Root water uptake and myco-rhizosphere hydraulic properties

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Key points

- Water loss from leaves creates a potential gradient in the plant that drives water uptake from soil.
- Stomata regulate the rate of water loss from leaves.
- At high rates of water loss from leaves, the rate of water movement to roots through soil can be the limiting factor of transpiration.
- Roots can increase the rate of water capture from soil by improving root-soil contact, secreting compounds or by associations with mycorrhizal fungi.

Introduction

The uptake of soil water by roots is driven by water losses from the leaves into the atmosphere. Plants are big movers of water and understanding the factors controlling root water uptake is necessary for properly modelling and predicting water exchange between the soil and the atmosphere. Root water uptake is driven by a gradient in water potential across the soil-plant-atmospheric continuum. Water evaporates from the leaves into the atmosphere across stomata. The transpiration rate depends on the difference in vapor pressure between stomata and the atmosphere (also referred to as vapor pressure deficit or VPD) and on the canopy conductance. The latter depends on stomatal conductance (which plants can regulate at short time scale) and boundary layers.

The water loss from the leaves generates a decrease in leaf water potential that passively drives the water from the soil, into the roots, along the xylem, and finally to the stomata. The gradients in water potential that drive water along this pathway depend on the hydraulic conductivities of key elements: the soil, the rhizosphere (soil in vicinity of and affected by roots), the root-soil interface, the roots (including its radial and axial components and their arrangement along the root architecture), and the xylem up to the leaves. All these conductivities are variable and are affected, to a different extent, by water potential.

In this chapter, we focus on the conductivity of the soil, of the root, and of the mycorrhizosphere (Fig. 1). Particular attention is dedicated to the water flow across the rhizosphere, which is defined as the soil in the vicinity of and affected by roots (i.e., a few mm around the roots). Large gradients in water potential occur across the rhizosphere in dry soil with low conductivity and eventually trigger stomatal closure. Plants have mechanisms to mediate these gradients by growing root hairs, symbiosis with mycorrhizae or by altering the rhizosphere hydraulic properties, such as mucilage secretion. After a short review of water flow in soil and roots, we discuss physical and biological mechanisms shaping water flow across the rhizosphere and the impact of root hairs, mycorrhiza and mucilage on root water uptake.

Principles of water flow from the soil into the roots

Soil water flow

Soil water fluxes are driven by gradients in soil water potential. In soils, the water potential [hPa] is made of three components: gravimetric (ψ_g), matric (ψ_m) and osmotic (ψ_o) potentials, with the latter not affecting water flow in soils. Volumetric soil water content θ [$m^3\ m^{-3}$] and matric potential ψ_m are related through a function called the soil water retention curve. The amount of plant

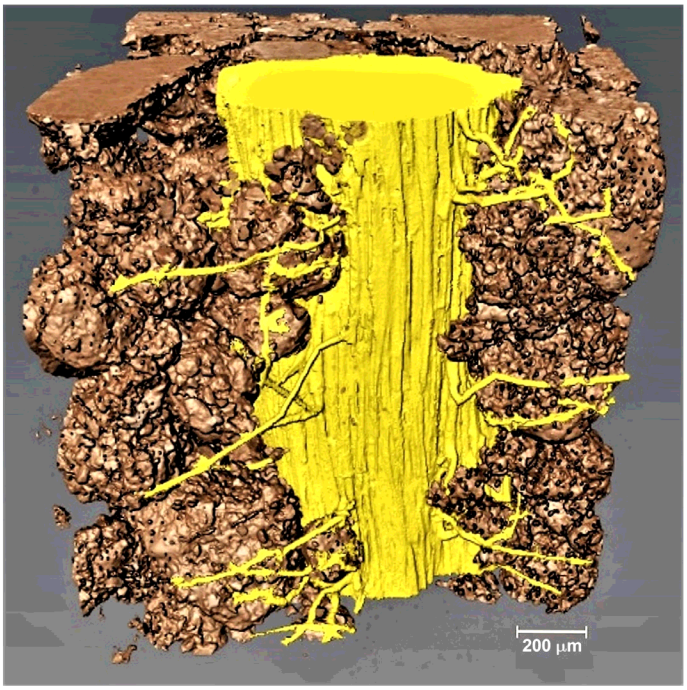

Fig. 1 Rendering of a synchrotron-based X-ray CT of a maize root in a loamy soil with root hairs protruding across the rhizosphere. Image courtesy by Patrick Duddek and Mutez Ahmed. Details on the image are in Duddek P, Carminati A, Koebernick N, Ohmann L, Lovric G, Delzon S, Rodriguez-Dominguez CM, King A, and Ahmed MA (2022) The impact of drought-induced root and root hair shrinkage on root–soil contact. *Plant Physiology*.

available water in a soil depends on typical points of this retention function (field capacity and wilting points) and on the plant root depth. Soil water holding capacity provides a buffer for plants to endure dry spells and is an important bulk soil characteristic in the long term (days-weeks). Typical values for soil water holding capacity range between 4% and 30%.

Besides its ability to store water, soil is also characterized by its ability to conduct water, called soil hydraulic conductivity $\mathrm{k}(\theta)$ [m s^{-1}]. This is a highly nonlinear function of water content because not only do the number of wet pores decrease with water content, but also their diameter, and thereby the resistance that water has to overcome to flow. In addition, smaller pores are often more tortuous and less connected. The soil conductivity curve controls soil water fluxes within the soil profile and toward roots. In the rhizosphere, the role of the soil hydraulic conductivity is crucial as it generates an important resistance when the soil dries out.

