



## Tansley review

# The role of height-driven constraints and compensations on tree vulnerability to drought

Author for correspondence:  
Laura Fernández-de-Uña  
Email: [laura.fernandezdeuna@gmail.com](mailto:laura.fernandezdeuna@gmail.com)

Received: 13 March 2023  
Accepted: 7 June 2023

Laura Fernández-de-Uña<sup>1,2</sup> , Jordi Martínez-Vilalta<sup>1,3</sup> ,  
Rafael Poyatos<sup>1,3</sup> , Maurizio Mencuccini<sup>1,4</sup> and Nate G. McDowell<sup>2,5</sup>

<sup>1</sup>CREAF, Bellaterra (Cerdanyola del Vallès), Catalonia, 08193, Spain; <sup>2</sup>Pacific Northwest National Laboratory, Richland, WA 99354, USA; <sup>3</sup>Universitat Autònoma de Barcelona, Bellaterra (Cerdanyola del Vallès), Catalonia, 08193, Spain; <sup>4</sup>ICREA, Barcelona, 08010, Spain; <sup>5</sup>School of Biological Sciences, Washington State University, Pullman, WA 99164, USA

## Contents

Summary	2083	IV. Conclusions	2093
I. Introduction	2083	Acknowledgements	2094
II. Physiological shifts with height and drought	2084	References	2094
III. Potential implications of tree height on vulnerability to drought-induced mortality	2091		

*New Phytologist* (2023) **239**: 2083–2098  
doi: 10.1111/nph.19130

**Key words:** drought vulnerability, functional adjustments, hydraulic limitations, structural adjustments, tree height, tree size.

## Summary

Frequent observations of higher mortality in larger trees than in smaller ones during droughts have sparked an increasing interest in size-dependent drought-induced mortality. However, the underlying physiological mechanisms are not well understood, with height-associated hydraulic constraints often being implied as the potential mechanism driving increased drought vulnerability. We performed a quantitative synthesis on how key traits that drive plant water and carbon economy change with tree height within species and assessed the implications that the different constraints and compensations may have on the interacting mechanisms (hydraulic failure, carbon starvation and/or biotic-agent attacks) affecting tree vulnerability to drought. While xylem tension increases with tree height, taller trees present a range of structural and functional adjustments, including more efficient water use and transport and greater water uptake and storage capacity, that mitigate the path-length-associated drop in water potential. These adaptations allow taller trees to withstand episodic water stress. Conclusive evidence for height-dependent increased vulnerability to hydraulic failure and carbon starvation, and their coupling to defence mechanisms and pest and pathogen dynamics, is still lacking. Further research is needed, particularly at the intraspecific level, to ascertain the specific conditions and thresholds above which height hinders tree survival under drought.

## I. Introduction

Large trees play crucial roles in forest ecosystems, providing food and shelter for numerous forest-dwelling species, accumulating large amounts of carbon, redistributing nutrients and modulating the water cycle through their effect on evapotranspiration and

rainfall interception (Lindenmayer & Laurance, 2016; Gora & Esquivel-Muelbert, 2021). Global environmental change processes, such as increasing drought severity and vapour pressure deficit (VPD), can gravely threaten tree survival (Williams *et al.*, 2013). Due to differences in resource acquisition, regulation and use, tree size (diameter or height) can affect a tree's chances of

survival under stress. Larger trees frequently show higher mortality rates under drought (Bennett *et al.*, 2015; Stovall *et al.*, 2019); however, the opposite pattern has often been observed (Galiano *et al.*, 2010; Bennett *et al.*, 2015; Crouchet *et al.*, 2019; Fettig *et al.*, 2019; Stephenson *et al.*, 2019; Hajek *et al.*, 2022), hindering the determination of the mechanisms resulting in size-dependent drought-induced mortality. Because of their value to biodiversity and biogeochemical cycles, the loss of large trees is of particular concern under a warming climate in which droughts are becoming more severe and potentially driving greater size-dependent mortality (McDowell & Allen, 2015; Lindenmayer & Laurance, 2016; Gora & Esquivel-Muelbert, 2021).

The mechanisms behind size-dependent drought vulnerability are largely speculative and may vary across species and ecosystems (Bennett *et al.*, 2015; Hember *et al.*, 2017; Stephenson & Das, 2020), as well as a function of drought severity (da Costa *et al.*, 2010; Meir *et al.*, 2018; Stovall *et al.*, 2019). Because taller trees are expected to have greater constraints to hydraulic function and carbon uptake, it has been suggested that they may have a smaller margin for survival under water stress (McDowell & Allen, 2015). Drought-induced mortality of large trees is often attributed to these height-related hydraulic constraints (e.g. Bennett *et al.*, 2015); however, tree size in demographic studies is usually determined by tree diameter rather than height (da Costa *et al.*, 2010; Bennett *et al.*, 2015). While there exists a relationship between these two size measures, this is generally asymptotic and species and site dependent owing to differences in, for example, tree morphology or climatic conditions. Moreover, size-dependent mortality patterns have often been assessed at the community level (Bennett *et al.*, 2015; Stovall *et al.*, 2019), confounding size and species effects on mortality during drought (Stephenson & Das, 2020). In cases where insect attacks are associated with drought mortality, species-specific, size-dependent mortality rates frequently follow insect colonization rates (Fettig *et al.*, 2019; Stephenson *et al.*, 2019), with host preferences and reduced resource allocation to defence becoming interdependent (Guérard *et al.*, 2007; Gaylord *et al.*, 2013; Kolb *et al.*, 2016; McDowell *et al.*, 2022), thus hindering the determination of the relative contribution of predisposing physiological mechanisms on drought-related mortality. Furthermore, trait responses to drought have mostly been studied at the interspecific or interpopulation levels, generally neglecting the effect of intraspecific variability associated to tree diameter or height (Trugman *et al.*, 2021).

To bridge the gaps between the theory and existing evidence regarding the drivers and mechanisms of size-related drought vulnerability, we performed a quantitative synthesis of the existing data regarding physiological and structural changes as a function of tree height and then interpreted these patterns in relation to the expectations of drought impacts on plant function and survival. We adopted a reference hydraulic framework and focused on the effect of height (i.e. tall vs short trees), rather than diameter, because large tree drought vulnerability has often been associated to height-related hydraulic constraints (e.g. Bennett *et al.*, 2015). Nonetheless, we occasionally refer to studies evaluating traits as a function of tree diameter (i.e. large vs small trees) when height data were scarce or missing, under the assumption that, for a specific

ecosystem, the largest trees would also be the tallest. Unlike previous efforts (e.g. Liu *et al.*, 2019), we focused on studies analysing the effect of height on different trees or tree height categories of the same species within the same site (Supporting Information Table S1) to avoid species or site confounding effects. We further separated the inter- and intraspecific patterns in height-driven trait variation through the analyses performed (see Methods S1 for a detailed description of paper selection and data analyses). Likewise, we focused on mature trees to minimize the confounding effect of trait changes during early development and resource allocation to reproduction (Thomas, 2011). We also reviewed patterns within the vertical profile of individual trees, as well as patterns across species, in focal cases.

## II. Physiological shifts with height and drought

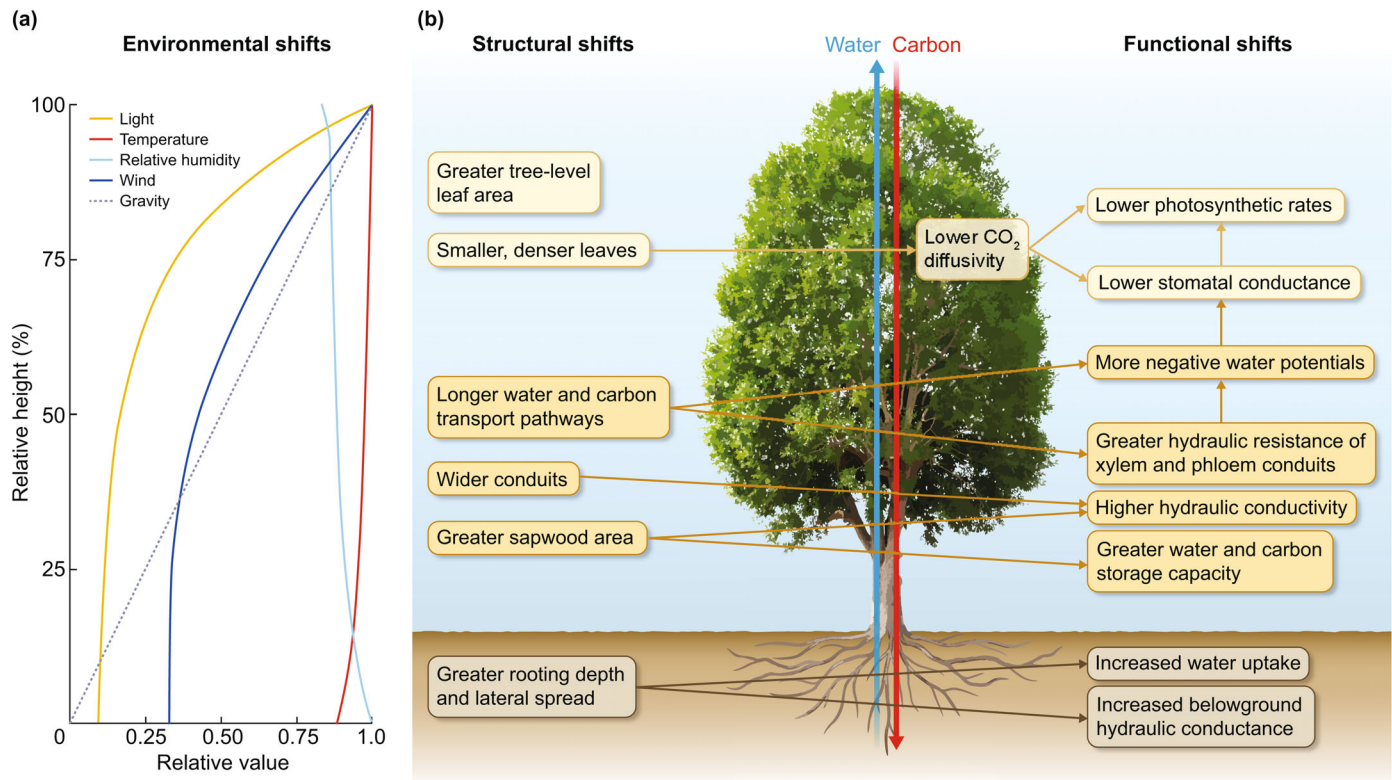
Plants use a variety of mechanisms to cope with drought. Stomatal closure during drought regulates leaf water potential ( $\Psi_{\text{leaf}}$ ) and the associated risk of embolism. This reduces the likelihood of hydraulic failure, or irreversible and complete loss of hydraulic conductance, and subsequent permanent dehydration of distal tissues (McDowell *et al.*, 2002a,b). Simultaneously, reduced photosynthesis induced by stomatal closure may also decrease carbon availability to maintain metabolic and hydraulic function (e.g. through osmoregulation; McDowell, 2011; Tomasella *et al.*, 2020; McDowell *et al.*, 2022) and to defend against pathogen and pest attacks (McDowell, 2011; Gaylord *et al.*, 2013; Netherer *et al.*, 2015), which may, in turn, exacerbate hydraulic failure and/or carbon starvation processes under drought (McDowell, 2011).

While trees of different heights all have risk of mortality via hydraulic failure and/or carbon starvation, these risks may be aggravated in tall trees that must withstand a harsher climate in the canopy (Fig. 1a) and large structural challenges to balance increasing demands for mechanical strength and hydraulic function (Fig. 1b; King, 2011). Within closed-canopy forests, taller trees tend to experience more extreme temperatures (but see McGregor *et al.*, 2021) and higher light levels, VPD, wind speeds and lightning exposure than shorter-statured trees (Fig. 1a; Phillips *et al.*, 2001; Ambrose *et al.*, 2016; Gora & Esquivel-Muelbert, 2021; McGregor *et al.*, 2021). Height growth also comes with an associated increase in the hydrostatic gradient due to gravity ( $-0.01 \text{ MPa m}^{-1}$ ) and hydraulic resistance due to the longer path and increased number of internodes and conduit connections water must cross (Mencuccini, 2003). In turn, this can intensify canopy water stress, inducing stomatal closure and limiting photosynthesis in taller trees (Ryan *et al.*, 2006).

These height-related limitations result in theoretical predictions that taller trees should be more vulnerable to drought events than shorter ones (McDowell & Allen, 2015). A plant hydraulic corollary to Darcy's law can be formulated as:

$$\Psi_{\text{leaf}} \approx \Psi_{\text{soil}} - \frac{G_s \cdot A_l \cdot \text{Height} \cdot \text{VPD}}{A_s \cdot K_s} \quad \text{Eqn 1}$$

where  $\Psi_{\text{soil}}$  is soil water potential,  $G_s$  is crown-scale conductance to water vapour,  $K_s$  is whole-tree sapwood-specific hydraulic



**Fig. 1** Expected changes in environmental factors (a) and structural and functional traits (b) with tree height. (a) Simulated environmental changes with height in a forest between the soil and the top of the canopy of the tallest trees in relative units, with temperatures becoming more extreme with height (i.e. warmer during the day and colder during the night). (b) Feedbacks expected to occur among structural and functional shifts as a result of the mechanical and hydraulic constraints imposed by increasing height as trees grow. In addition to increases in tree-level leaf, sapwood and root area and biomass, changes in the relative carbon investment to each organ, thus in the ratios between these traits (e.g. leaf : sapwood or leaf : root area ratios) are expected to occur as trees grow taller, causing additional shifts in tree-level hydraulic performance.

conductivity, and  $A_l : A_s$  is the whole-tree leaf : sapwood area ratio (Whitehead *et al.*, 1984). Predictions using Darcy's law suggest that, without concomitant changes in other traits, taller individuals will either suffer stronger declines in  $\Psi_{\text{leaf}}$  (Fig. 2a) or require greater adjustments in  $G_s$  (McDowell & Allen, 2015) than shorter trees with rising VPD or dropping  $\Psi_{\text{soil}}$ . This would theoretically increase their likelihood of suffering drought-induced hydraulic failure (through dropping  $\Psi_{\text{leaf}}$ ) or carbon starvation (through decreasing  $G_s$ ) under climate change. However, compensating shifts, such as increasing  $K_s$  or decreasing  $A_l : A_s$  or  $G_s$ , may mitigate the drop in  $\Psi_{\text{leaf}}$  with height (Fig. 2b). The net impact of tree height increase on hydraulic- and carbon-safety margins thus results from the balance between limiting and compensating mechanisms.

