; Volaire *et al.*, 1998; Ewers *et al.*, 2000; Hacke *et al.*, 2000; Lloret *et al.*, 2004; West *et al.*, 2007b); (vi) ratio of root absorbing area to leaf area (Ewers *et al.*, 2000; Hacke *et al.*, 2000; Magnani *et al.*, 2000); (vii) ratio of sapwood area to leaf area (Mencuccini & Bonosi, 2001; McDowell *et al.*, 2002b, 2006; Barnard & Ryan, 2003); (viii) leaf shedding (Tyree *et al.*, 1993; Suarez *et al.*, 2004; Hultine *et al.*, 2006); (ix) height (McDowell *et al.*, 2005; Addington *et al.*, 2006); and (x) capacitance (water storage, Goldstein *et al.*, 1998; Phillips *et al.*, 2003). Others, such as osmotic regulation of leaf turgor (Kozlowski & Pallardy, 2002), foliar water absorption (Breshears *et al.*, 2008), aquaporin mediation of hydraulic conductance (McElrone *et al.*, 2007) and cellular desiccation tolerance (Gaff, 1971; Dace *et al.*, 1998; Sherwin *et al.*, 1998), may also play a role in drought tolerance or avoidance. Each of these factors may strongly impact the likelihood of plants to survive or succumb to drought. For example, the observation that tall trees tend to die is consistent with Eqns 1 and 2 because height constrains K_l and E such that the margin of safety is reduced. Likewise, the observation that seedlings often die is consistent with their having insufficient soil-to-root K_l during drought.

Note that differences in structural parameters between our case study species, piñon and juniper, are consistent with Eqn 2 with respect to susceptibility to drought-related mortality. Relative to piñon, juniper has more cavitation-resistant xylem (Fig. 4), lower leaf area to sapwood area ratio (Grier *et al.*, 1992), lower leaf area to root area ratio (West *et al.*, 2008), a larger water potential gradient from soil to leaf (Lajtha & Barnes, 1991; West *et al.*, in press), and is shorter (2.7 vs 5.6 m at Mesita del Buey New Mexico).

Over diurnal timescales, plants maintain E below E_{crit} through stomatal closure. Plants reduce G_s in response to increasing E (Mott & Parkhurst, 1991), with the degree of closure linked to Ψ_{crit} that causes embolism (Sperry *et al.*, 2002). G_s is in turn regulated not only by water supply and demand, and their impact on E, but also by plant structural adaptations that impact the supply or demand for water, for example rooting volume or leaf area, respectively (Eqn 2). While reducing G_s serves the benefit of reducing water loss, it has the cost of reducing CO_2 diffusion from the atmosphere to the site of carboxylation, and thereby constraining photosynthetic CO_2 uptake (Cowan & Farquhar, 1977). As we show, this balance between water loss and CO_2 uptake may partition plants between survival, hydraulic failure or carbon starvation during drought.

3. Isohydry and anisohydry

Plants fall into two categories across the continuum of stomatal regulation of water status, labeled isohydric and anisohydric regulation (Tardieu, 1993; Tardieu & Simonneau, 1998). Isohydric plants reduce G_s as soil water potential decreases and atmospheric conditions dry, maintaining a relatively constant midday Ψ_l regardless of drought conditions. Anisohydric species, by contrast, allow midday Ψ_l to decline as soil Ψ declines with drought. Piñon is a good example of isohydric regulation, maintaining leaf water potentials at *c.* −2.0 MPa despite severe soil drying (Fig. 7, and see Lajtha & Barnes, 1991; Williams & Ehleringer, 2000; West *et al.*, 2008; Breshears *et al.*, in press). Although no specific thresholds and ranges of isohydric control are generalized in the literature, isohydric behavior has been observed in temperate hardwoods, C_4 grasses, Australasian and neotropical trees, and other species of gymnosperms (Tardieu & Davies, 1992; Loewenstein & Pallardy, 1998a,b; Tardieu & Simonneau, 1998; Niinemets *et al.*, 1999; Bonal & Guehl, 2001; Fisher *et al.*, 2006). Anisohydric plants maintain higher G_s for a given Ψ_l than isohydric species, effectively allowing Ψ_l to decline with decreasing soil water potential (Fig. 8, Barnes, 1986). Anisohydric behavior has been observed across the same diversity of plant groups: species such as juniper, sugar maple (*Acer saccharum*), sunflower (*Helianthus annuus*), and eucalyptus (*Eucalyptus gomphocephala*) allow a greater Ψ_l range than isohydric species (Loewenstein & Pallardy, 1998a,b; Tardieu & Simonneau, 1998; Franks *et al.*, 2007; West *et al.*, 2008). Anisohydric species tend to occupy more drought-prone habitats compared with isohydric species

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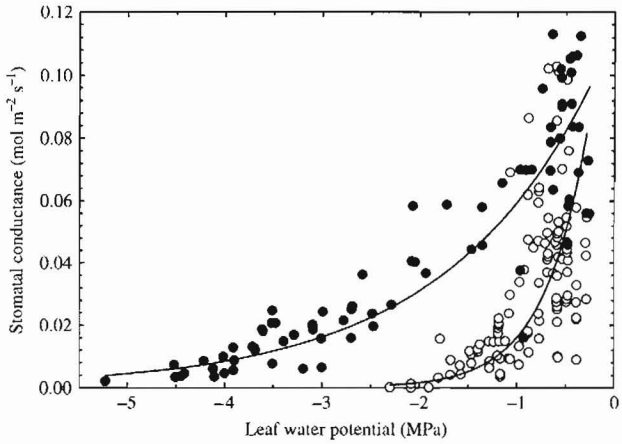

