

Letter

Stomatal closure prevents the drop in soil water potential around roots

The recent paper by Rodriguez-Dominguez & Brodribb (2020) shows that the loss in soil–root hydraulic conductance is the primary constraint on water flow during water stress (soil water potential below -1 MPa) and that this initiates stomata closure. This is an important result as it highlights the link between stomatal regulation and belowground soil–root interactions, particularly those taking place at the root–soil interface and in the adjacent soil, the *rhizosphere*.

This conclusion was obtained combining different methods to estimate the total hydraulic conductance of soil and plant, as well as their components. The hydraulic conductance of the soil–plant continuum was assessed by monitoring transpiration and stem water potential in drying soils. Additionally, the hydraulic conductance of shoot and roots (including and not the interface with the soil) were measured with excised plants using a rehydration method. Remarkably, as the soil dried out, root and soil–root interface hydraulic conductances dropped significantly and became the primary constraint on water flow, more than xylem cavitation. In particular, the conductance of the root–soil interface was the one that dropped the most.

The conductance of the root and its interface to the soil ($K_{\text{root}+i}$; using the notation of Rodriguez-Dominguez & Brodribb, 2020) were measured during both, dehydration and rehydration experiments. In the dehydration method, the total soil–root conductance was estimated by dividing the midday transpiration E by the difference between soil water potential ψ_{soil} and midday stem water potential $\psi_{\text{stem-md}}$:

$$K_{\text{soil-root}} = \frac{E}{\psi_{\text{soil}} - \psi_{\text{stem-md}}} \quad \text{Eqn 1}$$

where $K_{\text{soil-root}}$ includes the effect of soil hydraulic conductivity, which is expected to decrease significantly as the soil dries:

$$\frac{1}{K_{\text{soil-root}}} = \frac{1}{K_{\text{soil}}} + \frac{1}{K_i} + \frac{1}{K_{\text{root}}} \quad \text{Eqn 2}$$

where K_{soil} , K_i and K_{root} are the hydraulic conductances of the soil, the root–soil interface, and the root. Eqn 2 implies that the element with the lowest conductance has the strongest impact on the total conductance.

At negative soil water potentials, it is expected that K_{soil} drops by many orders of magnitude, becoming the limiting element in Eqn 2

and thus controlling the loss of $K_{\text{soil-root}}$ (Passioura, 1988; Draye *et al.*, 2010). The drop in K_{soil} is concomitant with the steepening of the gradients in soil water potential around the roots. These gradients have two characteristic scales: (1) a microscopic, single-root scale ($<$ millimeters) at which the water potential around a single root becomes increasingly steeper toward the root surface (Metselaar & De Jong van Lier, 2011; Fig. 1a) (these small-scale gradients change diurnally with the transpiration rate); (2) a root architecture scale ($>$ decimeter) at which soil water is depleted in the soil regions with the highest density of roots active in water extraction (Koch *et al.*, 2018; Fig. 1b) (these gradients develop over weeks as the soil progressively dries). Both gradients contribute to limiting the water extraction from the soil, impacting the apparent $K_{\text{soil-root}}$. Note that these gradients and K_{soil} nonlinearly change with water uptake rate and transpiration.

In the rehydration method, instead of being slowly dried, the soil was quickly rewetted. Obviously, the gradients in soil water potential affecting the rehydration kinetics are not representative of those occurring during soil water extraction by roots (i.e. during dehydration). Additionally, hysteresis in soil hydraulic properties can be expected. To compare the two methods, it can be assumed that the soil hydraulic conductivity rapidly increased after rewetting and that the water potential around the roots reached a potential close to zero ($\ll$ megapascal) in a short time. In this case the soil hydraulic conductivity should not reduce the rehydration kinetics and the measured conductance is:

$$\frac{1}{K_{\text{root}+i}} = \frac{1}{K_i} + \frac{1}{K_{\text{root}}} \quad \text{Eqn 3}$$

Despite the fundamental difference between the rehydration and dehydration measurements, Rodriguez-Dominguez & Brodribb (2020) observed that $K_{\text{soil-root}}$ (Eqns 1, 2) matched very well with $K_{\text{root}+i}$ (Eqn 3), which implies that K_{soil} was not limiting during the dehydration experiments and that the gradients in water potential around the roots were not large. This is a surprising result considering that at $\psi_{\text{soil}} < -1$ MPa the soil hydraulic conductivity is expected to be a major limit to water flow to roots in most soil textures (Draye *et al.*, 2010). The fact that this was not the case indicates that stomata closed before or immediately after significant water potential gradients started to form around the roots.