The soil water flux is a function of the soil water potential gradient, which is described by the Buckingham-Darcy equation:

$$q = -k(\theta)\left(\frac{\partial h}{\partial \mathbf{x}} + \frac{\partial z}{\partial \mathbf{x}}\right) \tag{1}$$

where $\mathbf{x}$ is the position vector ($\mathbf{x} = [x,y,z]$) [m], the matric head is $h = \frac{\psi_m}{\varrho g}$ [m], ϱ is the water density [kg m^{-3}] and g is the gravitational acceleration [m s^{-2}].

The transfer of water within a soil profile is governed by the Richardson-Richards equation, which in three dimensions is expressed as:

$$\frac{\partial \theta}{\partial t} = \frac{\partial}{\partial \mathbf{x}}\left[k(\theta)\left(\frac{\partial h}{\partial \mathbf{x}} + \frac{\partial z}{\partial \mathbf{x}}\right)\right] - S \tag{2}$$

where t is time [s] and S is the sink term corresponding to the volumetric root water uptake ($S > 0$) or release ($S < 0$) [m^3 m^{-3} s^{-1}]. The sink term in Eq. (2) represents the net uptake per volume of soil, V [m^3]. In the literature, two different approaches have been proposed for estimating S. Some authors define S as a function of macroscopic volumetric properties like root length density or soil water status like matric potential or matric flux potential (van Lier et al., 2006). On the other hand, microscopic approaches compute S from an explicit simulation of the segment root water uptake:

$$S = \frac{\sum_i jr,\, i\, Ai}{V} \tag{3}$$

where $j_{r,i}$ [m sec^{-1}] is the root water uptake per root surface (Ai) of a root segment i ($i = 1{:}n$) located within the soil volume V. In such a case, j_r must be explicitly calculated for each root segment between bulk soil and root xylem and will be a function of the hydraulic conductance in the rhizosphere K_{rh} [m s^{-1} MPa^{-1}] and in the root radial pathway K_r [m s^{-1} MPa^{-1}]:

$$j_r = \frac{1}{\frac{1}{Krh} + \frac{1}{Kr}}(\psi_b - \psi_x) \quad (4)$$

where ψ_b and ψ_x are the water potential (including all the three components: gravimetric, matric/hydraulic and osmotic) in the bulk soil and the root xylem, respectively [MPa].

Calculating *Krh* can be extremely challenging given the complex nature of the rhizosphere and the different possible pathways for water between the bulk soil and the root surface. Different pathways have been identified: the matrix pathway, i.e., through the soil pores, the root hair pathway, and the mycorrhiza pathway. The two latter pathways will be further developed in the last sections.

The flow through the soil matrix is obtained by solving the Richardson-Richards equation axisymmetrically, by considering the concentric flux of water from the bulk soil to the root surface (and neglecting gravity):

$$\frac{\partial\theta}{\partial t} = \frac{1}{r}\frac{\partial}{\partial r}\left[rk(\theta)\left(\frac{\partial h}{\partial x}\right)\right] \quad (5)$$

where r is the radial coordinate [m]. Numerous authors have provided semi-analytical solutions to this equation under steady-state ($\partial\theta/\partial t = 0$) or steady rate ($\partial\theta/\partial t$ = constant) using the flux matric potential approach (van Lier et al., 2006). One important aspect of these solutions is that the soil resistance to water flux becomes a function of the water flux itself. An increase of transpiration demand generates a lower water potential at the root interface, which decreases the hydraulic conductivity in the soil. Solving Eq. (5) using steady rate conditions allows calculating an effective rhizosphere conductance K_{rh} for varying j_r (Fig. 2).

In addition to the conductivity drop, rhizosphere matric conductance also depends on the contact between the root surface and the liquid phase. If the contact between root and the liquid phase decreases, water uptake concentrates on a narrow part of the root-soil interface and further increases the conductivity drop. When the soil dries, soil and roots may shrink and adversely affect the partial contact between soil and roots. For example, Faiz and Weatherley (1982) found that the roots of sunflowers shrank by 25% when the leaf water potential dropped to around −1.5 MPa. These observations suggest that under soil drying conditions, the contact between roots and their surrounding soil is reduced due to root and soil shrinkage, decreasing the hydraulic conductance of the rhizosphere and limiting water flow between roots and soil.

Water flow in the root

Down to the subcellular scale, primary cell walls are "corridors" for water between protoplasts that contain the cytosol and organelles. Just like in soil, in these fully hydrated corridors whose porosity is about 70%, water flow is driven by gradients in water potential, which is given by the hydrostatic (Ψ_m) (similar to the matric potential defined in soil) and gravitational (Ψ_g) potential. However, pore size in cell walls is extremely small – about 5 10^{-9} – relative to the dominant porosity class in soils with the finest texture – the clay "ultra-microporosity" spanning the 10^{-7} to 5 10^{-6} m spectrum. As a consequence, despite large uncertainties, the hydraulic conductivity of cell walls is thought to be orders of magnitude lower than that of heavy clay soils at water saturation. The respective orders of magnitude are: 10^{-10} to 10^{-7} versus 10^{-6} to 10^{-4} m^2 MPa^{-1} s^{-1} as reviewed by Couvreur et al. (2018).