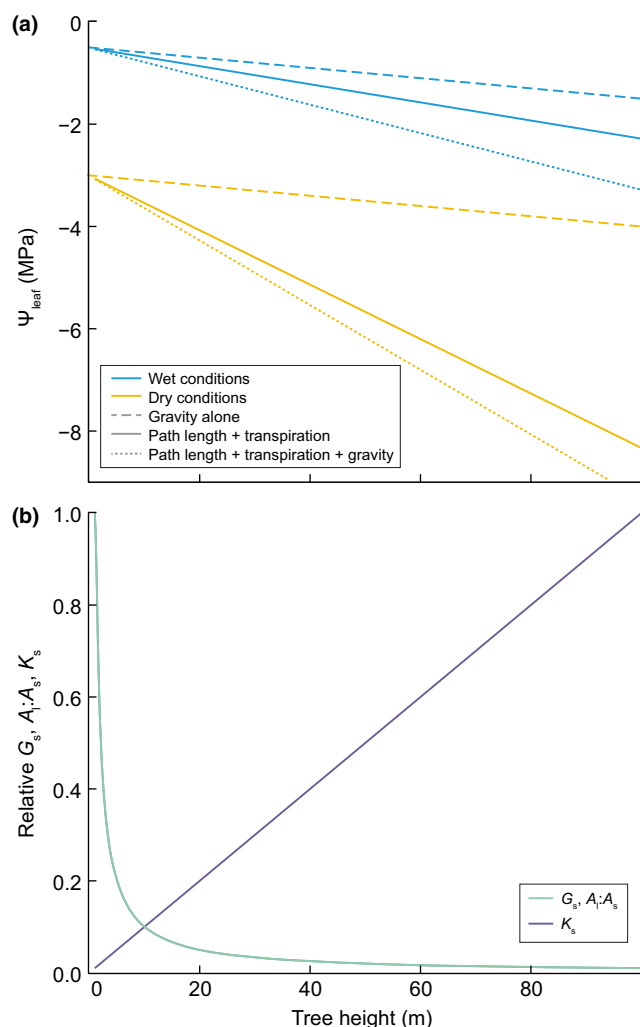
## 1. Canopy and stomatal conductance to water vapour

Our quantitative synthesis shows that both canopy ( $G_s$ ; Fig. 3a) and leaf-level stomatal conductance to water vapour (per leaf area,  $g_s$ ; Figs 3b, S2; Table S2, and per leaf mass,  $g_{s \text{ mass}}$ , Fig. S2; Table S2) generally decrease with increasing tree height within a species. However, this reduction was only significant for  $g_s$  when upper-crown, sun-exposed leaves were measured across tree heights (Fig. S3; Table S3), with the relationship becoming not significant

when all data (sun-exposed and shaded leaves) were analysed, as some studies have found no changes with height (Grulke & Retzlaff, 2001; Ambrose *et al.*, 2016; Miyata & Kohyama, 2016) and even increases in tropical (Phillips *et al.*, 2001) and temperate (Dawson, 1996) angiosperm species. In addition, daily  $g_s$  dynamics tend to show an earlier stomatal closure in taller trees compared with shorter conspecifics (Yoder *et al.*, 1994).

## 2. Hydraulic conductivity and conductance

In contrast to the short-term adjustments in  $G_s$ , tree hydraulic architecture, which significantly influences hydraulic conductivity, can require years to adjust to height constraints. Stem and branch tracheid and vessel sizes increase tip-to-bottom along the stem (Fig. 4a). Smaller conduits near the top of the tree are predicted to occur because they have less distal foliage to provide water to, reducing carbon costs, whereas larger conduits towards the base reduce the cumulative flow resistance, thus optimizing water transport along the xylem network (Olson *et al.*, 2018; Koçillari *et al.*, 2021). Concurrently with conduit diameter, there also exists an increase in conduit length (Schulte, 2012; Lazzarin *et al.*, 2016), the number and size of conduit pits (Burgess *et al.*, 2006; Schulte, 2012; Lazzarin *et al.*, 2016) and sapwood area along the trunk (Dean & Long, 1986; James *et al.*, 2003). Conversely, the



**Fig. 2** (a) Predicted changes in leaf water potentials ( $\Psi_{\text{leaf}}$ ) with tree height under wet (VPD = 1 kPa,  $\Psi_{\text{soil}} = -0.5$  MPa) and dry (VPD = 3 kPa,  $\Psi_{\text{soil}} = -3$  MPa) conditions using Darcy's law (Eqn 1) with and without accounting for the hydrostatic gradient (i.e. gravity); all traits except VPD and  $\Psi_{\text{soil}}$  held static. (b) Adjustments needed in canopy-scale water vapour conductance ( $G_s$ ), leaf : sapwood area ratio ( $A_l : A_s$ ) or sapwood-specific hydraulic conductivity ( $K_s$ ) to keep  $\Psi_{\text{leaf}}$  constant as height increases; every other trait held static.

number of conduits per sapwood area increases towards the tip, which partially offsets the effect of decreasing conduit size and increasing path length on hydraulic conductivity (Savage *et al.*, 2010; Pfautsch *et al.*, 2018; Prendin *et al.*, 2018).

The within-tree conduit widening generally translates into larger conduits at a given height in taller than in shorter trees (Olson *et al.*, 2018; Williams *et al.*, 2019). In addition, taller angiosperm trees often have wider conduits at the top (Olson *et al.*, 2014). Consequently, upper-crown branch sapwood- ( $K_s$ ) and leaf-specific ( $K_l$ ) hydraulic conductivity tend to increase with tree height, particularly in angiosperms (Figs 3c,d, S2), although some instances have found them to decrease (in tropical savanna trees; Zhang *et al.*, 2009) or remain unchanged (Phillips *et al.*, 2001; Ambrose *et al.*, 2009; Domec *et al.*, 2012), rendering the effect of height on  $K_s$  nonsignificant at the intraspecific level (Fig. 3c;

Table S2). Similarly, the stem (Domec & Gartner, 2003; Mokany *et al.*, 2003; Domec *et al.*, 2005, 2012) and roots (Domec *et al.*, 2004) of taller trees have been reported to be more efficient in transporting water than those of shorter conspecifics. These changes in xylem conductivity are, however, not strong enough to offset the effect of increasing hydraulic path length on whole-tree leaf-specific hydraulic conductance ( $k_l$ ), which significantly decreases with height within species (Figs 3e, S2; Table S2). Most of this decrease in  $k_l$  has been estimated to result from increasing friction with path length rather than gravity (Hubbard *et al.*, 1999), as suggested by the modest differences in the response to height in  $k_l$  calculated with and without accounting for the hydrostatic gradient (Fig. 3e; Table S2).

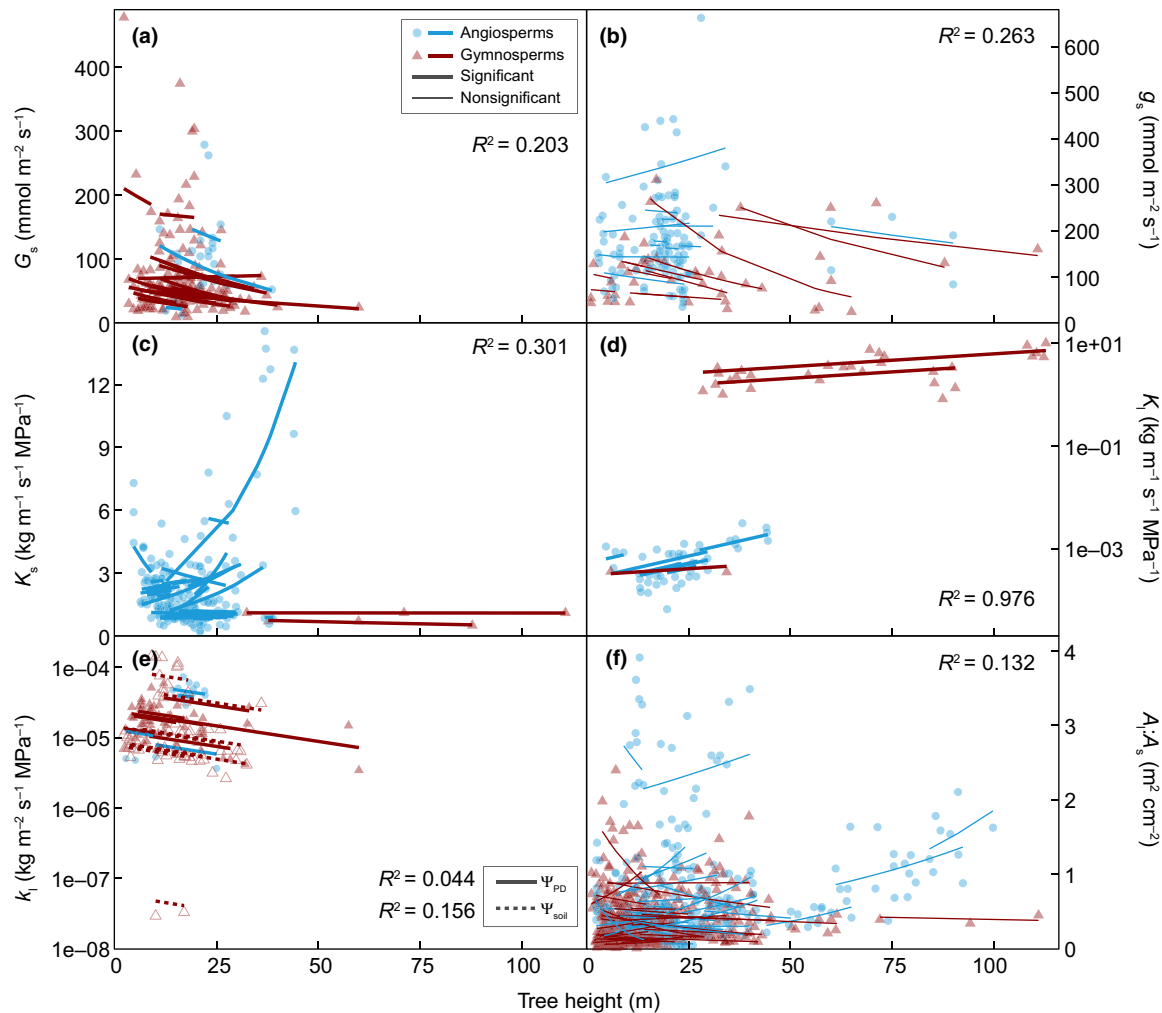
### 3. Leaf : sapwood area ratio

Trees may minimize the path-length-associated hydraulic constraints on canopy gas exchange by increasing resource allocation to sapwood (i.e. conductive) area relative to leaf area, thus reducing the leaf : sapwood area ratio ( $A_l : A_s$ ; Fig. 2b). Tree  $A_l : A_s$  has often been shown to decrease with increasing tree height (McDowell *et al.*, 2002a); however, exceptions to this pattern have been found in both conifer (Dean & Long, 1986; Domec *et al.*, 2012) and angiosperm species, particularly in tropical rainforests and temperate *Eucalyptus* and *Quercus* spp. (Mokany *et al.*, 2003; Phillips *et al.*, 2003a; Calvo-Alvarado *et al.*, 2008; Koch *et al.*, 2015), rendering the overall relationship with height nonsignificant, both within and across species (Figs 3f, S2; Table S2). An increase in  $A_l : A_s$  is expected to intensify height-associated hydraulic constraints, causing further reductions in  $G_s$  and  $k_l$  unless  $K_s$  increases proportionally more than  $A_l : A_s$  (Phillips *et al.*, 2003a; Domec *et al.*, 2012). Top branch and shoot  $A_l : A_s$  generally decrease (Ambrose *et al.*, 2009) or remain unchanged (Ambrose *et al.*, 2009; Osada *et al.*, 2014) with height in conspecific trees. Similarly, within a tree, branch  $A_l : A_s$  decreases (Hubbard *et al.*, 2002; Burgess *et al.*, 2006) or remains unchanged (Ambrose *et al.*, 2016) with height (Fig. 4b), which, together with decreases in trunk  $A_l : A_s$  (Domec *et al.*, 2005; Pfautsch *et al.*, 2018), could partially compensate for the effect of increasing path length on hydraulic resistance, maintaining and even increasing  $k_l$  along the stem (Fig. S2). Conversely, interspecific meta-analyses comparing top-branch  $A_l : A_s$  and species maximum height have observed an increase in this trait with height (Liu *et al.*, 2019; Mencuccini *et al.*, 2019). This suggests that height-related changes in  $A_l : A_s$  vary across scales (within tree, within species, across tree compartments and across species). The highly species-specific responses in whole-tree  $A_l : A_s$  (Fig. 3f) may thus indicate that shifts in  $G_s$  and  $K_s$  play a more consistent role in regulating changes in  $\Psi_{\text{leaf}}$  as trees grow (Fig. 2).