Fig. 8 Stomatal conductance vs leaf water potential for piñon (open circles) and juniper (closed circles) at Mesita del Buey, Los Alamos, New Mexico. Data from Barnes (1986).

and have xylem that is more resistant to negative water potentials (see Fig. 4). There are, however, exceptions to these generalizations and many comparative studies and syntheses (Pockman & Sperry, 2000; Maherali *et al.*, 2004) have not specifically characterized species as isohydric or anisohydric. Anisohydric vs isohydric regulation of water status may be a critical factor in the regulation of survival and mortality during drought (Fig. 3).

It is important to clarify that relating the hydraulic framework to plant mortality is based on the premise that whole-plant hydraulic failure will cause death. This premise may be false in cases of resprouting, xylem refilling, or if cells are desiccation-tolerant. Resprouting has been observed following cavitation-induced shoot dieback in shrubs (Davis *et al.*, 2002; Sperry & Hacke, 2002), mesic hardwoods (Tyree *et al.*, 1993), and riparian trees (Horton *et al.*, 2001). A benefit of reducing leaf area via shoot dieback is the resulting improvement in water status of the remaining foliage and subsequent survival of the individual (Tyree & Sperry, 1989; Davis *et al.*, 2002; Bréda *et al.*, 2006). Resprouters may die during drought, however, if persistent hydraulic failure leads to carbon starvation that prevents growth of new stems. Refilling of cavitated elements may occur in some species when drought is relieved by precipitation, although the mechanisms and frequency of refilling remain debated (Sperry *et al.*, 1987; Borghetti *et al.*, 1991; Holbrook & Zwieniecki, 1999; Tyree *et al.*, 1999; Salleo *et al.*, 2004; West *et al.*, 2007a). Refilling has been observed in piñon but not juniper (West *et al.*, 2007a). Desiccation-tolerant cells, such as the live cells of mosses, ferns, seeds and pollen of higher plants, and of resurrection plants (e.g. *Xerophyta*), can withstand complete drying, and upon wetting they regain complete physiological function (Gaff, 1971; Dace *et al.*, 1998; Sherwin *et al.*, 1998). This ancestral trait is rare amongst vascular plants (Oliver *et al.*, 2000); however, a lesser degree of cellular drought tolerance is common (Kozlowski & Pallardy, 2002). As plants have become larger and more complex, water transport has become more limiting to survival than cell physiology and so vegetative cells may have lost their capacity to tolerate air-drying (Oliver *et al.*, 2000). Based on evidence for correlations between cellular desiccation limits and hydraulic transport limits (Brodribb *et al.*, 2003), cellular drought tolerance may be as colimiting as hydraulics in determining plant physiological limits.

The large number of potential interactions between isohydry, anisohydry and parameters within Eqns 1 and 2 highlights that there is a large number of physiological and structural factors that may be adjusted to either tolerate or avoid water stress during drought. However, these factors may also have species or site-specific limits on how far they can be adjusted; these limits may subsequently predispose plants to hydraulic failure. Next we can apply the hydraulic framework to understand the hydraulically based hypotheses of hydraulic failure and carbon starvation.

4. Hydraulic failure

The concept underlying the hydraulic-failure hypothesis is that drought causes the species- and site-specific E_{crit} to be surpassed such that the plant irreversibly desiccates. Hydraulic failure occurs in small plants, as seedling mortality has been linked to excessive cavitation in the field (Williams *et al.*, 1997) and drying experiments with potted plants often result in rapid mortality (Sparks & Black, 1999). The limited rooting volume explored by seedlings exposes them to more negative soil water potentials than plants with larger root systems, decreasing soil-to-root K_l and hence the safety margin between realized E and E_{crit} (Fig. 6). For mature trees there are numerous anecdotal observations of mortality occurring in the absence of insect or pathogen attack; however, it is unknown if hydraulic failure or another mechanism was the cause of death.

The piñon–juniper comparison provides an interesting contrast with respect to mortality by hydraulic failure. Modeling E_{crit} vs Ψ_{soil} using piñon and juniper vulnerability curves (Fig. 4) and soil and plant architecture and water potential data (West *et al.*, 2008) yields the prediction that the anisohydric strategy of juniper makes it more susceptible to hydraulic failure than piñon, because the water-use envelope of juniper is closer to the xylem cavitation threshold (Fig. 9). Continued transpiration by juniper during drought reduced soil water potential to –6.9 MPa, bringing juniper plants close to hydraulic failure (Fig. 9, solid circle compared with E_{crit}) and induced an estimated 40–60% embolism in roots and shoots, respectively (West *et al.*, 2007a, 2008; Fig. 4). The species-specific difference in regulation of the hydraulic safety margins occurs in part via differential relationships between leaf water potential and G_s (Fig. 8; Barnes,