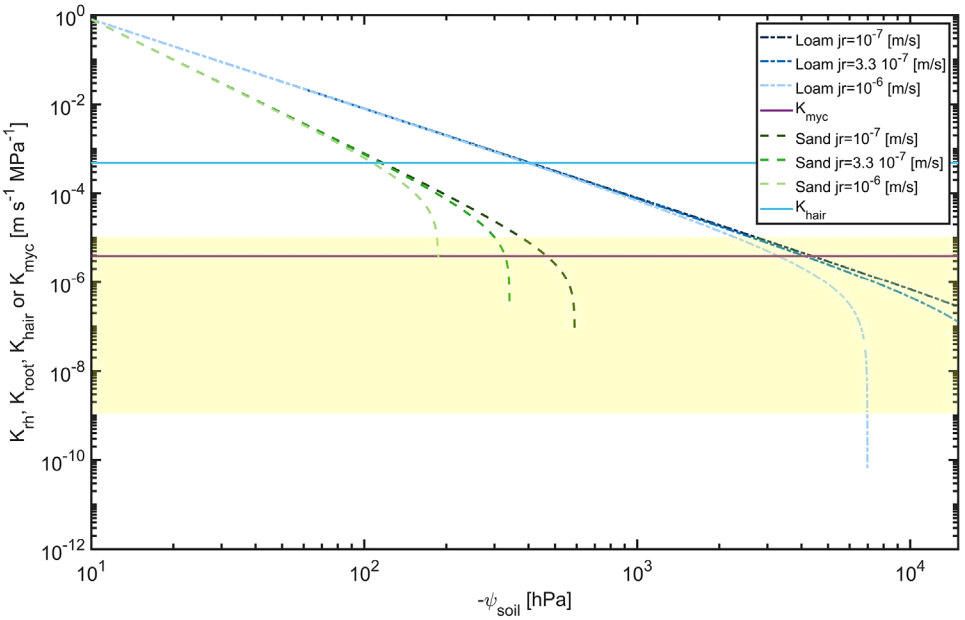

Fig. 2 Hydraulic conductance of the rhizosphere K_{rh} [m s^{-1} MPa^{-1}] of a sandy and a loamy soil and for three water fluxes at the root-soil interfaces j_r [m s^{-1}]. The large yellow bad is the range of root radial conductance K_r [m s^{-1} MPa^{-1}], according to Draye et al. (2010). K_{hair} and K_{myc} are the hydraulic conductances of the root hair zone and mycorrhiza estimated using the Hagen-Pouseuille law (Eq. 8).

The boundary between the cell wall and the cytosol is the plasma membrane. The inside of this phospholipid bilayer is hydrophobic, which drastically limits the transport of water. However, "gates" to the cytosol exist under the form of transmembrane water channels called aquaporins. Because they decouple the transport of water and solutes, membranes allow the formation of regions with distinct compositions in solutes and different osmolalities. Membranes thereby allow the process of osmosis, which explains how water molecules tend to spontaneously flow toward the side with highest osmolality as a result of their high affinity for solutes. To capture it mathematically, a new component is added to the potential of water: the osmotic potential (Ψ_o, more negative with increasing osmolality). Applying the second law of thermodynamics to water transport, water passively flows down differences of summed Ψ_m, Ψ_g and Ψ_o across selective membranes (the sum of these components is also called total water potential Ψ_{tot}). A membrane failing to decouple water and solute transport is considered as "leaky." A direct consequence of the leakiness is that the osmotic potential difference across the membrane is not as effective at driving water flow, and Ψ_o is then corrected by a "reflection coefficient" σ equal to zero if the membrane is fully permeable and up to one when fully selective. These principles translate mathematically as follows:

$$j_m = Lp\ (\Psi_{m,w} - \Psi_{m,c} + \sigma(\Psi_{o,w} - \Psi_{o,c})) \quad (6)$$

where j_m [m s^{-1}] is the water flow rate per unit membrane surface, Lp [m MPa^{-1} s^{-1}] is the membrane hydraulic conductance per unit surface, $\Psi_{m,w}$ and $\Psi_{m,c}$ [MPa] are the pressure potentials on the sides of the cell wall and cytosol, respectively, and $\Psi_{o,w}$ and $\Psi_{o,c}$ [MPa] the (negative) osmotic potentials on the sides of the cell wall and cytosol, respectively. Note that the gravitational potential is usually neglected at this scale. Lp is defined as conductance per root surface.

The composite nature of the root subcellular structures arranged in parallel and in series allows multiple pathways for water from the root surface to xylem vessels. The apoplastic, transmembrane and symplastic pathways (the last two frequently referred to as the combined cell-to-cell pathway) rely dominantly on water transport through cell walls, plasma membranes and plasmodesmata, respectively. While they have been conceptualized as pathways in parallel with their respective conductivities and reflection coefficients, recent unified modelling and experimental approaches suggest strong alterations of water pathways along the root radius (Couvreur et al., 2018) and the absence of a purely apoplastic pathway. Hydrophobic root diffusion barriers in the endodermis (and occasionally exodermis) play a key role in both of these observations. The lignin based Casparian strip forms a scaffold in radial cell walls and the suberin lamellae is deposited between all membranes and primary cell walls, drastically limiting permeation across these cell walls and membranes, respectively, in the concerned cell layers. Thereby, these structures locally force water through transmembrane or symplastic pathways, while functionally creating a filter for nutrients responding to the direct environment of roots. There appears to be a high level of coordination between the deposition of diffusion barriers and the expression of specific aquaporins in their direct vicinity so that the relative importance of these multiple factors has been hard to decipher.