### 4. Leaf water potential and hydraulic safety

Predawn ( $\Psi_{\text{PD}}$ ) and particularly midday ( $\Psi_{\text{MD}}$ ) water potentials are more negative in taller trees than in shorter conspecifics (Fig. 5a,b; Table S4).  $\Psi_{\text{leaf}}$  has also been reported to drop more steeply from predawn values during the day in taller than in shorter trees (Yoder

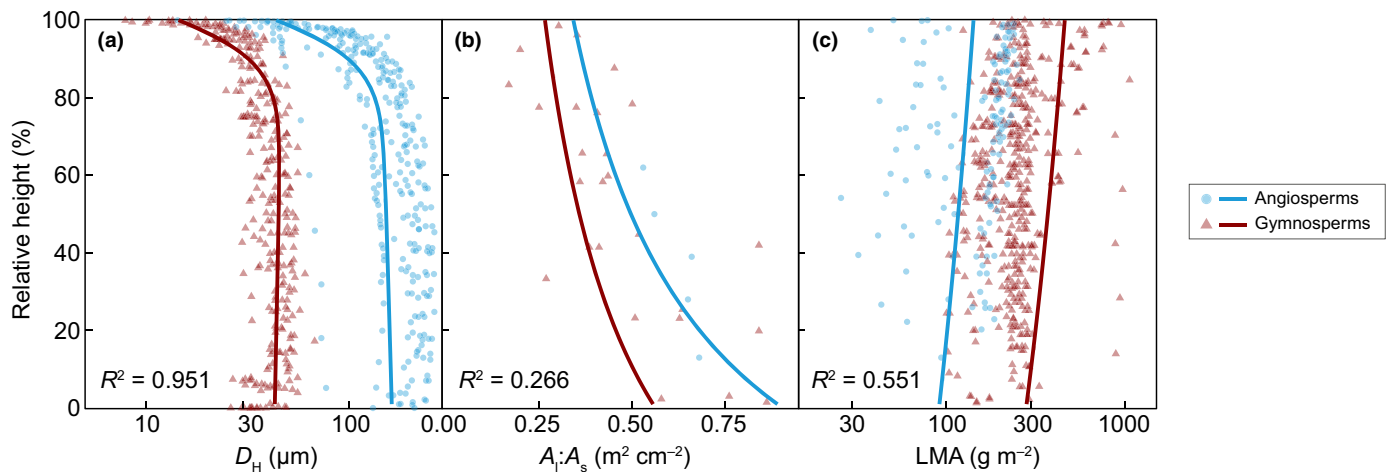




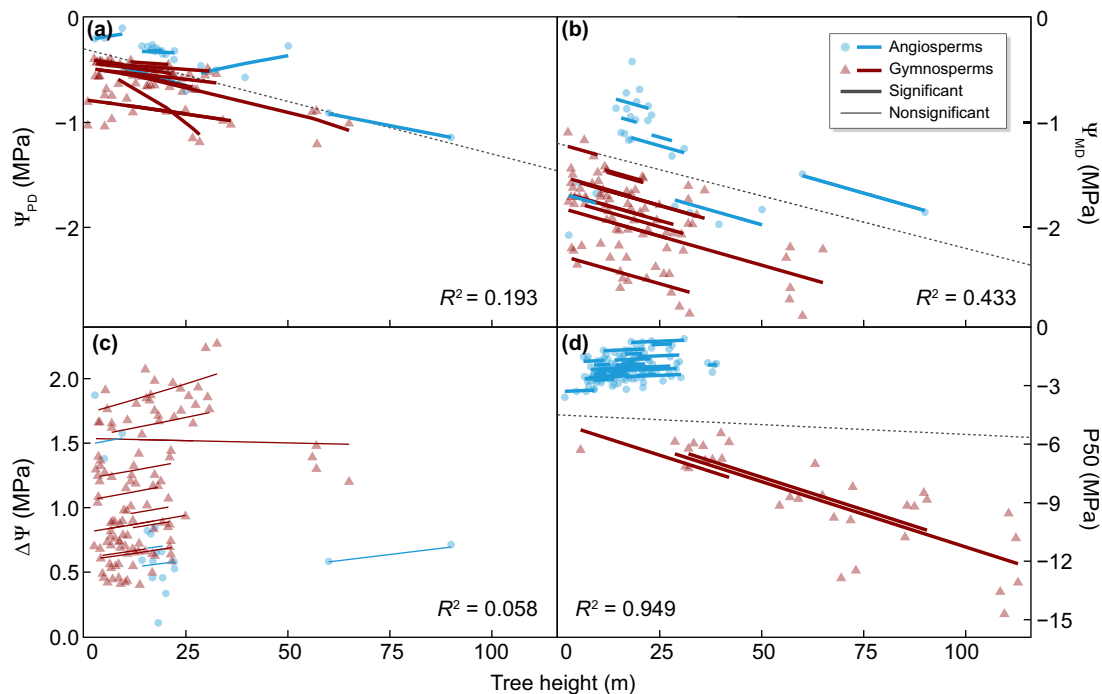
**Fig. 3** Changes with tree height per species and site in (a) tree-level canopy conductance ( $G_s$ ); (b) leaf stomatal conductance ( $g_s$ ); (c) upper-branch sapwood-specific hydraulic conductivity ( $K_s$ ); (d) upper-branch leaf-specific hydraulic conductivity ( $K_l$ ); (e) whole-tree leaf-specific hydraulic conductivity ( $k_l$ ); and (f) tree-level leaf : sapwood area ratio ( $A_1 : A_s$ ). Each point represents a tree or tree height category. Thinner lines denote nonsignificant relationships between the trait and height (see Supporting Information Table S2 for model structure and parameter values).  $R^2$  values are the variance explained by each model's fixed effects. Models were fit separately for  $k_l$  that had been calculated using predawn leaf water potentials ( $\Psi_{PD}$ ; solid symbols) and soil water potentials ( $\Psi_{soil}$ ; empty symbols). Data sources may be found in Table S1.

*et al.*, 1994; McDowell *et al.*, 2011). However, the significant declines in  $\Psi_{PD}$  and  $\Psi_{MD}$  with height disappear when the gravitational gradient ( $-0.01 \text{ MPa m}^{-1}$ ) is accounted for (Table S4). Similarly, within a tree, leaf and trunk  $\Psi$  decrease with height closely following the hydrostatic gradient (Fig. S4), although they can drop more steeply at midday under dry conditions (Ishii *et al.*, 2008). Consequently,  $\Delta\Psi$  (i.e.  $\Psi_{MD} - \Psi_{PD}$ ), which is a measure of the water-transport driving force, does not change significantly with height, neither across nor within trees or species (Figs 5c, S4; Table S4). This suggests that, while shifts in  $G_s$ ,  $K_s$  or  $A_1 : A_s$  (Figs 2b, 3) are not strong enough to offset the predicted drop in  $\Psi_{leaf}$  with height due to gravity constraints, they are largely able to compensate for increased path resistance (Fig. 2a). Additional enhancements in water uptake and storage (Dawson, 1996; Phillips *et al.*, 2003b; Domec *et al.*, 2004; Scholz *et al.*, 2011; see next section) may also increase tall-tree capacity to maintain transpiration needs without sacrificing hydraulic integrity.

The drop in  $\Psi$  with height is expected to increase embolism risk in tall trees, unless changes in hydraulic safety ensue. In upper-crown branches, the  $\Psi$  at which 50% of xylem conductivity is lost due to embolism ( $P_{50}$ ) tends to remain unchanged with height in angiosperms but becomes more negative in tall conifer trees (Fig. 5d; Table S4). This decrease has also been observed in the stems (Domec & Gartner, 2003) and roots (Domec *et al.*, 2004) of trees of different height and stems and branches within a tree (Fig. S4; Domec & Gartner, 2001; Domec *et al.*, 2005; Burgess *et al.*, 2006). On the contrary, Prendin *et al.* (2018) found that the  $P_{50}$  of *Picea abies* treetops asymptotically became less negative with height. Reductions in pit number, size and aperture and changes in the torus : pit aperture ratio, which may allow pits to resist higher water tensions (Burgess *et al.*, 2006; Domec *et al.*, 2008; Schulte, 2012; Lazzarin *et al.*, 2016), can contribute to enhance xylem capacity to withstand higher water tensions and thus embolism resistance with height, at least in gymnosperms (Fig. 5d).



**Fig. 4** Changes with height within a tree (100% being the tip) in (a) stem tracheid (gymnosperms) and vessel (angiosperms) hydraulic diameter ( $D_H$ ), (b) branch leaf : sapwood area ratio ( $A_l : A_s$ ) and (c) leaf mass per area (LMA).



**Fig. 5** Changes with tree height per species and site in (a) predawn leaf water potential ( $\Psi_{PD}$ ); (b) midday leaf water potential ( $\Psi_{MD}$ ); (c) difference between  $\Psi_{MD}$  and  $\Psi_{PD}$  ( $\Delta\Psi$ ); and (d) water potential at which 50% of branch conductivity is lost (P50). Each point represents a tree or tree height category. Dashed lines represent the expected change due to the hydrostatic force ( $-0.01 \text{ MPa m}^{-1}$ ). Thinner lines denote nonsignificant relationships between the trait and height (see Supporting Information Table S4 for model structure and parameter values).  $R^2$  values are the variance explained by each model's fixed effects. Data sources may be found in Table S1.

## 5. Whole-tree water transport, storage and uptake

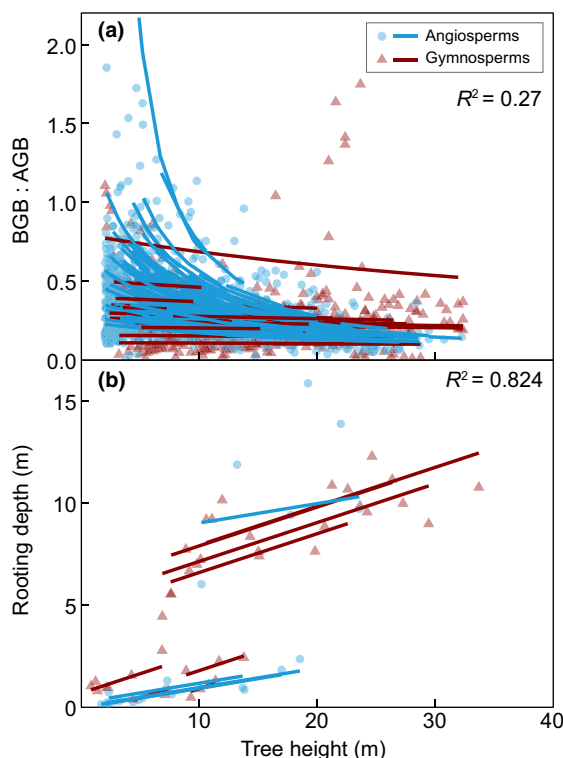
Both height-driven increases and decreases in stem sap flow rates per sapwood area ( $J_s$ ) have been observed, rendering the relationship with height nonsignificant (Fig. S5; Table S5). Whole-tree sap flow (i.e.  $Q = J_s \cdot A_s$ ) significantly increases with tree height both at the inter- and intraspecific levels (Fig. S5; Table S5), whereas height has no significant effect on sap-flux-

estimated transpiration per unit leaf area ( $E_L$ ), neither within nor across species (Fig. S5; Table S5). Thus, structural and physiological shifts could allow trees to maintain homeostatic water use per unit leaf area as they grow taller, both at the intra- and intertree levels (Fig. S5).

Increasing hydraulic capacitance and rooting depth with tree height have been suggested to be behind tall-tree capacity to maintain transpiration rates without compromising the hydraulic

system. Taller trees have a greater tree-level water storage capacity, even relative to their water use, than shorter ones, partly due to their greater sapwood area (Fig. S6; Goldstein *et al.*, 1998; Phillips *et al.*, 2003b). In addition, hydraulic capacitance, that is the ability to exchange water between storage tissues and xylem conduits per unit of water potential, increases with tree size, at least in temperate species (Domec & Gartner, 2001, 2003; Daley *et al.*, 2008; Scholz *et al.*, 2011). Larger trees have been found to use a greater proportion of, and thus rely more strongly on, stored water for transpiration than shorter ones, particularly under drought (Maherali & DeLucia, 2001; Phillips *et al.*, 2003b). Similarly, within a tree, the amount of transfusion tissue (Oldham *et al.*, 2010; Ishii *et al.*, 2014; Azuma *et al.*, 2016; Shiraki *et al.*, 2017), and thus, leaf capacitance per leaf area and water storage capacity increase with height (Ishii *et al.*, 2014; Azuma *et al.*, 2016; but see Shiraki *et al.*, 2017; Williams *et al.*, 2017), buffering turgor loss and potentially reducing transpiration reliance on water transport with increasing height (Ishii *et al.*, 2014).

Growth in root extent and depth follows that in height, at least until the water table is reached (Sudmeyer *et al.*, 2004; Christina *et al.*, 2011). Therefore, concurrent with increases in leaf and sapwood area, belowground biomass significantly increases with tree height, both in terms of fine and coarse root biomass (Fig. S7; Table S5). However, the ratio of below- to aboveground biomass decreases with height (Fig. 6a). These biomass estimations include



**Fig. 6** Changes with tree height per species and site in (a) the below : aboveground biomass ratio (BGB : AGB) and (b) rooting depth. Each point represents a tree or tree height category. In (a), an outlier (value 6.25) is hidden.  $R^2$  values are the variance explained by each model's fixed effects (see Supporting Information Table S5 for model structure and parameter values). Data sources may be found in Ledo *et al.* (2018) (a) and Table S1 (b).

