Moisture absorption by plant residue in soil

Turgut Kutlu [a,b], Andrey K. Guber [a,*], Mark L. Rivers [c], Alexandra N. Kravchenko [a]

[a] Department of Plant, Soil, and Microbial Sciences, Michigan State University, USA

[b] Bilecik Seyh Edebali University, Soil Science Department, 11210 Bilecik, Turkey

[c] Center for Advanced Radiation Sources, The University of Chicago, Argonne National Lab, Lemont, Illinois, USA

*Corresponding author, address: Michigan State University, 1066 Bogue St., Room 584D, East Lansing, MI 48824, phone: 517-355-0271 Ext. 269, email: akguber@msu.edu

Abstract

Oil incorporated plant residues are an important source of carbon inputs and its decomposition defines magnitudes of many soil processes. While soil properties, especially soil moisture levels, influence decomposition rates, the moisture level of plant residue itself can differ from that of the surrounding soil due to the so called "sponge effect" -water absorption by plant residue from the surrounding soil. Our study explored whether water absorption by plant residue varies depending on soil moisture and matric potential levels; and how soil characteristics and characteristics of the plant residue itself affect the magnitude of this effect. We examined water retention of two types of plant residue materials, namely, corn and soybean leaves, in soil materials with three contrasting particle size distributions (PSD); and analyzed water distribution patterns in the soil adjacent to the residue using X-ray computed micro-tomography. The results demonstrated that the sponge effect was especially pronounced when soil moisture levels ranged from 0.15 to 0.40 $cm^3 cm^{-3}$ (~30-80% water filled pore space). The leaves were fully saturated with gravimetric water content levels exceeding 2.0 $g g^{-1}$ even when the soil moisture level was only 0.15 $cm^3 cm^{-3}$. Subsequent increase in residue moisture level was achieved due to vertical swelling of residue and reached 3.0-4.0 $g g^{-1}$at soil moisture levels >0.30 $cm^3 cm^{-3}$. The sponge effect was greater in the coarse textured soil materials with lower soil water retention than in the fine textured soil material with high water retention; it was greater in

soybean than in corn, possibly due to greater porosity of soybean leaves. Our results indicate that plant residue fragments incorporated into soil likely create moisture microenvironments for microbial decomposers that differ from those of the surrounding soil; and which, in relatively dry soil, can be more beneficial for plant decomposition than what can be inferred from the information on moisture levels of the soil itself.

Keywords: water retention, plant residue, decomposition, soil.

Abbreviations: water filled pore space (WFPS), particle size distribution (PSD)

1. Introduction

Incorporation of plant residues in soil is an important contributor to soil fertility and sustainability. The use of agronomic practices that involve plant residue incorporation is continuously growing worldwide (Lal, 1997). Such practices, e.g., the use of green manures and cover crops, increase soil carbon sequestration, improve soil hydraulic properties, and reduce erosion (e.g., (Miguez and Bollero, 2005; Scholberg et al., 2010)), as well as potentially contribute to mitigation of greenhouse gas emissions (Liebig et al., 2012).

One of the key factors in defining C sequestration benefits as well as greenhouse gas emissions from soils subjected to plant residue incorporations is plant residue decomposition. Decomposition rates are affected by environmental factors, such as soil temperature, soil water content/potential, O_2 supply, pH, inorganic nutrients (Swift et al., 1979), by residue's size and contact with soil (Fruit et al., 1999; Garnier et al., 2008), and by properties of the residue, such as C:N ratio, lignin content, etc. (Gunnarsson et al., 2008).

