



# Tree growth strategies mediate drought resistance in species-diverse forests

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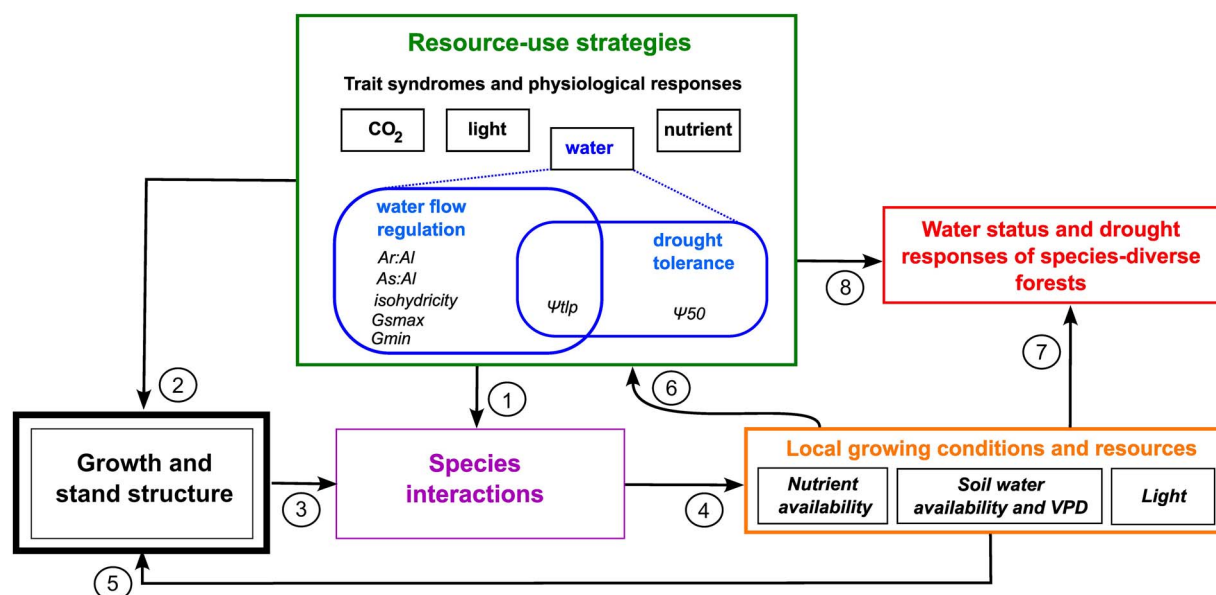
This scientific commentary refers to ‘Water status dynamics and drought tolerance of juvenile European beech, Douglas fir and Norway spruce trees as dependent on neighbourhood and nitrogen supply’ by Paligi et al. (2024).

The increasing frequency and severity of drought events associated with climate change are threatening forests worldwide. Therefore, the adaptation of managed forests to drier conditions is a crucial research priority (Keenan 2015). Increasing tree species diversity is often advocated as an important management option to achieve this goal, but the effect of tree species diversity on a forest’s ability to cope with drought remains elusive, with previous studies reporting positive, neutral and negative effects (Grossiord 2019, Haberstroh and Werner 2022). Writing in this issue of *Tree Physiology*, Paligi et al. (2024) conducted an innovative sapling experiment to explore drought responses in species-diverse forests. This timely work brings important new insights into a blind spot of tree diversity effects, and paves the way for future research endeavours. Here, we discuss a promising research direction illustrated by the work of Paligi et al. (2024): tree growth dynamics, shaped by the ecological strategies of tree species, mediates drought resistance in species-diverse forests.

Paligi et al. (2024) conducted a three-factorial sapling experiment to explore the effect of diversity (i.e., pure versus mixed neighbourhoods) on tree water status under contrasted levels of water and nitrogen availability. They measured tree growth and a set of key water-relation traits: stomatal conductance (i.e., hydroscape area), shoot water potential (at predawn:  $\psi_{PD}$ , at midday:  $\psi_{TMD}$ , at turgor loss point:  $\psi_{TLP}$ , and the point where  $\psi_{PD} = \psi_{MD}$  denoted  $\psi_{INT}$ ), branch xylem embolism vulnerability ( $\psi_{50}$ ) and minimum epidermal conductance ( $G_{min}$ ). Paligi et al. (2024)’s results show that drought-induced hydraulic risk in tree mixtures is not well predicted by water-relation trait plasticity. Although Douglas fir and spruce exhibited comparable trait values, the associations ‘beech–Douglas fir’ and ‘beech–spruce’ yielded contrasting results, with beech exhibiting enhanced water stress in neighbourhood of Douglas, but improved water

status (and growth) when mixed with spruce. This may stem from the fact that tree drought resistance is determined by an interacting set of traits (Delzon 2015), many of which are potentially affected by tree diversity (Figure 1). For example, Moreno et al. (2024) showed that mixture benefits the anisohydric *Quercus ilex* with no negative impact on the isohydric *Pinus halepensis* only because, in addition to their differences in stomatal regulation stringency, *P. halepensis* is able to reduce water losses to the soil and the atmosphere (i.e., low leaf residual and soil-root conductance under drought). Recently developed tree hydraulic and water-use models can help predict the outcome of drought in (diverse) forests by integrating the influence of interacting traits related to water flow and water status regulation (De Cáceres et al. 2021, Ruffault et al. 2022).

