Viewpoint
Plants control soil gas exchanges possibly *via* mucilage

Adrian Haupenthal[1]*, Mathilde Brax[2], Jonas Bentz[3], Hermann F. Jungkunst[4], Klaus Schützenmeister[4], and **Eva Kroener[1]**

[1] Institute for Bio- and Geosciences, IBG-3 Agrosphere, Forschungszentrum Jülich GmbH, Wilhelm-Johnen-Straße, 52428 Jülich, Germany
[2] iES Landau, Institute for Environmental Sciences, Environmental and Soil Chemistry, University of Koblenz-Landau, Fortstraße 7, 76829 Landau, Germany
[3] iES Landau, Institute for Environmental Sciences, Geophysics, University of Koblenz-Landau, Fortstraße 7, 76829 Landau, Germany
[4] iES Landau, Institute for Environmental Sciences, Geoecology & Physical Geography, University of Koblenz-Landau, Fortstraße 7, 76829 Landau, Germany

Abstract

Background: Gaseous matter exchanges in soil are determined by the connectivity of the pore system which is easily clogged by fresh root exudates. However, it remains unclear how a hydrogel (*e.g.*, mucilage) affects soil pore tortuosity and gas diffusion properties when drying.
Aims: The aim of this viewpoint study is to extend the understanding of gas exchange processes in the rhizosphere by (a) relating it to the patterns formed by drying mucilage within pore space and (b) to give a concept of the effect of drying mucilage on soil gas diffusivity using the combination of experimental evidence and simulations.
Methods: To describe the effect of mucilage on soil gas exchanges, we performed gas diffusion experiments on dry soil–mucilage samples and took images of glass beads mixed with mucilage to visualize the formation of mucilage after drying, using Environmental Scanning Electron Microscopy. Finally, we set up simulations to characterize the geometric distribution of mucilage within soil during the drying process.
Results: Experiments of gas diffusion show that mucilage decreases gas diffusion coefficient in dry soil without significantly altering bulk density and porosity. Electron microscopy indicates that during drying mucilage forms filaments and interconnected structures throughout the pore space reducing gas phase connectivity. The evolution of these geometric structures is explained via pore scale modelling based on identifying the elastic strength of rhizodeposition during soil drying.
Conclusion: Our results suggest that releasing mucilage may be a plant adaption strategy to actively alter gas diffusion in soil.

Key words: gas diffusion coefficient / liquid bridges / mucilage / pore connectivity / pore scale simulation / respiration / rhizosphere

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1 Introduction

The availability of life-sustaining resources in the Earth's Critical Zone (*National Research Council*, 2000) is highly dependent on solute and energy transportation. Gas and water transport in air and water is quite well calculable. Gas and water transport in and out of soils is, due to the heterogeneous nature of soils, more complex. The connectivity of the pore system determines liquid and gaseous flows in the porous media soil. The basic route network for matter flow through soils is set by the solid mineral phase like soil texture. However, the tortuosity of the pore connectivity through soils is highly influenced by organic matter locking pores. Furthermore, the highly dynamic and variable liquid phase is locking pores for the gaseous flow, as gas diffusion is 10^4 times lower in water than in gas (*Ferrell* and *Himmelblau*, 1967). Therefore, it remains very challenging to predict matter flow through soils like greenhouse gas emissions from soils to the atmosphere. Above all, soil is a living environment and therefore biology comes into play and the diversity of biological influences is still not yet fully understood. When growing in soil, roots create the rhizosphere. The rhizosphere is a small layer of soil particles around roots, where interactions between plants and soil take place and which is actively modified by plant root rhizodeposits and growth rate (*Bais* et al., 2006; *Gregory*, 2006; *Hinsinger* et al., 2009). Depending on the root density, the rhizosphere frequently covers a dense layer at the interface of the soil to the atmosphere. Therefore, plants influence is decisive for all matter flow at the interfaces soil–plant and soil–atmosphere. By releasing hydrogels, roots influence both the organic matter and the liquid phase of the soil and consequently pore tortuosity. One of the most prominent

* Correspondence: A. Haupenthal;
e-mail: a.haupenthal@fz-juelich.de

hydrogel root releases is mucilage, known to affect soil hydraulic properties (*Carminati* et al., 2010; *Kroener* et al., 2014, 2018). In contact with water, it swells and is able to adsorb water up to 10^3 times its own weight depending on the type (*Muñoz* et al., 2012). During drying mucilage forms liquid bridges between soil particles, filling larger parts of the pore space (*Albalasmeh* and *Ghezzehei*, 2014 *Carminati* et al., 2017; *Benard* et al., 2018).