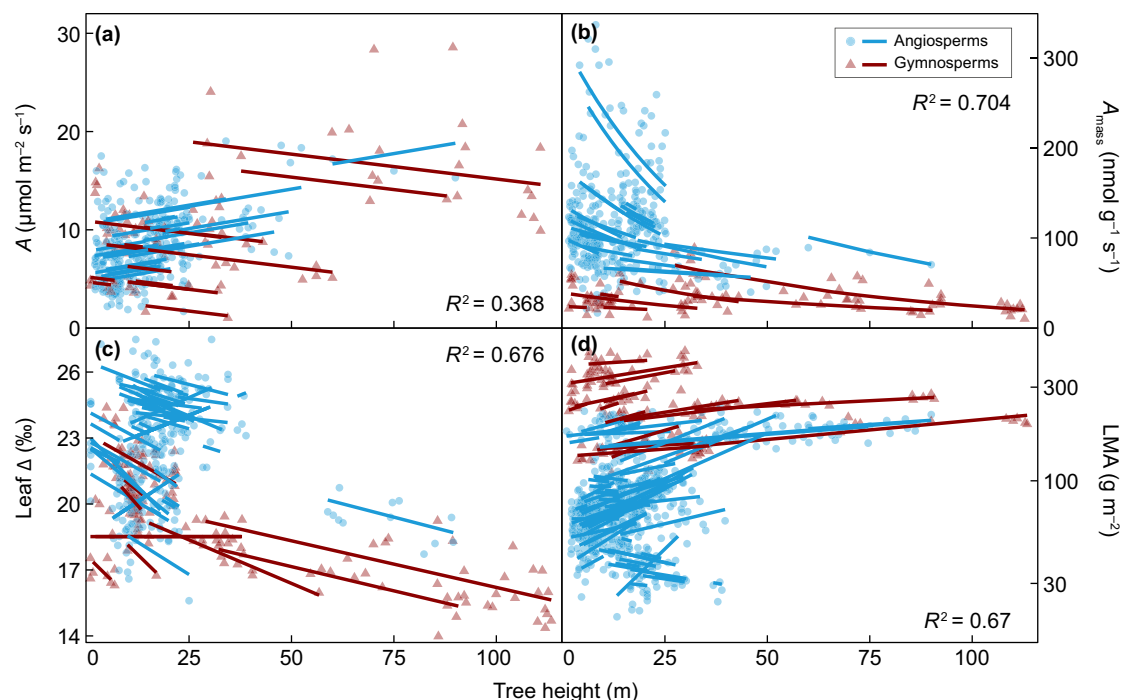
nonfunctional heartwood (Ledo *et al.*, 2018) and therefore the extent to which the reduction in this ratio imposes a limitation on water and nutrient supply to the canopy in taller trees remains unknown. Moreover, root lateral extent (Sudmeyer *et al.*, 2004) and depth (Fig. 6b) increase with tree height, enhancing water access as trees grow. Isotopic analyses have found that larger trees tend to draw water from deeper soil layers than smaller trees, both at the inter- (Stahl *et al.*, 2013; Brum *et al.*, 2019; Ding *et al.*, 2021) and intraspecific levels (Dawson, 1996; Duursma *et al.*, 2011; Kerhoulas *et al.*, 2013; Ripullone *et al.*, 2020). Taller trees may also have a greater hydraulic lift capacity than shorter conspecifics (Dawson, 1996; Domec *et al.*, 2004). Hydraulic lift or redistribution consists of the transfer of water from deeper to drier upper soil layers through the root system as water is lost during the night from the roots into soil that has a lower  $\Psi$ . This may allow tall trees (and potentially nearby shorter ones) to draw this water from the soil during the day to further sustain transpiration (Dawson, 1996) and minimize shallow root embolism (Domec *et al.*, 2004).

## 6. Photosynthesis and growth

Given the widespread decrease in  $G_s$  with height (Fig. 2a), photosynthetic rates ( $A$ ) would be expected to decrease with height accordingly. In gymnosperms, this expectation holds true (Fig. 7a), with few exceptions (Grulke & Retzlaff, 2001; McDowell *et al.*, 2002b). In angiosperms,  $A$  decreases with height when upper-crown, sun-exposed leaves are measured (Fig. S3; Table S3) but increases with height when all data are considered (Figs 7a, S8; Table S6). This suggests that, at least in this functional type, the greater access to light experienced by taller trees compared with shorter conspecifics (Fig. 1a) could partially compensate for the hydraulically driven reduction in  $g_s$  in closed forests. Nonetheless, when leaf construction costs are considered, photosynthetic rates per unit mass ( $A_{\text{mass}}$ ) significantly decrease with height in both functional types regardless of sun exposure (Figs 7b, S3; Tables S3, S6).

Leaf isotopic discrimination during photosynthesis ( $\Delta$ ), which is an assimilation-weighted measure of intrinsic water-use efficiency ( $iWUE = A/g_s$ ), decreases, and thus,  $iWUE$  increases (Nabeshima & Hiura, 2004; Woodruff *et al.*, 2009; Zhang *et al.*, 2009; Brien *et al.*, 2017), as trees grow taller, with few exceptions (Figs 7c, S3, S8; Tables S3, S6). This increase in  $iWUE$  is thought to be primarily driven by the decrease in stomatal conductance with height (McDowell *et al.*, 2011). However, some studies have found decreases in  $\Delta$  despite  $g_s$  not changing with height (Grulke & Retzlaff, 2001; Ambrose *et al.*, 2016), indicating  $\Delta$  may be further affected by changes in light conditions,  $CO_2$  isotope ratios within the canopy (McDowell *et al.*, 2011) or fractionation and diffusion resistances associated to changes in leaf morphology with height (Niinemets, 2002; Whitehead *et al.*, 2011).

Light intensity can have a significant effect on the physiological response to height at the intratree level (Scartazza *et al.*, 2016; Shiraki *et al.*, 2017). Similarly, we found that sun exposure affected the intertree response of  $A$  and  $g_s$  to height, with the negative effect of height on those variables being partially offset in closed-canopy forests, at least in angiosperms (Figs 3, 7, S3). Height *per se* has however been found to influence leaf morphological features more



**Fig. 7** Changes with tree height per species and site in (a) photosynthetic rate on a leaf area basis ( $A$ ); (b) photosynthetic rate on a leaf mass basis ( $A_{\text{mass}}$ ); (c) leaf  $^{13}\text{C}$  discrimination ( $\Delta$ ); and (d) leaf mass per area (LMA). Each point represents a tree or tree height category.  $R^2$  values are the variance explained by each model's fixed effects (see Supporting Information Table S6 for model structure and parameter values). Data sources may be found in Table S1.

strongly than light levels at the intertree level (Sendall & Reich, 2013; Shiraki *et al.*, 2017). Smaller, thicker, denser leaves (i.e. with higher leaf mass per area, LMA) are found in the upper canopy of individual trees (Fig. 4c) and in taller compared with shorter trees (Figs 7d, S3, S8; Tables S3, S6). Increasing LMA results from decreases in leaf area (Figs S3, S8) and increases in leaf density (e.g. through increases in cuticle and cell-wall thickness; England & Attiwill, 2006; van Wittenberghe *et al.*, 2012). Decreasing the transpiring area minimizes water loss while promoting heat exchange by reducing the boundary layer thickness, facilitating leaf cooling and protecting the leaf from heat damage (Richardson *et al.*, 2000; England & Attiwill, 2006). These and other adaptations (see e.g. Richardson *et al.*, 2000; England & Attiwill, 2006; van Wittenberghe *et al.*, 2012; Scartazza *et al.*, 2016) confer protection against herbivores and increasing environmental stress (chiefly water stress and radiation damage; Fig. 1a), albeit at the cost of lower  $\text{CO}_2$  diffusivity within the leaf due to increasing mesophyll limitations (Niinemets, 2002; Oldham *et al.*, 2010; Han, 2011; Whitehead *et al.*, 2011), potentially decreasing mesophyll conductance and increasing iWUE with height (Fig. 7c). Denser leaves in the upper canopy of tall trees have also been suggested to have greater maintenance costs due to the associated increase in respiration rates along a tree's stem (Ellsworth & Reich, 1993; Scartazza *et al.*, 2016); however, leaf and shoot respiration rates have been found to be equal (Grulke & Retzlaff, 2001; Koch *et al.*, 2015) and even lower (Sendall & Reich, 2013) in taller than in shorter trees, minimizing the detrimental effect of denser leaves on the carbon balance of tall trees.

In addition to morphological shifts, changes in photosynthetic rates and iWUE could be a result of height-driven biochemical adjustments. However, the maximum carboxylation activity of

Rubisco and rate of photosynthetic electron transport per leaf area do not follow a consistent pattern with height (Phillips *et al.*, 2003a; Woodruff *et al.*, 2009; Drake *et al.*, 2010; Whitehead *et al.*, 2011), with photosynthetic rates often changing in a different direction from them (McDowell *et al.*, 2002b; Woodruff *et al.*, 2009; Drake *et al.*, 2010). Decreasing nitrogen concentrations have also been proposed to potentially limit photosynthesis in taller trees (Niinemets, 2002). However, N concentrations tend to remain unchanged with height on a per leaf mass basis and increase on a per leaf area basis, both across and within trees (Ellsworth & Reich, 1993; Hubbard *et al.*, 1999; Delzon *et al.*, 2004; Nabeshima & Hiura, 2008; Whitehead *et al.*, 2011; Miyata & Kohyama, 2016; Azuma *et al.*, 2019), causing photosynthetic nitrogen use efficiency to decline with height (Nabeshima & Hiura, 2004; Miyata & Kohyama, 2016). The increase in iWUE with height is therefore likely related to changes in substomatal leaf  $\text{CO}_2$  concentrations due to reductions in  $\text{CO}_2$  diffusion from the atmosphere to the site of carboxylation, rather than to biochemical limitations (Drake *et al.*, 2010; Han, 2011). Consistent with this, morning photosynthetic rates of taller trees have been found to equal or even surpass those of smaller trees (Yoder *et al.*, 1994), despite their stronger midday declines, indicating that photosynthetic capacity *per se* might not be strongly constrained by tree height (although tree age may have a negative effect, see Azuma *et al.*, 2019).

Limitations in canopy processes associated with height may affect other tree-scale processes, such as growth. Lower productivity (Ryan *et al.*, 2006) and growth efficiency (i.e. annual stem biomass production per unit leaf area; Yoder *et al.*, 1994; McDowell *et al.*, 2002b; Phillips *et al.*, 2002; Delzon *et al.*, 2004; Martínez-Vilalta *et al.*, 2007; Genet *et al.*, 2010) have been frequently



reported in taller trees. This decrease has often been linked to decreasing photosynthetic rates; however,  $A$  may increase with height in angiosperms (Fig. 7a). Nutrient (Martínez-Vilalta *et al.*, 2007) and turgor (Woodruff *et al.*, 2004) limitations, greater and more frequent reproductive output (Thomas, 2011), and increased belowground carbon allocation (Magnani *et al.*, 2000; Baret *et al.*, 2015) have also been suggested to underlie the observed growth reductions in taller trees. These productivity measurements are however often based on stem growth and do not account for the tree's total cambial surface (Silett *et al.*, 2010). Tree-level studies have found that aboveground mass growth rates increase with tree size (either height or diameter) due to the increase in branch growth and crown complexity compensating for the decrease in trunk mass growth (Silett *et al.*, 2010; Stephenson *et al.*, 2014). Nevertheless, growth efficiency, as measured in the stem and used as a proxy of tree vigour, has been found to be correlated to pest and pathogen (e.g. fungi) resistance (Christiansen *et al.*, 1987); hence, decreasing growth efficiency with height may be indicative of reduced defence capacity in taller trees. Moreover, potential height limitations on stem growth, and thus trees capacity to periodically renew the hydraulic network supporting the canopy, may be further compounded under drought, reducing drought resilience and thus taller tree capacity to recover from drought-induced hydraulic impairment (Bennett *et al.*, 2015; DeSoto *et al.*, 2020; McGregor *et al.*, 2021).

### III. Potential implications of tree height on vulnerability to drought-induced mortality

All the above-described physiological and structural shifts with height (Figs 3–7) could play a significant role on the potentially increased vulnerability of tall trees to hydraulic failure, carbon starvation and/or biotic agents under drought (Table 1).

#### 1. Hydraulic failure

Increasing VPD (Stovall *et al.*, 2019) and soil drought (Rowland *et al.*, 2015) have been associated with increased mortality probability with height; however, height-dependent drought-induced mortality sensitivity has been found to be highly species-specific (Hember *et al.*, 2017). Increasing VPD and/or decreasing  $\Psi_{\text{soil}}$  should theoretically increase the hydraulic constraints faced by

taller trees (Fig. 2), which would presumably predispose them to both hydraulic failure and carbon starvation. Xylem water potentials, and thus hydraulic safety margins, that is  $\Psi - P50$ , are expected to decrease with dropping  $\Psi_{\text{soil}}$  under drying conditions, with this decrease being potentially steeper as height increases due to gravitational and frictional constraints (Fig. 2). At the tree level, the first signs of dieback are generally observed in the upper canopy, which experiences more negative  $\Psi$  (Fig. S4) and higher VPD (Fig. 1). Indeed, upper branches have greater native xylem embolism and lower hydraulic safety margins, suggesting that xylem embolism underlies intratree die-back patterns (Fang *et al.*, 2021). Likewise, given their intrinsically more negative  $\Psi_{\text{leaf}}$  (Fig. 5), if  $P50$  increases across tree heights (Olson *et al.*, 2018; Prendin *et al.*, 2018), remains unchanged (Fig. 5, angiosperms) or decreases at a lower rate than  $\Psi$ , safety margins will decrease, increasing the risk of embolism and leaf desiccation in the upper canopy of tall trees as drought progresses. On the contrary, if the height-driven drop in branch  $P50$  is steeper than that of  $\Psi$  (Fig. 5, gymnosperms; Domec *et al.*, 2008), then the hydraulic safety margins will increase, reducing the risk of hydraulic failure as trees grow. While  $\Psi_{\text{leaf}}$  are significantly more negative in taller than shorter trees under nondrought conditions (Fig. 5), changes in  $\Psi_{\text{leaf}}$  with height tend to decrease under dry conditions (McDowell *et al.*, 2011), as evidenced by the lack of differences frequently observed in minimum water potentials ( $\Psi_{\text{min}}$ ) between tree heights (Ryan *et al.*, 2000; Phillips *et al.*, 2003a; Nabeshima & Hiura, 2008). Greater capacitance, water storage capacity (Domec & Gartner, 2001, 2003; Daley *et al.*, 2008; Scholz *et al.*, 2011) and rooting depth (Fig. 6), as well as stomatal control, may thus minimize the drop in plant  $\Psi$  under drought in taller trees.