The mainstream model for radial water flow across vascular plant roots has remained untouched for multiple decades and is a common building block in Functional-Structural Plant Models. It simply assumes that root tissues are analogous to a "big-membrane," hence its formulation very close to Eq. (6):

$$j_r = k_r\ (\Psi_{m,s} - \Psi_{m,x} + \sigma_r(\Psi_{o,s} - \Psi_{o,x})) \quad (7)$$

where j_r [m s^{-1}] is the radial water flux at the root surface, k_r is the root radial conductance per root surface as defined in Eq. (4), σ_r is the root reflection coefficient, $\Psi_{m,s}$ and $\Psi_{m,x}$ [MPa] are the water pressure potentials at root surface and in xylem, respectively, and $\Psi_{o,s}$ and $\Psi_{o,x}$ [MPa] the (negative) osmotic potentials at root surface and in xylem, respectively.

Measured k_r values range between 10^{-9} and 10^{-5} [m s^{-1} MPa^{-1}] according to Draye et al. (2010) (yellow region in Fig. 2).

Rhizosphere processes and their impact on root water uptake

Root hairs

Root hairs represent about 2% of the root mass but they greatly increase the root surface area, which can be up to 3-fold larger in the presence of root hairs. The volume of soil influenced by roots in the presence of root hairs is further increased by their ability to access finer pores than the main root axis.

Controlled laboratory studies have demonstrated that root hairs facilitate water uptake. Segal et al. (2008) reported a greater depletion of soil water in the root hair zone of the barley (*Hordeum vulgare*) wild type compared with the hairless mutant. Similarly, Tanaka et al. (2014) showed a 47% reduction in water absorption for the hairless mutant of *Arabidopsis thaliana* relative to the wild type. In terms of plant water status, under low evaporative demand in controlled environmental conditions, Dodd and Diatloff (2016) showed no difference in the transpiration rate of the no root hairs mutant of barley and the wild-type plants. In contrast, under higher evaporative demands, the ability of root hairs to take up water from drying soil was reported by Carminati et al. (2017b). As soil dried, the leaf water potential of the 'no root hairs' mutant decreased more rapidly than that of the wild type, implying a reduced capacity to take up water at high transpiration rates. Root hairs facilitate water uptake by bridging the gaps between roots and soil, either by directly taking up water or by creating a capillary bridge for water to flow across the gap (Carminati et al., 2017b) and thereby reducing the decline in water potential at the root-soil interface in rapidly transpiring plants.

Field evidence of the significance of root hairs for water uptake by barley under drought was reported by Marin et al. (2021). The field experiment was carried out in Scotland during a typically wet growing season (2017) and during the driest growing season ever

recorded at the site (2018), under contrasting soil textures (clay loam and sandy loam). The study showed that root hairs did not confer a notable advantage to barley under optimal conditions, but under soil water deficit, root hairs enhanced plant water status and stress tolerance. This resulted in less negative leaf water potential and lower leaf abscisic acid concentration in the presence of root hairs for plants grown in clay loam, while no significant effect of root hairs was found in sandy loam soil (Marin et al., 2021).

The role of root hairs in plant water uptake has been elucidated mainly in barley. Cai et al. (2021) evaluated the effects of maize root hairs on plant-soil water relations in sand and loam and found no clear effect of root hairs in either soil textures. This might be related to the early shrinkage of root hairs in maize (Duddek et al., 2022). Root hairs show intra- and interspecific variations in length and density. In angiosperms, root hairs vary in length from zero (i.e., species with no root hairs) to 1.5 mm. If comparing barley and maize for instance, barley produces significantly longer root hairs (2-fold) and at a greater root hair length density (6-fold) than maize. Therefore, the role of root hairs in plant water uptake is equivocal, apparently being species and soil specific.

To give an approximate estimation of the capacity of root hairs to transport water, we calculate the effective conductance of root hairs, treating them as capillaries arranged in parallel and using the Hagen-Poiseuille law:

$$j_r = \frac{N \pi r^4 \Delta\psi}{8\mu L} \tag{8}$$

where j_r is the water flux at the root soil interface [m s^{-1}], N is the number of root hairs per root surface [m^{-3}], r is the hair radius, $\Delta\psi$ is the difference in water potential, μ is viscosity [Pa s] and L is the hair length [m]. K_{hair} is calculated as:

$$K_{hair} = \frac{N \pi r^4}{8\mu L} \tag{9}$$

Using $N = 9.5$ (assuming 30 hairs per root length and a root radius of 0.5 mm), hair radius $r = 6$ μm, and setting L = 10 mm (to compare it to other domains that were set to 10 mm), we obtain 4.8×10^{-3} m s^{-1} MPa^{-1} (Fig. 2). This is a pretty large value and it might be an overestimate by assuming that viscosity is the same as water and by not adding the permeability of the root membrane. Water has to cross at least one membrane to be taken up by roots. However, it shows how the number of hairs and their radius is potentially sufficient to constitute a significant parallel pathway for water uptake.

Mucilage

Plants contribute a large portion of their photosynthetic products to the soil via their roots in a process called rhizodeposition. Rhizodeposition comprises the release of water-soluble components, the secretion of insoluble components, such as mucilage, the sloughing off of root border cells, the senescence of root epidermis and root hairs, and the release of gases such as CO_2 and ethylene. Mucilage is a polymeric gel that is mainly secreted by the Golgi apparatus of the root cap, but it can also be secreted by the epidermal cells of mature roots (McCully and Boyer, 1997). Its formation is readily visible in air-born roots of maize (Fig. 3). The root tip continuously secretes mucilage in the soil, and as the root elongates, mucilage is translocated along roots. Major components of root mucilage are galactose (~39–42%), fucose (~22–30%), mannose (~11–14%), arabinose (~8–11%), xylose (~1–4%), glucose (~1–4%) and glucuronic acid (~3–5%).

