Effects of Mucilage on Rhizosphere Hydraulic Functions Depend on Soil Particle Size

Eva Kroener*, Maire Holz, Mohsen Zarebanadkouki, Mutez Ahmed, and Andrea Carminati

Mucilage secreted by roots alters hydraulic properties of soil close to the roots. Although existing models are able to mimic the effect of mucilage on soil hydraulic properties for specific soils, it has not yet been explored how the effects of mucilage on macroscopic soil hydraulic properties depend on soil particle size. We propose a conceptual model of how mechanistic pore-scale interactions of mucilage, water, and soil depend on pore size and mucilage concentration and how these pore-scale characteristics result in changes of macroscopic soil hydraulic properties. Water retention and saturated hydraulic conductivity of soils with different ranges of particle sizes mixed with various mucilage concentrations were measured and used to validate the conceptual model. We found that (i) at low mucilage concentrations, the saturated conductivity of a coarse sand was a few orders of magnitude higher than that of a silt, (ii) at an intermediate concentration, the hydraulic conductivity of a fine sand was lower than that of a coarse sand or a silt, and (iii) at a high concentration, all soils had a hydraulic conductivity of the same magnitude. At low matric potentials, mucilage increased the water content in all soils in all soils. In coarser soils, higher mucilage concentrations were needed to induce an increase in water content of >0.05 g g⁻¹ at low matric potentials. This study shows how pore-scale interactions between mucilage, water, and soil particles affect bulk soil hydraulic properties in a way that depends on soil particle size, including such effects in quantitative models of root water uptake remains challenging.

Abbreviations: EPS, extracellular polymeric substances; REV, representative elementary volume.

Mucilage secreted from plant roots and extracellular polymeric substances (EPS) produced by microorganisms have a strong impact on soil hydraulic properties (McCully and Boyer 1997; Or et al., 2007a; Carminati et al., 2010; Kroener et al., 2014; Volk et al., 2016). Extracellular polymeric substances have been suggested to buffer fast and strong oscillations in soil water content, maintaining the microenvironment where microorganisms live at a rather constant water content during drying and rewetting (Or et al., 2007b). Similarly, it has been proposed that mucilage maintains the rhizosphere wet and hydraulically conductive during drying, while it delays rewetting after irrigation and might temporarily limit root water uptake during a rewetting phase subsequent to severe soil drying. This hypothesis was based on observations of water content around plant roots (Carminati et al., 2010; Moradi et al., 2012; Zarebanadkouki et al., 2016).

Experiments with a mucilage analog (from chia seeds [Salvia hispanica L.]) supported the hypothesis that mucilage plays a key role in shaping the hydraulic properties of the rhizosphere. Mucilage from chia seeds increases the capacity of soils to hold water against negative water potential. A sandy soil mixed with mucilage at a concentration of 1.25% (w/w dry gel/dry soil) had higher water contents at negative matric potentials than the same sandy soil without mucilage (Kroener et al., 2014). Similar results were obtained by Ghezzehei and Albalsameh (2015) using glass beads and sand mixed with polygalacturonate acid as an analog of mucilage. Mucilage also affects soil hydraulic conductivity: at high concentrations, it decreases the saturated conductivity of a sandy soil by a few orders of magnitude.

Core Ideas
- We propose a model of mechanistic pore-scale interactions of mucilage, water, and soil.
- Effect of mucilage on saturated hydraulic conductivity is stronger in coarse soils.
- Coarse soils require higher mucilage concentration to increase water content.
- Upscaling to macroscopic soil hydraulic properties remains challenging.
- The model was validated on measured water retention and saturated hydraulic conductivity.
magnitude—at a concentration of 0.4% the saturated conductivity is already reduced 20 times (Kroener et al., 2014). The observation that mucilage from chia seeds (Kroener et al., 2015; Benard et al., 2016), maize (*Zea mays* L.) roots (Ahmed et al., 2016), and from a series of different plants (Zickenrott et al., 2016) turns hydrophobic on drying explains the water repellency of the rhizosphere observed during severe drying and wetting cycles.

Based on this experimental evidence, Carminati (2012) and Kroener et al. (2014) developed a model of unsaturated water flow in soils mixed with mucilage, which they used to explain water dynamics in the rhizosphere. Ghezzehei and Albalasmeh (2015) and Kroener et al. (2014) postulated that mucilage absorbs water and decreases the soil water potential at any water content. The absorptive potential of mucilage was assumed to be dependent only on the concentration of mucilage in the liquid phase. Similarly, Kroener et al. (2014) assumed that the soil hydraulic conductivity decreases with increasing mucilage concentrations. The model by Kroener et al. (2014) has been recently used to simulate root water uptake (Schwartz et al., 2016) and to fit existing observations of water dynamics in the rhizosphere (Kroener et al., 2016). The model development and its assumptions were based on experiments with a quartz sand of a medium particle size, but it is not clear if the results can be extended to other soil particle sizes.

