



Tansley review

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

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Summary

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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 (Ψ_{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 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:

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

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

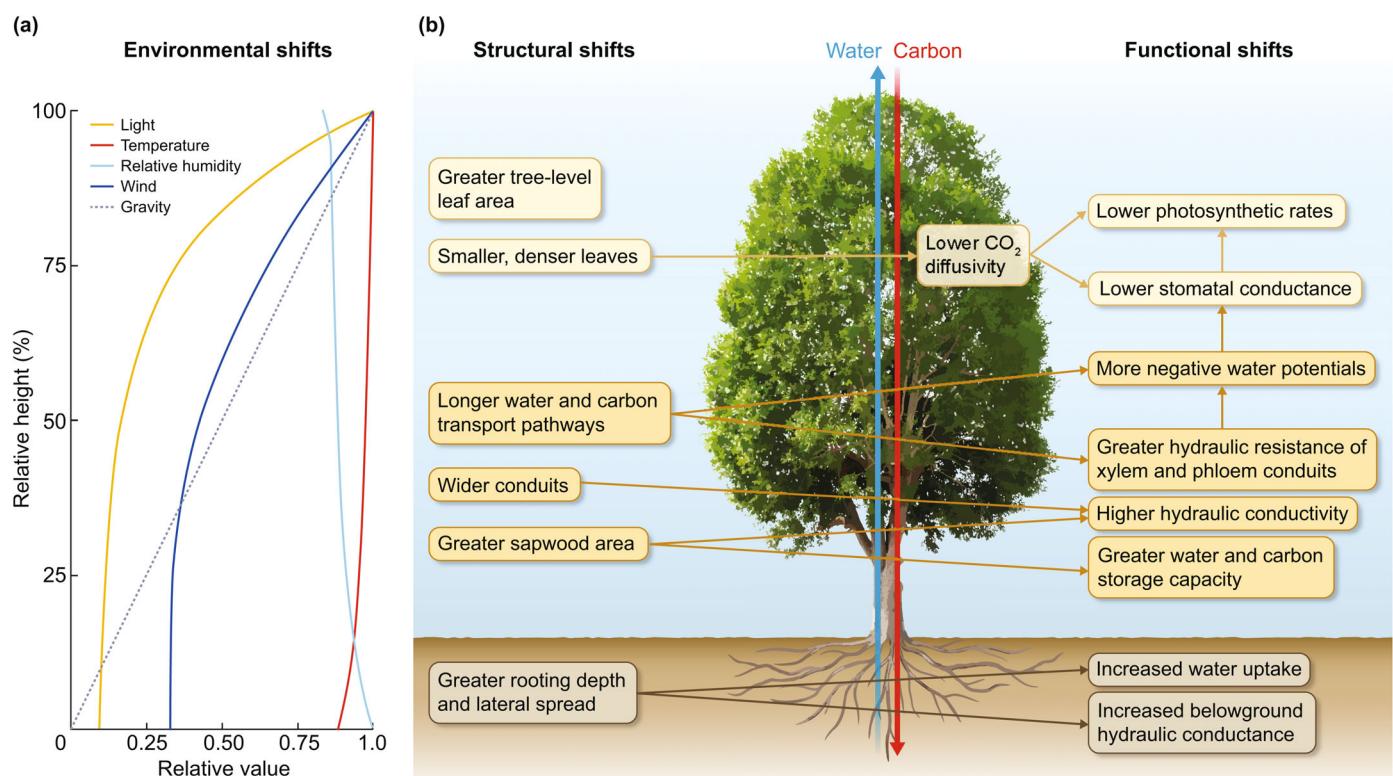


Fig. 1 Expected changes in environmental factors (a) and structural and functional traits (b) with tree height. (a) Simulated environmental changes with height in a forest between the soil and the top of the canopy of the tallest trees in relative units, with temperatures becoming more extreme with height (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 Ψ_{leaf} (Fig. 2a) or require greater adjustments in G_s (McDowell & Allen, 2015) than shorter trees with rising VPD or dropping Ψ_{soil} . This would theoretically increase their likelihood of suffering drought-induced hydraulic failure (through dropping Ψ_{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 Ψ_{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; Kocíllari *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