Yet, another reason may explain why it is so hard to predict the effects of tree diversity on drought resistance: tree drought resistance in species-diverse forests is not only influenced by water-relation traits, but also by the growth strategies of the species mixed. The resource-use strategy of a tree species (i.e., the rates of acquisition and processing of water, carbon and nutrient) crucially influences its growth rate. In a species-diverse forest, the association of contrasting resource-use strategies (hence, contrasting species growth rates) determines over time the size of a tree relative to its (heterospecific) neighbours, and the amount of resources available for this tree at a given point in time. For example, the size of root apparatus (water acquisition organ), the size of leaf area (transpiring organ) and the height-related water relation constraints of the neighbours will influence their water use and the amount of water available for the target tree. The contrast in growth strategies among tree species is advocated in Paligi et al. (2024) as an important determinant of diversity effects in water status, as Douglas fir outperformed beech in growth rate, and therefore, in sapling size, leaf area and water use. The importance of growth strategies in driving drought resistance in tree mixtures was also reported by another recent pot experiment study (Mas et al. 2024a). Differences in growth strategies (and therefore in tree size distributions) may also



**Figure 1.** Tree drought resistance in mixed forests is influenced by water-relation traits but also by the ecological strategies driving tree species resource-use and growth, which is partly mediated by nutrient cycling. The water-use strategies of the trees in mixture determine the species interaction effects on resource use (arrow no. 1). Resource-use strategies (including strategies for acquisition and processing of CO<sub>2</sub>, light, water and nutrient) drive growth dynamics and stand structure (arrow no. 2), which influence species interactions over time (these interactions include facilitation, selection and resource partitioning, arrow no. 3). These species interaction determine the local resource available for each tree in mixture, as well as the atmospheric water demand (arrow no. 4), which impacts growth (arrow no. 5). On the long term, nutrient and water availability, and light exposure can influence traits related to water regulation and drought tolerance (arrow no. 6). Tree water stress and associated drought responses are then determined jointly by local growing conditions (e.g., local soil water availability) and the species' traits (arrows nos 7 and 8). See references supporting these links in the main text.  $A_r:A_l$  is root area: leaf area ratio,  $A_s:A_l$  is sapwood area: leaf area,  $G_{smax}$  is the maximum stomatal conductance,  $\psi_{tlp}$  is the turgor loss point,  $G_{min}$  is minimum epidermal conductance,  $\psi_{50}$  is the xylem pressure inducing 50% loss in conductance.

explain why field and pot experiment studies reach, in some instances, contrasting conclusions. For example, two recent studies of oak–pine mixtures showed a positive effect for oaks, but only the field study reported a negative effect for pines (Mas et al. 2024b, Moreno et al. 2024), which may be a consequence of their bigger size and shallower root exploration (which cannot be evaluated in pot experiments).

Over the long term, differences in growth strategies among species drive stand structure in diverse forests, with implications for micro-climate buffering (Zhang et al. 2022, Ma et al. 2023) and total leaf area (therefore, total water-use), which can strongly affect the water stress of the mixed species (Decarsin et al. 2024). This view is synthesized in Figure 1, where species interactions with regard to drought resistance are shaped not only by water-use strategies, but also by the other dimensions of a species' resource-use strategy, through growth. In turn, these interactions determine the local soil water availability and atmospheric water demand of a tree in mixture. Tree water stress and associated drought responses are then determined jointly by local conditions and the species' traits.

The view proposed in Figure 1 implies that the coordination of species' drought resistance with the other ecological strategies governing growth rate will crucially determine the way a diverse forest copes with drought. Paligi et al. found total sapling growth to be largely independent from the axes describing hydraulic traits. Yet, the way drought resistance relates to the trait trade-off axes governing tree functions and forest demography is still debated in the literature (Torres-Ruiz et al. 2024). Other studies conducted at larger scale found significant coordination between drought resistance

and ecological strategies and growth (Eller et al. 2018, Guillemot et al. 2022). A better understanding of these trade-offs and synergies in local and regional tree species communities will help predict the drought responses of diverse forests.

Importantly, this perspective on growth and resource-use strategy put the focus on the implication of resources other than water, especially nutrients, in the drought resistance of diverse forests. Paligi et al. (2024) found that nitrogen addition increased stomatal conductance in the studied species, without deteriorating water status. This result adds to a growing body of evidence that suggests that nutrient availability influences a variety of tree drought responses (Gessler et al. 2017). Because tree diversity can influence local nutrient availability and tree nutrition (Richards et al. 2010, Figure 1), e.g., through diversity-mediated changes in nutrient return through litterfall (Huang et al. 2017, Beugnon et al. 2023), the nutrient cycle may indirectly affect the drought resistance of species-diverse forests. However, this remains largely unknown and warrants further research.

Finally, the importance of growth and size-distribution in the drought resistance of diverse forests also implies that we need long-term field tree experiments to evaluate the effects of tree diversity on forest drought resistance. This is the purpose of the TreeDivNet, an international network of field tree experiments designed to test for biodiversity effects on forest functioning (Verheyen et al. 2016, Depauw et al. 2024). A recent study conducted in this network revealed that tree diversity can strongly improve the resistance of dominated species to extreme drought, probably through greater

microclimate buffering (Decarsin et al. 2024). Furthermore, integrating ecological strategies in our understanding of tree diversity effect on drought resistance is also crucial to better understand how tree species interactions change over time (Urgoiti et al. 2022), as well as to evaluate the long-term persistence of interesting species mixtures during forest succession and how this can be influenced by management.

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## Data availability

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