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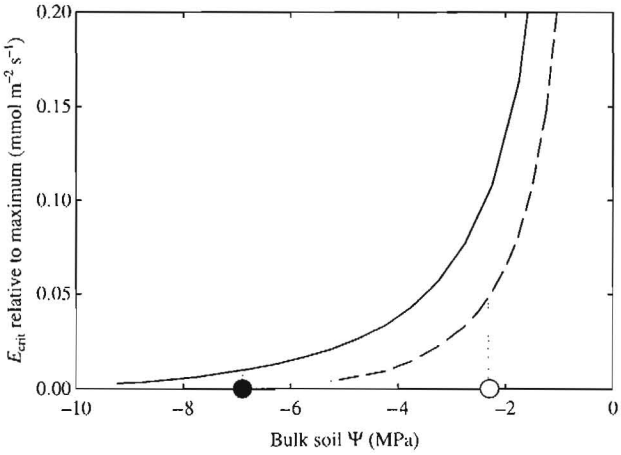

Fig. 9 Modeled critical transpiration threshold as a function of soil water potential for piñon (dashed line) and juniper (solid line) and observed minimum leaf water potential for each (filled and open symbol, respectively). Data from West *et al.* (2008). Dotted vertical lines represent the species-specific margins of hydraulic safety, which are 0.05 and 0.01 mmol m^{-2} s^{-1} for piñon and juniper, respectively.

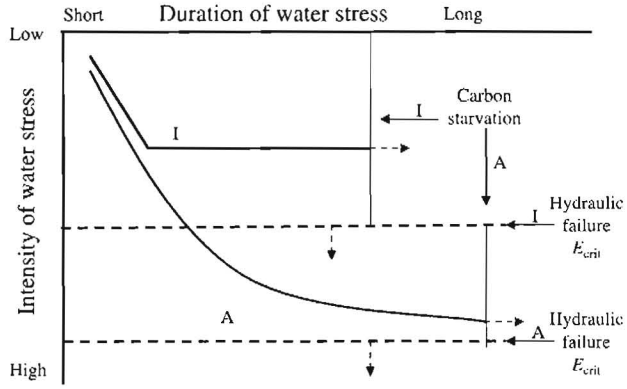

Fig. 10 Theoretical predictions of the mechanisms of drought-related mortality for species utilizing isohydric vs anisohydric regulation of water potential. This figure is a more detailed representation of the hypotheses exemplified in Fig. 3, highlighting differences between isohydric (I) and anisohydric (A) functional types. The dashed horizontal line represents the point of hydraulic failure for each functional type. Carbon starvation is hypothesized to occur primarily for isohydric species that close stomata relatively early in a drought (solid isohydric line), initiating the phase of reliance on carbohydrate reserves earlier than anisohydric plants (compare solid isohydric and anisohydric lines). Isohydric species may experience hydraulic failure in cases of severe intensity of drought (dotted isohydric line). Anisohydric species have a more curvilinear response (similar to Fig. 9) and are predicted to maintain positive carbon gain for a longer period than isohydric species, thus prolonging the duration of drought they can withstand before carbon starvation (solid anisohydric line). However, anisohydric species have a smaller margin of safety, thus increasing their likelihood of mortality via hydraulic failure (dotted anisohydric line).

1986; Williams & Ehleringer, 2000; West *et al.*, 2008). Although this strategy allows juniper to maintain photosynthetic activity during drought, ultimately it may result in patchy dieback of crowns if drought is prolonged, as has been observed in juniper during the 2000–2002 severe drought in the southwestern USA (authors' personal observations). Whether this partial dieback can explain whole tree mortality is unknown, but given a drought of sufficient intensity and duration, it seems a logical hypothesis that hydraulic failure may cause whole-plant mortality in anisohydric plants (Fig. 3).

By contrast, the isohydric behavior of piñon prevents excessive cavitation even during extreme drought, making it unlikely to be a victim of hydraulic failure. Piñons lose only an estimated 5–40% of their xylem conductivity (all in their root systems) because stomatal closure keeps xylem water potentials above −2.5 MPa during drought (Figs 7–9). Safety margins from hydraulic failure are relatively large (Fig. 9, compare open circle with E_{crit}). Of course, this control of cavitation in piñon comes at the price of negligible gas exchange, which leads to the carbon-starvation hypothesis, which we discuss in the next section.

A notable insight that emerges from the hydraulic framework is that although isohydric species appear more vulnerable to embolism (Fig. 4), isohydric plants should actually be less likely to experience hydraulic failure because they close their stomata rather than risk cavitation. Anisohydric plants instead have higher rates of gas exchange during drought, but risk greater cavitation as a consequence (Fig. 10). Both isohydric and anisohydric species are capable of carbon starvation or hydraulic failure; however, the isohydric species will probably maintain Ψ_l above its hydraulic failure threshold until carbon starvation occurs (Fig. 10, thick line) and will only reach hydraulic failure if the drought is sufficiently intense to force whole-system cavitation via xylem equilibration with severely dry soil. By contrast, the anisohydric species will allow Ψ_l to approach (or even surpass, e.g. Fig. 9) its cavitation threshold, thus allowing a longer time period before zero carbon assimilation and hence a longer time period before carbon starvation occurs. However, the closer proximity that the anisohydric species has to its cavitation threshold increases the risk of catastrophic hydraulic failure if drought intensity continues to increase, particularly because it maintains Ψ_l in realms where both soil moisture release curves and cavitation response curves (i.e. Fig. 4) are steep, such that small changes in water availability can have very large impacts on water potential.