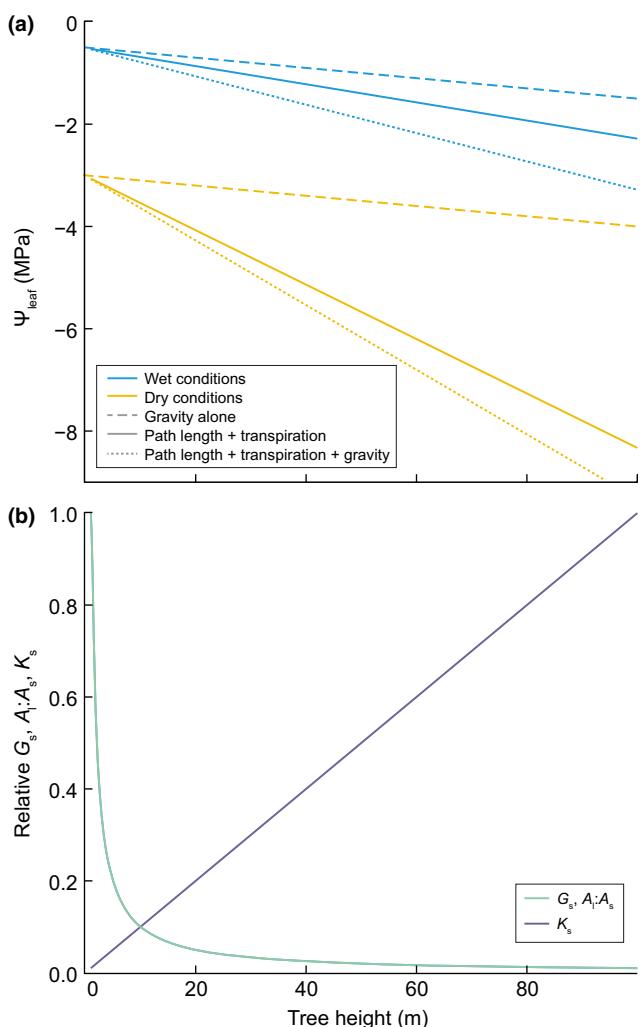


Fig. 2 (a) Predicted changes in leaf water potentials (Ψ_{leaf}) with tree height under wet (VPD = 1 kPa, $\Psi_{soil} = -0.5$ MPa) and dry (VPD = 3 kPa, $\Psi_{soil} = -3$ MPa) conditions using Darcy's law (Eqn 1) with and without accounting for the hydrostatic gradient (i.e. gravity); all traits except VPD and Ψ_{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 Ψ_{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 Ψ_{leaf} as trees grow (Fig. 2).