The effect of soil moisture is of particular importance for plant residue decomposition as it affects production and activity of microbial extracellular enzymes (Sardans and Penuelas, 2005; Sardans et al., 2008; Alarcon-Gutierrez et al., 2010), which are the main drivers of decomposition processes (Sinsabaugh and Moorhead, 1994; Moorhead and Sinsabaugh, 2000; Smart and Jackson, 2009; Waring, 2013). Decomposition is typically the highest when soil moisture levels are within 50-60% of water filled pore space (WFPS), a condition known to be optimal for microbial growth and metabolic activity (Sommers et al., 1981). Lower decomposition rates are expected both in soils drier and wetter than the optimal WFPS range. However, despite an overall understanding of the mechanisms by which soil moisture influences plant residue decomposition (i.e. controlling motility, transport and activity of microorganisms, gas and nutrients fluxes in pore space, connectivity between pores populated by microorganisms and residue location, etc.), published results on relationships between soil moisture levels and decomposition remain controversial. Some studies report no decomposition response to water additions (Steinberger et al., 1990; Li et al., 2016a), while others observe positive response (Strojan et al., 1987; Austin and Vitousek, 2000; Yahdjian et al., 2006; Setia and Marschner, 2013; Li et al., 2016b). Among proposed explanations for the discrepancies are differences in soil texture and structure of the studied soils (Adu and Oades, 1978; Gunnarsson et al., 2008), as well as masking effects of temperature, e.g. (Howard and Howard, 1979).

An additional emerging explanation is a possibility that moisture level of plant residue can differ from that of the surrounding soil. Kravchenko et al. (2017) recently brought attention to this phenomenon, reporting that plant residue located in soil with 30-45% WFPS had gravimetric moisture levels as high as 150-250%. The authors referred to the phenomenon as the "sponge effect" and explained it by the absorption of water by the residue from the surrounding soil. Such absorption is possible due to strong capillary forces generated by fine pores within the residue. Indeed, in an early study, Sommers et al. (1981) demonstrated that decomposition of various plant residues in the absence of soil might occur at water potentials considerably lower than those in soils, thus suggesting that the water retention properties of the residue itself may play an important role in its decomposition.

The possibility of water absorption by plant residue from the surrounding soil implies that conditions for decomposition within the residue might differ from those of the surrounding soil. This would explain only modest success in using soil moisture for predicting soil processes that relay on plant residue decomposition, including greenhouse gas emissions (Groffman et al., 2009; Ball, 2013). Understanding this phenomenon and possibly incorporating it in process-based models has the potential to improve the accuracy in predicting a number of soil processes important for both soil management decisions and for future climate assessments. However, at present this phenomenon remains largely unexplored. Questions to consider: (i) does water absorption by plant residues vary depending on soil moisture and matric potential levels; and (ii) how the soil characteristics and characteristics of the plant residue itself affect the magnitude of this effect.

The main hypothesis of the present study is that the water retention capacity of the plant residue incorporated into soil is greater than the water retention of the soil, leading to a sponge effect - water absorption by the residue from the surrounding soil. Our objectives are 1) to examine water retention of two types of plant residue materials, namely, corn and soybean leaves in soil materials with three contrasting particle size distributions (PSD), and 2) to explore water distribution patterns in the soil adjacent to the residue using X-ray computed micro-tomography (μCT).

2. Materials and Methods

2.1. Soil and plant residue sampling and analysis

Soil samples were taken in September 2016 from the Long Term Ecological Research (LTER) site located at Kellogg Biological Station in southwest Michigan, USA (85°24' W, 42°24' N). The soil of the experimental site is fine-loamy, mixed, mesic Typic Hapludalf (Kalamazoo series) developed on glacial outwash. We sampled plots of the LTER's biologically-based agronomic treatment from three blocks of the LTER experiment. The treatment is in corn-soybean-winter wheat rotation with cereal rye (*Secale cereal* L.) and clover (*Trifolium pretense* L.) cover crops. The treatment does not receive any chemical inputs. Rye cover crop is planted after corn harvest in fall, red clover is frost seeded into wheat in late winter. Cover crops are terminated and their residues are incorporated in soil by chisel plowing prior to main crop planting in spring. Additional details on soil, climatic, and management characteristics of the experimental site can be found in Robertson and Hamilton (Robertson and Hamilton, 2015). The biologically-based agronomic treatment was selected for this study since it receives substantial amounts of plant residues in the course of the rotation and, thus, relies on the decomposition of the residue of the legume cover crop for its main nutrient input and soil C sequestration (Syswerda et al., 2011).