It could be argued that as the plants were grown in small pots, the root length density (root length per soil volume) was sufficient to avoid the formation of large hydraulic gradients in the soil (such as those shown in Fig. 1a,b), and in more realistic conditions the soil might have more markedly limited $K_{\text{soil-root}}$. However, these gradients depend on the flux and they would have been very large if the stomata had been fully open. In that case the authors would have measured a lower $K_{\text{soil-root}}$ in the dehydration experiments than in

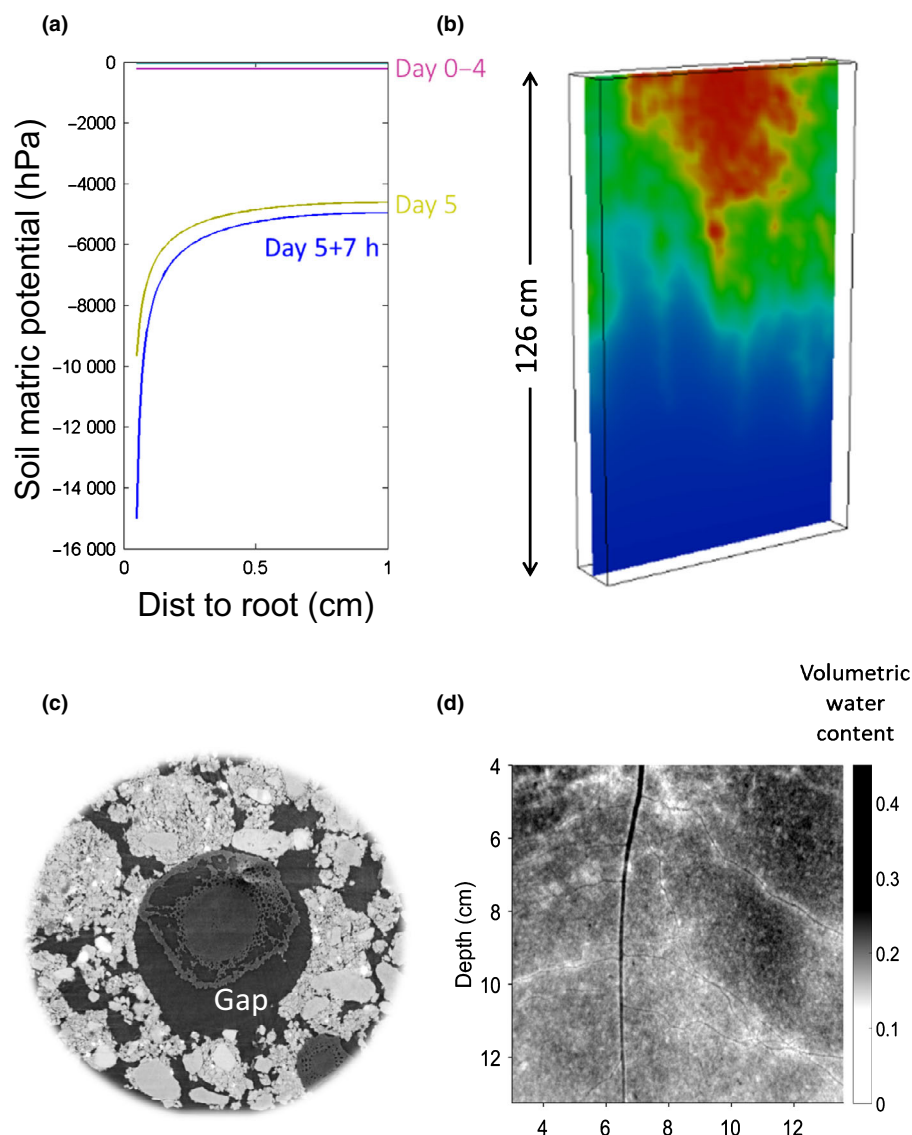


Fig. 1 Processes limiting water flow to roots. (a) Gradients in soil matric potential around a single root taking up water at constant rate from a drying soil. As the soil water potential decreases, large gradients in matric potential develop near the root surface, ultimately limiting water flow to the root surface (lines corresponding to different times) (simulations adapted from Carminati & Vetterlein, 2013). (b) Decrease in water content (red, dry soil; blue, wet soil) in the soil regions with high water extraction from roots (simulations from Koch *et al.*, 2018). (c) Synchrotron X-ray computed tomography of maize roots in a relatively dry loamy soil showing an air-filled gap between the root and the soil matrix (field of view c. 1 mm at a pixel size of $0.65 \times 0.65 \mu\text{m}^2$; air is black, soil is light gray and root is dark gray). (d) Neutron radiography of lupin roots in a sandy soil showing that the rhizosphere remained temporarily dry (due to its water repellency) after irrigation. The gray values are proportional to volumetric water contents (wet is dark) (modified from Zarebanadkouki *et al.*, 2018).

the rehydration (i.e. $K_{\text{soil-root}} < K_{\text{root+}i}$). The fact that this was not the case indicates that stomata closure avoided the drop in soil–plant conductivity, as hypothesized by Sperry & Love (2015). In Rodriguez-Dominguez & Brodribb (2020), however, the loss of hydraulic conductivity was belowground and not in the xylem. This is a remarkable result, showing a close link between stomata regulation and water potential gradients in the soil.

Despite stomatal closure alleviating the loss of soil hydraulic conductance K_{soil} , soil drying caused a large drop of hydraulic conductance at the root–soil interface K_i . The authors explained the drop in K_i with the loss of contact between soil and root surface. Indeed, gaps between root and soil have been shown and their recovery is not immediate (Carminati *et al.*, 2013). An illustrative example of the loss of contact between roots of maize and the soil matrix is shown in Fig. 1(c). In this case, it would be the loss of contact area between root and soil that limits the hydraulic conductance. Possibly, as roots shrink, the conductivity of their cortex is likely to decrease too (note the air-space in the cortex in Fig. 1(c)). Disentangling the changes in the conductivity of the cortex

