

How the interactions between atmospheric and soil drought affect the functionality of plant hydraulics

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Rising temperature and vapor pressure deficit (VPD) are predicted to increase transpiration demand and to cause a decline in stomatal conductance and photosynthesis (Novick et al., 2016). To avoid excessive drops in leaf water potential, plants down-regulate water use by reducing stomatal conductance. Typically, stomatal closure anticipates hydraulic failure of the xylem, with the leaf water potentials at which stomata close being less negative than those at which the xylem cavitates (Anderegg et al., 2017). The coordination between stomatal closure and hydraulic limitations is a well-accepted principle of plant water relations (Sperry et al., 2017). Yet, it is not clear which hydraulic element of the soil–plant continuum is the primary limit to transpiration. Recent experimental findings indicated that outer-xylem tissues (Albuquerque et al., 2020) and the root–soil interface (Abdalla et al., 2022; Rodriguez-Dominguez & Brodribb, 2019) have a controlling role on stomatal regulation. Carminati and Javaux (2020) proposed that the loss of soil hydraulic conductivity is the first trigger of stomatal closure.

The recent paper by Schönbeck et al. (2022) investigated the effect of rising VPD and temperature on plant hydraulics. The authors observed that VPD and temperature led to losses in stem hydraulic conductivity independently from soil drought. They examined young trees (3 years old) of *Fagus sylvatica* L., *Quercus pubescens* Willd., and *Quercus ilex* L. and evaluated the responses of multiple hydraulic and physiological traits to increasing VPD and temperature. Significant losses in stem xylem hydraulic conductivity, up to about 75% in *F. sylvatica* and *Q. pubescens*, were observed. The authors concluded that ‘VPD and temperature can cause major hydraulic dysfunctions’ (Schönbeck et al., 2022).

Interestingly, despite substantial loss in stem xylem conductivity, both in *F. sylvatica* and *Q. pubescens*, there was no ‘functional’ hydraulic damage, in the sense that there was no loss in conductance of the entire soil–plant hydraulic system (Figure 1a–c). The total soil–plant hydraulic conductance K_{sp} [$\text{mmol s}^{-1} \text{MPa}^{-1}$] is defined as:

$$K_{sp} = \frac{E}{\psi_{\text{leaf,pd}} - \psi_{\text{leaf,md}}}$$

where E is transpiration rate [mmol s^{-1}], $\psi_{\text{leaf,pd}}$ and $\psi_{\text{leaf,md}}$ are leaf water potential at predawn and midday [MPa]. The relation between leaf-level transpiration rate and the difference in leaf water potentials between midday and predawn remained relatively constant over the course of the experiment (Figure 1d–f), despite the decline in stem xylem conductivity (Figure 4 in Schönbeck et al. [2022]). This means that stem xylem conductance did not limit the total conductance of the soil–plant continuum and that the nonembolized xylem tissues were sufficient to sustain the observed fluxes under these conditions. It appears that in their case the stem xylem was more conductive than the entire soil–plant system even under substantial embolism formation.

Schönbeck et al. (2022) highlighted that the observations of xylem hydraulic damage were found ‘without soil drought’. Indeed, in their study there was no decline in soil–plant hydraulic conductance, and presumably neither xylem embolism nor partial soil drying limited transpiration. Therefore, it is reasonable to assess their environmental conditions as ‘without soil drought’. Yet, we would like to raise the general issue that defining soil drought is not obvious. A plausible definition of soil drought is related to the inability of the soil water supply to sustain the transpiration demand. Note that such

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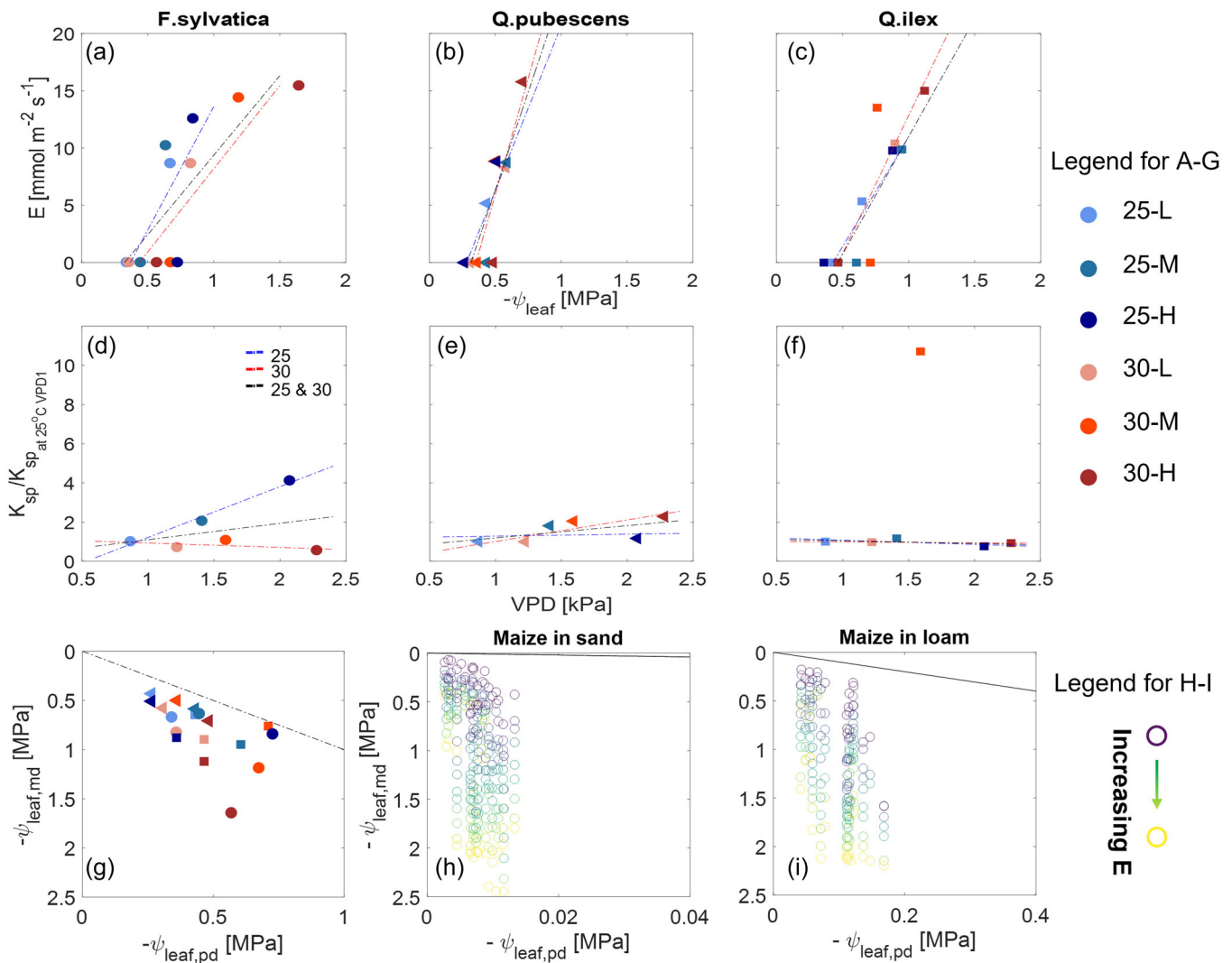