In this study, we investigated the effect of mucilage on the hydraulic properties of soils with varying particle sizes: a coarse sand, a fine sand, and a silty soil. We measured the water retention curve and hydraulic conductivity of the different soils at varying mucilage concentrations. Our hypothesis was that the way mucilage affects the soil hydraulic properties is soil particle size specific and that the differences in mucilage behavior in the different soils depend on the microscopic distribution of mucilage in the pore space. We present a conceptual model that describes how—depending on mucilage concentration and soil particle size—different basic physical pore-scale processes become dominant and that suggests how these processes affect soil hydraulic properties, that is, the water retention curve and saturated hydraulic conductivity. The model was validated with measurements using soils of various particle sizes and mucilage concentrations.

**Theory and Conceptual Model**

**Saturated Hydraulic Conductivity**

In the following paragraphs, we propose a conceptual model of the pore scale interactions between mucilage, water, and soil particles and how their interactions affect the saturated hydraulic conductivity. First, the classical theory of saturated water flow without the presence of mucilage is recalled; second, dynamics at high mucilage concentrations are discussed; and finally, the interplay between both dynamics at an intermediate concentration are mentioned.

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**Fig. 1.** Conceptual model of the saturated hydraulic conductivity as a function of particle size and mucilage concentration. The concentration of mucilage increases from top to bottom and particle size decreases from left to right. In each row, the concentration of mucilage per unit of soil volume is constant for all soils. At medium concentration (middle row), this is indicated by the same number of stars (eight) in all samples. Note that those on the boundaries count half. The positions of the stars indicate the place where mucilage deposits on the particle surface when the sample gets dry.
The Darcy–Brinkman equation describes the flow velocity profile inside a saturated capillary containing a high-porosity porous matrix—a similar scenario to a mucilage-filled pore. It combines Stokes equation (describing flow at the boundary of the capillary that is dominated by viscous forces) with Darcy law (describing flow dynamics inside the porous medium within the capillary):

$$\mu \nabla^2 \mathbf{u} - \nabla p - \mu a^2 \mathbf{u} = 0 \quad \text{and} \quad \nabla \cdot \mathbf{u} = 0$$

where \( \mathbf{u} = (u_x, u_y, u_z) \) and \( p \) are velocity vector and pressure, \( \mu \) is the Newtonian fluid viscosity and \( a^2 \) is the permeability. The Darcy–Brinkman equation has been used widely to describe flow through high-porosity porous media (Liu et al., 2007; Givler and Altobelli, 1994; Koplik et al., 1983).

Close to the boundary (Fig. 2b) the flow velocity \( \mathbf{u} \) is small and the term \( \mu a^2 \mathbf{u} \) can be neglected; now the pressure gradient \( \nabla p \) balances the Brinkman-term \( \mu \nabla^2 \mathbf{u} \) and the flow is essentially viscous. Far from the boundary, the velocity \( \mathbf{u} \) increases, making the term \( \mu a^2 \mathbf{u} \) more important; for low permeabilities (when \( a^2 \) is large) this term dominates over the Brinkman term, balances the pressure gradient \( -\nabla p - \mu a^2 \mathbf{u} \approx 0 \) and the velocity profile becomes rather uniform \( \mathbf{u} \approx -\nabla p/\mu a^2 \). The characteristic length (Brinkman screening length) distinguishes between these two domains and is given by the square root of permeability \( a^{-1} \) (Durlofsky and Brady, 1987). To better understand the relation between flow profile and permeability, the Darcy–Brinkman equation is numerically solved in cylindrical pores of radius \( R = 50, 100, \) and \( 200 \mu\text{m} \) with no-slip boundary conditions (Fig. 2b). Here, from symmetry reasons, Eq. [1] simplifies to \( u_z = 0, u_y = 0, \) and

$$\frac{1}{r} \frac{\partial}{\partial r} r \frac{\partial}{\partial r} u_z - \frac{\partial^2 p}{\mu} (a^2 u_z) = 0$$

This ordinary differential equation was solved using the Finite Difference Method with Thomas-Algorithm being applied to solve the linear equation system. The implementation was adapted from the Python-based programs provided by Bittelli et al. (2015). The solution of the Darcy–Brinkman equation suggests that in large pores, a lower permeability strongly reduces the cumulative flow, whereas in small pores, the total flow is mainly affected by the friction at the pore walls and is only marginally affected by changes of permeability within the pore. At a low permeability of, for example, \( a^2 = 500 \mu\text{m}^2 \), the flow velocity \( u_z \approx 500 \mu\text{m}^2 \times \partial p/\mu \) is similar in all the three pores.