from those of the root–soil interface is challenging. An additional process impacting K_i is the modification of rhizosphere hydraulic properties due to root activity. For example, mucilage was found to maintain the rhizosphere wet during drying and to delay its rewetting upon irrigation (Carminati & Vetterlein, 2013) (Fig. 1d). Zarebanadkouki *et al.* (2018) proved that rhizosphere water repellency limits the recovery of K_i after rewetting. It follows that K_i is not simply a function of the contact area between root and soil, but it depends on the specific hydraulic properties of the volume of soil surrounding the roots, the rhizosphere. To what extent gaps (Fig. 1c), mucilage (Fig. 1d) and alteration of pore structure in the rhizosphere impact K_i remains an open question. Most likely, root hairs play a role in this process. Carminati *et al.* (2017) showed that root hairs enable plants to sustain high transpiration rates in dry soils. However, root hairs might also break-up due to tensile forces during severe drying. An additional potential source of high resistance to flow is the build-up of solutes at the root–soil interface driven by water flow toward the root surface (Stirzaker & Passioura, 1996). Solutes accumulate at the

root surface (or inside the root cortex) when their uptake and back diffusion are slower than the convective transport toward the root driven by transpiration (mass flow) and would slowly diffuse back when transpiration decreases. This build-up of solutes would result in an apparent decrease in K_i . All these processes suggest that K_i is dynamic, hysteretic and it depends on several root traits, including root hair length and density and mucilage secretion and can have an impact on soil–plant water relations (Ahmed *et al.*, 2018).

In summary, the results of Rodriguez-Dominguez & Brodribb (2020) show that stomatal closure prevents the formation of large gradients in water potential around the roots. They demonstrate the importance of hydraulic processes at the root–soil interface and call for accurate measurements of the hydraulic properties of the rhizosphere and approaches linking belowground and aboveground hydraulic properties. According to their measurements, the loss of conductance of the root–soil interface and of the rhizosphere, more than that of the soil, impacts the total hydraulic conductance of the soil–plant continuum; and this result is partly explained by the prompt closure of stomata. Testing this result across plant species, soil types and for variable atmospheric conditions should be a research priority for understanding the coordination between stomata and soil drying.

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Author contributions

AC, MAA, MZ, GC and MJ discussed this study and wrote the manuscript. GL provided support to produce Fig. 1.

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