Soil samples were collected from 0–15 cm depth and air-dried. Air-dry soil was mechanically crashed and sieved with RO-TAP test sieve shaker (Model RX-29, OH, USA) for one minute to obtain three soil fractions with <0.05, 0.10–0.50 and 1.00–2.00 mm size ranges. We will refer to these fractions as fine, medium and coarse fractions, respectively. Particle size distributions were measured in the three soil fractions using the pipet method (Gee and Or, 2002), after dispersion in 5% sodium hexametaphosphate solution. For each fraction, three lab replicates were analyzed for data from each of the three LTER plots for a total of 9 measurements per fraction. Particle diameter groups were <0.002, 0.002-0.005, 0.005-0.01, 0.01-0.022, 0.022-0.05, 0.05–0.1, 0.1-0.25, 0.25-0.5, 0.5-1.0, and 1.0-2.0 mm.

Leaves of corn and soybean plants were collected from experimental fields in summer of 2016. The leaves were dried in a herbarium press; then, 8 mm and 22 mm diameter disks were cut from the leaves with a puncher for subsequent water retention and X-ray computed micro-tomography (μCT) experiments.

2.2. Soil Water Retention

Water retention was measured in the three soil fractions using a 15 Bar ceramic pressure plate extractor (Model CAT.#1500, Soilmoisture Equipment Corp, Santa Barbara, CA). For each fraction, three lab replicates were analyzed for data from each of the three LTER plots for a total of 9 measurements per fraction. The soil was placed into metal rings (10 mm height, 39 mm ID) and gradually saturated from the bottom overnight. The water retention was measured at saturation and at the pressure head levels of -56, -102, -336 -1020, -3060, -5608, -10200 and -14080 cm. Additional measurements were conducted using controlled vapor pressure method (Nimmo and Winfield, 2002) in a desiccator with saturated solutions of $CaCl_2$ to obtain soil water content at a pressure head level of $-1.05 \cdot 10^6$ cm. We express pressure head levels as pF, which is a $\log_{10}$ of water pressure head in centimeters.

2.3. Leaf Water Retention Experiment

Leaf water retention was measured in soybean and corn leaves at six levels of WFPS, roughly corresponding 10%, 20%, 40%, 50%, 60% and 80%, as determined for each respective soil fraction based on its full saturation. Note that since the total soil volume decreases as soil dries during water retention experiment, it is not possible to precisely determine WFPS of each sample corresponding to each pressure head level. Thus, water retention results are reported in terms of soil water content levels, and approximate WFPS are only mentioned when discussing the results, in order to place the findings in perspective of this commonly used metric.

For the measurements, we prepared soil columns with 22 mm diameter and 20 mm height. In each column, an air-dry leaf disk (22 mm in diameter) was placed between two soil layers, each layer 10 mm thick. Prior to leaf placement the soil layers were brought to the specified soil water content. The prepared samples were left overnight to reach an equilibrium between the moisture in the soil and in the leaves. Then, the leaves were separated from the soil, and gravimetric water content of the leaves was determined from the weights of wet leaves and after drying them for 48 hours at 60ºC. In addition, after drying, the leaves were ashed at 500ºC. The mass of ashed leaves was used to correct the leaf water content measurements for occasional soil particles attached to leaf surfaces (Blair, 1988). We report the resulting relationships between leaf gravimetric water contents and soil volumetric water contents, as well as relationships between leaf gravimetric water contents and pF. We used soil water retention curves measured individually for each soil fraction as described in 2.2 to convert soil water contents from this experiment into pF values.

2.4. X-ray µCT scanning and image analysis

X-ray µCT was used to measure the leaf thickness and to examine the patterns of spatial distribution of water in the pore space and in the leaves. The X-ray scanning was conducted on the bending magnet beam line, station 13-BM-D of the GeoSoilEnvironCARS at the Advanced Photon Source, Argonne National Laboratory, IL. We used potassium iodine as a dopant for visualization of the added liquid in soil and in leaves. Two scanning experiments were conducted.