At very low permeabilities, that is, high concentrations of mucilage, flow through a single pore has a uniform velocity profile, total water flow scales with the cross-section \( \sim r^2 \), the number of
pores scale with \( r^{-2} \), and as a result, it is expected that, at high concentrations of mucilage, hydraulic conductivity does not scale with mean pore diameter and that the hydraulic conductivities of a coarse and a fine soil are of same magnitude (Fig. 1, bottom).

When immersed in water, dry mucilage swells to a certain extent into the saturated pore body. In a medium soil, it might swell far enough to block a significant part of the pore space. In a coarse soil, instead, the distance from pore throat to center of pore can be larger than the swelling distance of the mucilage units, and a big part in the center of the pore remains free of mucilage. In a fine soil, where there are many more pores than mucilage units, we expect that because of the tortuous pathway, mucilage cannot swell across many different pores and that, even when saturated, not all pores are filled with swollen mucilage. We therefore hypothesize that at a medium mucilage concentration, the saturated hydraulic conductivity is lowest for a soil of medium particle size (Fig. 1, middle row) where the number of pores is small enough so that most of them contain mucilage and where most pore sizes are small enough so that a big part of each pore can be occupied by mucilage.

### Soil Water Retention Curve

Without mucilage, the Young–Laplace equation together with contact angle and pore geometry define water content inside a pore at a given water potential (solute and gravimetric potential not considered). The presence of chia seed mucilage increases water content at a given water potential (Ahmed et al., 2014; Kroener et al., 2014). Here we will present a conceptual model (Fig. 3) for the increased water retention and its dependency on soil particle size and mucilage concentration.

When immersed in water, mucilage (Fig. 3, stars) swells from the pore throats into the pore space. In fine soils, the pore size is smaller than the mean swelling distance, and mucilage can completely occupy some of the pores, building up a network connecting opposite sides of those pores (Fig. 3, top, right). In coarse soils, the pores are so large that at the same concentration the swelling distance of mucilage is not long enough to occupy the entire pore (Fig. 3, top, left). When the water potential decreases, the liquid phase is under tension. If the polymeric network does not connect opposite sides of the pores (left), the network retreats back into the pore throats. In fine pores, mucilage spans throughout the pore space (right). Similar to the soil matrix, the polymeric network itself creates an additional matric potential that contributes to the general water potential and causes an increase of water potential at a given water content; or, at a given water potential, it leads to an increase in water content.

Since the pore size of the polymeric network is very small, it can hold water till a very low matric potential. The polymeric network is stable as long as cross-linkings sustain the forces required to span the network across the pore and to hold water inside the network. This is very different from mucilage in a soilless medium (i.e., in a liquid solution) where the network will shrink when exposed to negative tensions.

To summarize, we hypothesize that during drying, especially at low water potentials when the mucilage network is under tension, mucilage increases the water content by adding an additional matric potential. A significant increase in water content occurs when mucilage forms a network connecting opposite sides of the soil pores. We expect that this network can form already at low mucilage concentrations in fine soils. In coarse soils, a much higher concentration is required to build up a network that spans across
the pore body and that significantly increases the water content at low water potentials.

Materials and Methods

Soil and Mucilage Preparation

The effect of mucilage on soil hydraulic properties was tested using a soil–mucilage mixture, which was chosen as an analog of the rhizosphere. Mucilage extracted from chia seeds was used as a model of plant mucilage. Mucilage extracted from chia seeds satisfied two important criteria: (i) it was easily extractable in a large quantity, which was needed for our measurements, and (ii) it had similar physical properties as plant mucilage (McCully and Boyer, 1997; Read and Gregory, 1997); it formed a gel-like substance after immersion in water (Kroener et al., 2014), and it turned hydrophobic after drying and rewetting (Kroener et al., 2015). Mucilage was extracted from chia seeds as follows: chia seeds were mixed with tap water at a gravimetric ratio of 1:10. The mixture was stirred for 2 h using a magnetic stirrer. The mixture was then passed through two successive sieves with mesh sizes of 0.5 and 0.2 mm by applying a suction of −800 hPa. The concentration of extracted mucilage was ~0.5% (w/w dry mucilage/water) and was determined by comparing the oven-dry mass with the initial wet mass of the mucilage solution.