4. Leaf water potential and hydraulic safety

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

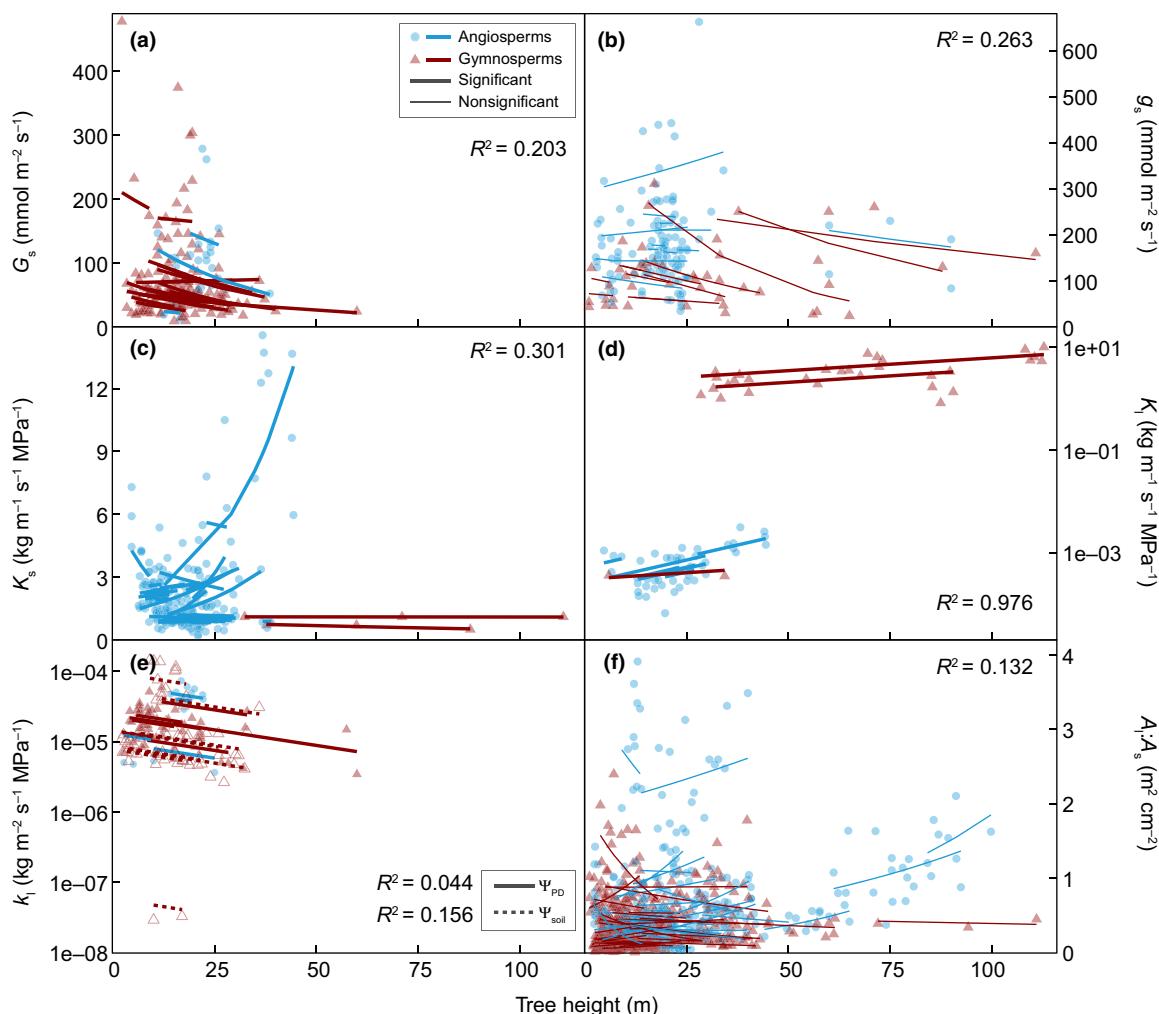


Fig. 3 Changes with tree height per species and site in (a) tree-level canopy conductance (G_s); (b) leaf stomatal conductance (g_s); (c) upper-branch sapwood-specific hydraulic conductivity (K_s); (d) upper-branch leaf-specific hydraulic conductivity (K_l); (e) whole-tree leaf-specific hydraulic conductivity (k_l); and (f) tree-level leaf : sapwood area ratio ($A_l : A_s$). 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 (Ψ_{PD} ; solid symbols) and soil water potentials (Ψ_{soil} ; empty symbols). Data sources may be found in Table S1.

et al., 1994; McDowell *et al.*, 2011). However, the significant declines in Ψ_{PD} and Ψ_{MD} with height disappear when the gravitational gradient (-0.01 MPa m^{-1}) is accounted for (Table S4). Similarly, within a tree, leaf and trunk Ψ 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 $A_l : A_s$ (Figs 2b, 3) are not strong enough to offset the predicted drop in Ψ_{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 Ψ with height is expected to increase embolism risk in tall trees, unless changes in hydraulic safety ensue. In upper-crown branches, the Ψ at which 50% of xylem conductivity is lost due to embolism (P50) 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 P50 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).