The first experiment aimed at measuring volume of leaves when air-dry and when fully saturated in a solution. Four air-dry soybean and corn leaf disks (8 mm ID) were placed in tubes separated by plastic spacers and scanned at 28 keV energy with 4.03 µm resolution. Then, the tubes were filled with 10% KI solution, the leaves were allowed to saturate for 8 hours, and scanned again. The leaves were clearly visible on the images, thus we assessed their sizes by determining leaf thickness and diameter. For that, the thickness of each leaf disks was measured using line tool of ImageJ/Fiji software (Schindelin et al., 2012). Each leaf was measured at 15 randomly selected locations. The leaf diameters were measured in 3-4 replications by rotating the leaf images.

The purpose of the second experiment was, first, to explore changes in leaf size when in contact with soil of different fractions at different soil water content levels and, second, to assess the spatial distribution of water in soil and leaves. This experiment was conducted using only soybean leaves. For each studied soil fraction we prepared soil micro-columns (8 mm diameter, 10 mm height) with air-dry soybean leaf disks (8 mm in diameter) placed in the middle of the columns. Prior to the experiment, the air-dry leaf disks were scanned (28keV energy with 4.03 μm resolution). During micro-column construction the soil received 10% solution of KI in the amounts needed to bring soil moisture levels of 0.1, 0.25, and 0.40 cm^3 cm^{-3}. The micro-column tubes were closed with rubber stoppers to prevent evaporation and allowed to equilibrate for 8 hours. In order to visualize the liquid added to the soil, the micro-columns were scanned at two energies, 33.269 keV and 33. 069 keV, which are above and below the iodine K absorption edge, respectively. Subtraction of the images scanned at two energies visualized patterns of the iodine distribution and hence distribution of the liquid added to the system (Wildenschild et al., 2013). The thickness and diameter of the leaves within the micro-columns was measured the same way as for the air-dry leaves.

The reconstructed image sequences were subject to 3D median filtering. The images produced by above and below absorption edge subtraction were then segmented using global threshold values estimated based on the applied amounts of iodine. When the porosity of the segmented samples exceeded the values measured in the soil fractions, the global threshold was set close to the Fiji default value with minor adjustments.

2.5. Statistical analysis

For comparisons between the soil fractions in terms of soil PSDs and in terms of soil water retentions, the statistical models consisted of two fixed factors and their interaction. The first factor was soil fraction and the second factor was either particle size or pF level for soil particle size distribution and water retention data, respectively. The second factor was treated as a repeated measure factor with individual sample used as the subject of repeated measurements. The variance-covariance structure for the repeated measures factor was selected using Akaike Information Criterion as described in Milliken and Johnson (Milliken and Johnson, 2009). Because of substantial differences in variability at different particle size and pF levels all the selected variance-covariance structures were the structures that account for heterogeneous variances. The statistical model also included the LTER experimental blocks as a random factor. Significant interaction effects were examined using analysis of simple effects, aka slicing (Winer, 1971). When simple effects of soil fraction within individual levels of either particle size or pF were found to be statistically significant ($p<0.05$), comparisons among the fractions were conducted using t-tests and least significant difference values were calculated for visual presentation on the figures.

The relationships between leaf and soil water contents and between leaf water contents and pressure heads were assessed using analysis of covariance (ANCOVA) (Milliken and Johnson, 2001). We tested performance of polynomial regression models in describing the relationship between leaf water content and soil water contents/pressure heads as the models that would enable straightforward comparisons between plant types and soil fractions within ANCOVA framework. The relationships were found to be best described by a cubic regression. ANCOVA model included the effects of plant and fraction size and their interaction, as categorical variables, and soil water content, as a continuous covariate with separate linear, quadratic, and cubic terms for each plant and fraction. Comparisons between corn and soybean leaves and among the fractions were conducted at ten levels of soil moisture, ranging from 0.01 cm^3cm^{-3} to 0.50 cm^3cm^{-3} in ~0.05 cm^3cm^{-3} intervals.