FIGURE 1 Relationship between transpiration rate (E) and leaf water potential (ψ_{leaf}) at predawn ($\psi_{\text{leaf,pd}}$) and midday ($\psi_{\text{leaf,md}}$), and soil-plant hydraulic conductance (K_{sp}) at different vapor pressure deficits (VPD). E was normalized by leaf area. The data in subplots (a-g) are from Schönbeck et al. (2022) while those in subplots (g-i) are from Cai et al. (2022). L, M, and H refer to low, middle, and high vapor pressure deficit. VPD1 on the y-axis label in subplot (d) is the lowest VPD with 25°C. Black regression lines are for all points in each subplot while blue and red lines are for the conditions of 25°C and 30°C, respectively. Values of r^2 of the black line in subplots (a-c) are 0.63, 0.76, 0.76, while in subplots (d-f) they are 0.11, 0.33, 0.31 (the high red square in subplot [f] was not considered for the fitting), respectively. The symbol shapes (round, triangle, and square) in subplots (a-g) refer to the three species. Colours from dark blue to yellow in subplot (h) and (i) represent increasing transpiration rate.

definition is pertinent to plant water use regulation, rather than to irreversible hydraulic failure. Soil limiting conditions for plant water uptake and transpiration rate can occur at relatively high soil water potentials, when large gradients in water potential develop around the roots when soil water flow becomes limiting. For instance, Cai et al. (2022) reported that in sandy soils, the soil became limiting already at water potentials of -0.01 MPa due to the extremely steep hydraulic conductivity curves of coarse textured soils, while in fine-textured soils, which have a less steep hydraulic conductivity curve, the limiting soil water potential was around -0.1 MPa (Figure 1g). These values are higher than the reported predawn leaf water potentials observed by Schönbeck et al. (2022) (see Figure 4 in Schönbeck et al. [2022]), which were around -0.5 MPa (assuming

that predawn leaf water potential approached the soil water potential), and in general are higher than those often used in studies on plant water relations during drought. Therefore, we can expect transpiration limitations also in soils that would one would consider 'relatively wet'. Note that these soil water potential thresholds refer to stomatal closure and not to irreversible hydraulic failure, which occur at more negative potentials.

While the results by Schönbeck et al. (2022) enable us to rank the effects of VPD, temperature and soil drought on plant hydraulic responses, which is definitely important, in this commentary we advocate for the importance of evaluating the interactions between atmospheric and soil drought. The reason is that the effects of VPD and temperature become increasingly and nonlinearly larger as the

soil dries, given that rising VPD and temperature cause an increase in transpiration rate. This is true until stomatal closure prevents the increase in transpiration, which comes at the cost of reduced photosynthesis. In this sense, the effect of VPD on photosynthesis increases as the soil dries. Figure 1g-i shows that the deviation of midday leaf water potential from the predawn leaf water potential is a function of transpiration rate (dark blue to yellow) and soil water potential (which decreases with decreasing predawn leaf water potential). The figure is drawn from Schönbeck et al., 2022 (Figure 1g) and Cai et al. (2022, Figure 1h-i). It shows that the loss in midday leaf water potential for a given transpiration rate becomes larger as the soil dries. In other words, the effects of VPD and temperature on the soil-plant hydraulic system are exacerbated by soil drying.

In summary, Schönbeck et al. (2022) importantly disentangled the effects of rising VPD and temperature on plant hydraulics and showed that they can induce substantial loss of stem xylem hydraulic conductivity. Moreover, their observations indicate that a loss of conductance within one part of the soil-plant continuum (i.e., stem xylem) does not automatically imply a loss of conductance of the entire water transport system. This commentary aims therefore at emphasizing the importance of studying the entire soil-plant hydraulic system. Finally, we advocate for giving more emphasis to the interactions between VPD (and temperature) and soil drying, as the effects of VPD and temperature become increasingly important with soil drying.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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