5. Carbon starvation

The carbon-starvation hypothesis predicts that stomatal closure to prevent desiccation (e.g. by isohydric plants, Figs 8 and 9), causes photosynthetic carbon uptake to diminish to near zero (Fig. 10). Continued demand for carbohydrates to maintain metabolism will deplete carbohydrate reserves,

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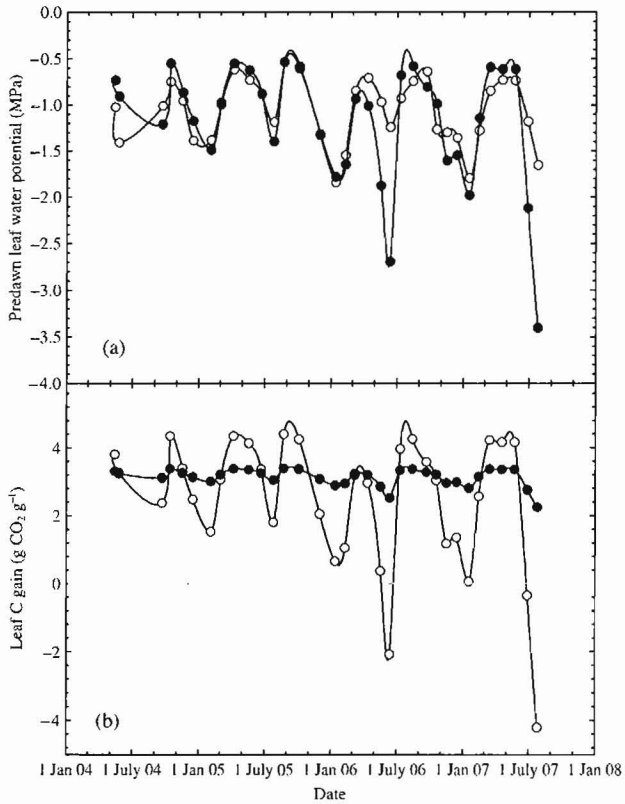

Fig. 11 (a) Three years of monthly observations of predawn water potential of piñon (open circles) and juniper (closed circles) from Mesita del Buey, Los Alamos, New Mexico. Twigs were sampled at least 20 min before sunrise and kept in plastic bags until measurement, which took place within 1 h of collection. Samples consisted of two twigs per tree and a minimum of five trees per species per time period. (b) Seasonal leaf carbon gain for piñon and juniper modeled using Barnes (1986) and the predawn water potentials from (a).

leading eventually to starvation or an inability to fend off attack from biotic agents, whichever comes first (Fig. 3). Similar to the hydraulic-failure hypothesis, the carbon starvation hypothesis lacks direct tests, although variations on this theme have been modeled as a driver of mortality for decades (Waring, 1987; Manion, 1991; Martínez-Vilalta *et al.*, 2002; Guneralp & Gertner, 2007). Empirical evidence supporting a link between carbon availability and mortality is derived from the numerous studies reporting that trees that die have lower stemwood growth rates, increased growth variability, or increased climatic sensitivity, particularly after severe droughts (Kolb & McCormick, 1993; Pedersen, 1998; Demchik & Sharpe, 2000; Ogle *et al.*, 2000; Lloret *et al.*, 2004; Rolland & Lemperiere, 2004; Suarez *et al.*, 2004; Guarin & Taylor, 2005; Bigler *et al.*, 2006). However, still other studies have shown higher growth rates in trees predisposed to die, particularly in oak species (Jenkins & Pallardy, 1995, T. Levanič & N. McDowell, unpublished data). Modeling studies typically support the carbon-starvation hypothesis (Pedersen, 1998; Guneralp & Gertner, 2007), including models that predict carbon starvation initiated by stomatal closure (Martínez-Vilalta *et al.*, 2002).

The primary means of reduced photosynthesis by isohydric species during drought is the constraint on CO_2 diffusion into leaf intercellular spaces as a result of stomatal closure (Figs 8 and 9). For example, piñon net photosynthesis is halved at a rhizosphere water potential of −1.0 MPa, and reaches zero at a water potential of −2.3 MPa (Lajtha & Barnes, 1991). However, respiratory consumption of stored carbohydrates continues during drought to maintain plant metabolism, even if growth is zero (Amthor, 2000). Accounting for nocturnal leaf respiration costs, piñon leaf carbon gain reaches zero at approx. −2.0 MPa (Barnes, 1986). If we make the simple assumption that whole-plant respiration consumes 55% of assimilation (Ryan *et al.*, 1994; Waring *et al.*, 1998; Litton *et al.*, 2007) then piñon trees achieve negative whole-plant carbon balance around rhizosphere water potentials of −1.0 MPa. By contrast, making this same 55% assumption, we predict that juniper reaches a zero whole-plant carbon balance at a rhizosphere water potential of *c.* −3.0 MPa. In effect, this difference allows the anisohydric species to maintain positive carbon gain for a greater duration of the drought (Fig. 10).

The hypothesis that carbon starvation, not hydraulic failure, is a likely driver of mortality in isohydric species can be examined by parameterizing Barnes' (1986) empirical model of leaf carbon gain using measurements of predawn water potential generated from the same field site (Mesita del Buey). Three years of monthly predawn water potential measurements demonstrate that piñon regulates water potential within a much narrower range than juniper (Fig. 11a). By contrast, modeled leaf carbon gain is substantially more variable for piñon than juniper (Fig. 11b), owing to the greater stomatal sensitivity of piñon to water stress (Fig. 8). During the 2000–2002 drought, when piñon experienced region-scale mortality, Breshears *et al.* (in press) observed that piñon and juniper predawn water potential was below −2.0 MPa for 11 months before observed mortality, effectively precluding carbon gain for a year.