To reproduce an analog of the rhizosphere, soils of different particle sizes were mixed with various amounts of wet mucilage to obtain the desired mucilage concentration in the soil. To enable a rather homogeneous mixing of gel and soil, the extracted mucilage was diluted with water to achieve a minimum gravimetric water content of 25% of the wet soil–mucilage mixture. After mixing, the porosity of the wet soil–mucilage mixture depended on the mucilage concentration; at the highest measured concentration, >160 g of wet and very viscous mucilage was mixed with 100 g of dry soil, resulting in a very high porosity of the mixture. The mixture was poured into a flat and wide container and dried at a temperature of 30°C for 48 h before being packed for the respective experiment. By being packed after drying, samples of each of the soil types had a rather similar porosity and packing density.

Saturated Soil Hydraulic Conductivity Measurement

The effect of varying concentrations of mucilage on the saturated hydraulic conductivity was evaluated in soil samples consisting of different soil particle sizes. Soil samples sieved to five different ranges of particle sizes, from coarse sand to silt (630–1000, 360–630, 200–500, 60–200, and <20 μm), were prepared with varying concentrations of mucilage (0, 0.1, 0.4, and 0.8% w/w dry mucilage/dry soil). Washed quartz sand from a sand pit in southern Florida (organic matter content <0.2%) was sieved to obtain soils having the two coarsest particle size ranges; washed quartz sand from a sand pit located near Duingen, Germany (organic matter content <0.1%), was sieved to obtain soil of the finest particle size range.

The saturated hydraulic conductivity was measured using a constant-head permeameter (Eijkelkamp Equipment). Often, cylinders of ~5-cm diameter are chosen as soil sample holders. For mucilage–soil mixtures, especially at high mucilage concentrations, it is rather difficult to create a sample that is homogeneous at a scale of 5 cm. To exclude the effect of larger heterogeneities and considering that the extension of the rhizosphere is in the range of millimeters, we used cylinders of 1.9-cm diameter. The cylinders were filled with 10 g of dry mucilage–soil mixture and compressed by shaking and adding 10 g of coarse gravel on top (~2-mm diameter). The soil columns had heights of 2.2 (630–1000 μm) to 3.3 cm (~20 μm). Via capillary rise from the bottom, the soil columns were saturated with tap water. In coarse soil prepared at high mucilage concentrations, the saturation took 48 h because the samples were initially hydrophobic. By pumping water into a water reservoir, a constant water level was established outside the samples at 3 cm above the samples’ surface. Within the sample holders, bent pipes were used to establish a water level at 1 cm above the samples’ surface. In this way, a constant difference in pressure head (~2 cm) was imposed between the top and bottom of samples, and water outflow from the samples was collected in burettes. The burettes were covered with foil to reduce evaporation. After monitoring the outflow with time and confirming that the outflow rate was static, collection of water for hydraulic conductivity estimation was initiated. Hydraulic conductivity was calculated using the following form of Darcy’s equation:

\[ Q = A K_s \frac{\Delta H}{\Delta z} \]

where \( Q \) (mL s\(^{-1}\)) is the flow rate, \( A \) is the cross-section of the column (2.75 cm\(^2\)), \( K_s \) (cm s\(^{-1}\)) is saturated hydraulic conductivity, \( \Delta H \) (cm) is the hydraulic head difference across the column, and \( \Delta z \) (cm) is the height of the column; \( \Delta H \) and \( \Delta z \) varied slightly among the samples and have been measured for each of them.

The measurement time was between 1 min and 1 d, and the number of pore volumes flowing through a sample were between 5 and 10; for the samples with the highest concentrations, ~0.7 to 3 pore volumes were flowing through the sample. No significant changes in the outflow rate were observed with time, suggesting that mucilage was well bound to the particle surface and that no significant amount of mucilage was leaching out during the experiment. Three replicates were prepared for each combination of soil particle size and mucilage concentration.