At the interspecific level, a trade-off between capacitance and  $P50$  has been observed, with  $\Psi_{\text{min}}$  and safety margins decreasing with increasing capacitance across species (Meinzer *et al.*, 2009). However, at the intraspecific level, larger trees have greater capacitance while maintaining or even decreasing  $P50$  (Fig. 5), thus relying on both xylem structural features and release of stored water to sustain their greater xylem tensions and avoid embolism. Hence, while water reserves last, capacitance may minimize conductivity loss in tall trees during drought. Moreover, water uptake has been found to switch towards deeper soil levels as drought progresses and the upper soil dries out (Duursma *et al.*, 2011). Thanks to their deeper roots (Fig. 6), taller trees

**Table 1** Implications of the observed height-driven patterns on height-dependent drought-induced mortality.

	Compounding factors	Compensating factors	Key unknowns
Hydraulic failure	$\downarrow \Psi$ (hydrostatic gradient)	$\downarrow G_s$ $\uparrow iWUE$ $\uparrow$ <i>Water storage and capacitance</i> $\uparrow$ <i>Rooting depth</i>	$P50$ and hydraulic safety margin trends with height
Carbon starvation	$\downarrow G_s$ $\downarrow A_{\text{mass}}$	$\uparrow NSC$ <i>reserves</i>	Size-dependent minimal NSC thresholds
Biotic attacks	<i>Pathogen host preferences</i>	$\uparrow LMA$ $\uparrow NSC$ <i>reserves</i>	Height-driven changes in defence status under drought

Traits in italics were only reviewed qualitatively.  $A_{\text{mass}}$ , photosynthetic rate on a leaf mass basis;  $G_s$ , canopy conductance;  $iWUE$ , intrinsic water-use efficiency;  $LMA$ , leaf mass per area;  $NSC$ , nonstructural carbohydrates;  $P50$ , water potential at which 50% of conductivity is lost;  $\Psi$ , water potential.

would thus be at a competitive advantage compared with shorter ones under drought as long as soil water reserves are within reach. Comparing species within a subtropical karst ecosystem, smaller species with shallower roots and lower iWUE were found to experience greater drought-induced crown defoliation and mortality than larger species with deeper roots and higher iWUE (Ding *et al.*, 2021). In addition, the turgor loss point ( $\pi_{\text{tlp}}$ , i.e. the  $\Psi_{\text{leaf}}$  at which wilting occurs, triggering stomatal closure) has been found to remain unchanged (Zhang *et al.*, 2009) or decrease towards more negative values with height following the gravitational gradient (Woodruff *et al.*, 2007; also within trees, Ishii *et al.*, 2014; Azuma *et al.*, 2016, 2019; Shiraki *et al.*, 2017; Williams *et al.*, 2017), likely ensuring stomatal closure occurs before P50 is reached.

Studies directly assessing shifts in safety margins with height under drought conditions are scarce; however, they found that leaf desiccation occurred often in taller trees because  $\Psi_{\text{leaf}}$  dropped below leaf P50 (Zhang *et al.*, 2009; Ambrose *et al.*, 2018). Yet, the drop of  $\Psi_{\text{leaf}}$  below the  $\pi_{\text{tlp}}$  and consequent stomatal closure and leaf abscission largely prevented  $\Psi_{\text{branch}}$  from declining below critical levels (Zhang *et al.*, 2009; Ambrose *et al.*, 2018). This, together with the abovementioned shifts in water uptake and storage (Dawson, 1996; Domec & Gartner, 2001; Phillips *et al.*, 2003b; Domec *et al.*, 2004; Scholz *et al.*, 2011; Kerhoulas *et al.*, 2013; Crouchet *et al.*, 2019), might indicate that tall trees adjust to their larger heights to minimize extensive drought-induced cavitation (Woodruff & Meinzer, 2011), at least under short-term drought while tree and deep soil water reserves last. Thus, albeit hydraulic limitations are expected to underlie large tree vulnerability to drought (Bennett *et al.*, 2015; Rowland *et al.*, 2015; Stovall *et al.*, 2019), unequivocal evidence of greater hydraulic failure in tall trees is missing. Due to the multiple mechanisms involved in embolism prevention, such as stomatal closure, hydraulic safety, capacitance and leaf abscission, a better understanding of height-dependent hydraulic safety margins at the intraspecific level is still needed to elucidate its role in increased tall-tree drought-induced mortality.

## 2. Carbon starvation

Given the decrease in  $G_s$  with increasing VPD, whole-tree carbon assimilation is expected to be limited under drought. This decline could be predicted to be larger in taller than in shorter trees, particularly in gymnosperms, which already show declining  $A$  with height under nondrought conditions (Fig. 7). However, because of their higher maximum  $G_s$  (Fig. 2), shorter trees exhibit a steeper response to drying (either through decreasing  $\Psi_{\text{soil}}$  or increasing VPD) than taller conspecifics (Dawson, 1996; Schäfer *et al.*, 2000; Drake *et al.*, 2010). Tall trees tend to have, therefore, lower time-integrated assimilation rates but lower variability in response to environmental conditions (Yoder *et al.*, 1994; Schäfer *et al.*, 2000; Ambrose *et al.*, 2010), with differences among heights approaching zero under severe drought (Delzon *et al.*, 2004; McDowell *et al.*, 2005; but see Hubbard *et al.*, 1999; Phillips *et al.*, 2002). Likewise, intra-annual branch nonstructural carbohydrate (NSC) fluctuations have been found to closely follow  $\Psi_{\text{soil}}$  in short *Pseudotsuga menziesii* trees, whereas in taller ones, NSC concentrations barely changed regardless of soil water availability (Woodruff

& Meinzer, 2011). NSC reserves are often higher in taller than shorter conspecifics (Sala & Hoch, 2009; Day & Greenwood, 2011; Woodruff & Meinzer, 2011; Carbone *et al.*, 2013; Lahr & Sala, 2014; but see Genet *et al.*, 2010). While this accumulation has been associated with height-driven limitations to phloem transport (Woodruff & Meinzer, 2011), assimilate movement occurs along the gravity direction and, similar to the xylem (Fig. 4), phloem hydraulic resistance decreases from the top of the stem to the roots thanks to sieve tube and plate adjustments (Jyske & Hölttä, 2015; Savage *et al.*, 2017). Therefore, there is no conclusive evidence that phloem transport is more constrained in tall trees. This NSC pattern across height classes is however consistent with the expected greater sensitivity to water stress of carbon sinks (growth and respiration) than sources (photosynthetic rates), which results in increased NSC storage under drought (McDowell, 2011; Huang *et al.*, 2021). Greater NSC reserves in taller trees could buffer drought effects for longer than in short ones by maintaining metabolic and defence processes and regulating osmotic potential, as well as through their potential role in maintaining hydraulic integrity (Woodruff *et al.*, 2004; Woodruff & Meinzer, 2011; Tomasella *et al.*, 2020). The large-scale mortality patterns observed in conifer-dominated forests of California's Sierra Nevada mountains (USA), with higher mortality rates shifting from shorter trees early in the drought period to tall trees after several years of drought (Stovall *et al.*, 2019), could thus be partly associated with a greater tall-tree capacity to endure short-term drought thanks to their larger carbon and water reserves but not longer-term dry periods (Trugman *et al.*, 2018; but also see next section on III). Their higher photosynthetic rates under non-drought conditions (Fig. 7a) may provide tall broadleaf trees, particularly in closed forests, a significant carbon reserve pool to sustain drought periods, which would explain why taller trees have been found to have greater growth resilience and recovery after drought in angiosperms (Merlin *et al.*, 2015; González de Andrés *et al.*, 2021; McGregor *et al.*, 2021), whereas the opposite has been observed in conifers (Merlin *et al.*, 2015; Serra-Maluquer *et al.*, 2018). Unfortunately, paired NSC measurements for tall and short trees as they die are lacking, and thus the possible role of carbon starvation in height-related mortality remains speculative.

## 3. Biotic attacks

Counter to hydraulic limitations imposed by increasing VPD (Stovall *et al.*, 2019), host-specific relationships have been suggested as the cause of the widespread and severe mortality in Sierra Nevada gymnosperms and its associated height-related patterns as the drought progressed (Fettig *et al.*, 2019; Stephenson *et al.*, 2019; Stephenson & Das, 2020). Size-dependent drought-induced mortality has often been associated to pest attacks, particularly from bark beetles (mostly *Ips* spp. and *Dendroctonus* spp.) upon gymnosperms (Bennett *et al.*, 2015; Fettig *et al.*, 2019; Stephenson *et al.*, 2019), which may kill the tree directly through tissue (e.g. phloem) damage or indirectly through infection of mutualistic fungi and bacteria. This size dependency is however host and biotic-agent species-specific and can even shift between normal and outbreak conditions (Raffa *et al.*, 2008; Kolb

*et al.*, 2016). While bark-feeding insects may favour larger trees due to their thicker phloem, most pest insects (including bark beetles) preferentially attack smaller trees as they are often suppressed and hence have a lower defensive capacity (Boone *et al.*, 2011; Gaylord *et al.*, 2013; Nahrung *et al.*, 2014; Takagi *et al.*, 2018; Martinson *et al.*, 2019; Davis *et al.*, 2022). Taller trees have higher LMA (Fig. 7), which confers them protection against herbivores, as well as greater NSC reserves that may be used in defence compound production (Lahr & Sala, 2014), with resin flow and monoterpene concentrations generally increasing with tree size (Boone *et al.*, 2011; Davis & Hofstetter, 2014; but see Raffa *et al.*, 2013). However, once populations increase to outbreak levels, bark beetles are more likely to overcome the defences of healthy trees, thus preferring larger ones due to their deeper, more nutritious phloem (Raffa *et al.*, 2008; Boone *et al.*, 2011; Tai *et al.*, 2019; Korolyova *et al.*, 2022). Whether the infestation of weakened trees becomes an outbreak depends on multiple interacting factors, including the insect's population density, forest structure, climatic conditions and host physiological status (Raffa *et al.*, 2008).

Drought and warming may affect pest activity, performance and population dynamics, potentially increasing the chances of attack (Wermelinger & Seifert, 1998; Kolb *et al.*, 2016). Moreover, tree physiological stress and pest dynamics may interact to drive size-dependent mortality during drought episodes, with one acting as a predisposing or compounding factor of the other. On the one hand, water stress can shift and limit trees' defensive capacity against pests and pathogens (Guérard *et al.*, 2007; Gaylord *et al.*, 2013; Netherer *et al.*, 2015; Kolb *et al.*, 2019; Gely *et al.*, 2021; Öhrn *et al.*, 2021), as well as induce the release of signals that may make drought-stressed trees more easily identifiable to pest insects (Kolb *et al.*, 2016). On the other hand, previously existing, size-dependent pathogen-induced damage (Klesse *et al.*, 2021) and parasitic-plant presence, such as mistletoe (which preferentially infects dominant trees), may debilitate tree response to and exacerbate water stress during drought and thus promote mortality through carbon starvation and/or hydraulic failure or predispose trees to further biotic attacks (Kolb *et al.*, 2016; Fernández-de-Uña *et al.*, 2017; Erbilgin *et al.*, 2021). Drought has been found to predispose trees to bark beetle (Netherer *et al.*, 2015) and other pest insect attacks (Gely *et al.*, 2021), with large-scale bark beetle outbreaks often being preceded by drought (Christiansen *et al.*, 1987). Ensuing damage has been found to be greater in both large trees (bark beetle-associated fungus, Öhrn *et al.*, 2021) and small ones (wood boring insects, Gely *et al.*, 2021), depending on the infecting species. Drought may also compound the effect of beetle attack and bark-beetle-associated fungi alone by accelerating or enhancing carbon depletion, thus promoting tree death (Kolb *et al.*, 2019; Stephenson *et al.*, 2019; Erbilgin *et al.*, 2021). Resulting mortality may be size dependent (e.g. Korolyova *et al.*, 2022, with larger trees having greater chances of mortality) or independent (Kolb *et al.*, 2019; Tai *et al.*, 2019). Nevertheless, physiological vulnerability and predisposition to biotic attacks may also be decoupled, particularly during an outbreak (Fettig *et al.*, 2019; Stephenson *et al.*, 2019; Trugman *et al.*, 2021). For instance, Tai *et al.* (2019) found that tree diameter had a stronger effect on bark beetle attack than the host's hydraulic stress for three

conifer species, with drought-related mortality being size-dependent only for *Pinus contorta*. Similarly, larger *Pinus* spp. trees of Sierra Nevada were found to have higher mortality rates as a result of bark beetle attack regardless of their chronic stress levels (Stephenson *et al.*, 2019). Given the significant association between pest attacks (chiefly bark beetles) and size-dependent drought-related mortality (Bennett *et al.*, 2015), disentangling the feedbacks between physiological stress, biotic-agent defence mechanisms and host preferences is key to fully understand height-dependent drought-induced mortality.

#### IV. Conclusions

As trees become taller, they undergo shifts in  $G_s$  and  $K_s$  (Fig. 3) that mitigate the expected drop in  $\Psi_{\text{leaf}}$  with height due to path-length-related hydraulic resistance, but not the hydraulic limitations imposed by gravity (Fig. 5). Additionally, taller trees have higher water uptake capacity (Fig. 6) and frequently lower P50 (Fig. 5) which, together with increased water storage capacity and capacitance, minimize hydraulic risk. The stronger stomatal regulation translates into a reduction in carbon assimilation rates with height, particularly on a per leaf mass basis, and an increase in water-use efficiency (Fig. 7). These height-driven shifts are expected to influence tree response to drying conditions, thus highlighting the importance of considering height-related intraspecific changes in functional traits on assessing species vulnerability to drought. The observed structural and physiological adjustments associated with tree height allow tall trees to endure short-term droughts, often offering a competitive advantage over smaller ones. How these adaptations will affect height-dependent drought-induced mortality rates under longer, warmer droughts like those foreseen under climate change scenarios remains uncertain.