The theory that carbon starvation and hydraulic failure are the dominant mechanisms of mortality for isohydric and anisohydric species, respectively, is further supported when a broader set of plant species is considered. In Fig. 12 we plotted a typical rhizosphere drying curve for a drought period after a precipitation event at time zero. We have overlaid measured Ψ of zero G_s for all isohydric species and Ψ of 100% cavitation for all anisohydric species. These species are described in our literature review from the 'Isohydry and anisohydry' section. An assumed time lag of 10 months from zero G_s to carbon starvation is applied uniformly to all isohydric species (from observations of piñon pine; Breshears *et al.*, in press). Figure 12 demonstrates that the isohydry/anisohydry continuum

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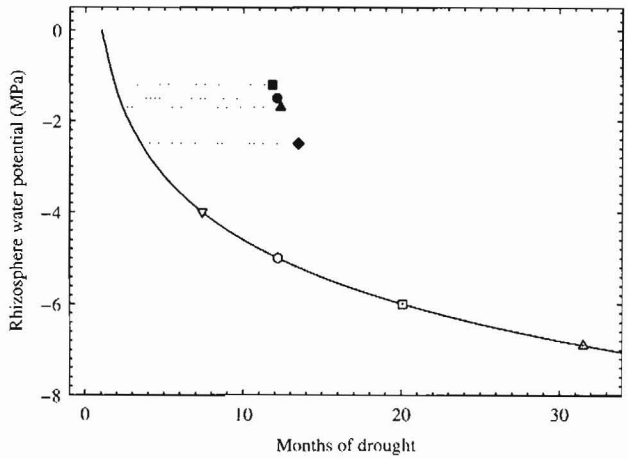

Fig. 12 Theoretical mortality response of isohydric and anisohydric species to drought. The curve illustrates the decline in rhizosphere water potential under a 30 month drought scenario. For isohydric species, the horizontal dotted lines extend from where the Ψ_{leaf} at zero G_s crosses the rhizosphere Ψ curve to the date of death via carbon starvation (filled symbols). For anisohydric species, Ψ_{crit} is the Ψ_{stem} or Ψ_{leaf} at which some portion of the plant xylem experiences $K_s = 0$, and is plotted on top of the rhizosphere Ψ curve (open symbols). For isohydric species, the length of time until carbon starvation is based on observations of piñon pine (see text). Isohydric species (solid symbols): flowering dogwood (square), tatuba (circle), black elderberry (triangle), piñon pine (diamond). Anisohydric species (open symbols): sunflower (downward triangle), sugar maple (hexagon), eucalyptus (square), juniper (upward triangle). Sources are from the literature review provided in Section V.3, Isohydry and anisohydry.

partitions species vulnerability to drought as a function of drought duration. For example, if drought were relieved by precipitation after 10 months, one anisohydric species (sunflower) would have died but all other species would have survived. By contrast, if drought-relieving precipitation did not occur until 15 months then all isohydric species would have died. If the drought were more intense, such that the drying curve were steeper, then the likelihood of more anisohydric species succumbing earlier would increase; and vice versa, if the drought were less intense, such that the drying curve was shallower, proportionally more isohydric species would succumb because they would reach carbon starvation long before anisohydric species reach Ψ_{crit}. Perhaps the most important observation from Fig. 12 is the clear need for information regarding the time required for carbon starvation to occur. Likewise, this analysis points to the need to understand interactions with biotic mortality agents and within-species variation in Ψ of zero G_s (isohydric) and Ψ_{crit} (anisohydric); such variation is known to occur in response to tree height (Yoder *et al.*, 1994; McDowell *et al.*, 2002a; Barnard & Ryan, 2003) or soil texture (Hacke *et al.*, 2000), and may occur in other situations. However, variation in these variables is likely to move species timing of mortality only slightly relative to the larger general pattern of mortality shown in Fig. 12. The patterns in Fig. 12 support the concept that isohydric species are more likely to die of carbon starvation than hydraulic failure, and that partitioning of mortality between isohydric and anishydric plants is a function of drought intensity and duration (Figs 3 and 10).

Drought may also reduce photosynthesis by other mechanisms, such as loss of leaf turgor (Dreyer *et al.*, 1992; Rodriguez *et al.*, 1993; Kolb & Sperry, 1999) and leaf shedding (Tyree *et al.*, 1993 and citations mentioned earlier). When elevated temperatures accompany drought (Breshears *et al.*, 2005), a nonhydraulic mechanism of reduced photosynthesis may result from the impact of temperature on photosynthetic optima, both on electron transport and Rubisco activity (Berry & Bjorkman, 1980; Sage & Kubien, 2007). For our case study, juniper has a higher temperature optima for peak photosynthesis (21 vs 17°C) and a broader temperature range above which 90% of maximum photosynthesis is sustained (16.5 vs 14.2°C) than does piñon (Barnes, 1986). Adaptation of the biochemical machinery driving photosynthesis to rising temperatures may occur if the temperature rise is consistent and slow, but will be insufficient if temperature extremes happen rapidly and infrequently. Temperature impacts on photosynthesis occur in broadleaf species that have high interception of solar radiation, and may possibly occur in needleleaf species during periods of low wind speed and high radiative load (Kolb & Robberecht, 1996; Martin *et al.*, 1999). Atmospheric conditions that promote high leaf temperatures in needleleaf species are not frequent; however, just a single day of lethal conditions could severely impede future photosynthesis if there are no stored carbohydrates for use in repair of the photosynthetic apparatus, such as during a severe drought. Mesophyll conductance to CO_2 also shows temperature optima, and therefore may also be a constraint on photosynthesis under temperature extremes (Diaz-Espejo *et al.*, 2007).

