

Roots at the percolation threshold

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The rhizosphere is the layer of soil around the roots where complex and dynamic interactions between plants and soil affect the capacity of plants to take up water. The physical properties of the rhizosphere are affected by mucilage, a gel exuded by roots. Mucilage can absorb large volumes of water, but it becomes hydrophobic after drying. We use a percolation model to describe the rewetting of dry rhizosphere. We find that at a critical mucilage concentration the rhizosphere becomes impermeable. The critical mucilage concentration depends on the radius of the soil particle size. Capillary rise experiments with neutron radiography prove that for concentrations below the critical mucilage concentration water could easily cross the rhizosphere, while above the critical concentration water could no longer percolate through it. Our studies, together with former observations of water dynamics in the rhizosphere, suggest that the rhizosphere is near the percolation threshold, where small variations in mucilage concentration sensitively alter the soil hydraulic conductivity. Is mucilage exudation a plant mechanism to efficiently control the rhizosphere conductivity and the access to water?

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Worldwide, 8.6×10^{10} tons of water flow across the soil-plant-atmosphere continuum every day [1]. This water flow is necessary to sustain vegetation, carbon sequestration, and food production. One of the least understood but very important interfaces in this water cycle is the rhizosphere, the soil region surrounding the roots that is effected by them.

Since the early 1960s the Gardner model [2] has been applied to model root water uptake. In the Gardner model the Richards equation [3] is solved in radial coordinates and the root system is simplified as a single root. Since then, models have been developed that account for more complex three-dimensional root architecture [4–6]. All of these models are based on the assumption of homogeneous properties around the roots. However, there is increasing evidence that the rhizosphere differs from the bulk soil in its physical, chemical, and biological properties.

Root growth induces soil compaction in the vicinity of roots [7,8]. Variations in soil water content lead to expansion and shrinkage of roots and can produce air-filled gaps around roots under dry conditions [9,10]. Furthermore, the rhizosphere is affected by mucilage, a polymeric gel exuded by roots. Mucilage is capable of absorbing large volumes of water, up to 1000 times its own dry weight [11]. Hydrated mucilage facilitates root water uptake from dry soil [12]. However, when mucilage dries it turns hydrophobic and it makes the rhizosphere temporarily water repellent [13], limiting root water uptake [14].

Swelling and shrinking rates of mucilage within the soil pore space depend on mucilage elasticity and viscosity and they can be significantly slower than the change in water potential in the bulk soil near the root. The slow rewetting rate of the rhizosphere is illustrated in Fig. 1, which shows a neutron radiography of the root zone of a young lupine plant after irrigation subsequent to a drying period [15]. Carminati [15]

reported that during a drying period the rhizosphere of lupines had a higher water content than the adjacent bulk soil. In contrast, after irrigation the rhizosphere remained markedly drier than the bulk soil for approximately 1–2 days. However, the recovery in transpiration rate as well as root swelling rates had faster kinetics, i.e., water was able to flow across the rhizosphere into the root without rewetting the rhizosphere significantly.

To describe these nonequilibrium dynamics Kroener *et al.* [16] proposed a dynamic relation between water content θ ($\text{cm}^3 \text{cm}^{-3}$) and water potential ψ (h Pa) in the rhizosphere:

$$\frac{d\theta}{dt} = RC_{\text{bu}}(\psi) \frac{d\psi}{dt} + (1 - R) \frac{1}{\tau} [\psi - \psi^{\text{eq}}(\theta_M)], \quad (1)$$

where R and τ (s h Pa) are parameters affecting the nonequilibrium dynamics, $\psi^{\text{eq}}(\theta_M)$ (h Pa) is the equilibrium water potential, and $C_{\text{bu}}(\psi)$ (h Pa^{-1}) is the bulk soil water holding capacity. The resulting dynamic relation is illustrated in Fig. 2.

When combined with the Richards equation [3], Eq. (1) is capable of reproducing the observed nonequilibrium dynamics in the bulk soil-rhizosphere-root continuum. The model, however, increases the complexity of previous root water uptake models and adds further parameters that need to be fitted. Additionally, although Eq. (1) can effectively describe the observed hydraulic dynamics, it still needs to be physically justified at the pore scale.

The objective of this study is to understand the nonequilibrium dynamics using a percolation approach and to determine the concentrations where this nonequilibrium relation becomes relevant. We apply a classic percolation model where a fraction of bonds is impermeable. An impermeable pore describes a pore covered with dry, hydrophobic mucilage. The percolation model predicts the fraction of disconnected pores above which the rhizosphere turns impermeable.