There is widespread evidence of a size effect on drought-induced mortality (Bennett *et al.*, 2015; Stovall *et al.*, 2019), with increased height-associated hydraulic constraints often being inferred as the potential mechanism driving either or both hydraulic failure (through increased embolism) and carbon starvation (through decreased assimilation). However, our review shows that further evidence is still needed at both the intra- and interspecific levels to elucidate how height-driven shifts in hydraulic, carbon and defence traits respond to drought, and the thresholds above which height becomes a limitation and triggers mortality. Most of the studies on size-dependent drought-induced mortality have assessed mortality patterns either at the community level (da Costa *et al.*, 2010; Bennett *et al.*, 2015; Stovall *et al.*, 2019), thus confounding height and species-specific physiological effects, or as a function of tree diameter rather than height (da Costa *et al.*, 2010; Bennett *et al.*, 2015), thus potentially confounding height and ontogenetic effects as well as physiological differences related to species-specific tree morphology. Our quantitative review suggests that, at the intraspecific level, taller trees may be able to better withstand short-term droughts than shorter conspecifics. This evidence was however largely gathered in temperate ecosystems (Table S1), thus precluding disentangling whether the observed patterns are universal or biome specific. Given that the traits and environmental factors increasing vulnerability to drought-induced mortality, including tree size, may be biome dependent



(O'Brien *et al.*, 2017), it is key to unveil how different traits change within species and under drought across a broad array of plant functional (e.g. leaf habit, xylem properties and tree morphology) and ecosystem types (including tropical forests and those in the southern hemisphere, which are underrepresented in the literature). Further research is thus needed to elucidate whether height actually increases tree vulnerability to drought-induced mortality within species and the specific conditions (e.g. ecosystem type, drought duration and pest and pathogen presence) under which height hinders tree survival. Due to the multiple mechanisms involved in the prevention of hydraulic failure, a better understanding of height-dependent stomatal and hydraulic safety margins across tree compartments, and their feedbacks with plant water pools and water uptake capacity (including rooting depth), is required at the intraspecific level for a broad range of species to elucidate its role in drought-induced mortality in tall trees. Likewise, how dynamic drought responses, such as whole-tree water-use regulation in response to varying VPD and soil moisture, change with tree height must be ascertained. As well as xylem hydraulic constraints, path length-induced limitations to phloem transport and the carbon budget, including NSC reserves, need further study to evaluate the hydraulically driven risk of carbon starvation in taller trees under severe drought. In addition to trait adjustments (both above- and belowground), a better understanding of the potentially different roles that  $\Psi_{\text{soil}}$  and VPD may play in drought vulnerability as trees grow taller, and their feedbacks with gravity effects, is still needed. This entails studying trees of different heights in different environmental settings, that is open forests where microenvironmental conditions differ little across tree heights vs closed-canopy forests where a gradient in environmental constraints co-occurs with gravity and path length limitations. Finally, given the significant role played by pest and pathogen attacks on drought-associated mortality (Bennett *et al.*, 2015; Fettig *et al.*, 2019; Stephenson *et al.*, 2019), the interactions between water stress and biotic agents, including host size dependency pre- and postdrought, should be concurrently explored to disentangle exacerbating and triggering causes of drought-induced mortality. This involves discerning the causes of tree mortality during drought, and thus how often tall-tree mortality events are linked to insect or pathogen attacks, and if so, whether infestation occurred as a result of the tree's weakened state due to drought (i.e. water stress precedes insect or pathogen attacks) or solely due to pest-host species-specific size preferences (i.e. biotic attacks escalate water stress). Ultimately, paired tests of tall and short trees exposed to severe drought (within and among species) are required to assess the interacting mechanisms associated with height dependence of drought-induced death.

## Acknowledgements

We would like to thank J. Abend for his assistance in collecting data. LF-d-U was supported by the European Union's Horizon 2020 Marie Skłodowska-Curie Individual Fellowship no. 844028. NGM was supported by the Next Generation Ecosystem Experiment-Tropics, a project sponsored by the U.S. Department of Energy, Office of Biological and Environmental Research, and a National Science Foundation grant. MM and JM-V were supported by the Spanish Ministry of Science and Innovation

(MICINN) via competitive grant CGL2017-89149-C2-1-R. JM-V benefited from an ICREA Academia award. RP was supported by the MICINN grant RTI2018-095297-J-I00.

## Competing interests

None declared.

## ORCID

Laura Fernández-de-Uña  <https://orcid.org/0000-0001-8136-2545>

Jordi Martínez-Vilalta  <https://orcid.org/0000-0002-2332-7298>

Nate G. McDowell  <https://orcid.org/0000-0002-2178-2254>

Maurizio Mencuccini  <https://orcid.org/0000-0003-0840-1477>

Rafael Poyatos  <https://orcid.org/0000-0003-0521-2523>

## References

- Ambrose AR, Baxter WL, Martin RE, Francis E, Asner GP, Nydick KR, Dawson TE. 2018. Leaf- and crown-level adjustments help giant sequoias maintain favorable water status during severe drought. *Forest Ecology and Management* **419**: 257–267.
- Ambrose AR, Baxter WL, Wong CS, Burgess SSO, Williams CB, Næsberg RR, Koch GW, Dawson TE. 2016. Hydraulic constraints modify optimal photosynthetic profiles in giant sequoia trees. *Oecologia* **182**: 713–730.
- Ambrose AR, Sillett SC, Dawson TE. 2009. Effects of tree height on branch hydraulics, leaf structure and gas exchange in California redwoods. *Plant, Cell & Environment* **32**: 743–757.
- Ambrose AR, Sillett SC, Koch GW, Van Pelt R, Antoine ME, Dawson TE. 2010. Effects of height on treetop transpiration and stomatal conductance in coast redwood (*Sequoia sempervirens*). *Tree Physiology* **30**: 1260–1272.
- Azuma W, Ishii HR, Kuroda K, Kuroda K. 2016. Function and structure of leaves contributing to increasing water storage with height in the tallest *Cryptomeria japonica* trees of Japan. *Trees – Structure and Function* **30**: 141–152.
- Azuma W, Ishii HR, Masaki T. 2019. Height-related variations of leaf traits reflect strategies for maintaining photosynthetic and hydraulic homeostasis in mature and old *Pinus densiflora* trees. *Oecologia* **189**: 317–328.
- Baret M, Pepin S, Ward C, Pothier D. 2015. Long-term changes in belowground and aboveground resource allocation of boreal forest stands. *Forest Ecology and Management* **350**: 62–69.
- Bennett AC, McDowell NG, Allen CD, Anderson-Teixeira KJ. 2015. Larger trees suffer most during drought in forests worldwide. *Nature Plants* **1**: 15139.
- Boone CK, Aukema BH, Bohlmann J, Carroll AL, Raffa KF. 2011. Efficacy of tree defense physiology varies with bark beetle population density: a basis for positive feedback in eruptive species. *Canadian Journal of Forest Research* **41**: 1174–1188.
- Brienen RJW, Gloor E, Clerici S, Newton R, Arppe L, Boom A, Bottrell S, Callaghan M, Heaton T, Helama S *et al.* 2017. Tree height strongly affects estimates of water-use efficiency responses to climate and CO<sub>2</sub> using isotopes. *Nature Communications* **8**: 1–10.
- Brum M, Vadeboncoeur MA, Ivanov V, Asbjørnsen H, Saleska S, Alves LF, Penha D, Dias JD, Aragão LEOC, Barros F *et al.* 2019. Hydrological niche segregation defines forest structure and drought tolerance strategies in a seasonal Amazon forest. *Journal of Ecology* **107**: 318–333.
- Burgess SSO, Pittermann J, Dawson TE. 2006. Hydraulic efficiency and safety of branch xylem increases with height in *Sequoia sempervirens* (D. Don) crowns. *Plant, Cell & Environment* **29**: 229–239.
- Calvo-Alvarado JC, McDowell NG, Waring RH. 2008. Allometric relationships predicting foliar biomass and leaf area: sapwood area ratio from tree height in five Costa Rican rain forest species. *Tree Physiology* **28**: 1601–1608.



- Carbone MS, Czimczik CI, Keenan TF, Murakami PF, Pederson N, Schaberg PG, Xu X, Richardson AD. 2013. Age, allocation and availability of non-structural carbon in mature red maple trees. *New Phytologist* **200**: 1145–1155.
- Christiansen E, Waring RH, Berryman AA. 1987. Resistance of conifers to bark beetle attack: searching for general relationships. *Forest Ecology and Management* **22**: 89–106.
- Christina M, Laclau JP, Gonçalves JLM, Jourdan C, Nouvellon Y, Bouillet JP. 2011. Almost symmetrical vertical growth rates above and below ground in one of the world's most productive forests. *Ecosphere* **2**: 27.
- da Costa ACL, Galbraith D, Almeida S, Portela BTT, da Costa M, De Athaydes Silva Junior J, Braga AP, De Gonçalves PHL, De Oliveira AA, Fisher R *et al.* 2010. Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. *New Phytologist* **187**: 579–591.
- Crouchet SE, Jensen J, Schwartz BF, Schwinning S. 2019. Tree mortality after a hot drought: distinguishing density-dependent and - independent drivers and why it matters. *Frontiers in Forests and Global Change* **2**: 21.
- Daley MJ, Phillips NG, Pettijohn JC, Hadley J. 2008. Hydraulic responses to environmental perturbations in *Tsuga canadensis* and *Betula lenta*. *Tree Physiology* **28**: 1341–1348.
- Davis GA, Lowrey L, Eckberg T, Hicke JA, Smirnova E. 2022. Characterizing balsam woolly adelgid infestations and associated tree mortality in Idaho. *Journal of Forestry* **120**: 361–378.
- Davis TS, Hofstetter RW. 2014. Allometry of phloem thickness and resin flow and their relation to tree chemotype in a southwestern ponderosa pine forest. *Forest Science* **60**: 270–274.
- Dawson TE. 1996. Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: the roles of tree size and hydraulic lift. *Tree Physiology* **16**: 263–272.
- Day ME, Greenwood MS. 2011. Regulation of ontogeny in temperate conifers. In: Meinzer FC, Lachenbruch B, Dawson TE, eds. *Size- and age-related changes in tree structure and function*. Dordrecht, the Netherlands: Springer, 91–120.
- Dean TJ, Long JN. 1986. Variation in sapwood area–leaf area relations within two stands of lodgepole pine. *Forest Science* **32**: 749–758.
- Delzon S, Sartore M, Burlett R, Dewar R, Loustau D. 2004. Hydraulic responses to height growth in maritime pine trees. *Plant, Cell & Environment* **27**: 1077–1087.
- DeSoto L, Cailleret M, Sterck F, Jansen S, Kramer K, Robert EMR, Aakala T, Amoroso MM, Bigler C, Camarero JJ *et al.* 2020. Low growth resilience to drought is related to future mortality risk in trees. *Nature Communications* **11**: 545.
- Ding Y, Nie Y, Chen H, Wang K, Querejeta JI. 2021. Water uptake depth is coordinated with leaf water potential, water-use efficiency and drought vulnerability in karst vegetation. *New Phytologist* **229**: 1339–1353.
- Domec J-C, Gartner BL. 2001. Cavitation and water storage capacity in bole xylem segments of mature and young Douglas-fir trees. *Trees – Structure and Function* **15**: 204–214.
- Domec J-C, Gartner BL. 2003. Relationship between growth rates and xylem hydraulic characteristics in young, mature and old-growth ponderosa pine trees. *Plant, Cell & Environment* **26**: 471–483.
- Domec J-C, Lachenbruch B, Meinzer FC, Woodruff DR, Warren JM, McCulloh KA. 2008. Maximum height in a conifer is associated with conflicting requirements for xylem design. *Proceedings of the National Academy of Sciences, USA* **105**: 12069–12074.
- Domec J-C, Lachenbruch B, Pruyn ML, Spicer R. 2012. Effects of age-related increases in sapwood area, leaf area, and xylem conductivity on height-related hydraulic costs in two contrasting coniferous species. *Annals of Forest Science* **69**: 17–27.
- Domec J-C, Pruyn ML, Gartner BL. 2005. Axial and radial profiles in conductivities, water storage and native embolism in trunks of young and old-growth ponderosa pine trees. *Plant, Cell & Environment* **28**: 1103–1113.
- Domec J-C, Warren JM, Meinzer FC, Brooks JR, Coulombe R. 2004. Native root xylem embolism and stomatal closure in stands of Douglas-fir and ponderosa pine: mitigation by hydraulic redistribution. *Oecologia* **141**: 7–16.
- Drake JE, Raetz LM, Davis SC, Delucia EH. 2010. Hydraulic limitation not declining nitrogen availability causes the age-related photosynthetic decline in loblolly pine (*Pinus taeda* L.). *Plant, Cell & Environment* **33**: 1756–1766.
- Duursma RA, Barton CVM, Eamus D, Medlyn BE, Ellsworth DS, Forster MA, Tissue DT, Linder S, McMurtrie RE. 2011. Rooting depth explains  $[CO_2] \times$  drought interaction in *Eucalyptus saligna*. *Tree Physiology* **31**: 922–931.
- Ellsworth DS, Reich PB. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia* **96**: 169–178.
- England JR, Attiwill PM. 2006. Changes in leaf morphology and anatomy with tree age and height in the broadleaved evergreen species, *Eucalyptus regnans* F. Muell. *Trees – Structure and Function* **20**: 79–90.
- Erbilgin N, Zanganeh L, Klutsch JG, Chen S, Zhao S, Ishangulyyeva G, Burr SJ, Gaylord M, Hofstetter R, Keefover-Ring K *et al.* 2021. Combined drought and bark beetle attacks deplete non-structural carbohydrates and promote death of mature pine trees. *Plant, Cell & Environment* **44**: 3866–3881.
- Fang LD, Ning QR, Guo JJ, Gong XW, Zhu JJ, Hao GY. 2021. Hydraulic limitation underlies the dieback of *Populus pseudo-simonii* trees in water-limited areas of northern China. *Forest Ecology and Management* **483**: 118764.
- Fernández-de-Uña L, Rossi S, Aranda I, Fonti P, González-González BD, Cañellas I, Gea-Izquierdo G. 2017. Xylem and leaf functional adjustments to drought in *Pinus sylvestris* and *Quercus pyrenaica* at their elevational boundary. *Frontiers in Plant Science* **8**: 1200.
- Fettig CJ, Mortenson LA, Bulaon BM, Foulk PB. 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, US. *Forest Ecology and Management* **432**: 164–178.
- Galiano L, Martínez-Vilalta J, Lloret F. 2010. Drought-induced multifactor decline of *Scots pine* in the Pyrenees and potential vegetation change by the expansion of co-occurring oak species. *Ecosystems* **13**: 978–991.
- Gaylord ML, Kolb TE, Pockman WT, Plaut JA, Yezzer EA, Macalady AK, Pangle RE, McDowell NG. 2013. Drought predisposes piñon-juniper woodlands to insect attacks and mortality. *New Phytologist* **198**: 567–578.
- Gely C, Laurance SGW, Stork NE. 2021. The effect of drought on wood-boring in trees and saplings in tropical rainforests. *Forest Ecology and Management* **489**: 119078.
- Genet H, Bréda N, Dufrêne E. 2010. Age-related variation in carbon allocation at tree and stand scales in beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) using a chronosequence approach. *Tree Physiology* **30**: 177–192.
- Goldstein G, Andrade JL, Meinzer FC, Holbrook NM, Cavelier J, Jackson P. 1998. Stem water storage and diurnal patterns of water use in tropical forest canopy trees. *Plant, Cell & Environment* **21**: 397–406.
- González de Andrés E, Rosas T, Camarero JJ, Martínez-Vilalta J. 2021. The intraspecific variation of functional traits modulates drought resilience of European beech and *Pubescent oak*. *Journal of Ecology* **109**: 3652–3669.
- Gora EM, Esquivel-Muelbert A. 2021. Implications of size-dependent tree mortality for tropical forest carbon dynamics. *Nature Plants* **7**: 384–391.
- Gulke NE, Retzlaff WA. 2001. Changes in physiological attributes of ponderosa pine from seedling to mature tree. *Tree Physiology* **21**: 275–286.
- Guérard N, Maillard P, Bréchet C, Lieutier F, Dreyer E. 2007. Do trees use reserve or newly assimilated carbon for their defense reactions?  $\Delta^{13}C$  labeling approach with young *Scots pine* inoculated with a bark-beetle-associated fungus (*Ophiostoma brunneo ciliatum*). *Annals of Forest Science* **64**: 601–608.
- Hajek P, Link RM, Nock CA, Bauhus J, Gebauer T, Gessler A, Kovach K, Messier C, Paquette A, Saurer M *et al.* 2022. Mutually inclusive mechanisms of drought-induced tree mortality. *Global Change Biology* **28**: 3365–3378.
- Han Q. 2011. Height-related decreases in mesophyll conductance, leaf photosynthesis and compensating adjustments associated with leaf nitrogen concentrations in *Pinus densiflora*. *Tree Physiology* **31**: 976–984.
- Hember RA, Kurz WA, Coops NC. 2017. Relationships between individual-tree mortality and water-balance variables indicate positive trends in water stress-induced tree mortality across North America. *Global Change Biology* **23**: 1691–1710.
- Huang J, Hammerbacher A, Gershenzon J, van Dam NM, Sala A, McDowell NG, Chowdhury S, Gleixner G, Trumbore S, Hartmann H. 2021. Storage of carbon reserves in spruce trees is prioritized over growth in the face of carbon limitation. *Proceedings of the National Academy of Sciences, USA* **118**: e2023297118.
- Hubbard RM, Bond BJ, Ryan MG. 1999. Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. *Tree Physiology* **19**: 165–172.