In addition to reductions in carbon uptake there are increases in carbon use for maintenance respiration and perhaps belowground root production during drought. Carbon allocation to maintenance respiration may increase as a result of elevated temperatures of foliage, sapwood and roots (Amthor, 2000), although acclimation to temperature and drought may occur that would minimize this effect (Bryla *et al.*, 1997; King *et al.*, 2006). During relatively mild droughts, allocation to roots and sapwood may increase to maintain adequate K_l if there are carbohydrates available (Gower *et al.*, 1994; Cinnirella *et al.*, 2002; Kozlowski & Pallardy, 2002).

Carbon starvation may facilitate mortality from biotic agents (Fig. 3) when carbon starvation and the population abundance of these agents are synchronous (Schoeneweiss, 1981; Marçais & Bréda, 2007). This synchrony is mediated by the degree of water stress imposed on the trees. The growth-differentiation balance hypothesis (Herms & Mattson, 1992; Reeve *et al.*, 1995; Stamp, 2003; Fine *et al.*, 2006) predicts a

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curvilinear relationship between water stress and carbon allocation to resin because moderate water stress impacts photosynthesis slightly but shifts carbon allocation from growth to storage and defensive chemicals. This shift in carbon allocation results in greater resin flow from phloem wounds in moderately stressed compared with nonstressed trees (Lorio, 1986; Dunn & Lorio, 1993). However, severe droughts cause a cessation of carbon allocation to all sinks, including resin defense, when photosynthetic carbon gain is near zero (Christiansen *et al.*, 1987; Waring, 1987; Herms & Mattson, 1992; Lewinsohn *et al.*, 1993; Reeve *et al.*, 1995; Stamp, 2003). Consistent with the carbon-starvation hypothesis, ponderosa pine (*Pinus ponderosa*) resin flow decreases with stresses that reduce radial growth (Kolb *et al.*, 1998; McDowell *et al.*, 2007). Drought duration is important because stored carbohydrates may temporarily buffer effects on carbon allocation to resin (consistent with Fig. 10). Studies examining carbohydrate content of tissues in relation to drought and mortality are consistent with the idea that reduced carbon storage is associated with susceptibility to biotic mortality agents (Marçais & Bréda, 2007).

Carbon starvation may also facilitate biotic attack via changes in the release of volatile attractants or changes in the quality of forage for biotic agents. The production of ethanol and other volatiles changes during drought in order to preserve cellular function (Kimmerer & Kozlowski, 1982; Tadege *et al.*, 1999) and perhaps as a byproduct of increased tissue temperatures associated with reduced transpiration (Hietz *et al.*, 2005). Such increases in volatile emissions may be used by insects to locate stressed plants (Kelsey, 2001; Kelsey & Joseph, 2003; Manter & Kelsey, 2008). The composition of defensive compounds within plant tissues may also shift during drought, though little conclusive evidence yet exists (Tognetti *et al.*, 1997; Thoss & Byers, 2006). Host palatability may improve or decline during drought, depending in part on soil nutrient availability (Price, 1991; Waring & Cobb, 1992; Warren *et al.*, 1999; Erbilgin & Raffa, 2000; Campo & Dirzo, 2003; Rieske *et al.*, 2003; Hui & Jin, 2004) and phloem thickness (Amman, 1972; Haack *et al.*, 1984; Amman & Pasek, 1986). Lastly, predisposition to biotic agents from carbon starvation may feed back to hydraulic failure as the proximal cause of mortality. For many pine species, bark beetles attack stressed trees and inoculate them with fungi that occludes the xylem, functionally halting transpiration (Larsson *et al.*, 1983; Waring & Pitman, 1985; Lorio, 1986; Christiansen *et al.*, 1987). It remains an open question whether hydraulic failure or carbon starvation *per se* leads to mortality in these cases (Wullschleger *et al.*, 2004).

VI. Implications of future climate on hypothesized mortality mechanisms

The hypothesized mechanisms of mortality presented in previous sections and their relationships to intensity and duration of water stress have key implications for how tree mortality may occur in response to global climate change. Climate models generally agree that over the next 50 yr the Earth's surface temperatures will increase along with shifts in precipitation that result in greater drought severity and frequency (Cook *et al.*, 2004; IPCC, 2007; Seager *et al.*, 2007). Thus, the recent drought-related mortality events that have been observed worldwide (Suarez *et al.*, 2004; Breshears *et al.*, 2005; Ciais *et al.*, 2005; Jurskis, 2005; Breda *et al.*, 2006; Gitlin *et al.*, 2006; Allen & Breshears, 2007) have the potential to become more frequent and exert an impact on larger areas (Jentsch *et al.*, 2007). Warmer air temperature will exacerbate the impact of drought on plant water loss by elevating the vapor pressure deficit of the atmosphere (D), thereby placing a greater demand on transpiration, as evident in the basic relationship:

