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Commentary

Faster drought recovery in anisohydric beech compared with isohydric spruce

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This scientific commentary refers to ‘Physiological recovery of tree water relations upon drought release-response of mature beech and spruce after five years of recurrent summer drought’ by [Hesse et al.](#) (doi: [10.1093/treephys/tpac135](https://doi.org/10.1093/treephys/tpac135)).

With drought and heat events increasing in frequency and intensity worldwide, global drought-induced tree decline ([Allen et al. 2010](#), [Hammond et al. 2022](#)) has resulted in widespread interest in understanding the physiological mechanisms that underlie tree death. Unprecedented mortality rates threaten forest function and ecosystem services, including carbon (C) sequestration, clean air and water, and recreational and emotional value. Researchers have aimed to understand the mechanisms of tree mortality to better predict which trees will die or survive, inform future forest dynamics and improve forest management practices ([McDowell et al. 2008, 2011](#), [Raffa et al. 2008](#), [Sevanto et al. 2014](#), [Gaylord et al. 2015](#), [Adams et al. 2017](#)).

With intense investigation of the physiological mechanisms of tree mortality came research identifying species-specific stomatal regulation strategies along with the iso–anisohydric continuum ([Tardieu and Simonneau 1998](#), [Klein 2014](#)), first identified by [Berger-Landefeldt \(1936\)](#). More specifically, research addressed how contrasting stomatal regulation strategies under drought may contribute to species-specific mortality vulnerability ([McDowell et al. 2008](#)). An isohydric behavior is commonly described for species that exhibit a stringent stomatal response to drought and close stomata with declining soil moisture to maintain constant midday leaf water potentials. In contrast, anisohydric species exhibit a less severe stomatal response to

drought than isohydric ones, allowing leaf water potentials to track declining soil moisture. The initial appeal of classifying species based on isohydricity to predict tree mortality has led to a burgeoning number of studies over recent years ([Figure 1](#)). Most of this work compared co-occurring species from opposite ends of the iso–anisohydric (isohydricity) continuum, including (but not limited to) evergreen species (*Pinus edulis*, *Juniperus monosperma*: [McDowell et al. 2008](#), [Limousin et al. 2013](#), [Woodruff et al. 2015](#), and *Picea wilsonii*, *P. tabuliformis*, *J. przewalskii*: [Wang et al. 2021](#)), grapevine varieties (*Vitis vinifera*: [Schultz 2003](#)), deciduous hardwood species (*Acer saccharum*, *Liriodendron tulipifera*, *Quercus alba*: [Kannenberget al. 2019](#)), shrubs (*Sorbus aucuparia*, *Sambucus nigra*: [Vogt 2001](#)) and a mix of evergreen and deciduous species (*Q. fusiformis*, *Diospyros texana*, *Prosopis glandulosa*, *J. ashei*: [Johnson et al. 2018](#)). Based on these findings, anisohydric species are often viewed as more drought resistant than isohydric ones, as exhibited by their lower turgor loss point and osmotic potential at full turgor ([Meinzer et al. 2014, 2016](#)), greater stored nonstructural carbohydrates ([Dickman et al. 2015](#), [Woodruff et al. 2015](#)), greater wood density ([Meinzer et al. 2017](#), [Chen et al. 2021](#)), higher resistance to embolism (e.g., a more negative water potential at which 50% of hydraulic conductivity is lost, P₅₀) ([Linton et al. 1998](#), [Martínez-Vilalta et al. 2014](#)) and often, deeper rooting systems (e.g., [Grossiord et al. 2017](#)). However, the opposite has also been found with anisohydric species having narrower hydraulic safety margins and lower embolism resistance ([Benson et al. 2022](#)) (which may be because of the anisohydric species in the study being ring-porous;