Soil Water Retention Curve

The effect of varying concentrations of mucilage on the water retention curve was tested on soils with different particle sizes.
We used a coarse sand (washed quartz sand from a sand pit in southern Florida, sieved to 360–1000 µm, organic matter content <0.05%), a fine sand (washed quartz sand from a sand pit located near Duingen, Germany, with particle size distribution of 0.1 [200–630 µm], 91.4 [125–200 µm], 8.0 [63–125 µm], and 0.5% [<63 µm] and organic matter content <0.2%), and a silt soil (collected from Reinhausen, Lower Saxony, Germany; sieved to <20 µm, organic matter content <0.1%). The different soils were mixed with varying concentrations of mucilage: 0, 0.1, 0.4, and 0.8% (w/w dry mucilage/dry soil). The silt soil was sieved to break aggregates and to enable a more homogeneous mixing with the mucilage. After drying, the dry soil–mucilage mixtures (60 g for the coarse and fine sand samples, 40 g for the silt samples) were packed in soil cores of 6-cm diameter. The samples were saturated with water for 48 h by setting the water potential to zero at the bottom of the samples and letting water flow from the bottom to the top of the samples to minimize air entrapment. When saturated, the samples had porosities of 0.4 (coarse sand), 0.46 (fine sand), and 0.58 to 0.67 cm$^3$ cm$^{-3}$ (silt). Note that especially at high concentrations of mucilage, the silt swelled during saturation, resulting in a higher porosity than the untreated silt. In the coarse and fine sands, no significant swelling was observed.

Using the hanging column method (Dane and Hopmans, 2002a), water potentials of 0, −10, −30, and −60 cm were imposed. The water potential, equilibrium was reached after different times for each combination of particle size and mucilage concentration. The conversion between volumetric and gravimetric water content was proportional to the concentration in the liquid phase ($\rho_w/\rho_b$). During measurement of the water retention curve of the coarse and fine sands, compaction of the soil was not significantly affected by changes in mucilage or water content, and the soil density ($\rho_b$) could be considered constant. Then, volumetric and gravimetric water contents were proportional throughout the experiment. Silt, however, showed shrinkage of the soil matrix and a decrease in total porosity at water potentials greater than −100 cm, which resulted in a reduction in water content while still at saturation. These dynamics of the soil matrix are not covered in our model. Therefore, only the water retention curves of the coarse and fine sands were fitted.

Results

Saturated Hydraulic Conductivity

Without mucilage, the saturated hydraulic conductivity (Fig. 4a) decreased with pore size, spanning three orders of magnitude, ranging from $2.4 \times 10^{-1}$ cm s$^{-1}$ in the coarse sand (630–1000 µm) to $2.4 \times 10^{-4}$ cm s$^{-1}$ in the silty soil (<20 µm). In the log–log plot (Fig. 4b) of the saturated conductivity as a function of mean particle size, the parabolic fit (red line) falls well within the error bars of the measurement, showing that hydraulic conductivity scales approximately well with the quadratic mean particle size $r^2$.

In general, with an increasing concentration of mucilage, the saturated hydraulic conductivity decreased (Fig. 4a). With the addition of 0.8 g dry mucilage to 100 g of dry soil, the saturated hydraulic conductivity was reduced by factors of $1.8 \times 10^{-4}$, $1.3 \times 10^{-3}$, $1.7 \times 10^{-3}$, $1.9 \times 10^{-3}$, and $3.0 \times 10^{-3}$ (Fig. 4c) compared with the conductivity of the untreated soil of the corresponding range of soil particle sizes (630–1000, 360–630, 200–500, 60–200, and <20 µm). The effect of mucilage in
reducing the saturated hydraulic conductivity depended strongly on the soil particle size; for the coarse soil, the reduction was >1000 times larger than the reduction in the silty soil.

It is striking that at a concentration of 0.8% the hydraulic conductivities of the soils of different particle sizes were of the same magnitude. Indeed, a constant hydraulic conductivity of $6.3 \times 10^{-5}$ cm s$^{-1}$ is within the error bars of the measured data points (Fig. 4b, violet line). At a concentration of 0.4%, the hydraulic conductivity of the fine sand was the lowest among the different soils ($4.8 \times 10^{-5}$ cm s$^{-1}$), and it was smaller by a factor of 6.7 than the silty soil and by a factor of 77.0 than the coarse sand at the same mucilage concentration.

The relative decrease in saturated hydraulic conductivity with increasing concentration of mucilage (Fig. 4c) strongly depends on the mean particle size, indicating that the saturated hydraulic conductivity does not simply depend on mucilage concentration but also on the local distribution defined by pore-scale interactions among mucilage, soil particle surface, and water.