The chemical composition and quantity of mucilage varies across species, developmental stages of plants, and environmental conditions. Despite these variations, mucilage shares common intrinsic properties. Mucilage increases viscosity and lowers the surface tension and water potential of the soil solution. Read and Gregory (1997) showed that the viscosity of maize mucilage is twice that of water already at concentrations of 0.7 mg g^{-1} (weight of dry mucilage per unit weight of the liquid solution), and it increases non-linearly as the concentration of mucilage increases (1000 times higher than pure water at ca. 10 mg g^{-1}). The higher viscosity of mucilage compared to water causes a reduction in the hydraulic conductivity of the rhizosphere. At low concentrations, mucilage increases the saturated hydraulic conductivity of soils with small mean particle size (fine-textured soils), probably due to its swelling capacity and the consequent increase in soil porosity. However, as mucilage concentration increases, the saturated hydraulic conductivity decreases dramatically. Mucilage has a smaller surface tension than pure water, probably due to the presence of phospholipid components in the root exudates. Read and Gregory (1997) found that the surface tension rapidly declined with increasing mucilage concentration, decreasing from 72 [mN m^{-1}] down to 45–50 mN m^{-1} at concentrations of 1 mg g^{-1} in water. McCully and Boyer (1997) found that when fully saturated mucilage exuded by the nodal roots of the maize plant can hold an amount of water 300 times its dry weight, but a large fraction of this water could not be held against negative water potentials as the soil dries. These authors concluded that mucilage should not play a significant role in soil-plant water relations. However, when mucilage is embedded into a solid matrix, it increases the water holding capacity of the soil at any given water potential (Carminati et al., 2017a). This evidence suggests that the effect of mucilage on soil water retention must be amplified in soils by additional forces that emerge from the interaction between polymers and soil matrix.

Mucilage of most plants contains a small fraction of phospholipids and anionic polysaccharides. These components are amphiphilic substances that contain both hydrophilic and hydrophobic functional regions. Therefore, when mucilage dries, the hydrophilic regions of these components may bind to each other or to the soil and expose the hydrophobic parts toward the air-filled phase of the pore space, causing water repellency in the rhizosphere (Hallett et al., 2003).

Several hypothetical functions have been attributed to mucilage such as impacting the dynamics of nutrients in the rhizosphere, keeping the soil surrounding the root tip wet and hydrated (McCully and Boyer, 1997) and therefore protecting root tips from dehydration in drying soil, acting as a lubricant at the root surface, thereby improving root penetration in soil, and improving the

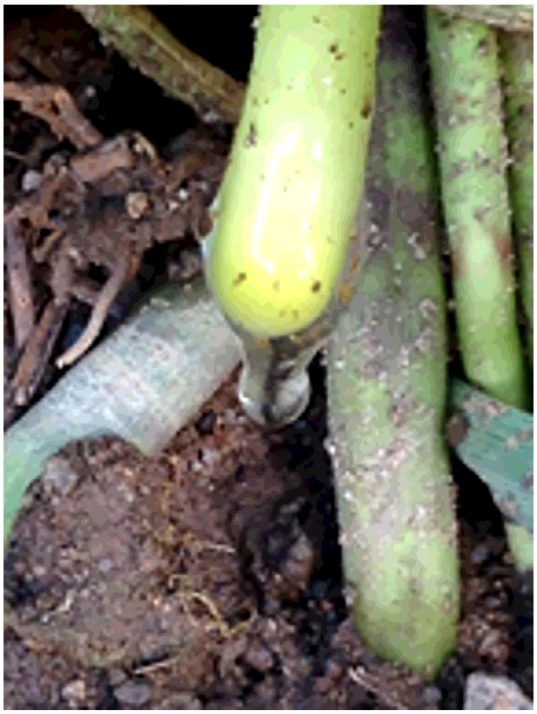

Fig. 3 Mucilage secreted by nodal roots of the maize plant. The photo was taken a day after a rain event in the field.

contact between roots and soil particles. Another putative function attributed to mucilage is the facilitation of water and nutrient uptake by roots. This beneficial function is related to an improved contact between roots and the soil, improving the soil's water-holding capacity, and improved connectivity of the liquid phase within soil pores by altering the liquid configuration. Carminati et al. (2017a) conceptualized the function of mucilage in the retention and flow of water in drying soil. They showed that the combination of increased viscosity and decreased surface tension of the liquid phase could alter the spatial configuration of the liquid phase within the soil pores, enhancing the connectivity of the liquid phase during soil drying.

Mycorrhizal fungi

The vast majority of land plants form associations with mycorrhizal fungi. Four main types of mycorrhizas are recognized based on morphological characteristics of root tissues and host plants: arbuscular mycorrhizas, ectomycorrhizas, ericoid mycorrhizas and orchid mycorrhizas, that form associations with 72%, 2%, 1.5% and 10% of vascular plants, respectively. Arbuscular mycorrhizal fungi (AMF) are therefore, by far, the more widespread, distributed in the majority of terrestrial ecosystems and which concern the vast majority of agricultural and horticultural crops. We will thus focus our attention on this main guild of mycorrhizal fungi.

Arbuscular mycorrhizal fungi are obligate root symbionts that have co-evolved with land plants for more than 400 million years. Their roles in plant nutrition and growth as well as alleviation of biotic and abiotic stresses have been repeatedly demonstrated, making these soil microorganisms key players in crop production (Smith and Read, 2008) and plant ecology in natural systems. AMF colonize the cortical cells of the root system, developing intraradical mycelium (IRM) and arbuscules, and extend tens of cm away from the roots into the soil as extraradical mycelium (ERM), colonizing soil pores with hyphae having diameters up to 10 times finer than that of root hairs. They produce up to 100 m of hyphae per gram of soil in pastures and prairies (Miller et al., 1995). ERM can thus be considered as an extension of the root system, increasing the uptake of minerals (e.g., phosphorus, nitrogen) and water, meeting plant nutritional needs, in exchange for organic compounds issued from the photosynthesis.