$$E = G_s \times D \qquad \text{Eqn 3}$$

with D being a function of relative humidity and temperature. An increase in temperature will raise D, and hence E, thus forcing isohydric and anisohydric plants closer towards their respective mechanisms of mortality. For example, from Eqn 3 we can predict that a rise in the Earth's surface temperature of 1.1–6.4°C (IPCC, 2007) will result in a 7–48% increase in D and E if G_s remains constant. For isohydric species, G_s will decline to hold E below E_{crit}, pushing them closer towards carbon starvation. For anisohydric species, failure to sufficiently reduce G_s in response to rising D will push them closer towards Ψ_{crit}. Increased D will also exacerbate drought by increasing evaporative losses of water from canopy and soil surfaces, and altered net radiation associated with climate change could also increase E (e.g. via the Penman–Monteith relationship on leaf temperature, Monteith & Unsworth, 1990). Rising surface temperatures could also facilitate carbon losses to maintenance respiration as a result of the exponential dependency of respiration on temperature (Amthor, 2000) if temperature acclimation does not keep up with temperature changes (Ciais *et al.*, 2005; King *et al.*, 2006), effectively reducing the time plants may survive on stored carbohydrates. Therefore, increased intensity and duration of future droughts will increase rates of mortality by either hydraulic failure or carbon starvation.

A logical hypothesis is that the increased droughts predicted to occur over the next century will initially result in increased mortality of isohydric species because these species have shown greater susceptibility to drought. However, droughts of sufficient intensity could push anisohydric species past their threshold for hydraulic failure (e.g. Fig. 10). These hypotheses can be shown via a modeling exercise using the piñon–juniper case study (Fig. 13). We predicted leaf carbon gain in the same manner as for Fig. 11(b) and hydraulic failure with a Ψ_{leaf} for zero G_s set to –2.5 MPa for piñon and Ψ_{crit} of 100% cavitation set to –6.9 MPa for juniper (West

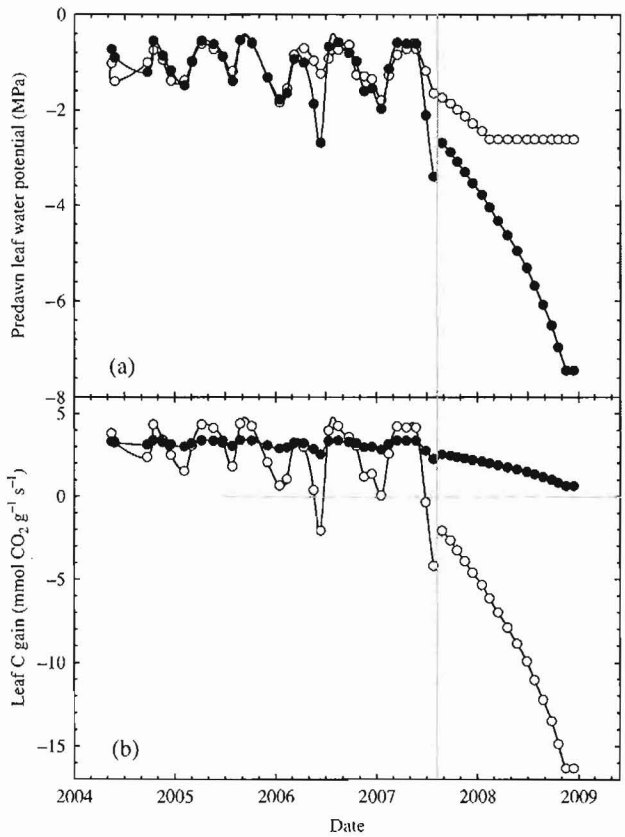

Fig. 13 (a) To the left of the gray bar are 3 yr of monthly observations of predawn water potential for piñon (open circles) and juniper (closed circles) as from Fig. 11(a), and to the right of the gray baris a simulation of the water potential response to a severe drought. A description of the simulation is given in the text. (b) Seasonal leaf carbon gain modeled as per Fig. 11(b) using values of juniper predawn water potential as observed between 2004 and 2007 (left of gray bar) or simulated for 2007–2009 (right of gray bar).

et al., 2008), using predawn water potentials for 2004–2007 from Mesita del Buey as a starting point. We assumed a 3 yr, 50% reduction in rainfall, as occurred in 2000–2002, (Breshears *et al.*, 2005) and a conservative 7% increase in evaporative losses resulting from a D increase associated with a 1.1°C surface temperature increase (IPCC, 2007). Under this scenario, predawn water potential reached Ψ of zero G_s and Ψ_{crit} in 7 and 15 months, respectively (Fig. 13a). Piñon never achieved a positive carbon balance during the simulated drought because the starting Ψ value was already below the zero carbon balance point, whereas juniper maintained a positive carbon gain until Ψ_{crit} was reached (Fig. 13b). This simple exercise assumes no physiological acclimation, but is conservative relative to climate predictions for the next century (IPCC, 2007; Seager *et al.*, 2007).