- Hubbard RM, Bond BJ, Senock RS, Ryan MG. 2002. Effects of branch height on leaf gas exchange, branch hydraulic conductance and branch sap flux in open-grown ponderosa pine. *Tree Physiology* 22: 575–581.
- Ishii HR, Azuma W, Kuroda K, Sillett SC. 2014. Pushing the limits to tree height: could foliar water storage compensate for hydraulic constraints in *Sequoia sempervirens*? *Functional Ecology* 28: 1087–1093.
- Ishii HT, Jennings GM, Sillett SC, Koch GW. 2008. Hydrostatic constraints on morphological exploitation of light in tall *Sequoia sempervirens* trees. *Oecologia* 156: 751–763.
- James SA, Meinzer FC, Goldstein G, Woodruff D, Jones T, Restom T, Mejia M, Clearwater M, Campanello P. 2003. Axial and radial water transport and internal water storage in tropical forest canopy trees. *Oecologia* 134: 37–45.
- Jyske T, Hölttä T. 2015. Comparison of phloem and xylem hydraulic architecture in *Picea abies* stems. *New Phytologist* 205: 102–115.
- Kerhoulas LP, Kolb TE, Koch GW. 2013. Tree size, stand density, and the source of water used across seasons by ponderosa pine in northern Arizona. *Forest Ecology and Management* 289: 425–433.
- King DA. 2011. Size-related changes in tree proportions and their potential influence on the course of height growth. In: Meinzer FC, Lachenbruch B, Dawson TE, eds. *Size- and age-related changes in tree structure and function*. Dordrecht, the Netherlands: Springer, 165–192.
- Klesse S, Von Arx G, Gossner MM, Hug C, Rigling A, Queloz V. 2021. Amplifying feedback loop between growth and wood anatomical characteristics of *Fraxinus excelsior* explains size-related susceptibility to ash dieback. *Tree Physiology* 41: 683–696.
- Koch GW, Sillett SC, Antoine ME, Williams CB. 2015. Growth maximization trumps maintenance of leaf conductance in the tallest angiosperm. *Oecologia* 177: 321–331.
- Koçillari L, Olson ME, Suweis S, Rocha RP, Lovison A, Cardin F, Dawson TE, Echeverría A, Fajardo A, Lechthaler S *et al.* 2021. The Widened Pipe Model of plant hydraulic evolution. *Proceedings of the National Academy of Sciences, USA* 118: e2100314118.
- Kolb T, Keefover-Ring K, Burr SJ, Hofstetter R, Gaylord M, Raffa KF. 2019. Drought-mediated changes in tree physiological processes weaken tree defenses to bark beetle attack. *Journal of Chemical Ecology* 45: 888–900.
- Kolb TE, Fetting CJ, Ayres MP, Bentz BJ, Hicke JA, Mathiasen R, Stewart JE, Weed AS. 2016. Observed and anticipated impacts of drought on forest insects and diseases in the United States. *Forest Ecology and Management* 380: 321–334.
- Korolyova N, Buechling A, Ďuračiová R, Zabihi K, Turčáni M, Svoboda M, Bláha J, Swarts K, Poláček M, Hradecký J *et al.* 2022. The last trees standing: climate modulates tree survival factors during a prolonged bark beetle outbreak in Europe. *Agricultural and Forest Meteorology* 322: 109025.
- Lahr EC, Sala A. 2014. Species, elevation, and diameter affect whitebark pine and lodgepole pine stored resources in the sapwood and phloem: implications for bark beetle outbreaks. *Canadian Journal of Forest Research* 44: 1312–1319.
- Lazzarin M, Crivellaro A, Williams CB, Dawson TE, Mozzi G, Anfodillo T. 2016. Tracheid and pit anatomy vary in tandem in a tall *Sequoiadendron giganteum* tree. *IWA Journal* 37: 172–185.
- Ledo A, Paul KI, Burslem DFRP, Ewel JJ, Barton C, Battaglia M, Brooksbank K, Carter J, Eid TH, England JR *et al.* 2018. Tree size and climatic water deficit control root to shoot ratio in individual trees globally. *New Phytologist* 217: 8–11.
- Lindenmayer DB, Laurance WF. 2016. The ecology, distribution, conservation and management of large old trees. *Biological Reviews* 92: 1434–1458.
- Liu H, Gleason SM, Hao G, Hua L, He P, Goldstein G, Ye Q. 2019. Hydraulic traits are coordinated with maximum plant height at the global scale. *Science Advances* 5: eaav1332.
- Magnani F, Mencuccini M, Grace J. 2000. Age-related decline in stand productivity: the role of structural acclimation under hydraulic constraints. *Plant, Cell & Environment* 23: 251–263.
- Maherali H, DeLucia EH. 2001. Influence of climate-driven shifts in biomass allocation on water transport and storage in ponderosa pine. *Oecologia* 129: 481–491.
- Martínez-Vilalta J, Vanderklein D, Mencuccini M. 2007. Tree height and age-related decline in growth in Scots pine (*Pinus sylvestris* L.). *Oecologia* 150: 529–544.
- Martinson SJ, Fernández Ajó AA, Martínez AS, Krivák-Tetley FE, Villacide JM, Ayres MP, Corley JC. 2019. Attack rates of *Sirex noctilio* and patterns of pine tree defenses and mortality in northern Patagonia. *Bulletin of Entomological Research* 109: 141–149.
- McDowell NG. 2011. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiology* 155: 1051–1059.
- McDowell NG, Allen CD. 2015. Darcy's law predicts widespread forest mortality under climate warming. *Nature Climate Change* 5: 669–672.
- McDowell NG, Barnard H, Bond BJ, Hinckley T, Hubbard RM, Ishii H, Köstner B, Magnani F, Marshall JD, Meinzer FC *et al.* 2002a. The relationship between tree height and leaf area : sapwood area ratio. *Oecologia* 132: 12–20.
- McDowell NG, Bond BJ, Dickman LT, Ryan MG, Whitehead D. 2011. Relationships between tree height and carbon isotope discrimination. In: Meinzer FC, Lachenbruch B, Dawson TE, eds. *Size- and age-related changes in tree structure and function*. Dordrecht, the Netherlands: Springer, 255–286.
- McDowell NG, Licata J, Bond BJ. 2005. Environmental sensitivity of gas exchange in different-sized trees. *Oecologia* 145: 9–20.
- McDowell NG, Phillips N, Lunch C, Bond BJ, Ryan MG. 2002b. An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. *Tree Physiology* 22: 763–774.
- McDowell NG, Sapes G, Pivovarov AL, Adams HD, Allen CD, Anderegg WRL, Arend M, Breshears DD, Brodribb TJ, Choat B *et al.* 2022. Mechanisms of woody-plant mortality under rising drought, CO<sub>2</sub> and vapour pressure deficit. *Nature Reviews Earth and Environment* 3: 294–308.
- McGregor IR, Helcoski R, Kunert N, Tepley AJ, Gonzalez-Akre EB, Herrmann V, Zailaa J, Stovall AEL, Bourg NA, McShea WJ *et al.* 2021. Tree height and leaf drought tolerance traits shape growth responses across droughts in a temperate broadleaf forest. *New Phytologist* 231: 601–616.
- Meinzer FC, Johnson DM, Lachenbruch B, McCulloh KA, Woodruff DR. 2009. Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. *Functional Ecology* 23: 922–930.
- Meir P, Mencuccini M, Binks O, Da Costa AL, Ferreira L, Rowland L. 2018. Short-term effects of drought on tropical forest do not fully predict impacts of repeated or long-term drought: gas exchange versus growth. *Philosophical Transactions of the Royal Society B. Series B: Biological Sciences* 373: 20170311.
- Mencuccini M. 2003. The ecological significance of long-distance water transport: short-term regulation, long-term acclimation and the hydraulic costs of stature across plant life forms. *Plant, Cell & Environment* 26: 163–182.
- Mencuccini M, Rosas T, Rowland L, Choat B, Cornelissen H, Jansen S, Kramer K, Lapenis A, Manzoni S, Niinemets Ü *et al.* 2019. Leaf economics and plant hydraulics drive leaf : wood area ratios. *New Phytologist* 224: 1544–1556.
- Merlin M, Perot T, Perret S, Korboulewsky N, Vallet P. 2015. Effects of stand composition and tree size on resistance and resilience to drought in sessile oak and Scots pine. *Forest Ecology and Management* 339: 22–33.
- Miyata R, Kohyama TS. 2016. Light-exposed shoots of seven coexisting deciduous species show common photosynthetic responses to tree height. *Oecologia* 182: 373–383.
- Mokany K, McMurtrie RE, Atwell BJ, Keith H. 2003. Interaction between sapwood and foliage area in alpine ash (*Eucalyptus delegatensis*) trees of different heights. *Tree Physiology* 23: 949–958.
- Nabeshima E, Hiura T. 2004. Size dependency of photosynthetic water- and nitrogen-use efficiency and hydraulic limitation in *Acer* mono. *Tree Physiology* 24: 745–752.
- Nabeshima E, Hiura T. 2008. Size-dependency in hydraulic and photosynthetic properties of three *Acer* species having different maximum sizes. *Ecological Research* 23: 281–288.
- Nahrung HF, Smith TE, Wiegand AN, Lawson SA, Debusse V. 2014. Host tree influences on longicorn beetle (Coleoptera: Cerambycidae) attack in subtropical Corymbia (Myrtales: Myrtaceae). *Environmental Entomology* 43: 37–46.
- Netherer S, Matthews B, Katzensteiner K, Blackwell E, Henschke P, Hietz P, Pennerstorfer J, Rosner S, Kikuta S, Schume H *et al.* 2015. Do water-limiting conditions predispose Norway spruce to bark beetle attack? *New Phytologist* 205: 1128–1141.
- Niinemets Ü. 2002. Stomatal conductance alone does not explain the decline in foliar photosynthetic rates with increasing tree age and size in *Picea abies* and *Pinus sylvestris*. *Tree Physiology* 22: 515–535.
- O'Brien MJ, Engelbrecht BMJ, Joswig J, Pereyra G, Schuldt B, Jansen S, Kattge J, Landhäusser SM, Levick SR, Preisler Y *et al.* 2017. A synthesis of tree functional