The movement of gas is triggered by concentration gradients that develop due to autotrophic (mainly plants) and heterotrophic (microbes) respiration in the rhizosphere between soil and atmosphere and by concentration gradients within the soil. Soil-gas diffusion is controlled by soil gas diffusion coefficient D_p which is mostly affected by the soil structure, air-filled porosity, bulk density, and pore connectivity and tortuosity (*Fujikawa* and *Miyazaki*, 2005; *Hamamoto* et al., 2009). The main barriers for gas movement in soil is altered pore structure due to compaction, water saturation and organic matter fraction (*Xu* et al., 1992; *Moldrup* et al., 2000; *Thorbjørn* et al., 2008; *Hamamoto* et al., 2012, 2009).

The composition of soil gas is affected by atmospheric diffusion and respiration of roots and microorganisms (*Fujikawa* and *Miyazaki*, 2005). During respiration oxygen is used by heterotrophic organisms producing carbon dioxide. Other gases like methane and nitrous oxide are produced and used as well. At high soil moisture there is a limited availability of oxygen in soil pore-space leading to hypoxia (*Badri* and *Vivanco*, 2009). As a result of hypoxia respiration change from aerobic to anaerobic leading to an accumulation of ethanol, lactic acid and alanine at phytotoxic levels (*Rivoal* and *Hanson*, 1994). It is reported that roots protect themselves from toxication by secreting exudates from their roots (*Xia* and *Roberts*, 1994). Thus, the process of diffusion in soil close to the roots is a key aspect in the survival of plants.

Despite several studies on the effect of physical properties and organic matter on soil gas diffusion, it is still unknown how mucilage affects gas movement in soils. *Benard* et al. (2019) showed that during drying maize mucilage and extracellular polymeric substances (EPS) form filaments and two-dimensional interconnected structures, which span across multiple pores. Due to a higher viscosity and a lower surface tension of mucilage and EPS compared to water, these structures will not break up easily. As a result, the formed network enhances water retention, keeps the liquid phase connected during drying, and decreases vapour diffusivity and local drying rates. They expect that mucilage and EPS layers limit the diffusion of gases. However, we still lack both, measurements and models of the effect of rhizodeposits on gas diffusion in soil.

In this study, we examined the effect of mucilage on soil gas diffusion coefficient during drying. Our hypothesis is that during drying mucilage forms a network that disconnects the gas phase, reducing soil gas diffusion. We present experimental data and a conceptual model with pore scale simulations of simplified drying scenarios. For the experiments, we mixed a sandy soil with chia seed mucilage at various concentrations and given bulk density, dried the samples and measured gas diffusion coefficient.

2 Material and methods

2.1 Theory and conceptual model

2.1.1 Soil gas diffusivity models

In a dry porous medium without mucilage, gas diffusion coefficient D_p ($cm^2\ s^{-1}$) strongly depends on soil physical properties. Particle size distribution and bulk density affect the pore structure of soil determining air-filled porosity ε as well as pore connectivity and tortuosity (*Hamamoto* et al., 2009). In coarse soils, pores are wider and less tortuous than in fine soils resulting in higher diffusion coefficients (*Thorbjørn* et al., 2008).

There are several models predicting D_p. Most of them are described as power-law functions of the soil–air content ε (*Buckingham*, 1904; *Marshall*, 1959; *Millington*, 1959; *Currie*, 1960; *Millington* and *Quirk*, 1961; *Moldrup* et al., 2000). Their general form is:

$$\frac{D_p}{D_0} = \varepsilon^{X'}, \tag{1}$$

where X' is the pore-tortuosity factor (dimensionless) and D_0 is the gas diffusion coefficient in free air. Based on measured D_p data, *Hamamoto* et al. (2012) proposed a pore-tortuosity factor of:

$$X' = 0.4 + 2.9\Phi, \tag{2}$$

where Φ is the total porosity.

In their model, *Hamamoto* et al. (2012) considered a percolation threshold ε_{th}, at which the gas-phase within pores is disconnected and gas diffusion is limited by the diffusion through the liquid phase—in water this is approximately10^4 times lower than in air. Thus, Eq. (1) can be written as:

$$\frac{D_p}{D_0} = (\varepsilon - \varepsilon_{th})^{X'}. \tag{3}$$

They proposed an estimation of the air-filled porosity threshold:

$$\varepsilon_{th} = 0.11\Phi^4. \tag{4}$$

In their experiments, ε_{th} ranges from 0–0.1 $m^3\ m^{-3}$, depending on total porosity.