It is less clear what the impact of an increased frequency of droughts, or increased climatic variability (IPCC, 2007), will be on mortality. Climatic variability in association with decadal and multidecadal Pacific and Atlantic Ocean oscillations certainly has large impacts on vegetation mortality (Swetnam & Betancourt, 1998; McCabe *et al.*, 2004). However, it is difficult to predict a generalized response to climate oscillations because there is a lack of consistency between observations and predictions of mortality response to climate oscillations. According to the hydraulic framework, nonlethal droughts should promote drought resilience, or ability to survive droughts. This is because plants typically respond to nonlethal drought by acclimation of key hydraulic parameters from Eqn 2 such as leaf area (reductions), root and sapwood area (increases), and cavitation resistance (increases), which should bolster trees against future droughts (Cinnirella *et al.*, 2002; Holste *et al.*, 2006). However, some field observations have shown that trees that die are predisposed to death by a prior drought period. This may depend on species and edaphic circumstances. Some species have shown increased cavitation susceptibility after exposure to drought (Hacke *et al.*, 2001) or a feedback spiral of reduced carbon gain leading to reduced growth and subsequent inability to fight off pathogens or insects in later droughts (Pedersen, 1998). In contrast to dry periods, the hydraulic framework predicts that particularly wet periods will promote susceptibility to future drought via increased growth of leaf area and reduced growth of roots and sapwood, resulting in trees that have high ratios of hydraulic demand (leaf area) to supply (root area) (e.g. Eqn 2; McDowell *et al.*, 2006). This is consistent with the observation of increased mortality in fast-growing compared with slow-growing oak trees (Jenkins & Pallardy, 1995, T. Levanič & N. McDowell, unpublished data). Likewise, this may in part explain the high mortality rates in 1996 and 2002 for piñon pine because southwestern USA experienced above-normal precipitation between the late 1970s and early 1990s (Breshears *et al.*, 2005).

Climate change-driven drought will also increase tree mortality via wildfires, both directly through combustion and, more pertinent to this review, indirectly via structural damage that predisposes trees to biotic attack (McHugh & Kolb, 2003; Sieg *et al.*, 2006). Wildfire extent and severity are strongly influenced by regional temperature and global climate systems such as the El Niño-Southern Oscillation, and are expected to increase with climate change (Swetnam & Betancourt, 1998; Westerling *et al.*, 2006). Trees are killed by fire when exposed to temperatures greater than 60°C, and death of remaining above-ground tissues occurs as a result of disruption of water and carbohydrate transport when heat damages phloem and xylem (Ducrey *et al.*, 1996). For trees that survive, fire reduces whole-tree leaf area and subsequent photosynthesis and carbon allocation to insect defenses (Wallin *et al.*, 2003) and may increase olfactory signals (Kelsey & Joseph, 2003), leading to preferential attack from biotic agents such as bark beetles (Bradley & Tueller, 2001; McHugh & Kolb, 2003; Parker *et al.*, 2006; Perrakis & Agee,

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2006). Mortality of fire-damaged trees with low resin defenses caused by bark beetle attacks is likely a consequence of carbon starvation in which the source of low carbon reserves is defoliation from drought-associated fire, rather than from prolonged stomatal closure. Future fires will preferentially shift the landscape towards species that can resprout or quickly recolonize.

VII. Conclusions

The hydraulic framework allows quantitatively informed analyses of the mechanisms of mortality. Hydraulically mediated carbon starvation, and subsequent predisposition to attack from biotic mortality agents, is a likely cause of mortality in isohydric species because of their large margins of hydraulic safety. Mortality of isohydric species is particularly likely during prolonged droughts of intermediate intensity. This conclusion is consistent with prior theoretical modeling exercises and empirical results. Hydraulic failure is a potential cause of mortality in plants with isohydric constrained hydraulic conductance, such as particularly tall trees with a long hydraulic pathlength or plants with small rooting volumes such as seedlings. Ironically, the relatively drought-tolerant anisohydric species are more likely to die from hydraulic failure than carbon starvation because they maintain a thin margin of hydraulic safety. Mortality of anisohydric species is particularly likely during intense droughts. Demographics of biotic mortality agents may interact with carbon starvation or hydraulic failure to facilitate mortality because periods of drought are generally favorable to increased abundance of insects and pathogens. Mortality in the absence of drought should occur at low rates because some trees may suffer from carbon limitation even during wet climatic periods as a result of prior injury (e.g. from drought or mechanical impact) and the eventual exposure to the ever-present population of biotic mortality agents.

We hypothesize that future droughts will kill isohydric species first via carbon starvation and subsequent predisposition to insect and pathogen attacks, and will result in mortality of anisohydric species only if hydraulic failure is reached as a result of particularly intense droughts, prolonged drought duration, or in cases of edaphic (e.g. soil) or size (i.e. seedling and trees at maximum height) related constraints on hydraulic conductance (Figs 10 and 12). Preferential mortality of isohydric species may have large demographic impacts through a reduction in seed sources, shifting the landscape towards anisohydric species (Mueller *et al.*, 2005). The potential for long-term changes to regional vegetation composition is significant, supporting the need for biogeochemistry and climate models to continue refinement of dynamic vegetation simulations (Neilson *et al.*, 2005; Bonan & Levis, 2006; Scholze *et al.*, 2006). These demographic implications may be exacerbated by shifts in the ranges of biotic mortality agents associated with climate change (Simberloff, 2000). The greater likelihood of extreme climate events during this century, as many climate models predict, together with chronic climate warming will most likely lead to increased vegetation mortality and declining forest cover in many regions. Isohydric and anisohydric regulation of leaf water potential may partition species survival and mortality, and may be an effective approach to modeling plant survival and mortality under future climate conditions.

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