Statistical analysis was conducted using PROC MIXED in SAS (SAS 9.4). The results with p-value less than 0.05 will be referred to as statistically significant, while those with p-values in 0.05-0.1 range will be referred to as tendencies or trends.

3. Results

3.1. Soil characteristics and water retention

As expected, the three studied soil fractions substantially differed in their PSDs (Fig. 1). The fine fraction was dominated by particles in 0.01-0.05 mm size range (~70%), while the medium fraction was dominated by particles in 0.25-0.5 mm size range (~40%). The coarse fraction consisted of soil particles ranging in size from < 2 μm to 2 mm, with relatively even proportions of all sizes present in the fraction.

The observed differences in PSDs resulted in different water retention properties of the three fractions (Fig. 2). For the same pF values, water contents were the highest in the fine fraction, the smallest in the medium fraction and intermediate in the coarse fraction. The differences between water contents were the greatest for pF values ranging from 1.7 to 3.0, followed by the differences for pF > 3.5. The differences between fine and medium soil fractions were statistically significant in the whole range of pF values ($p<0.05$). The differences between the fine and coarse fractions tended to be significant in the 2-3 pF range, and between the medium and coarse fractions for pF < 2.5 ($p<0.1$).

3.2. Plant water retention

The water contents of soybean and corn leaves increased with increasing soil water content; however, the relationship between them was not linear (Fig. 3). Leaf water contents increased sharply as soil water content rose to 0.10-0.15 cm^3cm^{-3}, followed by only gradual increases as soil water contents increased to ~0.40 cm^3cm^{-3}, with then a tendency for sharper increase at soil water contents >0.40 cm^3cm^{-3}. These overall trends were present in both corn and soybean leaves and in all three studied fractions; however, the increase in leaf water contents in 0.15-0.40 cm^3cm^{-3} range of water contents was sharper in soybean leaves of medium and coarse fractions, than in the rest of the treatments.

Water contents of corn and soybean leaves were not significantly different from each other at soil water contents <0.20 cm^3cm^{-3}. Water content of soybean leaves was higher than that of corn at 0.25-0.35 cm^3cm^{-3} soil water contents in the large fraction and at >0.35 cm^3cm^{-3} soil water contents in the medium fraction.

Water content of soybean leaves in medium and large fractions were significantly higher than that in the fine fraction at soil moisture contents within 0.20-0.40 cm^3cm^{-3} range. Water contents of corn leaves tended to be higher in medium and large fractions than in the fine fraction at soil moisture contents within 0.10-0.25 cm^3cm^{-3} range ($p<0.1$). The differences between coarse and medium fractions were not statistically significant either in corn or in soybean leaves.

Assuming that an equilibrium was achieved between pressure heads in soil and leaves during the overnight leaf saturation, we plotted leaf water contents vs. pF values corresponding to the water contents measured in the soil (Fig.4). To find the pF values we used a linear interpolation of the soil water retention curves shown in Fig. 2. The leaf water retention curves were quite different from those for the soil (Fig. 4 and Fig. 2). Water content increased sharply and almost linearly from 0.1 g g^{-1} to 1.5 – 2.9 g g^{-1} in both soybean and corn leaves as pF values decreased from 6 to 4.8, followed by relatively gradual increase in leaf water content up to 4.2 g g^{-1} with decrease in pF values from 4.8 to 0 (Fig. 4). These trends were similar in the three studied soil fractions and in both corn and soybean leaves. There were no statistically significant differences across the pF values either between corn and soybean leaves or among different soil fractions ($p<0.05$).

3.3. Plant porosity and swelling upon wetting

When air-dry, the soybean leaves were thicker than the corn leaves and had markedly higher porosity, 0.522 vs. 0.341 cm^3 cm^{-3}, respectively (Table 1). After full saturation, leaf thickness almost doubled in both crops. Porosity in soybean increased by a factor of 1.4, and in corn by a factor of 2, reaching ~ 0.7 cm^3 cm^{-3} in both crops.