The model of *Moldrup* et al. (2004) also originates from a gas diffusivity model of *Millington* and *Quirk* (1961) and can be written as:

$$\frac{D_p}{D_0} = \frac{\varepsilon^{10/4}}{\Phi^2}, \tag{5}$$

where Φ is the total porosity ($m^3\ m^{-3}$).

In their study on gas diffusivity in soil (*Moldrup* et al., 2013) presented a structure-dependent water-induced linear reduction (SWLR) model with the ability to express pore network complexity and water blockage effect. They introduced a porous media complexity factor C_m to specify soil conditions, *e.g.*, repacked or intact soils. The SWLR-model can be written as:

$$\frac{D_p}{D_0} = \varepsilon^{[1+C_m\Phi]}\left(\frac{\varepsilon}{\Phi}\right). \quad (6)$$

They have shown that for dry soil conditions ($\varepsilon = \Phi$) $C_m = 1$ provides a good prediction of gas diffusivity. Comparison with literature data for gas diffusivity in dry porous media had shown that $C_m = 3$ represents lower limit D_p/D_0 models and gives a good description of pore networks with high tortuosity, like clay soils.

2.1.2 Mucilage and organic matter dependent gas diffusion models

When mucilage is added to the soil, we assume a blocking effect. *Oleghe* et al. (2019) recognized that adding mucilage can result in an increase of soil water retention without bulk porosity being affected by chia seed mucilage and thus suggested that pores got clogged by mucilage. It is very straightforward to postulate that hydrogel is clogging pores, so the challenge now lies in conceptualizing the effects of soil gas exchanges when mucilage (hydrogel) is drying or has dried out. The addition of mucilage results in an increase of viscosity of the liquid phase which leads to a formation of mucilage bridges between soil particles during drying (*Albalasmeh* and *Ghezzehei*, 2014; *Benard* et al., 2018, 2019). At low concentrations of mucilage within soil (mass of dry mucilage per mass of dry soil) the bridges between particles are shaped like thin filaments. With higher concentrations the amount of mucilage per soil increases and instead of filaments, hollow structures or even interconnected surfaces of dry mucilage are formed which are spanning across the pore space (Fig. 1). Similar to a foil, these very thin layers break the connectivity of the gas phase and we expect that gas diffusion may get strongly reduced. Due to its low volumetric content, dry mucilage does not affect total air-filled porosity in sandy soils significantly. We hypothesize that, in dry soils, mucilage increases the tortuosity of gas diffusion pathways until disconnecting the gas phase which results in a reduction of the gas diffusion coefficient (Fig. 1).

Since dry mucilage does not affect air-filled porosity significantly, models such as Eq. (3) by *Hamamoto* et al. (2012) considering a reduction of air-filled porosity due to organic matter cannot serve as a suitable model to predict D_p in the rhizosphere. There is the possibility to adjust the complexity factor C_m of the model of (*Moldrup* et al., 2013) to represent the complexity of the air-filled pore network. However, in *Moldrup* et al. (2013) C_m is supposed to be related to total porosity—a parameter that is, in our case, not significantly affected by mucilage.

The described models may serve as a first rough approximation to predict the influence of mucilage on soil gas diffusion.

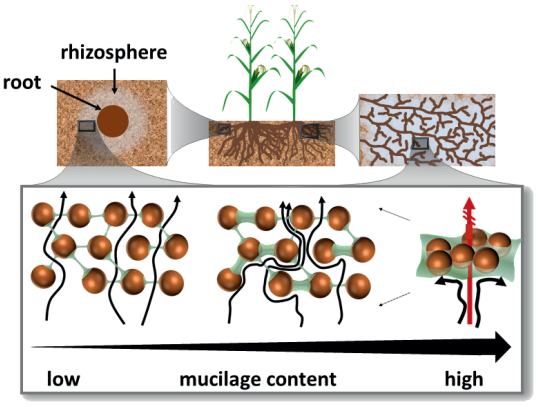

Figure 1: Schematic of increasing mucilage content at constant dry soil condition for (left) the rhizosphere of a single root and (right) a soil with many roots coated with mucilage. Depending on mucilage concentration, liquid bridges form thin filaments (low), hollow structures or interconnected surfaces (high) between soil particles.

But these models are developed for organic matter in general instead of mucilage. To develop more suitable models an understanding of underlying pore scale processes affecting gas phase connectivity is needed.