The role of AMF in the water supply of plants has been reported since the early 1970s. Safir et al. (1971) were the first to suggest that the symbiosis of AMF with soybean affects the water relations, probably via improved phosphorus (P) nutrition. This hypothesis was supported up to the 1980s until a couple of studies demonstrated that AMF could also affect water relations by other mechanisms than P nutrition (Harris et al., 1985). Since then, several hypotheses have been proposed and are still being explored.

Fungal ERM allow AMF-colonized plants to explore more soil, accessing pores unreachable to roots and root hairs, taking up more water than non-colonized plants and transporting water via the hyphae from far distances to the roots. The tridimensional ERM structures maintain water continuity from soils to plant by by-passing air gaps. The hyphal length per unit soil mass (m g^{-1}) reported in the field varies from 68 to 101 in prairie (Miller et al., 1995), 45 to 74 in ungrazed pasture (Miller et al., 1995) and 10 to 35 in maize cropping (Kabir and Koide, 2002). The diameter of hyphae in the soil generally varies from 1.2 to 18 μm with the smallest ones involved in uptake being approximately 2 μm. Their growth is estimated between 0.3 and 3.3 mm a day with values

reported for *Rhizophagus fasciculatum* symbiotic with *Trifolium subterraneum* of 10 m g^{-1} after four weeks and 20 m g^{-1} after 5 weeks (Scheltema et al., 1985).

AMF strongly affects the expression of aquaporins (i.e., water channels) involved in the transport of water. Aquaporins have been reported in the hyphae developing within the soil (favoring the entry of water within the hyphae) as well as in the peri-arbuscular membrane, which is the membrane that surrounds an arbuscule and is contiguous to the plasma membrane of the cortical cell (it plays a central role in nutrient exchange between the symbionts). Kikuchi et al. (2016) proposed a model in which plant transpiration creates a water potential gradient, allowing water to move within the extraradical hyphae through the cytosol toward the cortical cells. A mycorrhiza-inducible plant aquaporin on the periarbuscular membrane and an aquaglyceroporin located on the fungal plasma membrane (responsible for water transport across the plasma membrane) further mediate the water flow from fungal cell to root cell. Thus, root colonization impacts gene expression of aquaporins, which is correlated with changes in root hydraulic properties that increase water transport capacity of mycorrhizal roots. In the model proposed by Kikuchi et al. (2016), water may also move through the lumen of tubular vacuoles containing aquaporins. Interestingly, inorganic phosphorus accumulates within these tubular vacuoles and is translocated toward the roots by the water flow. Host transpiration and the fungal aquaporin thus play key roles in P translocation.

Stimulation of root hair growth and protection of host plants against the oxidative damage under abiotic, including osmotic stresses, have also been reported. Gas exchange capacities were also increased in AMF-colonized plants, probably associated with a decrease in stomatal resistance and increase in transpiration as reported by Zhu et al. (2011) in maize. Finally, AMF have been shown to impact plant water uptake capacity indirectly by the production of exudates, which alter soil pore structure through aggregation and can also influence hydrophobicity.

We repeated the calculations described above for root hairs but using $r = 1$ μm, L = 1 cm and $N = 100$ (estimated assuming 20 m of ERM per gram of soil, a root length density of 2 cm cm^{-3}) appropriate for AMF hyphae. Using Eq. (8), we obtain $K_{myc} = 3.9\ 10^{-6}$ [m s^{-1} MPa^{-1}] (Fig. 2). This value is much smaller than that calculated for root hairs, due to the smaller radius of ERM hyphae, however it is larger than the conductance of a sandy soil for soil matric potentials more negative than –200 hPa to – 500 hPa, while it needs 10 times more negative water potential in a loam for mycorrhiza to be as conductive as the soil matrix. This simple calculation suggests that a significant flow across mycorrhizae can take place, particularly in coarse textured soils.

Rhizosphere hydraulic properties

Plant water uptake from the soil is influenced by the hydraulic properties of the rhizosphere, which differ from those of bulk soil as a result of biophysical processes occurring at the root-soil interface as discussed above. Processes affecting rhizosphere hydraulic properties include soil compaction by root growth, air-filled gaps caused by roots and soil shrinking and swelling during drying and wetting cycles, root hair intrusion, and mucilage production. Imaging methods have provided insight into the dynamics of water content and soil structure around the roots. X-ray CT has been particularly useful for resolving the soil structure dynamics around the roots. Aravena et al. (2011) showed that root-induced compaction increases contact areas between aggregates, leading to an increase in unsaturated hydraulic conductivity of the rhizosphere soil. Koebernick et al. (2017) investigated the effect of root hairs on soil porosity and pore connectivity, reporting increased soil macroporosity in the rhizosphere in the presence of root hairs. As roots shrink, they create gaps between soil and roots, reducing water transfers and therefore helping plants to prevent water loss when the soil dries.

Neutron radiography and tomography have been useful to reveal unexpected gradients in water content around the roots, with increasing water contents toward the root surface during the drying phase (Carminati et al., 2010). These contradictory observations were explained as the effect of mucilage exuded by roots on water holding capacity and rhizosphere hydrophobicity of the rhizosphere. Hallett et al. (2003) directly measured the hydraulic characteristics of the rhizosphere using a miniaturized infiltrometer device and found reduced water sorptivity in moist rhizosphere soil of barley compared with bulk soil, due to increased water repellency in the rhizosphere.