Percolation models are idealized representations of a medium at the microscopic scale used to derive macroscopic properties. Percolation has been applied to various disciplines: elasticity and formation of gels [17–19], metal-insulator transition [20,21], and flow and transport in porous media [22–25]. When applied to hydraulic processes in soils, the pore space

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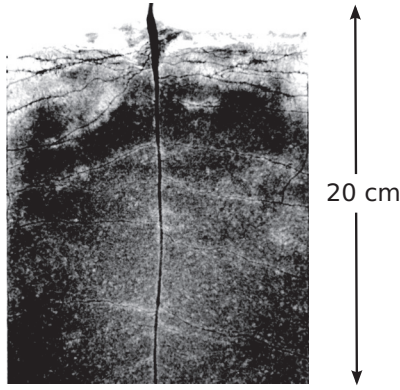


FIG. 1. Water content distribution in the root zone of a young lupine after irrigation as imaged with neutron radiography. The gray values are proportional to the water content (dark denotes wet). The radiograph shows that the water content in the rhizosphere was markedly drier than in the adjacent bulk soil. The image is taken from the experiments described in [15].

is usually represented as a regular lattice consisting of sites that are connected by bonds of simple shapes, i.e., cylindrical tubes, channels, or angular prisms [22,26–28]. The importance of percolation for flow in porous media consists in relating large-scale flow phenomena at the Darcy scale to pore scale heterogeneities [29].

In this study we focus on water infiltration through the rhizosphere during the first minutes after irrigation. Consider an initially dry rhizosphere [Fig. 3(a)]. A pore covered with mucilage is initially water repellent [Fig. 3(b)]. The small part of the gel in contact with water starts adsorbing water, wets, and the contact angle relaxes. The wetting front advances and the gel continues swelling. The wetting of this pore is controlled by the advancing contact angle, the swelling rate of mucilage, and the flow of water across mucilage. Since these processes happen at a time scale of several minutes to hours, we consider a mucilage covered pore as impermeable during the first minutes after irrigation. To incorporate this idea into a percolation model we set a random number of pores as covered

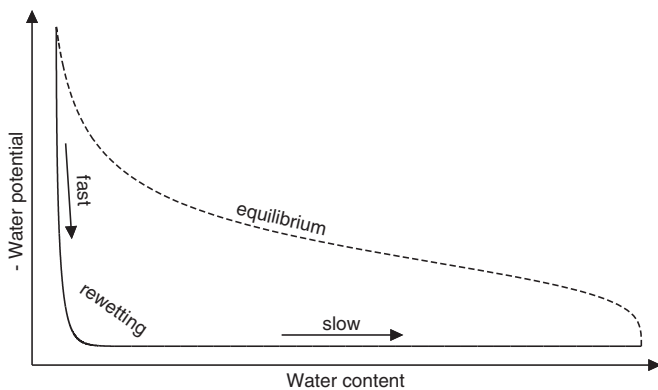


FIG. 2. Nonequilibrium relation (1) between rhizosphere water content and water potential in the rhizosphere during the rewetting phase [16]. The water content recovers more slowly than the water potential, resulting in a deviation from the equilibrium curve.

with mucilage; these pores are assumed to be impermeable [Fig. 3(c)].

We simulate the percolation through a cubic lattice. We use the bond percolation model, in which the nodes between the sites can be either connected or disconnected. The simulations show a distinct dual behavior [Fig. 4(a)]: When 73% of the bonds are disconnected water can easily flow across the region, most nodes of the domain get filled with water, and the wetting front is rather uniform. At 74% water can still cross the region, but the wetting front becomes irregular and only a fraction of pores is rewetted. Above a percentage of 75% water can no longer percolate. This value is consistent with the more accurate value of 24.881 26(5)% of connected bonds determined by [30] using extensive Monte Carlo simulations. Close to the percolation threshold, a small change in the number of disconnected nodes extremely alters the rhizosphere hydraulic behavior [Figs. 4(b) and 4(c)].

Steenhuis *et al.* [31] used a percolation model to explain water repellency in soils containing a fraction of hydrophobic particles. Experimentally, they found that 5% of hydrophobic particles can impede infiltration unless ponded. Our experiments differed in two ways: (i) All particles were uniformly treated and (ii) the longitudinal dimension was shorter than the lateral ones, as in the rhizosphere, while in their theoretical considerations they followed the approach of Raikh and Ruzin [32], who described the longitudinal conductivity of a narrow channel.