- traits related to drought-induced mortality in forests across climatic zones. *Journal of Applied Ecology* 54: 1669–1686.
- Öhrn P, Berlin M, Elfstrand M, Krokene P, Jönsson AM. 2021. Seasonal variation in Norway spruce response to inoculation with bark beetle-associated bluestain fungi one year after a severe drought. *Forest Ecology and Management* 496: 119443.
- Oldham AR, Sillett SC, Tomescu AMF, Koch GW. 2010. The hydrostatic gradient, not light availability, drives height-related variation in *Sequoia sempervirens* (Cupressaceae) leaf anatomy. *American Journal of Botany* 97: 1087–1097.
- Olson ME, Anfodillo T, Rosell JA, Petit G, Crivellaro A, Isnard S, León-Gómez C, Alvarado-Cárdenas LO, Castorena M. 2014. Universal hydraulics of the flowering plants: vessel diameter scales with stem length across angiosperm lineages, habits and climates. *Ecology Letters* 17: 988–997.
- Olson ME, Soriano D, Rosell JA, Anfodillo T, Donoghue MJ, Edwards EJ, León-Gómez C, Dawson T, Camarero Martínez JJ, Castorena M *et al.* 2018. Plant height and hydraulic vulnerability to drought and cold. *Proceedings of the National Academy of Sciences, USA* 115: 7551–7556.
- Osada N, Okabe Y, Hayashi D, Katsuyama T, Tokuchi N. 2014. Differences between height- and light-dependent changes in shoot traits in five deciduous tree species. *Oecologia* 174: 1–12.
- Pfautsch S, Aspinwall MJ, Drake JE, Chacon-Doria L, Langelaan RJA, Tissue DT, Tjoelker MG, Lens F. 2018. Traits and trade-offs in whole-tree hydraulic architecture along the vertical axis of *Eucalyptus grandis*. *Annals of Botany* 121: 129–141.
- Phillips N, Bond BJ, McDowell NG, Ryan MG. 2002. Canopy and hydraulic conductance in young, mature and old Douglas-fir trees. *Tree Physiology* 22: 205–211.
- Phillips NG, Bond BJ, McDowell NG, Ryan MG, Schauer A. 2003a. Leaf area compounds height-related hydraulic costs of water transport in Oregon White Oak trees. *Functional Ecology* 17: 832–840.
- Phillips N, Bond BJ, Ryan MG. 2001. Gas exchange and hydraulic properties in the crowns of two tree species in a Panamanian moist forest. *Trees – Structure and Function* 15: 123–130.
- Phillips NG, Ryan MG, Bond BJ, McDowell NG, Hinckley TM, Čermák J. 2003b. Reliance on stored water increases with tree size in three species in the Pacific Northwest. *Tree Physiology* 23: 237–245.
- Prendin AL, Mayr S, Beikircher B, von Arx G, Petit G. 2018. Xylem anatomical adjustments prioritize hydraulic efficiency over safety as Norway spruce trees grow taller. *Tree Physiology* 38: 1088–1097.
- Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *Bioscience* 58: 501–517.
- Raffa KF, Powell EN, Townsend PA. 2013. Temperature-driven range expansion of an irruptive insect heightened by weakly coevolved plant defenses. *Proceedings of the National Academy of Sciences, USA* 110: 2193–2198.
- Richardson AD, Berlyn GP, Ashton PMS, Thadani R, Cameron IR. 2000. Foliar plasticity of hybrid spruce in relation to crown position and stand age. *Canadian Journal of Botany* 78: 305–317.
- Ripullone F, Camarero JJ, Colangelo M, Voltas J. 2020. Variation in the access to deep soil water pools explains tree-to-tree differences in drought-triggered dieback of mediterranean oaks. *Tree Physiology* 40: 591–604.
- Rowland L, da Costa ACL, Galbraith DR, Oliveira RS, Binks OJ, Oliveira AAR, Pullen AM, Doughty CE, Metcalfe DB, Vasconcelos SS *et al.* 2015. Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature* 528: 119–122.
- Ryan MG, Bond BJ, Law BE, Hubbard RM, Woodruff D, Cienciala E, Kucera J. 2000. Transpiration and whole-tree conductance in ponderosa pine trees of different heights. *Oecologia* 124: 553–560.
- Ryan MG, Phillips N, Bond BJ. 2006. The hydraulic limitation hypothesis revisited. *Plant, Cell & Environment* 29: 367–381.
- Sala A, Hoch G. 2009. Height-related growth declines in ponderosa pine are not due to carbon limitation. *Plant, Cell & Environment* 32: 22–30.
- Savage JA, Beecher SD, Clerx L, Gersony JT, Knoblauch J, Losada JM, Jensen KH, Knoblauch M, Holbrook NM. 2017. Maintenance of carbohydrate transport in tall trees. *Nature Plants* 3: 965–972.
- Savage VM, Bentley LP, Enquist BJ, Sperry JS, Smith DD, Reich PB, Von Allmen EI. 2010. Hydraulic trade-offs and space filling enable better predictions of vascular structure and function in plants. *Proceedings of the National Academy of Sciences, USA* 107: 22722.
- Scartazza A, Di Baccio D, Bertolotto P, Gavrichkova O, Matteucci G. 2016. Investigating the European beech (*Fagus sylvatica* L.) leaf characteristics along the vertical canopy profile: leaf structure, photosynthetic capacity, light energy dissipation and photoprotection mechanisms. *Tree Physiology* 36: 1060–1076.
- Schäfer KVR, Oren R, Tenhunen JD. 2000. The effect of tree height on crown level stomatal conductance. *Plant, Cell & Environment* 23: 365–375.
- Scholz FG, Phillips NG, Bucci SJ, Meinzer FC, Goldstein G. 2011. Hydraulic capacitance: biophysics and functional significance of internal water sources in relation to tree size. In: Meinzer FC, Lachenbruch B, Dawson TE, eds. *Size- and age-related changes in tree structure and function*. Dordrecht, the Netherlands: Springer, 341–362.
- Schulte PJ. 2012. Vertical and radial profiles in tracheid characteristics along the trunk of Douglas-fir trees with implications for water transport. *Trees – Structure and Function* 26: 421–433.
- Sendall KM, Reich PB. 2013. Variation in leaf and twig CO<sub>2</sub> flux as a function of plant size: a comparison of seedlings, saplings and trees. *Tree Physiology* 33: 713–729.
- Serra-Maluquer X, Mencuccini M, Martínez-Vilalta J. 2018. Changes in tree resistance, recovery and resilience across three successive extreme droughts in the northeast Iberian Peninsula. *Oecologia* 187: 343–354.
- Shiraki A, Azuma W, Kuroda K, Ishii HR. 2017. Physiological and morphological acclimation to height in cupressoid leaves of 100-year-old *Chamaecyparis obtusa*. *Tree Physiology* 37: 1327–1336.
- Sillett SC, Van Pelt R, Koch GW, Ambrose AR, Carroll AL, Antoine ME, Mifsud BM. 2010. Increasing wood production through old age in tall trees. *Forest Ecology and Management* 259: 976–994.
- Stahl C, Hérault B, Rossi V, Burban B, Bréchet C, Bonal D. 2013. Depth of soil water uptake by tropical rainforest trees during dry periods: Does tree dimension matter? *Oecologia* 173: 1191–1201.
- Stephenson NL, Das AJ. 2020. Height-related changes in forest composition explain increasing tree mortality with height during an extreme drought. *Nature Communications* 11: 1–4.
- Stephenson NL, Das AJ, Ampersee NJ, Bulaon BM, Yee JL. 2019. Which trees die during drought? The key role of insect host-tree selection. *Journal of Ecology* 107: 2383–2401.
- Stephenson NL, Das AJ, Condit R, Russo SE, Baker PJ, Beckman NG, Coomes DA, Lines ER, Morris WK, Rüger N *et al.* 2014. Rate of tree carbon accumulation increases continuously with tree size. *Nature* 507: 90–93.
- Stovall AEL, Shugart H, Yang X. 2019. Tree height explains mortality risk during an intense drought. *Nature Communications* 10: 1–6.
- Sudmeyer RA, Speijers J, Nicholas BD. 2004. Root distribution of *Pinus pinaster*, *P. radiata*, *Eucalyptus globulus* and *E. kochii* and associated soil chemistry in agricultural land adjacent to tree lines. *Tree Physiology* 24: 1333–1346.
- Tai X, Mackay DS, Ewers BE, Parsekian AD, Beverly D, Speckman H, Brooks PD, Anderegg WRL. 2019. Plant hydraulic stress explained tree mortality and tree size explained beetle attack in a mixed conifer forest. *Journal of Geophysical Research: Biogeosciences* 124: 3555–3568.
- Takagi E, Masaki D, Kanai R, Sato M, Iguchi K. 2018. Mass mortality of *Abies veitchii* caused by *Polygraphus proximus* associated with tree trunk diameter in Japan. *Forest Ecology and Management* 428: 14–19.
- Thomas SC. 2011. Age-related changes in tree growth and functional biology: the role of reproduction. In: Meinzer FC, Lachenbruch B, Dawson TE, eds. *Size- and age-related changes in tree structure and function*. Dordrecht, the Netherlands: Springer, 33–64.
- Tomasella M, Petrusa E, Petruzzellis F, Nardini A, Casolo V. 2020. The possible role of non-structural carbohydrates in the regulation of tree hydraulics. *International Journal of Molecular Sciences* 21: 144.
- Trugman AT, Anderegg LDL, Anderegg WRL, Das AJ, Stephenson NL. 2021. Why is tree drought mortality so hard to predict? *Trends in Ecology and Evolution* 36: 520–532.
- Trugman AT, Detto M, Bartlett MK, Medvigy D, Anderegg WRL, Schwalm C, Schaffer B, Pacala SW. 2018. Tree carbon allocation explains forest drought-kill and recovery patterns. *Ecology Letters* 21: 1552–1560.
- Wermelinger B, Seifert M. 1998. Analysis of the temperature dependent development of the spruce bark beetle *Ips typographus* (L.) (Col., Scolytidae). *Journal of Applied Entomology* 122: 185–191.



- Whitehead D, Barbour MM, Griffin KL, Turnbull MH, Tissue DT. 2011. Effects of leaf age and tree size on stomatal and mesophyll limitations to photosynthesis in mountain beech (*Nothofagus solandrii* var. *cliffortioides*). *Tree Physiology* 31: 985–996.
- Whitehead D, Edwards WRN, Jarvis PG. 1984. Conducting sapwood area, foliage area, and permeability in mature trees of *Picea sitchensis* and *Pinus contorta*. *Canadian Journal of Forest Research* 14: 940–947.
- Williams AP, Allen CD, Macalady AK, Griffin D, Woodhouse CA, Meko DM, Swetnam TW, Rauscher SA, Seager R, Grissino-Mayer HD *et al.* 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change* 3: 292–297.
- Williams CB, Anfodillo T, Crivellaro A, Lazzarin M, Dawson TE, Koch GW. 2019. Axial variation of xylem conduits in the Earth's tallest trees. *Trees – Structure and Function* 33: 1299–1311.
- Williams CB, Reese Næsborg R, Dawson TE. 2017. Coping with gravity: the foliar water relations of giant sequoia. *Tree Physiology* 37: 1312–1326.
- van Wittenbergh S, Adriaenssens S, Staelens J, Verheyen K, Samson R. 2012. Variability of stomatal conductance, leaf anatomy, and seasonal leaf wettability of young and adult European beech leaves along a vertical canopy gradient. *Trees – Structure and Function* 26: 1427–1438.
- Woodruff DR, Bond BJ, Meinzer FC. 2004. Does turgor limit growth in tall trees? *Plant, Cell & Environment* 27: 229–236.
- Woodruff DR, McCulloh KA, Warren JM, Meinzer FC, Lachenbruch B. 2007. Impacts of tree height on leaf hydraulic architecture and stomatal control in Douglas-fir. *Plant, Cell & Environment* 30: 559–569.
- Woodruff DR, Meinzer FC. 2011. Water stress, shoot growth and storage of non-structural carbohydrates along a tree height gradient in a tall conifer. *Plant, Cell & Environment* 34: 1920–1930.
- Woodruff DR, Meinzer FC, Lachenbruch B, Johnson DM. 2009. Coordination of leaf structure and gas exchange along a height gradient in a tall conifer. *Tree Physiology* 29: 261–272.
- Yoder BJ, Ryan MG, Waring RH, Schoettle AW, Kaufmann MR. 1994. Evidence of reduced photosynthetic rates in old trees. *Forest Science* 40: 513–527.
- Zhang YJ, Meinzer FC, Hao G-Y, Scholz FG, Bucci SJ, Takahashi FSC, Villalobos-Vega R, Giraldo JP, Cao KF, Hoffmann WA *et al.* 2009. Size-dependent mortality in a Neotropical savanna tree: the role of height-related adjustments in hydraulic architecture and carbon allocation. *Plant, Cell & Environment* 32: 1456–1466.

## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Fig. S1** Species colour legend for Figs S2, S4, S5, and S8.

**Fig. S2** Changes with height at different scales in canopy conductance ( $G_s$ ), stomatal conductance on a leaf area ( $g_s$ ) and leaf mass basis ( $g_{s\text{ mass}}$ ), branch sapwood-specific hydraulic conductivity ( $K_s$ ), branch leaf-specific hydraulic conductivity ( $K_l$ ), leaf-specific hydraulic conductance ( $k_l$ ) and leaf: sapwood area ratio ( $A_l : A_s$ ).

**Fig. S3** Changes with tree height per species and site in upper-crown, sun-exposed leaf stomatal conductance per leaf area ( $g_s$ ); stomatal conductance per leaf mass ( $g_{s\text{ mass}}$ ), photosynthetic rate per leaf area ( $A$ ); photosynthetic rate per leaf mass ( $A_{\text{mass}}$ );  $^{13}\text{C}$  discrimination ( $\Delta$ ); and leaf mass per area.

**Fig. S4** Changes in midday water potential ( $\Psi_{\text{MD}}$ ), predawn water potential ( $\Psi_{\text{PD}}$ ), difference between  $\Psi_{\text{MD}}$  and  $\Psi_{\text{PD}}$  ( $\Delta\Psi$ ), and the

water potential at which 50% of branch conductivity is lost (P50) with height at different scales.

**Fig. S5** Changes in sap flow density ( $J_s$ ), sap flow ( $Q$ ) and leaf-specific transpiration ( $E_l$ ) with height at different scales.

**Fig. S6** Changes with tree height per species and site in sapwood area ( $A_s$ ) at breast height.

**Fig. S7** Changes with tree height per species and site in belowground biomass, fine root biomass and coarse root biomass.

**Fig. S8** Changes in photosynthetic rate on a leaf area ( $A$ ) and leaf mass basis ( $A_{\text{mass}}$ ), leaf  $^{13}\text{C}$  discrimination ( $\Delta$ ), leaf mass per area and individual leaf area with height at different scales.

**Methods S1** Description of paper selection and data analyses.

**Table S1** Data sources.

**Table S2** Results of the generalized linear mixed models examining the effect of height on each trait ( $g_s$ ,  $g_{s\text{ mass}}$ ,  $G_s$ ,  $K_s$ ,  $K_l$ ,  $k_l$  and  $A_l : A_s$ ) within (centred height) and among species (mean height) as a function of species type (angiosperms vs conifers) and their interaction.

**Table S3** Results of the generalized linear mixed models examining the effect of height on each trait ( $g_s$ ,  $g_{s\text{ mass}}$ ,  $A$ ,  $A_{\text{mass}}$ ,  $\Delta$ , LMA and leaf area) within (centred height) and among species (mean height) as a function of species type (angiosperms vs conifers) and their interaction for measurements taken on upper-crown, sun-exposed leaves.

**Table S4** Results of the generalized linear mixed models examining the effect of height on each trait ( $\Psi_{\text{PD}}$ ,  $\Psi_{\text{MD}}$ ,  $\Delta\Psi$  and P50) within (centred height) and among species (mean height) as a function of species type (angiosperms vs conifers) and their interaction.

**Table S5** Results of the generalized linear mixed models examining the effect of height on each trait ( $J_s$ ,  $Q$ ,  $E_l$ ,  $A_s$ , belowground biomass, fine root biomass, coarse root biomass, BGB/AGB and rooting depth) within (centred height) and among species (mean height) as a function of species type (angiosperms vs conifers) and their interaction.

**Table S6** Results of the generalized linear mixed models examining the effect of height on each trait ( $A$ ,  $A_{\text{mass}}$ ,  $\Delta$ , LMA and leaf area) within (centred height) and among species (mean height) as a function of species type (angiosperms vs conifers) and their interaction.

Please note: Wiley is not responsible for the content or functionality of any Supporting Information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.