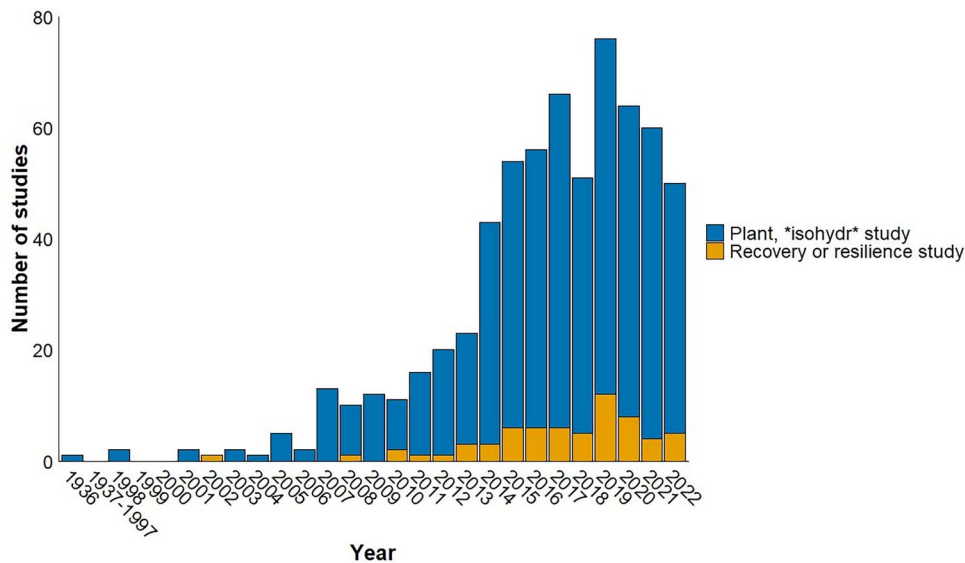


Figure 1. Web of Science search for the terms 'plant' and '*isohydr*' (1900–2022) yielded 577 articles in total (blue), and the number of these studies has increased substantially since 2008. Of these studies, 64 studies (11%) included the term 'recovery' or 'resilience' (orange). The number of recovery studies has been slowly increasing.

Kannenberg et al. 2019). Additionally, even anisohydric species that exhibit higher embolism resistance and hydraulic safety margins can experience higher mortality than co-occurring isohydric ones (Johnson et al. 2018), which further complicates our understanding of the link between isohydricity and drought vulnerability.

However, while much attention has been directed toward investigating drought-induced mortality mechanisms and identifying functional responses that could improve our understanding of mortality trajectories, being able to predict drought recovery (resilience) is of equal importance. Research investigating drought recovery and resilience mechanisms is ever more relevant today, given that we are undergoing warmer, drier climates than we had anticipated decades ago. Moreover, extreme events are occurring more frequently. Hence, the ability of trees to recover from past droughts is becoming a major component shaping future forests. Just 64 of the 577 studies (11%) on isohydricity included the term 'recovery' or 'resilience' (Figure 1), and we encourage research efforts on this critical knowledge gap to continue. Intensively examining how species spanning a broad range of stomatal regulation strategies recover from drought and whether drought-resistant species are also more drought-resilient will improve our understanding of species-specific drought vulnerability and enable more accurate predictions of forest dynamics. This is what makes studies like (Hesse et al. 2022) in the latest issue of *Tree Physiology* ever more needed. Their analysis and quantification of recovery time and resilience shed new light on how isohydricity may be linked to drought recovery.

In Hesse et al., the authors compared the resilience and recovery time between relatively anisohydric European beech

(*Fagus sylvatica* L.) and relatively isohydric spruce (*Picea abies* (L.) Karst.). In this mature temperate mixed forest in southeast Germany, the authors imposed a drought using precipitation exclusion shelters that withheld all precipitation and runoff at the KROOF experiment (Grams et al. 2021). After 5 years, they watered the droughted plots to the level of the soil water content of the control plots and monitored available plant water, leaf water potentials, stomatal conductance, osmoregulation, sap flow and leaf abscisic acid (ABA) concentration. Within 2 years, all traits (except spruce sap flow) achieved full resilience (i.e., no difference from control values) but varied in recovery times between species and traits. Generally, isohydric spruce recovered more slowly than anisohydric beech. Recovery times were the fastest for leaf water potentials, followed by stomatal conductance and osmoregulation. In both species, the function that recovered the slowest was sap flow, with spruce sap flow not fully recovering to control levels within 2 years. ABA, a plant hormone involved in stomatal closure, did not change in response to drought in beech, but increased in spruce before quickly and fully recovering within 7 days after rewatering.

Hesse et al.'s results suggest that anisohydric beech trees were more drought resilient with a faster recovery time than isohydric spruce (Figure 2). One might hypothesize that beech exhibited greater resilience and quicker recovery than spruce because the drought had less severe effects on the hydraulic functions in beech than spruce (i.e., beech was also more drought resistant than spruce). This is important because greater stress severity can reduce recovery time in various physiological traits, including gas exchange (Li et al. 2021), photosystem II function (Marias et al. 2017), hydraulic functions (Brodribb and Cochard 2009) and traits related to

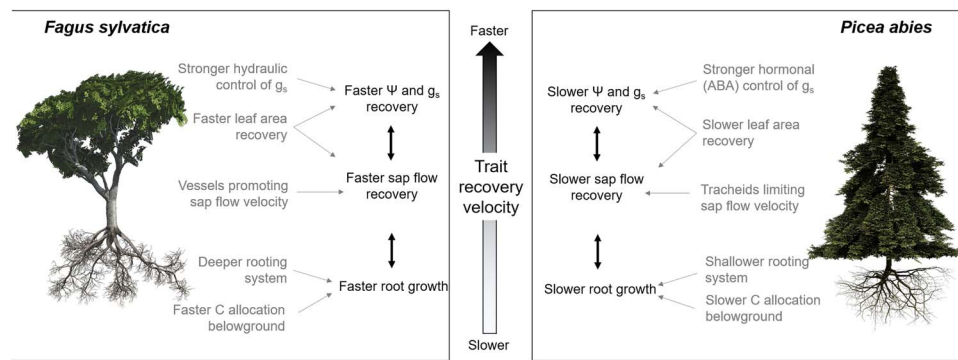


Figure 2. Mechanisms underlying drought recovery of predawn leaf water potential (ψ), stomatal conductance (g_s), sap flow and root growth in anisohydric beech (*Fagus sylvatica*) and isohydric spruce (*Picea abies*). Hesse et al. found that physiological and biochemical traits such as ψ and g_s recovered faster (from days to weeks) than traits related to morphology such as sap flow, which depends upon root and leaf area regrowth (from months to years).