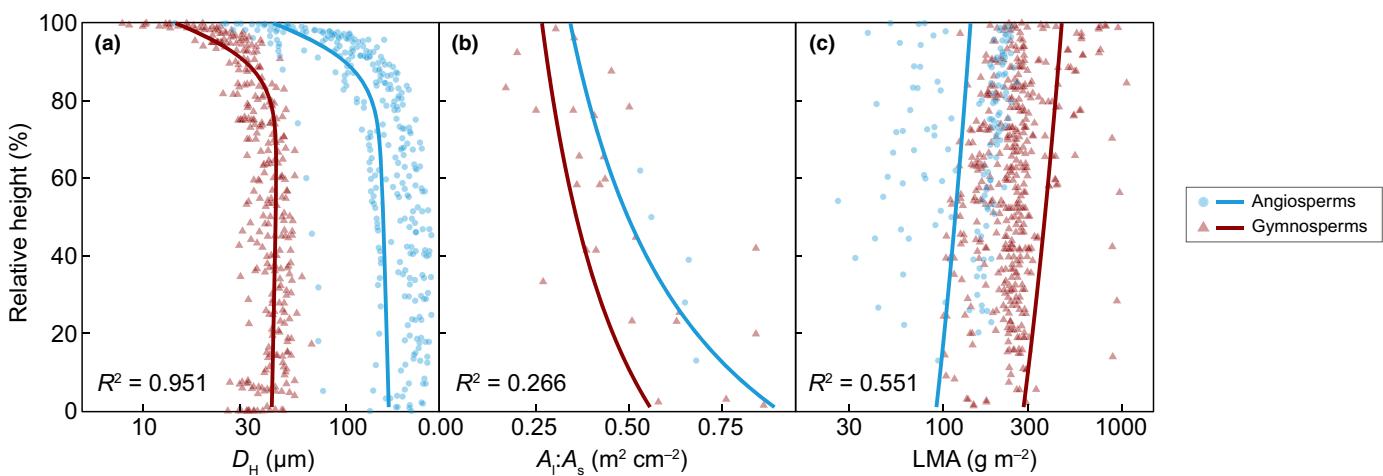


Fig. 4 Changes with height within a tree (100% being the tip) in (a) stem tracheid (gymnosperms) and vessel (angiosperms) hydraulic diameter (D_H), (b) branch leaf : sapwood area ratio ($A_l : A_s$) and (c) leaf mass per area (LMA).