2.1.3 Pore scale model of mucilage distribution during drying

To simulate the effect of mucilage on gas phase connectivity, a model is required that describes pore scale spatial distribution and dynamics of mucilage. At low concentrations of mucilage, *i.e.*, when there are large distances between polymers (Fig. 2a, left), mucilage behaves like a liquid, having a viscosity that increases with polymer concentration. Polymer chains start to build cross-links to create a network as muci-

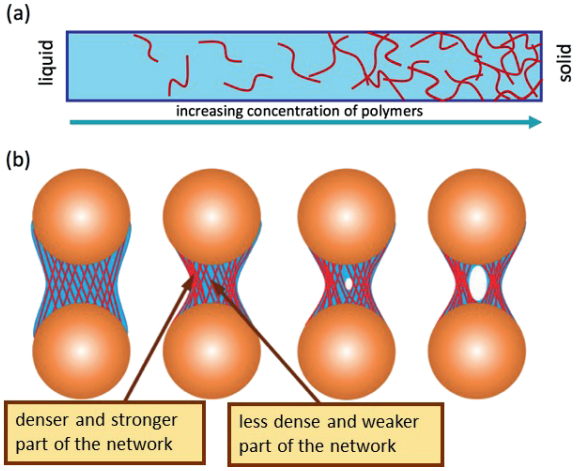

Figure 2: Conceptual idea of mucilage drying: (a) transition from low to high concentrated mucilage (*i.e.*, transition from high to low water content) corresponds to a transition from a liquid with large distances between polymers to a solid network where long chained polymers are connected via cross-links, (b) when mucilage is at high mucilage concentrations, during drying, its polymeric web shrinks, becomes denser and thus stronger at its outer parts and may break at its weakest parts in the centre forming a hollow structures.

lage dries out and the concentration of polymers increases, (Fig. 2a, right). Mucilage transforms from a liquid to a solid made of an elastic hydrogel that spans a three-dimensional solid web between the mineral soil particles. To properly simulate those drying processes at the pore scale, a description of the smooth transition from the rather liquid to the rather solid state is required. Here, we present a simplified case study. Simulations of the two extremes, the liquid and the solid network, only, without a transition between the two states. Lattice–Boltzmann methods are a suitable tool to simulate the pore scale dynamics of liquids (*Sukop* and *Or*, 2004; *Tuller* and *Or*, 2004; *Pot* et al., 2015; *Richefeu* et al., 2016). To simulate dynamics of the highly concentrated, rather solid mucilage, we applied the discrete element method which is a common tool to describe deformation and rupture processes of solids (*Munjiza* et al., 1995; *Bobet* et al., 2009) and has also been used to simulate fracture of hydrogels (*Kimber* et al., 2012; *Yang* et al., 2018). Using the description of highly concentrated mucilage as a network spanning across the pore space, one can explain the formation of hollow cylinders between particles (Fig. 2b). Upon drying the volume of water decreases, surface tension together with the attractive forces between polymers and water induce a tension on the network: it shrinks and as a result the density of polymers may locally increase near to the outer parts and strengthen the network there. Upon further tension the network may break at its weakest point which may be in the centre. Here, this concept is presented just in two dimensions. However, in the more complex three-dimensional pore space geometry this concept may not only describe the formation of hollow bridges between two particles but also the formation of connected surfaces of mucilage spanning across many pores (Fig. 1, right) and disconnecting the gas phase.

2.1.4 Setup of the simulations

For both simulations of the distribution of mucilage during drying (either as a liquid or as a polymeric network) we assume a slow drying process, *i.e.*, the system is assumed to be in a quasi-steady state in which viscosity and momentum do not need to be considered. For the liquid case, we implemented the Shan–Chen type multiphase lattice Boltzmann model (*Shan* and *Chen*, 1993) using the LBM simulation tool Yantra (*Patel* et al., 2017). For each drying step, a certain water content is chosen and its equilibrium distribution is simulated assuming a contact angle of the soil surface close to 0°. The model is based on the D2Q9 method: this means for each cell of the regular 2D-lattice, interactions with its eight neighbouring cells and the cell itself are considered to calculate streaming and collision at this step. These steps are repeated until equilibrium can be assumed, *i.e.*, changes in the liquid distribution are smaller than a certain threshold value. In each equilibrium state, the liquid–air interface adjusts such that its curvature is constant (compare Young–Laplace equation where interface curvature is related to surface tension and pressure difference). Upon further drying, *i.e.*, reduced water content, the negative curvature of the liquid phase becomes more and more negative.

In the highly concentrated case, mucilage is described as a polymeric network (Fig. 3) which consists of many nodes. These nodes are connected to their neighbouring nodes *via* springs of a certain stress-strain relation which represent the attractive forces. In our model, the stress-strain relation is represented by a simple linear relation between the elongation of the spring and the force F on the spring:

$$F(r) = -k \times (R_{equ} - r), \tag{7}$$

where k is a constant, and the elongation $(R_{equ} - r)$ is the difference between length of the spring R_{equ} in equilibrium and its current extension r. If a node gets close to the soil surface, it connects also to the soil surface *via* a spring, representing the attractive force towards the soil particle. During the drying process, each quasi-steady-state spatial distribution of the network is simulated stepwise: in each step, each node moves one step into the direction of the total force and proportional to the total force acting on it. If the tension on a spring gets larger than its breaking point, then the nodes get disconnected. Equilibrium is assumed when each node becomes stationary, *i.e.*, the forces on all the springs connected to this node sum up to approximately zero.