We did capillary rise experiments between pairs of glass plates to study the relation between mucilage concentration and contact angle. We used chia seed mucilage (*Salvia hispanica*) since it is easy to extract and has a chemical composition similar to lupine and maize mucilage (mainly xylose, glucose, and uronic acids, [33,34]). Additionally, it has similar physical behavior: When in contact with water it becomes a gel [33,35] and it turns hydrophobic after being dried. Mucilage extraction from chia seeds is described in [12,16]. Our experiments showed that the capillary rise in the angle between two glass plates was considerably reduced at a mucilage concentration of

$$c_{hy} = 6.0 \times 10^{-5} \text{ g cm}^{-2}. \tag{2}$$

The capillary rise between glass plates that were covered with a mucilage concentration lower than c_{hy} was finished within 5 min, while for plates covered with a higher concentration there was no capillary rise even after one day.

Once a threshold value of mucilage concentration per surface area was known, we calculated how much mucilage is needed to make the rhizosphere impermeable. Assuming that the soil particles are spheres with radius r , the specific soil surface area A (cm^{-1}) is

$$A = N4\pi r^2, \tag{3}$$

where N (cm^{-3}) is the number of soil particles per unit of volume; N is related to bulk soil density $\rho_{bu} = 1.6 \text{ g cm}^{-3}$ and soil mineral density $\rho_{mi} = 2.6 \text{ g cm}^{-3}$ according to

