Commentary

Connecting the dots: concurrent assessment of water flows and pools to better understand plant responses to drought

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Received April 17, 2023; Accepted June 15, 2023; handling Editor Sanna Sevanto

Keywords: isotope labelling, Pinus, Quercus, sap flow, water status regulation, water storage, water-use strategies.

This scientific commentary refers to ‘Contrasting stem water uptake and storage dynamics of water-saver and water-spender species during drought and recovery’ by Martín-Gómez et al. (doi: 10.1093/treephys/tpad032).

Drought is a key stress factor determining plant distribution and functioning (Woodward 1987). Because climate change is causing warmer and frequently drier conditions, the importance of drought in driving vegetation dynamics and functioning is expected to increase in many regions (Brodribb et al. 2020). As a result, the interest in understanding how plants respond to water shortage, which has always been high, is higher than ever for both ‘natural’ systems and croplands (Gupta et al. 2020).

Yet, despite the huge amount of research on this topic, important aspects of plant drought responses remain poorly understood. Our current understanding of plant–water relations is largely based on the regulation of water use and water status in terms of leaf water potential, which allows a consistent and thermodynamically grounded treatment of water transport along the soil–plant–atmosphere continuum (Slatyer and Taylor 1960, Kramer 1988). This approach has been extremely successful and led to the fast development of xylem hydraulics since the 1980s (Tyree and Sperry 1989, Tyree and Zimmermann 2002). Axial water flows in the xylem, however, are only part of the story. This is in part because extra-xylary processes in leaves (Scoffoni et al. 2017) and roots (Cuneo et al. 2016) frequently control plant hydraulic responses to drought. But, this is also due to the role of living cells in the xylem parenchyma and the phloem, which store water and may release it into xylem conduits, depending on the local water potential gradients. This capacitance allows buffering fluctuations in xylem water potentials induced by rapid changes in transpiration, and it is an essential component of whole-plant–water relations (Meinzer et al. 2009, McCulloh et al. 2019). Despite the increased recognition of the importance of plant–water pools in determining drought responses, including the vulnerability to drought-induced mortality (Martínez-Vilalta et al. 2019, McDowell et al. 2022), our knowledge of their distribution and temporal dynamics under drought remains limited.

In this current issue, Martín-Gómez et al. (2023) present a comprehensive study of water uptake and storage dynamics during and after a mild drought for saplings of two species with contrasting water-use strategies: a pine (Pinus sylvestris L.) and an oak (Quercus faginea Lam.). This study is important and timely for several reasons. First, because it combines different approaches that allow measurement of a diverse range of variables that are seldom assessed concurrently. These variables include plant and soil water status in terms of both water potential and water content, leaf-level gas exchange (assimilation, transpiration and stomatal conductance), whole-plant–water use (from sap flow sensors and gravimetric measures) and the dynamics of xylem water pools from a dual $\delta^{18}O$–$\delta^{12}H$ isotope-labelling experiment. Second, the study species represent the two tree families (Pinaceae and Fagaceae).
that dominate temperate forests in the northern hemisphere. Their comparison is particularly meaningful because these two families have been hypothesized to show opposite responses to climate warming (Carnicer et al. 2013), and an increased dominance of Fagaceae at the expense of Pinaceae species has been already observed across many temperate forests (Alfaro Reyna et al. 2018).

In addition, the two study species are characterized by contrasted drought response strategies: while the pine shows a strict regulation of water use (water saver) and water status (relatively isohydic regulation of leaf water potential), the oak presents a looser regulation in terms of both water fluxes (water spender) and status (relatively anisohydic). Note that this correspondence between the regulation of water use and that of water status is common but is by no means necessary. For instance, a plant can maintain relatively high water use under (climatic) drought (water spender strategy) and at the same time keep relatively constant water potentials (∼isohydic behaviour) if it has deep roots that allow access to reliable water stores in the soil (e.g., Jiang et al. 2020).

Martín-Gómez et al. provide evidence for a tight coordination between leaf-level water status and use and water uptake and storage patterns in stems (Figure 1). In particular, the more conservative water-use strategy of the pine was associated with rapid stomatal closure and fast declines in water use during drought, which avoided substantial declines in twig water content, but also with a faster recovery of xylem water potential and a slower replacement of xylem water after irrigation. By contrast, the oak’s more acquisitive strategy implied a generally looser stomatal regulation and higher sap flow before, during and after the drought. This behaviour was also associated with lower xylem water potentials and a substantial decline in the water content of twigs, which implied a slower recovery of water status despite its capacity to quickly replace xylem water after irrigation.

Like any good paper, the study by Martín-Gómez et al. provides interesting insights but also opens new questions. An important aspect is that the drought treatment imposed in the study is quite mild, and the plants (of either species) never reach water potentials expected to cause xylem hydraulic dysfunction. The water potential causing 50% loss of xylem hydraulic conductivity (Ψ50) is around −3 MPa for P. sylvestris (Martínez-Vilalta et al. 2009) and even lower for Q. faginea (Esteso-Martínez et al. 2006), so it is unlikely that plants experienced substantial (>20%) conductivity losses in the xylem. What would have happened under a more intense drought? It can only be hypothesized that lower water potentials would have induced even stronger reductions in water content and a reduced ability to replace water from conductive tissues, particularly after the hydraulic failure of the xylem. How the detailed dynamics of water pools in the plant around this inflexion point would reflect the different water-use strategies of the study species and would relate to their vulnerability to drought are far from trivial (Martínez-Vilalta and Garcia-Forner 2017) and remain to be explored.