The increased hydrophobicity induced by mucilage in the rhizosphere also results in a high contact angle between liquid phase and soil particles (Moradi et al., 2012). Zarebanadkouki et al. (2016) found that during a drying and wetting cycle in a sandy soil, the hydraulic conductivity of the root-soil interface creates a temporary limit to root water uptake as a result of rhizosphere hydrophobicity. They showed that water repellency of the rhizosphere reduced root water uptake by a factor of 6.5 times during the first 2–3 h after irrigation. Despite the occurrence and mechanisms of water repellency in the rhizosphere being partly clarified, their consequences on emerging water relations between soil and plants remain unclear. The reason is that rhizosphere hydrophobicity is often observed as a local phenomenon along the root system and it is not clear if this local limitation of root water uptake has any impact on the overall soil-plant water relationship. Rhizosphere hydrophobicity might even be a positive rhizosphere trait that hydraulically disconnects the root segments from the driest soil layers, therefore reducing leakage of water from root system to the dry soil. Rhizosphere hydrophobicity could locally and temporarily disconnect the root segment located in the driest soil layers, therefore reducing the risk of hydraulic failure.

Rhizosphere hydraulic properties also differ from those of bulk soil also as a result of other biofilms present in the soil, such as extracellular polymeric substances (EPS) secreted by bacteria and exudates from mycorrhizal fungi. Similar to mucilage, these materials connecting soil particles do not break up upon drying, due to their high viscosity and low surface tension, enhancing the soil water retention and connectivity of the liquid phase.

Root water uptake and rhizosphere properties in their ecological and environmental context

The physics of soil water flow indicates that soil drying and the consequent drop in soil hydraulic conductivity limit the availability of water to plants. The drop in soil hydraulic conductivity around the roots is exacerbated by soil and root shrinkage and the consequent reduction in root-soil contact, which causes a further loss of conductivity.

Plants can respond to such limitations in soil water availability with multiple strategies. One strategy is to reduce the transpiration demand by closing stomata, with the cost of reduced growth and carbon assimilation. A second strategy is to increase the surface of roots active in water uptake. A combination of both strategies is the allocation of more carbon to roots compared to shoot, which reduces the ratio between transpiration and root surface active in water uptake. An additional strategy is the modification of rhizosphere properties.

The three previous sections reviewed the several mechanisms that plants have to engineer the physical properties of their rhizosphere. Growth of root hairs and symbiosis with mycorrhiza increase the capacity of roots to extract water from dry and low conductive soils and thus increase the plant water potential needed to sustain transpiration during drought. However, their effectiveness is soil and plant specific. The additional strategy for plant roots is to modify their rhizosphere by the secretion of mucilage. Mucilage secretion leads to a wetter and more hydraulically connected rhizosphere compared to the bulk soil during drying, and to a less severe decrease in unsaturated hydraulic conductivity and diffusion coefficient. On the other hand, mucilage induces a temporary water repellency in the rhizosphere, particularly in sandy soils, which might be functional to maintain the region around the roots aerated upon rewetting and regulate water efflux from roots to dry soils layers. Despite its potential to maintain the connectivity between soil and roots, the relevance of mucilage on root water uptake has not yet been demonstrated due to challenges in quantifying the amount and properties of mucilage in-situ and to the lack of appropriate mucilage deficient genotypes. EPS produced by microorganisms have similar properties as mucilage and, one can speculate, have a similar beneficial role on root water uptake, indicating the important link between plants and soil microbiota for soil water resources.

Root strategies to improve the acquisition of water from the soil can be summarized in two groups: (1) root development and exploration of larger volumes of soil; and (2) improvement of the hydraulic conductivity of the rhizosphere via root hairs, mycorrhiza and the production of biofilms. Both strategies require a carbon input: the first strategy requires carbon input for plant growth; the second strategy consists in the investment of carbon into the rhizosphere. The two strategies are not alternatives and are likely to be coordinated in space and time. Hairs and mucilage are functional for some time, then hairs shrink (Duddek et al., 2022) and mucilage is degraded. Therefore, their production must match with the root development in such a way that these traits are active in the root segments that are hydraulically active (radially and axially).

In summary, we have shown the physics of soil water flow to the root and how, during soil drying, the local drop in conductivity around the roots becomes a limiting factor for transpiration. Plants have multiple mechanisms to cope with soil hydraulic limitation. Prominent examples are root hairs, mycorrhiza and mucilage exudation. Understanding plant and soil interactions in the rhizosphere is a key challenge in soil and plant research and it has important implications for the ability of plants to cope with drought. Finally, it should be noted that to fully comprehend the implications of rhizosphere processes, one should include these processes into a root system perspective, where roots dynamically grow in a variable (in space and time) soil.

References

Aravena JE, Berli M, Ghezzehei TA, and Tyler SW (2011) Effects of root-induced compaction on rhizosphere hydraulic properties - X-ray microtomography imaging and numerical simulations. *Environmental Science and Technology* 45: 425–431.

Cai G, Carminati A, Abdalla M, and Ahmed MA (2021) Soil textures rather than root hairs dominate water uptake and soil-plant hydraulics under drought. *Plant Physiology* 187: 858–872.

Carminati A, Moradi AB, Vetterlein D, Vontobel P, Lehmann E, Weller U, Vogel HJ, and Oswald SE (2010) Dynamics of soil water content in the rhizosphere. *Plant and Soil* 332: 163–176.