The next quasi-steady state of the drying process, *i.e.*, a reduced water content of the mucilage phase, is obtained by decreasing the equilibrium distance R_{equ} of the stress-strain relation of each spring. This way, the decreased equilibrium distance is related to the tension on the network induced by the reduced water content, *i.e.*, a reduced pore volume available for polymers.

To sum up, important parameters that need to be defined for the simulation are: k, the critical tension at which a connection breaks, the distance between two nodes at which a new

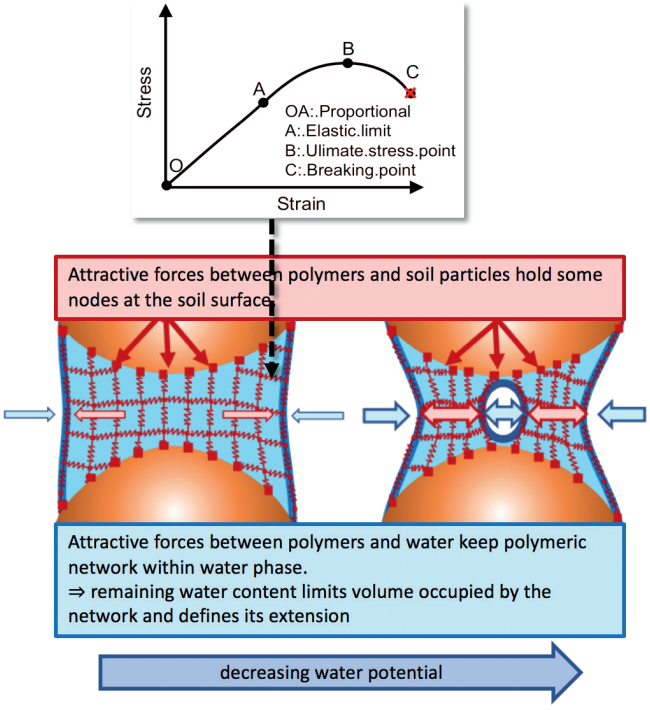

Figure 3: Setup of the simulation of drying dynamics at high concentrations using the discrete element methods.

connection can form between both nodes, the maximum number of springs one node can connect with, and the density of network nodes which may be related to the concentration of mucilage. An extensive analysis of the effect of each of these parameters exceeds the purpose of this viewpoint paper, here we only want to present qualitative results describing spatial structures that are created by hydrogel dynamics. Our two-dimensional simulations serve as a proposition of possible modelling tools to describe the observed pore space distributions of mucilage. For a quantitative analysis of these complex pore space dynamics, further advanced three-dimensional models, a transition between the two cases (low and high concentration of mucilage in the liquid phase) and knowledge of the changes of physico-chemical properties of the specific mucilage type during the drying process will be needed.

2.2 Mucilage collection

Mucilage was collected from chia seeds. Chia seed mucilage is easily available in large amounts and widely used as a model for plant mucilage. Its physical properties are similar to those of plant mucilage (*McCully* and *Boyer*, 1997; *Read* and *Gregory*, 1997; *Naveed* et al., 2017), but there are still differences, *e.g.*, a relatively high content of polysaccharides and a higher viscosity of chia seeds compared to barley mucilage or maize mucilage which contain more organic acid (*Naveed* et al., 2017; *van Veelen* et al., 2018). Mucilage was extracted from chia seeds according to the method of *Kroener* et al. (2018). The gel–water mixture was frozen and freeze-dried to obtain dry mucilage which was then pulverized.

2.3 Sample preparation

As an analogue of the rhizosphere, a soil–mucilage mixture was chosen to test the effect of mucilage on soil gas diffusion coefficient. Sand (soil) of particle sizes of 500–630 μm was mixed with chia mucilage to concentrations of 0.1%, 0.3%, and 0.6% (w/w, dry mucilage/dry soil). Dry mucilage was diluted with water and kept in a closed container for 15 min to swell. We set the amount of water for the gel–water mixture so that the volumetric water content was equal to the porosity. In this way, porosity was not affected during drying for all samples. Soil was mixed with wet mucilage, packed and allowed to dry for 48 h at 20°C ± 1°C. After drying, gravimetric water content of the samples was < 1%. While the simulations describe the effect of mucilage on pore scale dynamics of the liquid phase during drying, the following experiments were performed on already dried samples.