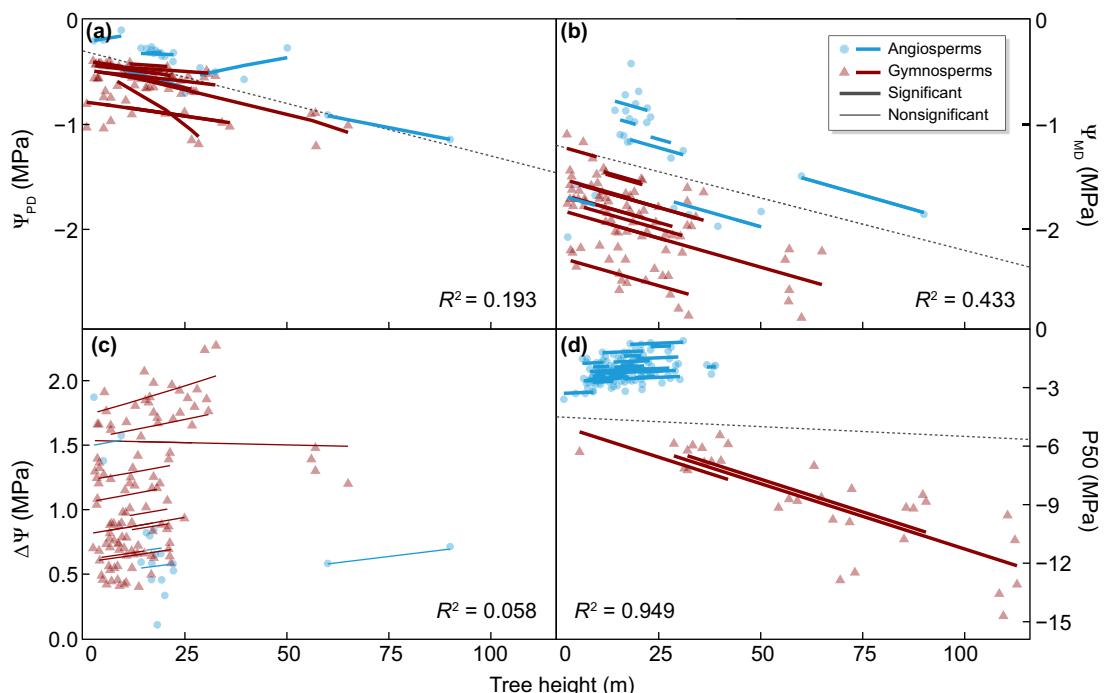


Fig. 5 Changes with tree height per species and site in (a) predawn leaf water potential (Ψ_{PD}); (b) midday leaf water potential (Ψ_{MD}); (c) difference between Ψ_{MD} and Ψ_{PD} ($\Delta\Psi$); and (d) water potential at which 50% of branch conductivity is lost (P_{50}). Each point represents a tree or tree height category. Dashed lines represent the expected change due to the hydrostatic force (-0.01 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

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 Ψ . 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_{mass}) significantly decrease with height in both functional types regardless of sun exposure (Figs 7b, S3; Tables S3, S6).

Leaf isotopic discrimination during photosynthesis (Δ), which is an assimilation-weighted measure of intrinsic water-use efficiency ($i\text{WUE} = A/g_s$), decreases, and thus, $i\text{WUE}$ increases (Nabeshima & Hiura, 2004; Woodruff *et al.*, 2009; Zhang *et al.*, 2009; Brienen *et al.*, 2017), as trees grow taller, with few exceptions (Figs 7c, S3, S8; Tables S3, S6). This increase in $i\text{WUE}$ 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 Δ despite g_s not changing with height (Grulke & Retzlaff, 2001; Ambrose *et al.*, 2016), indicating Δ 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

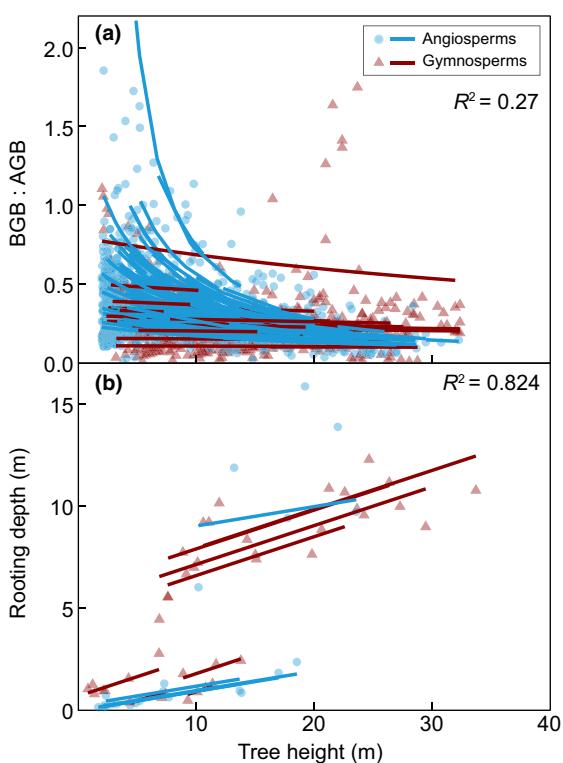


Fig. 6 Changes with tree height per species and site in (a) the below : aboveground biomass ratio (BGB : AGB) and (b) rooting depth. Each point represents a tree or tree height category. In (a), an outlier (value 6.25) is hidden. R^2 values are the variance explained by each model's fixed effects (see 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).