$$\rho_{bu} = N \frac{4}{3} \pi r^3 \rho_{mi}. \tag{4}$$

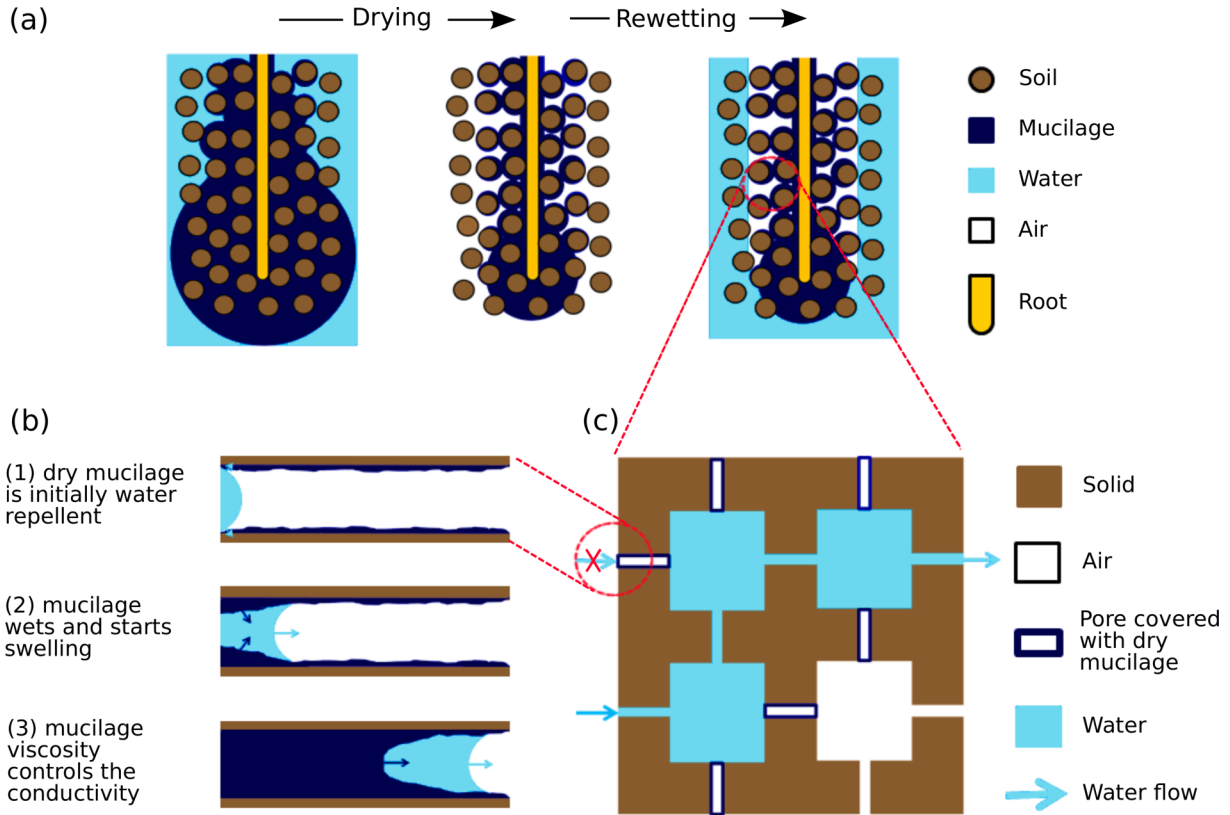


FIG. 3. (Color online) Conceptual model of rewetting of the dry rhizosphere. (a) Illustration of water content in the rhizosphere during drying and after rewetting, (b) rewetting of a pore covered with dry mucilage, and (c) pore network model of bonds covered with mucilage (disconnected) and bonds not covered with mucilage (connected).

Equations (3) and (4) give

$$A = \frac{3}{r} \frac{\rho_{bu}}{\rho_{mi}}. \quad (5)$$

The cubic percolation model predicts that around 75% of disconnected nodes are sufficient to make the soil impermeable. This means that we expect the percolation threshold at a mucilage concentration of $c_{th} = 0.75Ac_{hy}$. Combination with Eqs. (2) and (5) gives the mass of mucilage per unit volume of bulk soil required to make the soil impermeable:

$$c_{th} = \frac{1}{r} 8.3 \times 10^{-5} \text{ g cm}^{-3}. \quad (6)$$

Expressed as mass of dry mucilage per dry soil mass as a function of particle diameter d , it becomes

$$c_{th} = \frac{1}{d} 1.04 \times 10^{-4} \text{ g g}^{-1}. \quad (7)$$

We tested this theoretical relation by monitoring water infiltration through artificial rhizosphere layers of varying mucilage concentration and particle size. We mixed various amounts of wet mucilage with dry soil to obtain soil samples of the required mucilage concentration. The mucilage-soil mixture was dried for around 24 h at 40°C. To reduce accumulation of dry mucilage on the surface, we used very wide boxes so that the height of the soil was less than 1 mm. We packed soil samples representing a simplified model of the root-rhizosphere-soil system: We used a layer of dry untreated soil as an analog of the root, a layer of approximately 5 mm

of treated soil as rhizosphere, and again a region of untreated soil representing the bulk soil.

Neutron radiography was used to monitor the water content distributions during capillary rise. Water has a high attenuation coefficient for neutrons, making of neutron radiography an optimal noninvasive method to quantitatively image water distribution in thin samples with high accuracy [36]. The neutron radiographs were taken at the cold neutron imaging beam line NEUTRA [37] of the Paul Scherrer Institute, Switzerland.

The prepared dry samples were placed inside a box in front of the neutron beam. Then the box was filled with water until the water table was 2.5 cm below the layer representing the rhizosphere. The capillary rise in the samples was monitored with time-series neutron radiography. Figure 5 shows the water content distribution in the samples 5 min after the start of capillary rise. A typical threshold behavior appeared: When the concentration of mucilage in the rhizosphere was below a certain value water could easily cross the treated layer. In contrast, when the concentration exceeded this value water could no longer cross this region, at least during the first hours after irrigation. Neutron radiography was performed with soils of three different particle sizes. Four additional particle sizes were tested in our laboratory. Note that to determine the mucilage concentration at the percolation threshold it is sufficient to control if the surface of the sample turns wet. In this way we determined further threshold concentrations for different particle sizes without using neutron radiography.

Figure 6 shows the relation between mucilage concentration at the percolation threshold and particle size as predicted by