C and water relations (Ruehr et al. 2019). In Hesse et al., predawn leaf water potentials of both species dropped to -1.8 MPa after 5 years of drought. This predawn leaf water potential value for isohydric spruce should have more severe impacts on water use than for anisohydric beech. For example, species that have greater embolism resistance (e.g., P_{50}), wider hydraulic safety margins and more negative turgor loss points may be more drought tolerant and able to continue functioning under drought, as is widely observed with increasing anisohydricity (Martinez-Vilalta et al. 2014, Meinzer et al. 2016, Fu and Meinzer 2019). However, given that higher anisohydricity does not always indicate higher drought tolerance or survival (Johnson et al. 2018, Kannenberg et al. 2019), it is clear that the iso–anisohydric continuum of stringency of plant water–status regulation involves coordination and trade-offs among multiple coevolved traits (Bartlett et al. 2016, Ratzmann et al. 2019).

Hesse et al.'s study highlights this need to consider multiple traits in addition to stomatal sensitivity to drought in determining plant drought resistance, resilience and recovery. For example, Hesse et al. and previous studies at the same experimental site found beech and spruce to have similar P_{50} (-3.42 , -3.74 MPa, respectively; Tomasella et al. 2018) and turgor loss point (-2.40 , -2.43 MPa, respectively; Hesse et al. 2022). Unexpectedly, beech had a narrower hydraulic safety margin (1.54 MPa) than spruce (2.11 MPa) (Tomasella et al. 2018). Therefore, the findings of Hesse et al. suggest that other traits beyond those traits more frequently measured to assess drought resistance underlie the differences in recovery time between beech and spruce. These traits include ABA-driven stomatal closure in isohydric species versus more hydraulics-driven stomatal closure in anisohydric ones; slower regrowth of leaf area in spruce than beech, lowering and delaying the water demand by the spruce canopy; deeper rooting system of beech than spruce (Nikolova et al. 2009, Rötzer et al. 2017); slower regrowth of fine roots in spruce than beech after drought release

(Nickel et al. 2018, Zwetsloot and Bauerle 2021), limiting water uptake of spruce after watering and promoting faster C turnover in beech than spruce (Nikolova et al. 2020); and the presence of vessels in angiosperms promoting more efficient water transport versus the lack of vessels in gymnosperms (Figure 2). Spruce's slower recovery compared with beech may also be related to reductions in stored C reserves that more likely occur in isohydric species because of drought-induced restrictions on stomatal conductance and C assimilation (Sevanto et al. 2014, Woodruff et al. 2015). Additionally, anisohydric juniper has exhibited greater adjustment in response to hydration than isohydric pinyon (Meinzer et al. 2014), which may also contribute to beech's faster recovery. As emphasized by Hesse et al., isohydricity incorporates coordination among multiple traits, including stomatal regulation of leaf water potential under drought, drought resistance metrics (P_{50} , turgor loss point, hydraulic safety margin) and other traits (hormonal, morphological, structural, C balance and allocation) that deserve further attention.

Are more drought-resistant species also more drought-resilient? Previous work has suggested a tradeoff between resistance and resilience in gymnosperms (Gebauer et al. 2020, Li et al. 2020) and evergreen oak species (Fallon and Cavender-Bares 2018). However, Hesse et al.'s findings suggest that more resistant species may also be more resilient, which may be independent of stomatal regulation strategy (Kannenberg et al. 2019), and instead relate to wood density and hydraulic safety margins that increase drought resistance and resilience (Duan et al. 2013), as well as traits less frequently measured including leaf ABA concentration, morphology, structure and C balance and allocation (Hesse et al. 2022). Reduced recovery (legacy effects) was consistently prevalent in dry ecosystems among Pinaceae and species with low hydraulic safety margins (Anderegg et al. 2015).

Hesse et al.'s study nicely exemplifies the type of future work needed to understand how other traits beyond stomatal

regulation strategy affect drought recovery and to identify species' drought vulnerability, resistance and resilience. Like Hesse et al., we need more studies that focus on long-term (i.e., multi-year) effects of drought, particularly work including drought recovery. Future work should also measure multiple types of traits, including stomatal regulation of leaf water potential under drought, drought resistance metrics (P_{50} , turgor loss point, hydraulic safety margin), but also other traits that are less frequently included in our ecophysiology toolbox (hormonal, morphological, structural, C balance and allocation) to holistically understand plant physiological recovery mechanisms. Finally, more research should expand beyond these two species and assess resilience and recovery time in a wide range of species spanning leaf habit (evergreen, deciduous) as in Hesse et al., and the iso-anisohydric continuum. With more research on recovery time and resilience across species and functional groups, we may be able to identify an easier-to-measure proxy for recovery time and resilience that may improve broader predictions of forest vulnerability and resilience to drought.

Conflict of interest

None declared.

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