2.4 Environmental Scanning Electron Microscopy

Glass beads (0.2 mm) were mixed with chia seed mucilage at various concentrations and dried in the oven at 30°C for 24 h. ESEM images were taken with a FEI Quanta 250 ESEM (FEI Company Hillsboro, United States) under low vacuum with chamber pressures between 60 and 80 Pa. A large field detector was used with an acceleration voltage between 12.5 and 15 kV.

2.5 Gas diffusion measurements

To examine the effect of mucilage on gas diffusion in a dried sandy soil and to determine the diffusion coefficient D_p, a diffusion chamber method according to *Rolston* and *Moldrup* (2018) was set up (Fig. 4). D_p was measured as a function of mucilage concentration. For each concentration three replicates were prepared. Samples were repacked in 5.77 cm^3 soil cores, with a height of 0.6 cm, a cross section of 9.62 cm^2 and a weight of 10 g. Oxygen was used as a tracer gas with a gas diffusion coefficient in free air of D_0 = 0.231 cm^2 s^{-1} (*Wiegleb*, 2016). All measurements were performed at room temperature of 20°C ± 1°C.

3 Results

3.1 Gas diffusion measurements

Measurements of the diffusion coefficient D_p/D_0 for a dry sandy soil (500–630 μm) as a function of mucilage concentration show that with increasing mucilage concentration the relative diffusion coefficient D_p/D_0 decreases. Gas diffusion was reduced by about 50% as can be seen in Fig. 5.

Throughout all measurements bulk density (1.737 ± 0.002 g cm^{-3}) and porosity (0.343 ± 0.002 cm^3 cm^{-3}) were not affected. Dry weight of mucilage per sample ranged depending on concentration (0.1–0.6% gravimetric concentrations) from 0.01 to 0.06 g. Assuming a mucilage density of roughly 1 g cm^{-3} leads to a volumetric mucilage fraction of 0.17–1.04%. Thus, the volume occupied by mucilage is ≤ 1.04% of the volume of bulk soil and the effect of dry mucilage on air-filled porosity is negligible.

3.2 Environmental Scanning Electron Microscopy

The conceptual model (Fig. 1) is supported by images created using an environmental scanning electron microscope (Fig. 6). The formation of mucilage structures in glass beads after drying are shown in Fig. 6. At a concentration of 0.16% thin mucilage filaments spanning across various pores are

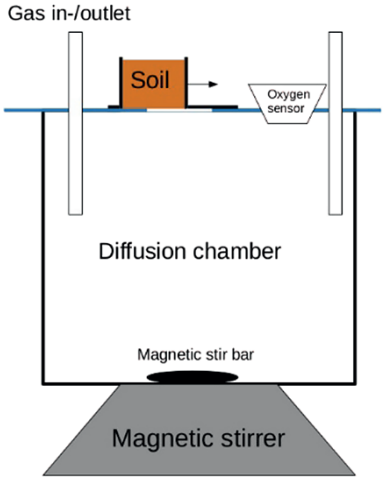

Figure 4: Experimental setup for gas diffusion measurements based on diffusion chamber method.

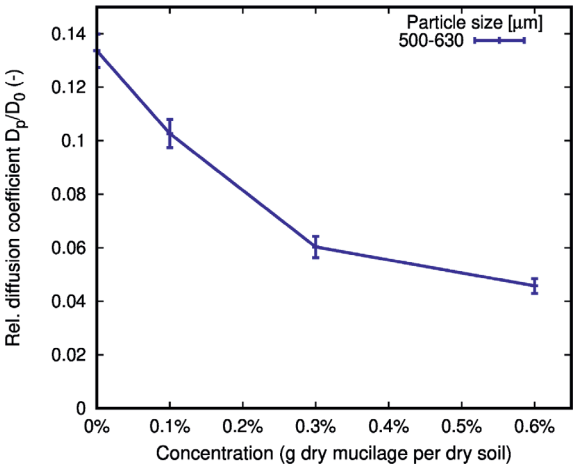

Figure 5: Relative diffusion coefficient D_p/D_0 as a function of mucilage concentration for a sandy soil with particle size of 500–630 µm.

shown (Fig. 6a, d), at intermediate concentration of 0.25% hollow cylinders emerge (Fig. 6b, e), and at high concentration of 0.49% mucilage forms interconnected surfaces throughout the pore-space (Fig. 6c, f).