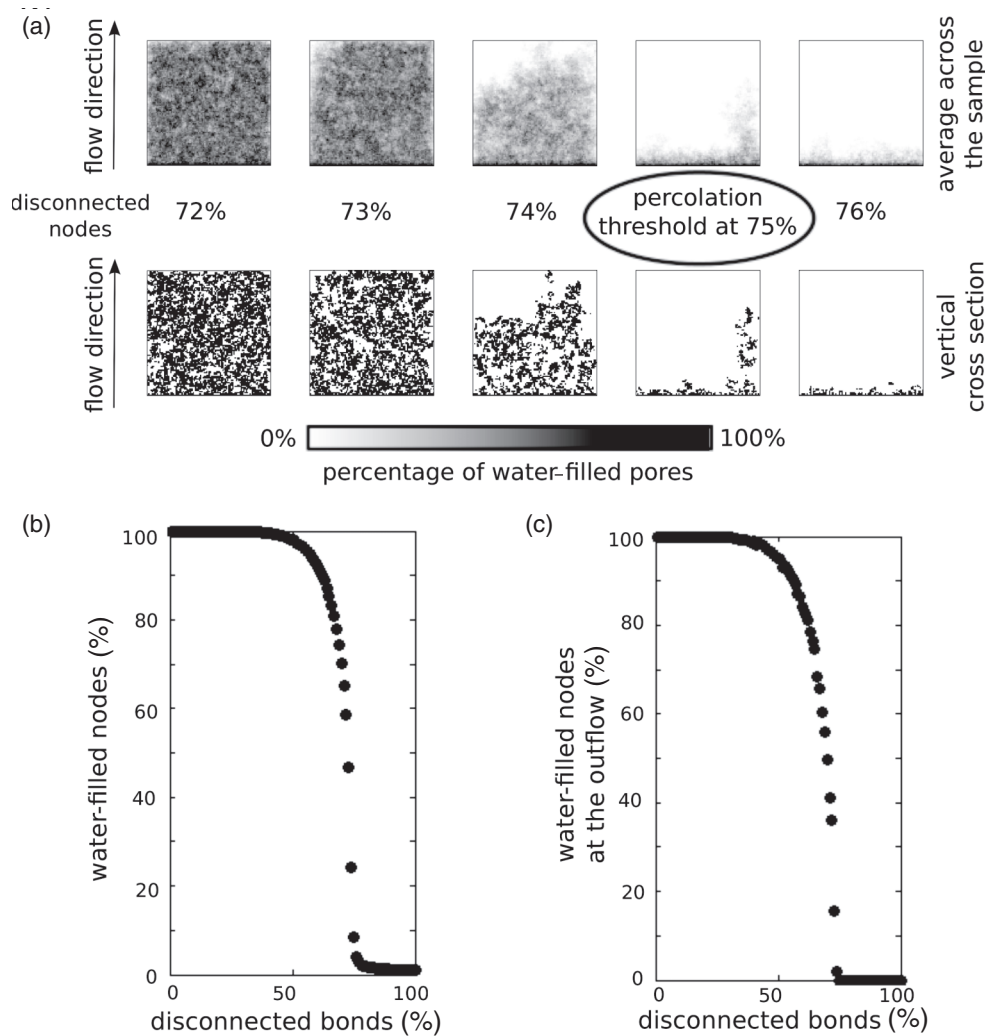


FIG. 4. Bond percolation in a cubic lattice with varying percentage of disconnected pores. (a) Water-filled pores averaged across the sample and for a horizontal cross section. (b) Water-filled nodes as a function of disconnected bonds. (c) Water-filled nodes at the outflow as a function of disconnected bonds. Close to the percolation threshold a small change in the number of disconnected nodes strongly affects the hydraulic behavior.

Eq. (7) and as observed in our experiments. The experimental results fit well with the theoretical relation. For the coarse sand the experimental points are slightly below the range of theoretical values. This can be explained by the small offset in the water potential during the experiments. At $\psi = -2.5$ cm the untreated, coarse rhizosphere layer [Fig. 5(c), sample on the left] was not fully saturated. Therefore, less surface was needed to be covered by mucilage to prevent capillary rise, i.e., the mucilage concentration at percolation threshold is smaller than the one we expect from our theory developed for saturated soil conditions.

Our pore network model and the capillary rise experiments showed a distinct dual behavior for the rewetting of dry rhizosphere. For mucilage concentrations lower than a certain threshold, water could uniformly and quickly cross the treated layer after rewetting of bulk soil. At slightly higher mucilage concentrations, the thin layer became almost impermeable. The mucilage concentration at the threshold strongly depended on particle size: The smaller the particle size, the larger the soil specific surface was and more mucilage was needed to

cover enough soil surface to induce water repellency. The percolation model could quantitatively reproduce well the threshold characteristics of the experiments.

Figure 5(b) demonstrates that near the percolation threshold water could flow across the rhizosphere layer without rewetting it significantly. In equilibrium, however, mucilage should lead to a higher water content [12]. This apparent contradiction is explained by the slow rewetting of mucilage compared to initial percolation of water, which results in nonequilibrium dynamics in the rhizosphere [16].