Carminati A, Benard P, Ahmed MA, and Zarebanadkouki M (2017a) Liquid bridges at the root-soil interface. *Plant and Soil* 417.

Carminati A, Passioura JB, Zarebanadkouki M, Ahmed MA, Ryan PR, Watt M, and Delhaize E (2017b) Root hairs enable high transpiration rates in drying soils. *New Phytologist* 216(3): 771–781.

Couvreur V, Faget M, Lobet G, Javaux M, Chaumont F, and Draye X (2018) Going with the flow: Multiscale insights into the composite nature of water transport in roots. *Plant Physiology* 178: 1689–1703.

Dodd IC and Diatloff E (2016) Enhanced root growth of the brb (bald root barley) mutant in drying soil allows similar shoot physiological responses to soil water deficit as wild-type plants. *Functional Plant Biology* 43: 199–206.

Draye X, Kim Y, Lobet G, and Javaux M (2010) Model-assisted integration of physiological and environmental constraints affecting the dynamic and spatial patterns of root water uptake from soils. *Journal of Experimental Botany* 61: 2145–2155.

Duddek P, Carminati A, Koebernick N, Ohmann L, Lovric G, Delzon S, Rodriguez-Dominguez CM, King A, and Ahmed MA (2022) The impact of drought-induced root and root hair shrinkage on root–soil contact. *Plant Physiology* 189(3): 1232–1236.

Faiz SMA and Weatherley PE (1982) Root contraction in transpiring plants. *New Phytologist* 92: 333–343.

Hallett PD, Gordon DC, and Bengough AG (2003) Plant influence on rhizosphere hydraulic properties: Direct measurements using a miniaturized infiltrometer. *New Phytologist* 157: 597–603.

Harris D, Pacovsky RS, and Paul EA (1985) Carbon economy of soybean-Rhizobium-Glomus associations. *New Phytologist* 101: 427–440.

Kabir Z and Koide RT (2002) Effect of autumn and winter mycorrhizal cover crops on soil properties, nutrient uptake and yield of sweet corn in Pennsylvania, USA. *Plant and Soil* 238: 205–215.

Kikuchi Y, Hijikata N, Ohtomo R, Handa Y, Kawaguchi M, Saito K, Masuta C, and Ezawa T (2016) Aquaporin-mediated long-distance polyphosphate translocation directed towards the host in arbuscular mycorrhizal symbiosis: Application of virus-induced gene silencing. *The New Phytologist* 211: 1202–1208.

Koebernick N, Daly KR, Keyes SD, George TS, Brown LK, Raffan A, Cooper LJ, Naveed M, Bengough AG, Sinclair I, et al. (2017) High-resolution synchrotron imaging shows that root hairs influence rhizosphere soil structure formation. *New Phytologist* 216: 124–135.

Marin M, Feeney DS, Brown LK, Naveed M, Ruiz S, Koebernick N, Bengough AG, Hallett PD, Roose T, Puértolas J, et al. (2021) Significance of root hairs for plant performance under contrasting field conditions and water deficit. *Annals of Botany* 128: 1–16.

McCully ME and Boyer JS (1997) The expansion of maize root-cap mucilage during hydration. 3. Changes in water potential and water content. *Physiologia Plantarum* 99: 169–177.

Miller RM, Jastrow JD, and Reinhardt DR (1995) External hyphal production of vesicular-arbuscular mycorrhizal fungi in pasture and tallgrass prairie communities. *Oecologia* 103: 17–23.

Moradi AB, Carminati A, Lamparter A, Woche SK, Bachmann J, Vetterlein D, Vogel H-J, and Oswald SE (2012) Is the rhizosphere temporarily water repellent? *Vadose Zone Journal* 11: vzj2011.0120.

Read DB and Gregory PJ (1997) Surface tension and viscosity of axenic maize and lupin root mucilages. *New Phytologist* 137: 623–628.

Safir GR, Boyer JS, and Gerdemann JW (1971) Mycorrhizal enhancement of water transport in soybean. *Science (New York, N.Y.)* 172: 581–583.

Scheltema MA, Abbott LK, Robson AD, and Death G (1985) The spread of glomus fasciculatum through roots of trifolium subterraneum and lolium rigidum. *New Phytologist* 100: 105–114.

Segal E, Kushnir T, Mualem Y, and Shani U (2008) Water uptake and hydraulics of the root hair rhizosphere. *Vadose Zone Journal* 7: 1027–1034.

Smith SE and Read D (2008) Mineral nutrition, toxic element accumulation and water relations of arbuscular mycorrhizal plants. *Mycorrhizal Symbiosis*. 145–VI.

Tanaka N, Kato M, Tomioka R, Kurata R, Fukao Y, Aoyama T, and Maeshima M (2014) Characteristics of a root hair-less line of Arabidopsis thaliana under physiological stresses. *Journal of Experimental Botany* 65: 1497–1512.

van Lier Q, de Metselaar JK, and van Dam JC (2006) Root water extraction and limiting soil hydraulic conditions estimated by numerical simulation. *Vadose Zone Journal* 5: 1264–1277.

Zarebanadkouki M, Ahmed MA, and Carminati A (2016) Hydraulic conductivity of the root-soil interface of lupin in sandy soil after drying and rewetting. *Plant and Soil* 398: 267–280.

Zhu XC, Bin SF, Liu SQ, and Liu TD (2011) Effects of arbuscular mycorrhizal fungus on photosynthesis and water status of maize under high temperature stress. *Plant and Soil* 346: 189–199.