Under the mild edaphic drought conditions imposed in the experiment by Martín-Gómez et al., processes at the root–soil interface are likely driving some of the observed differences between species and periods. Moderate soil water stress already reduces hydraulic conductance at the soil–root interface to a degree that the root and rhizosphere become the main hydraulic bottleneck and severely constrain plant gas exchange (Carmiñati and Javaux 2020, Rodriguez-Dominguez and Brodribb 2020). Belowground constraints to soil water uptake during edaphic drought have been reported for P. sylvestris under field conditions (Poyatos et al. 2018), and hydraulic disconnection from the soil may be a general water-saving strategy across Pinus species (e.g., Plaut et al. 2012). These reductions in the soil-to-root hydraulic conductance could be causing the slower labelling speed and the steeper decrease of whole-plant hydraulic conductance as a function of the soil water potential observed for P. sylvestris. In Q. faginea, sustained high transpiration rates during drought could also reduce the soil-to-root hydraulic continuity and explain the reductions in the whole-plant hydraulic conductance and the different response of gas exchange to soil water potential observed during the second drought cycle (see Figures 2 and 3 in Martín-Gómez et al. 2023). Of course, some of these soil-to-root hydraulic restrictions may be associated with the use of potted plants and the substantial size differences between the saplings of the two species, and how they would play under field conditions remains an open question.

The study by Martín-Gómez et al. provides new insights into the dynamics of xylem stored water and its use to supply transpiration during drought in species with contrasting wood structure and water-use strategies. Higher transpiration in oaks led to higher drought-driven twig xylem dehydration and delayed rehydration following irrigation when compared with pines. Water release into the transpiration stream is believed to have different sources, which are likely to dominate sequentially as water potentials decline in the xylem: capillary storage in intercellular spaces or already embolized vessels, tracheids and fibres; elastic storage in xylem parenchyma and phloem cells; and embolizing vessels and tracheids (Tyree and Yang 1990). Given the range of water potentials experienced by both species in the study, the capacitive effect of embolism is likely to be small. The authors associate the higher capacitance of Q. faginea with higher elastic storage in parenchyma cells due to the greater fraction of non-conductive tissue and parenchyma expected in this ring-porous species. Although wood parenchyma is often assumed to be a reservoir of capacitance water, recent studies have shown that wood porosity or parenchyma fraction is not necessarily related to capacitance in temperate tree species (Jupa et al. 2016, Zieminska et al. 2020), and they point towards capillary water (Knipfer et al. 2019) as a substantial source of water for transpiration in these
species. More detailed assessments of stem water pools are needed to quantify the role of different sources of capacitive water under different contexts. In addition, the focus of the study on xylem water pools (and small saplings) leaves some open questions as to the role of other storage compartments in roots (Scholz et al. 2011), leaves (Preisler et al. 2022) and the inner bark (Pfautsch et al. 2015, Peters et al. 2023), which can become critical to buffer drought stress in field-grown, mature trees (Salomón et al. 2022).

Studies combining isotope labelling, detailed monitoring of water fluxes and pools, and storage and transport traits face methodological challenges that are largely associated with the tracing of the isotopic label along the plant hydraulic pathway. First, the use of relatively small saplings greatly minimizes the logistic difficulties of studies on mature trees in the field (use of canopy cranes: James et al. 2003, Meinzer et al. 2006, or tree felling: Treydte et al. 2021) but at the expense of potential artefacts associated with repeated destructive samplings on small trees, as already acknowledged by Martin-Gómez et al. Second, the discrete sampling for the isotopic tracer hampers a more continuous detection of the label and limits the temporal resolution of the processes that can be addressed. The combination of isotopic labelling with in situ isotopic monitoring of soil, xylem and transpired water during experimental droughts (Volkmann et al. 2016, Gessler et al. 2022) has the potential to provide even more detailed information on the role and (re-)distribution of different plant–water pools under drought. This could help resolve, for instance, the puzzling fact that the dynamics of water potential and water content were partially disconnected in P. sylvestris, as the former declined noticeably during drought, whereas the latter was barely affected (cf., Figures 1 and 5 in Martín-Gómez et al.).

From the wider perspective of the ecological strategies of the two study species, which frequently coexist in the field, it is interesting to note that the leaf-level gas exchange and whole-plant–water use were higher in Q. faginea than in P. sylvestris throughout the study period regardless of water availability. The oak water use was also less impacted by drought, which is consistent with the fact that its xylem is both more efficient (higher conductivity) and safer (less vulnerable to embolism) than that of P. sylvestris. How can the water saver (and less carbon acquisitive) strategy of the pine be so successful then? Part of the answer could lie in species interactions and hydrological niche segregation (del Castillo et al. 2016), although similar dynamics of water use to those reported by Martín-Gómez et al. have been observed in field studies, both for the same species pair (Grossiord et al. 2015) and for similar oak–pine pairs in sub-Mediterranean forests (Forner et al. 2014, Aguadé et al. 2015, Martín-Gómez et al. 2017). Further studies should address the costs and benefits involved in both strategies under current and future climatic conditions and how hydraulic disconnection from the soil and a high capacity to retain water in their tissues help pines compensate for their apparently inferior hydraulic system. While we still lack a fully convincing framework linking plant–water use and drought resistance strategies with vulnerability to drought (Kannenberg et al. 2022), comprehensive studies such as the one by Martín-Gómez et al. clearly move us in the right direction.
Data availability statement

No new data were created or analysed in this study. Data sharing is not applicable to this article.

References