**Soil Water Retention Curve**

For all tested particle sizes (Fig. 5), the addition of mucilage increased the gravimetric water content at any given water potential, particularly at low water potentials (dry soil). Except for the silty soil, the water content in nearly saturated parts of the soil retention curve was not significantly affected by the addition of mucilage. In the silty soil, the saturated water content was also markedly affected by the presence of mucilage. In the fine sand, the air-entry potential was approximately $-30$ to $-60$ cm and did not seem to depend on mucilage concentration. In the coarse sand, the air-entry potential could not be resolved well in our experiments; however, at all concentrations, the air-entry potential was less than $-10$ cm.

In the coarse sand (Fig. 5a), with particle sizes ranging from 360 to 1000 μm and mixed at mucilage concentrations of 0.1, 0.4, and 0.8 g per 100 g dry soil, the soil water content at a water potential of $-500$ cm was 1.1, 2.2, and 6.6% higher, respectively, than in the control (1.1%). In the fine sand (Fig. 5b), with particle sizes ranging from 125 to 360 μm and mixed at the same mucilage...
concentrations, the soil water content at a water potential of −500 cm was 0.5, 5.1, and 5.5% higher than in the control (2.6%). In the silty soil (Fig. 5c), preparation of soil with mucilage of the same concentrations as above increased the soil water content at a water potential of −500 cm by 11.2, 8.3, and 12.5% compared with the control (22.5%).

In soils with larger particle sizes, higher concentrations of mucilage were needed to significantly increase the soil water content (Fig. 5, indicated by arrows). For the case of coarse sand, a significant increase in soil water content (>5%) was observed at a mucilage concentration of 0.8% (w/w mucilage/dry soil), in the fine sand at a mucilage concentration of 0.4%, and in the silty soil already at a mucilage concentration of 0.1%.

The water retention curves of coarse and fine sands have been fitted (Fig. 5) using the Brooks–Corey model (Eq. [4]) for untreated soil (Table 1) and the model of Kroener et al. (2014) (Eq. [5]) for the soil prepared with mucilage (Table 2). Different sets of parameters, for example with \( \beta \) having a lower value (not shown here), were also able to well reproduce the highest concentration. The magnitude of the fitted \( \omega_0 \) then strongly depends on the value of the exponent \( \beta \). Tables 1 and 2 also provide the values of \( R^2 \) and the standard errors of the fitting parameters. While these values are very helpful when analyzing parameters fitted to linear models, the use and interpretation of these values can be very misleading in the case of nonlinear models (Kvålseth, 1985; Spiess and Neumeyer, 2010). Equations [4] and [5] exponentially depend on the parameters \( l \) and \( b \) and are highly nonlinear. This could explain why the error \( \sigma(\omega_0) \) is bigger than the parameter \( \omega_0 \) (Table 2). The other values (\( R^2 \) and standard errors of parameters) are quite reasonable even if the interpretation criteria for parameters fitted to linear models are applied.

**Discussion**

Measurements of saturated hydraulic conductivity (Fig. 4) confirmed the main hypotheses of the conceptual model: (i) mucilage

<table>
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<th>Soil</th>
<th>( \theta_s )</th>
<th>( \theta_r )</th>
<th>( \psi_e )</th>
<th>( \lambda )</th>
<th>( R^2 )</th>
<th>( \sigma(\psi_e) )</th>
<th>( \sigma(\lambda) )</th>
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<td>0.9924</td>
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<td>0.9980</td>
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<th>( \omega_0 )</th>
<th>( \beta )</th>
<th>( R^2 )</th>
<th>( \sigma(\omega_0) )</th>
<th>( \sigma(\beta) )</th>
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<td>Coarse sand</td>
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<td>0.971</td>
<td>( 3.16 \times 10^{11} )</td>
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</tr>
<tr>
<td>Fine sand</td>
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<td>0.969</td>
<td>( 9.79 \times 10^{12} )</td>
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Fig. 5. Measured and fitted gravimetric water retention curves for (a) coarse sand, (b) fine sand, and (c) silt (without fitted curve) prepared at various mucilage concentrations (0–0.8% [w/w dry mucilage/dry soil]). At a water potential of −1000 cm, a significant increase (>5%) of water content is indicated by an arrow.
reduces saturated soil hydraulic conductivity; (ii) the effect of mucilage on soil hydraulic conductivity is stronger in coarse soils; (iii) at high mucilage concentration, the hydraulic conductivity no longer significantly depends on soil particle size; and (iv) at intermediate mucilage concentration (~0.4%), the hydraulic conductivities of coarse and fine soils are higher than that of a soil with a medium range of particle sizes.