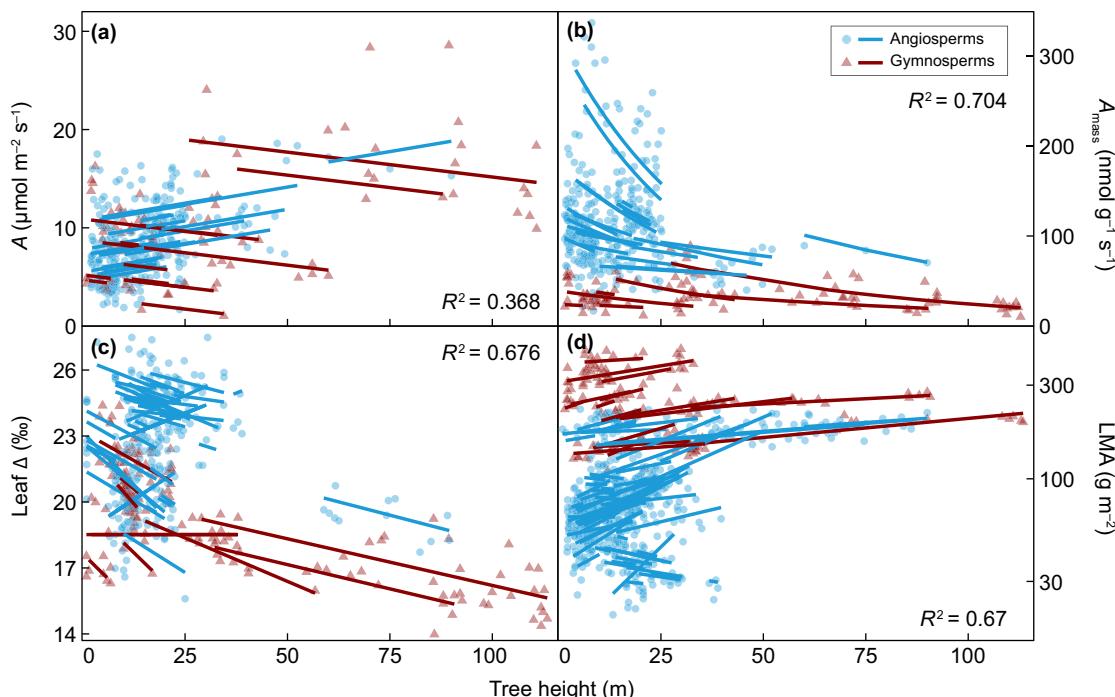


Fig. 7 Changes with tree height per species and site in (a) photosynthetic rate on a leaf area basis (A); (b) photosynthetic rate on a leaf mass basis (A_{mass}); (c) leaf ^{13}C discrimination (Δ); and (d) leaf mass per area (LMA). Each point represents a tree or tree height category. R^2 values are 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 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 CO_2 concentrations due to reductions in 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 (Sillett *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 (Sillett *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 Ψ_{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 Ψ_{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 Ψ (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 Ψ_{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 Ψ , 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 Ψ (Fig. 5, gymnosperms; Domec *et al.*, 2008), then the hydraulic safety margins will increase, reducing the risk of hydraulic failure as trees grow. While Ψ_{leaf} are significantly more negative in taller than shorter trees under nondrought conditions (Fig. 5), changes in Ψ_{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 (Ψ_{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 Ψ under drought in taller trees.

At the interspecific level, a trade-off between capacitance and P50 has been observed, with Ψ_{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)	$\downarrow G_s$ $\uparrow \text{iWUE}$ \uparrow Water storage and capacitance \uparrow Rooting depth	P50 and hydraulic safety margin trends with height
Carbon starvation	$\downarrow G_s$ $\downarrow A_{\text{mass}}$	\uparrow NSC reserves	Size-dependent minimal NSC thresholds
Biotic attacks	<i>Pathogen host preferences</i>	\uparrow LMA \uparrow NSC reserves	Height-driven changes in defence status under drought

Traits in italics were only reviewed qualitatively. A_{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; Ψ , 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 (π_{tlp} , i.e. the Ψ_{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 Ψ_{leaf} dropped below leaf P50 (Zhang *et al.*, 2009; Ambrose *et al.*, 2018). Yet, the drop of Ψ_{leaf} below the π_{tlp} and consequent stomatal closure and leaf abscission largely prevented Ψ_{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; Croucher *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 Ψ_{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 Ψ_{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 nondrought 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 monoterpenes 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 Ψ_{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 Ψ_{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.

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Competing interests

None declared.

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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_{mass}); ^{13}C discrimination (Δ); and leaf mass per area.

Fig. S4 Changes in midday water potential (Ψ_{MD}), predawn water potential (Ψ_{PD}), difference between Ψ_{MD} and Ψ_{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_{mass}), leaf ^{13}C discrimination (Δ), 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_{mass} , Δ , 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 (Ψ_{PD} , Ψ_{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_{mass} , Δ , LMA and leaf area) within (centred height) and among species (mean height) as a function of species type (angiosperms vs conifers) and their interaction.

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