3.3 Simulation of mucilage distribution during drying

Simulations of two simplified two-dimensional scenarios (either liquid or elastic network) can indeed reproduce pore scale dynamics observed for water and highly concentrated mucilage, respectively. For the liquid case (Fig. 7, left), simulations create the typical geometry of water bridges that break at low water contents. For the case of an elastic network (Fig. 7, right), simulations indeed show the formation of hollow structures between two particles upon drying. Here, the simulations are not meant to quantitatively describe processes, but they are rather a qualitative illustration of how interactions of polymer-like nanostructures may create the observed pore-scale distributions, *e.g.*, hollow cylinders, of mucilage which very much differ from those structures of water bridges.

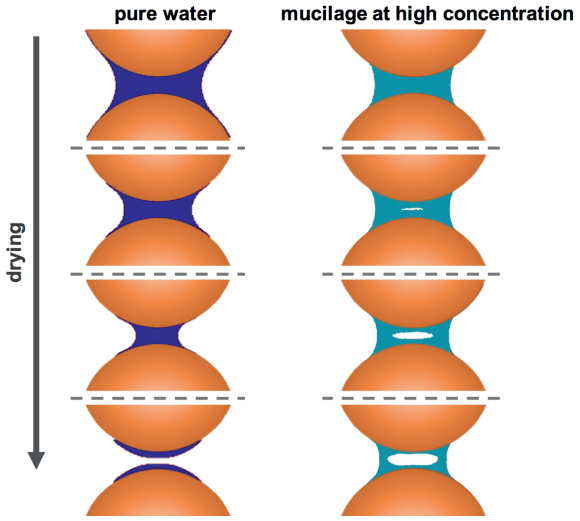

Figure 7: Simulated pore scale dynamics during a slow drying process of a liquid between two particles. In each step, the steady state spatial distribution of the liquid phase is simulated in each case at a certain water content.

4 Discussion

Gas diffusion measurements of dry soil (Fig. 5) confirmed the hypothesis of the conceptual model (Fig. 1): mucilage decreases the gas diffusion coefficient in dry soil without significantly affecting air-filled porosity. This can be explained by the formation of a mucilage dry surface spanning throughout the pore-space as imaged using Environmental Scanning Electron Microscopy (Fig. 6). These are in agreement with the observations by *Carminati* et al. (2017) and *Benard* et al. (2019), who discovered mucilage forming liquid bridges throughout the pore space during drying. The mucilage-based structures between neighbouring particles are able to disconnect the gas phase. This leads to an increased air-filled pore tortuosity and longer diffusion pathways resulting in a lower diffusion coefficient.

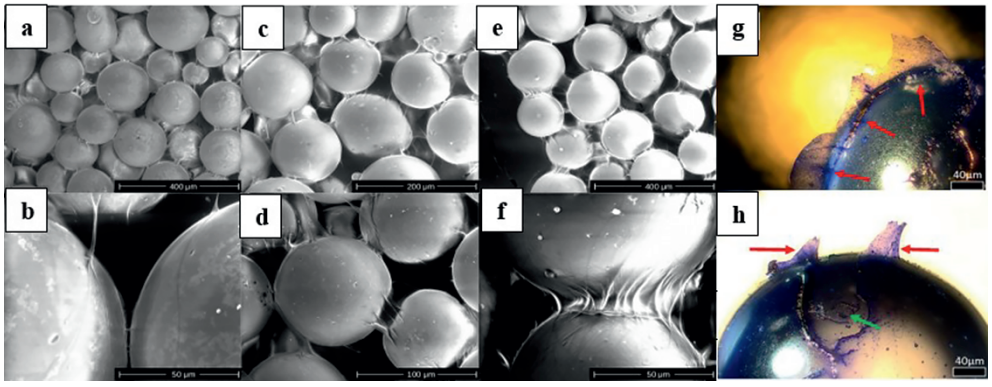

Figure 6: Environmental Scanning Electron Microscope (a–f) and Light Microscope (g, h) images of mucilage-based structures within the pore space of glass beads (0.2 mm diameter). Increasing concentration from left to right (0.16%, 0.25%, 0.49%). (a–f) Various structures can be seen depending on mucilage concentration (thin filaments, hollow cylinders, interconnected surfaces). (g, h) remains of broken mucilage filaments (red arrows) and former interparticle contact (green arrow) show that dry mucilage forms hollow structures during drying.

In their review on root respiration, *Ben-Noah* and *Friedman* (2018) presented a model to describe diffusion in a soil–mucilage layer. They assumed a homogeneous mucilage layer of a certain diffusion coefficient and thickness around the root. But neglecting the complex mucilage structures and considering mucilage as a uniform layer coating the root, is a simplification that might have a huge impact on predictions of gas diffusion through a soil–mucilage layer. We show that the pore scale dynamics of mucilage are more complex. Therefore, it is necessary to regard a more intricate spatial arrangement of mucilage within the pore-space.