The Darcy–Brinkman equation well described single-pore-scale processes and suggested that mucilage had a stronger impact on the saturated hydraulic conductivity of coarser soils, which was confirmed by our experiments. The Darcy–Brinkman equation might become a powerful tool to derive the flow field in a single pore based on molecular interactions between water and mucilage. However, it remains challenging to measure the permeability of pure mucilage–water mixtures directly; when not held between the pore walls of a soil, the structure of the polymeric network within mucilage might collapse, resulting in a different permeability.

In our conceptual model, swelling and shrinking of the soil matrix was not considered. In the experiments, swelling of soil samples was observed in the silt soil, especially at high mucilage concentrations. In the real rhizosphere, however, swelling might not occur because the soil is compacted by the surrounding soil. Indeed, by using X-ray tomography, Aravena et al. (2014) observed that the rhizosphere can even be more compacted than the bulk soil because of root growth.

In the past, models (Vandevivere, 1995; Clement et al., 1996; Rockhold et al., 2002) and measurements of bacterial-induced changes in hydraulic conductivity have been presented. Bacterial EPS have similar properties to root exudates; both are hydrogels and can turn hydrophobic when dry. Similar to our measurements, Vandevivere and Baveye, (1992a, 1992b) found that, in general, saturated hydraulic conductivity decreased with increasing concentration of EPS. To quantify this decrease, Rockhold et al. (2002) discussed various approaches: the biofilm model, the plug model (Vandevivere, 1995), and the composite media model (Rockhold et al., 2002). The biofilm model assumes that the gel covers all solid particles with a continuous impermeable layer of uniform thickness; in the plug model, it is assumed that bacterial colonies form discrete plugs at one end of each capillary. In these different models, the relative reduction of saturated hydraulic conductivity is proposed as a function of the fraction of pore volume occupied by bacterial colonies B:

$$\frac{K}{K_0} = \begin{cases} \frac{(1-B)^2}{a + B - aB} & \text{biofilm model} \\ \frac{a}{F(B)(1-B)^2} & \text{plug model} \\ \frac{1-F(B)}{a + B - aB} & \text{combined model} \end{cases}$$

where $a$ is considered to be the relative reduction when the system is completely plugged, and $F(B)$ is a weighting factor balancing the biofilm and the plug models. Using a cut-and-random-rejoin model, Clement et al. (1996) proposed a relative reduction in saturated hydraulic conductivity of $K/K_0 = (1 - n \phi/\phi)^{19/6}$, where $n$ is the volume of the attached biomass per bulk volume of the porous medium and $\phi$ is the porosity of the porous medium. All of these models suggest that the relative reduction in hydraulic conductivity is the same for all particle sizes. This is opposed to our measurements (Fig. 4c), where at high mucilage concentration, the absolute hydraulic conductivities were of same magnitude for soils having different particle sizes (Fig. 4a), while the relative hydraulic conductivity strongly depended on particle size (Fig. 4c). This dependency on soil particle sizes is expected when considering single-pore mechanisms as described by the Darcy–Brinkman equation (Fig. 2) and should be included in quantitative models.

Some differences should be considered when comparing models of hydraulic properties affected by root exudates and EPS:

1. It is not obvious how to relate the fraction of pore volume occupied by root exudates—a parameter used to estimate the saturated hydraulic conductivity in models of EPS-induced changes—to the mean mucilage concentration. One option is a linear function until a certain concentration, above which the entire pore space is occupied. Another option is an exponential function [e.g., $\exp(-a\phi)$] describing the decreasing non-mucilage-occupied pore space as a function of mucilage concentration with fitting parameter $a$ (Kroener et al., 2014).

2. Often EPS is considered as being localized around bacteria and having a constant permeability for water flow, whereas root exudates, especially those of low viscosity, might more easily diffuse through the pore space, resulting in a smooth transition from areas of high mucilage concentration and low permeability to areas of low mucilage concentration and high permeability, making it difficult to define the pore volume occupied by mucilage.

The measurements of the soil water retention curves supported the prediction of the conceptual model that mucilage increases the water content and that the effect is more pronounced at low water potentials (less than −1000 cm) similar to an increased residual water content, at least in medium and coarse soils. In the silt, the water content at saturation was also strongly affected. This was caused by expansion of the wet mucilage and the mechanical interactions between mucilage and soil particles. The higher the concentration of mucilage, the larger the swelling of the soil matrix. A similar swelling has already been reported by Chenu (1993), Or et al. (2007a), and Rosenzweig et al. (2012), who measured the water retention of sandy soils mixed with various concentrations of EPS.