No lateral swelling was observed on X-ray µCT images, suggesting that most of the leaf swelling took place perpendicular to the leaf's plane. The swelling of soybean leaves, assessed as a ratio of the leaf thickness at a certain soil water content and the thickness of the same leaf air-dry, depended on the soil fraction and soil water content levels (Fig. 5). As expected, leaf swelling increased with increasing soil water content and the maximum swelling occurred at soil water content of 0.4 cm^3 cm^{-3}. Leaf swelling was the greatest in medium and coarse soil fractions, where already at soil water content of 0.25 cm^3 cm^{-3} leaf thickness reached that of full saturation in water.

4. Discussion

Our results demonstrated presence of a sponge effect, i.e., water absorption by plant residues from the surrounding soil, across a wide range of soil moisture levels, in soil materials with contrasting physical characteristics, and in both studied plant species. The magnitude of this effect varied depending on soil moisture and matric potential levels (Figs. 3 and 4), however, there appeared to be a wide range of soil moisture and matric potential conditions across which residue water absorption remained relatively stable and fully saturated. Already when soil moisture level was at 0.15 cm^3 cm^{-3} (approximately 30% WFPS) the residues were swelled and fully saturated with gravimetric water content levels exceeding 2.0 g g^{-1}. Upon subsequent increase in soil moisture, residue continued to swell and remained fully saturated with gravimetric moisture levels exceeding 3-4.0 g g^{-1}.

4.1. Sponge effect and factors influencing it

Our observations suggest that even in relatively dry soil, fragments of incorporated plant residue with their fine porous structure can absorb large amounts of moisture from the surrounding soil, which then fills the entire pore space of the residue. With further increase in soil moisture, the residue swells as additional water enters it; subsequently, the residue remains fully saturated and just grows in size (Fig. 5). Vertical swelling appeared to be the mechanism driving the increases in residue water content within the 0.2-0.4 cm^3 cm^{-3} soil water content range. Specifically, at 0.25 cm^3 cm^{-3} soil water contents, the average measured amount of water stored within a soybean leaf was equal to 3.4 mg, and the amount of water stored within the leaf as estimated from the volume change due to leaf's vertical swelling was only slightly different, 3.1 mg. At 0.40 cm^3 cm^{-3} soil water content, both the measured and the swelling-estimated amounts of water stored within a soybean leaf were equal to 3.9 mg.

Water absorption by the residue can influence a number of soil processes, including plant residue decomposition. Even in relatively dry soil, plant residue fragments with their high amounts of absorbed water likely serve as micro-environments beneficial for microorganisms not only from perspective of nutrient supply, but also from perspective of adequate moisture levels. This phenomenon can explain some of the reported unexpectedly high plant residue decomposition results in relatively dry soils (Abera et al., 2014). Moreover, the micro-environmental conditions associated with the residue appear to remain relatively consistent across a wide range of soil conditions, both in terms of water content and pF, as plant residue just increases in volume due to swelling, while empty pores of the surrounding soil provide for adequate gas diffusion. It can explain absence of soil moisture effects on plant residue decomposition at 30% vs. 45% WFPS in the study by Kravchenko et al. (2017, in press). It is when soil water content reached the levels limiting gas diffusion, in particular influx of O_2, the anoxic conditions will start altering microbial activities within the residues.

The magnitude of the sponge effect was related to water retention characteristics of the surrounding soil, with lower absorption observed in the soil with higher water retention, i.e., fine fraction, and higher absorption in the soil with lower water retention, i.e., medium and coarse fractions (Fig. 3). The differences between the fractions in terms of the residue water contents were the biggest in the 0.2-0.4 cm^3 cm^{-3} soil water content range – the range where the differences in soil water retentions among the fractions were also the greatest (Fig. 2).