Existing models [Eqs. (1), (3), and (5)] describe gas diffusion processes in soil and how this is affected by organic matter in general, but they are not designed to describe how mucilage alters gas diffusion. As a consequence, the predicted values of these models [D_p/D_0 = 0.22, 0.22, and 0.238 using Eq. (1), (3), respectively (5)] when applied to our soil samples are much higher compared to our measured data. More flexible models, like the SWLR model [Eq. (6)] allow a better description of gas diffusion processes. Considering literature references of C_m = 2 (D_p/D_0 = 0.163), respectively C_m = 3 (D_p/D_0 = 0.114) allow a closer prediction of gas diffusion coefficient for a dry sandy soil with 0% (D_p/D_0 = 0.134) and 0.1% (D_p/D_0 = 0.103) mucilage concentration used in this study. However, a complexity factor of C_m = 2 provides a good estimation of gas diffusion coefficient for a variety of natural soils, while C_m = 3 gave a good description for specifically clay minerals (*Moldrup* et al., 2013). An adaption of the complexity factor on measured results only allows a comparison between gas diffusion coefficient of a sandy soil affected by mucilage and gas diffusion coefficient of soils with different soil texture. Since, in dry soil, air-filled porosity is not significantly affected by mucilage concentrations, these models would not predict an effect of dry mucilage on the relative diffusion coefficient. A reduction of the relative diffusion coefficient by a factor of 0.5 which we measured at 0.3% mucilage concentration could be predicted by Eq. (3) only if air-filled porosity was reduced from 34% to 11.4% opposed to our experiment where air-filled porosity was not significantly affected.

A better description of pore scale processes of the spatial formation of liquid mucilage bridges and surfaces is needed to create more appropriate gas diffusion models. Further experimental, theoretical and numerical studies may help to understand and describe the effect of mucilage on gas diffusion also at further water contents and soil conditions.

Although mucilage membranes reduce gas diffusion at dry soil conditions these structures may prevent roots from a deficiency of oxygen during a heavy rain fall event after drought: when dry, a hydrophobic mucilage surface that disconnects the pore space may prevent the pore space around the root from being completely filled with water while rewetting. In this way it may allow a better aeration of roots at the critical conditions close to saturation.

This results in a deceleration of gas movement in soil and by extending the pathway through the soil it may enhance possible redox reactions. Therefore, we hypothesize that it will affect soil–rhizosphere biogeochemistry and in consequence also the biogeochemical exchange between soil and atmosphere. Using greenhouse gases as a topic example, plants most likely may have a so far unaccounted biophysical effect on N_2O and CH_4 emissions. Both gases are highly reactive in the soil–rhizosphere being sources of energy for soil microbes. A decelerated diffusion through the soil increases the probability that N_2O will be denitrified to N_2 and CH_4 oxidized to CO_2 which reduces the climate warming feedback effect from soils. Additionally, soils and therefore plants will lose less water because water vapour will not move as fast to the open atmosphere. Since root exudates play a significant role in shaping rhizosphere bacterial community (*el Zahar Haichar* et al., 2008; *Dennis* et al., 2010), a next step would be to investigate the interactions with the microbial communities which may alter additionally our view on how plants control soil gas exchanges.

Our study does not only advance our understanding of gas diffusion in soil, but gas diffusion measurements may also be a useful tool to learn about the conditions at which mucilage forms connected surfaces in the pore space. In this way we want to contribute to further interdisciplinary rhizosphere research combining hydrology, gas transport and microbial activity as controlled by plant roots.

5 Conclusion

This study shows that plant derived mucilage increases air-filled pore tortuosity in soils by partly locking pores even when dry. During drying mucilage forms a polymeric network spanning throughout the pore space. Existing soil gas diffusion models (*e.g.*, *Hamamoto* et al., 2012; *Moldrup* et al., 2013) cannot provide a proper estimation of the influence of mucilage on soil gas diffusion, since mucilage increases pore tortuosity without affecting air-filled porosity. Most of these gas diffusion models do not have such a flexible tortuosity factor implemented. Therefore, a key to predict the effect of rhizodeposition on soil gas diffusion is at first to find a way to estimate tortuosity in rhizosphere soils and secondly to adjust gas diffusion models to consider a tortuosity factor. Such a decoupling of tortuosity from total porosity and air-filled porosity may help predicting the influence of rhizodeposition on soil gas diffusion. In summary, this study supports the concept that plants are capable of altering soil physical properties to their advantage.

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Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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