Similar to the findings of Rosenzweig et al. (2012), mucilage did not alter the air-entry potential in coarse and medium soils.
A significant increase in an apparent residual water content was found at concentrations of 0.4 to 0.8% in coarse sand, 0.1 to 0.4% in fine sand, and 0 to 0.1% in silt and supports the prediction of the conceptual model that in coarse soils more mucilage is needed to create a network that spans across the pore and can hold water at low matric potentials.

By using the model of Kroener et al. (2014) combined with Brooks and Corey (1966), the water retention curves of coarse and fine sand were fitted and the increase in residual water content could be reproduced. However, two different parameter sets (Table 2) were needed for the fine and coarse soils, indicating that soil pore size affects the ability of mucilage to increase the residual water content (Fig. 3), which is not yet incorporated into quantitative models such as Kroener et al. (2014).

Note that our experiments were based on mucilage from chia seeds. In general, the chemical, physical, and hydraulic properties of root mucilage depend on the plant species. Mucilage also contains surfactants (Read and Gregory, 1997). For the mucilage of some plant species, the effect of surfactants could overcome the effect of the hydrogel in holding water and might even result in a reduction of the water retention curve of the untreated soil.

Saturated hydraulic conductivity and its dependency on pore-scale interactions of mucilage, solid surface, and water is already very complex, making its extension to the unsaturated case even more challenging. Rockhold et al. (2002) proposed the composite porous media model to estimate unsaturated hydraulic conductivity in soils containing EPS as a function of the unsaturated hydraulic conductivity of bulk soil $K^\text{sand}(\theta_w^{\text{sand}})$ and of the biomass $K^\text{bio}(\theta_w^{\text{bio}})$ weighted by the volume of the attached biomass per bulk volume of porous medium $n_f$:

$$K^\text{comp}(\theta_w^{\text{comp}}) = K^\text{sand}(\theta_w^{\text{sand}}) + K^\text{bio}(\theta_w^{\text{bio}})n_f \quad [7]$$

Kroener et al. (2014) estimated the unsaturated conductivity of soil–mucilage mixtures by scaling the unsaturated conductivity of the bulk soil by the factor $\mu(\phi)$, which is related to mucilage viscosity and accounts for the reduced mobility of water to flow within the network: $K^\text{eff}(\theta_w) = K^\text{sand}(\theta_w)/\mu(\phi)$. Both models determine their parameters from bulk parameters, such as concentration of EPS or mucilage, and do not account for microscopic pore-scale interactions among mucilage, water, air, and solid particles and their dependency on the individual pore diameter (Fig. 1–3). In both models, at very low matric potentials, the unsaturated hydraulic conductivity of treated soil could become larger than that of the bulk soil. Carminati (2012) mentioned that this could be a strategy for plants to increase access to water under rather dry soil conditions. Volk et al. (2016) measured the unsaturated hydraulic conductivity of microbial biomass affected soils and found that, within their measured range of matric potentials, hydraulic conductivity was reduced by the presence of EPS and that the relative reduction in conductivity by EPS was largest in the saturated case.

Measurements of the unsaturated hydraulic conductivity of the rhizosphere remain challenging; tensiometers require a representative elementary volume (REV) of at least a few millimeters, while the extension of the rhizosphere itself is just 1 to 2 mm. Because of the low permeability of mucilage, it takes a long time until the system equilibrates at a certain water potential. As a result, it is hardly possible to judge whether the system is already in equilibrium at a given water potential or whether there are still significant microscopic heterogeneities between the water potential within the biomass and the REV-measured water potential. During long equilibration times, on the other hand, degradation of mucilage might become relevant.

In conclusion, the effects of mucilage on soil hydraulic properties have been related to basic physical properties at the pore scale. The presented concept provides a qualitative description of the effects of particle size and mucilage concentration on macroscopic soil hydraulic properties. The next challenge is to develop quantitative models of mucilage–soil interactions at the pore scale and to develop upscaling methods to predict rhizosphere hydraulic properties including the unsaturated conductivity, which has not been treated here. Existing models of rhizosphere hydraulic properties (e.g., Carminati, 2012; Kroener et al., 2014) provide a rough estimation of the relation between hydraulic properties and mucilage concentration, but they do not consider that mucilage–soil interactions are soil particle size specific. It is not yet clear whether the soil particle size specific relationship between pore scale soil–mucilage interactions and macroscopic hydraulic properties can be simply captured using different parameters or whether, depending on the specific distribution of soil particle sizes, even different effective functions and different equations need to be applied.

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References


Pathways to improve plant adaptation to drought. Vadose Zone J. 17:160090. doi:10.2136/vzj2016.09.0090