This tendency was present in both corn and soybean leaves, suggesting ubiquitous nature of the phenomenon. X-ray µCT analysis revealed that a substantial portion of medium and, especially, coarse soil fractions constituted of small aggregates, composed of particles in a variety of size groups (Fig. 6). Such composition resulted in presence of both fine intra-aggregate and coarse inter-aggregate pores in materials of these two fractions. The fine soil fraction was composed of relatively well-sorted fine material (Fig. 1) with no aggregation discernible at the studied resolution (4-5 µm). Thus, its pore space mostly consisted of fine pores with high capillary forces retaining soil moisture. Percentage of soil particles with size < 0.1 mm, which affected soil water retention in the range of high pressure heads, was almost the same in the medium and coarse soil fractions, resulting in their similar soil water retentions there. Abundance of sand/small stone particles of 0.25-0.50 mm size range in the medium fraction (Fig. 1) was the likely reason for its somewhat lower water retention as compared to the large fraction in the medium pF levels.

The magnitude of the sponge effect and the ranges of soil moisture levels and matric potentials at which it was most pronounced somewhat differed between corn and soybean, pointing to posisble role of the plant residue characteristics. Specifically, greater leaf water contents, as well as greater contrast between fine and coarse/medium fractions were observed in soybean than in corn leaves. Markedly higher porosity of soybean leaves in air-dry state (Table 1) can be one of the reasons for the observed differences. However, as corn and soybean leaves swelled upon wetting, their porosities became very similar. It is possible that not only porosity, but also leaf swelling capacity determine the magnitude of the sponge effect and soil moisture conditions at which it is most pronounced.

4.2. Possible mechanisms of sponge effect

The relatively slow decrease in the residue water content within the pF range between 0 and 5 was followed by the fast decrease for pF values > 5 in this study (Fig 4). Surprisingly, the leaf water content-potential relationships obtained for dead corn and soybean leaves here were very similar to those observed for live leaves in earlier studies. For example, experiments with a variety of plant species demonstrated that when water potentials increased from 0 to 4 pF the changes in water contents were relatively minor and constituted only 10-15%.
However, they were then followed by much bigger changes in water contents (30-40%) at higher pF values. Such observations were reported for tomato and Japanese privet (Weatherley and Slatyer, 1957), bulrush millet (Begg et al., 1964), dogwood (Knipling, 1967), corn and sorghum (Sanchez and Kramer, 1971). Such relationships between relative water content and water potential were described using piecewise linear regressions (Whiteman and Wilson, 1963; Wilson, 1967).

A number of studies also observed two distinct lines relating water content and energy state of the water (pressure) in leaf water retention (Gardner and Ehlig, 1965; Neumann et al., 1974; Steudle and Zimmermann, 1977). Presence of two lines, i.e., two regimes in the relationship, was associated with changes in the elastic properties of the leaf cells when the turgor pressure dropped below a critical value, which corresponded to the breakpoint between the two lines (Gardner and Ehlig, 1965). At low pF values, the dominant mechanism of the water retention was the tensile strength of the leaf cell walls. At high pF values, the dominant mechanism was the osmotic potential of the cell solution (Neumann et al., 1974) and presence of plant cell regions with different elasticity or stress-hardening effect within cell walls due to tension (Steudle and Zimmermann, 1977). We are not aware whether and to which extent these mechanisms remain relevant to dry leaves. Yet, our results showed that the leaf thickness increased almost linearly with increase in soil water content from 0.1 to 0.4 $cm^3\ cm^{-3}$ (Fig. 5), supporting observations regarding importance of leaf cell elasticity.

4.3. Spatial patterns in water distribution within plant residue and soil

Analysis of X-ray μCT images demonstrated that the differences in PSDs and arrangements of soil particles within the three soil fractions resulted in different spatial patterns in soil pores and in water. At low soil water content (0.1 $cm^3\ cm^{-3}$, WFPS ~20%), water occupied very fine soil pores between soil particles in the fine fraction (Fig. 7a) and inside soil aggregates in the medium and coarse fractions (Fig. 7d and 7g). Water formed clusters in the pore space with plenty of air-filled interconnected pores around them. Consistent with the direct measurements (Fig. 3) soybean leaves were almost completely filled with water. Such patterns in water's spatial distribution likely created favorable conditions for gas diffusion to/from the residue. However, soil water potential of 5 pF (-10 bar) at this water content might have been limiting catabolic capacity of soil microorganisms (Swift et al., 1979).