Of course our percolation model contains several simplifications. (a) Soils are not cubic lattices. More realistic networks, e.g., Voronoi networks, might provide a better prediction of the ratio of connected pores at the percolation threshold [38]. (b) While percolation is scale independent, we expect our experimental results to depend on the thickness of the rhizosphere: In thicker soil layers mucilage is expected to start swelling during the percolation time, leading to pore clogging mechanisms that are not included in this model [39]. Rhizosphere, however, is a very thin layer, so the percolation

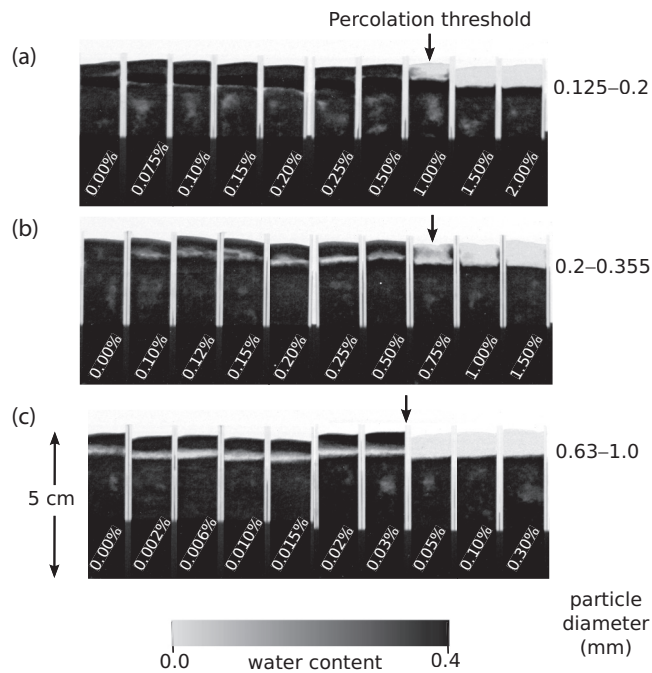


FIG. 5. Capillary rise in soil columns with a small layer of soil mucilage mixture as an analog of the rhizosphere. Among the soil columns particle size as well as mucilage concentration of the soil mucilage mixture varied: (a) fine sand (diameter of 0.125–0.2 mm), (b) medium sand (0.2–0.355 mm), and (c) coarse sand (0.63–1.0 mm). The gravimetric concentration (mass of dry mucilage per unit mass of dry soil) in the rhizosphere layer is given for each soil column.

time should be much faster than the swelling. Therefore, our model is justified to describe the initial phase of the rhizosphere rewetting. (c) In our study the capillary pressure was almost zero. For lower capillary pressures, however, one can expect that a lower mucilage concentration is needed to make the rhizosphere impermeable.

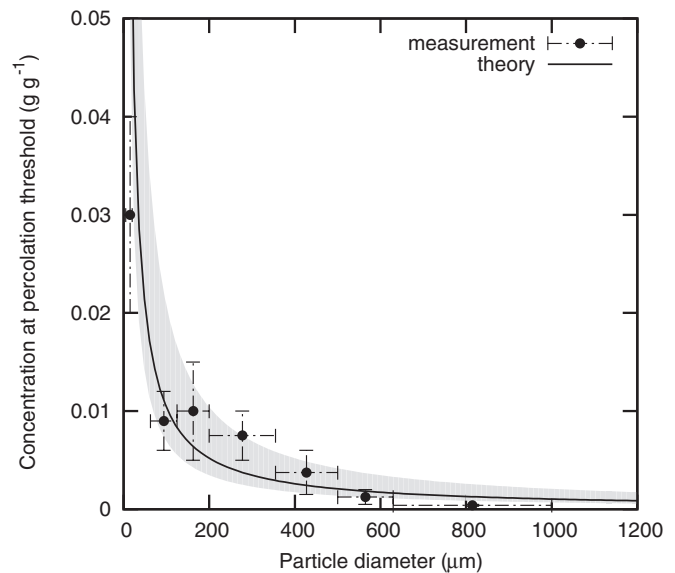


FIG. 6. Relation between particle diameter and threshold concentration (7). The gray region is related to the error in the measurement of c_{hy} .

Our experiments, together with former observations of water dynamics in the rhizosphere (Fig. 1), suggest that the rhizosphere is near the percolation threshold, where small variations in mucilage concentration sensitively alter the hydraulic behavior. It is tempting to conclude that mucilage exudation is an efficient mechanism to control the rhizosphere conductivity and the access to water.

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