Optimum water potentials for soil organic matter decomposition are believed to be within the - 0.2 to - 0.5 bar (3.3 to 3.7 pF) range (Sommers et al., 1981), of which our soil moisture content of 0.25 cm^3 cm^{-3} (WFPS ~50%) is a representation (Figs. 7b, 7e and 7h). At this condition, water is still clustered in the pore space, filling small and medium-size pores in all three fractions. However, much fewer interconnected air-filled pores can be visually detected on the images for this water content as compared to that of 0.10 cm^3 cm^{-3}. Importantly, only large inter-aggregate pores serve as pass-ways for airflow in the coarse soil fraction. Gas diffusion limitations likely can lead to less favorable conditions for decomposers in fine as compared to coarse fraction. This observation corroborates the results of slower corn leaf decomposition in fine as opposed to coarse soil fraction when incubated at 30-50% WFPS ((Negassa et al., 2015); Kravchenko et al., 2017 in press).

Further increase in soil moisture content to 0.4 cm^3 cm^{-3} considerably reduced air-filled porosity and, particularly, connected air flow pathways (Fig 7 c,f,i). This water content corresponded to pF values below 1.5 (Fig. 2), which is above the optimum range for soil microorganisms (Sommers et al., 1981).

It is interesting to note that, while water menisci were observed on the contacts between plant residue and soil at 0.40 cm^3 cm^{-3} water content, no visible water meniscus were present at soil water contents of 0.1 and 0.25 cm^3 cm^{-3} (Fig. 7), even though the leaves themselves there adsorbed appreciable amounts of iodine solution. We believe that the meniscus between soil particles and leaves at low water contents existed for a very short period of time, when the leaves were placed in contact with soil, and disappeared soon after the leaves adsorbed the iodine solution. In absence of such menisci the opportunities for movement of microorganisms and transport of enzymes and decomposition products from residue into adjacent soil was probably somewhat limited. Moreover, the lack of menisci also probably limited movement of protozoa from soil into the residue. Thus, a residue fragment might be likened to an island of processes and activities disparate of those taking place in soil.

Conclusions

Our study demonstrated that soybean and corn leaves had different water retention properties from those of the surrounding soil. The leaves of both crops acted as sponges absorbing water from relatively dry soil and increasing their water contents via swelling soil moisture increased. This finding implies that plant residue fragments likely create microenvironments for microbial decomposers that differ from those of the surrounding soil; and which, in relatively dry soil, can be more beneficial for enzyme diffusion and plant decomposition than what can be inferred from the information on moisture levels of the soil itself.

Ability of plant residue to absorb water from the surrounding soil was affected by soil water retention capacity and was lower in fine-texture soil with high water retention than in the coarser textured soils with lower water retention. The differences in the magnitude of sponge effect in response to soil texture were present at a wide range of soil moisture conditions spanning 20-80% WFPS.

Our results showed that soil properties might play a dua role in controlling activity of the microbial community in the soil, specifically via: (i) oxygen inflow to the decomposing material, and (ii) water saturation of the plant residue. It remains to be seen in further experimental studies to which extent these two mechanisms manifest itself in different soils and for plant residue of different origins and different decomposition duration.

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Captions

Figure 1. Particle size distributions of the fine (0.01–0.05 mm), medium (0.10–0.50 mm) and coarse (1.00–2.00 mm) soil fractions. Vertical lines represent standard errors (n=3). Grey bars represent least significant difference value ($p<0.05$) for each particle size.

Figure 2. Soil water retention measured in fine (0.01 – 0.05 mm), medium (0.1 – 0.5 mm) and coarse (1 – 2 mm) fractions. Horizontal lines represent standard errors (n=3). Grey bars represent least significant difference ($p<0.05$) for each pF level.

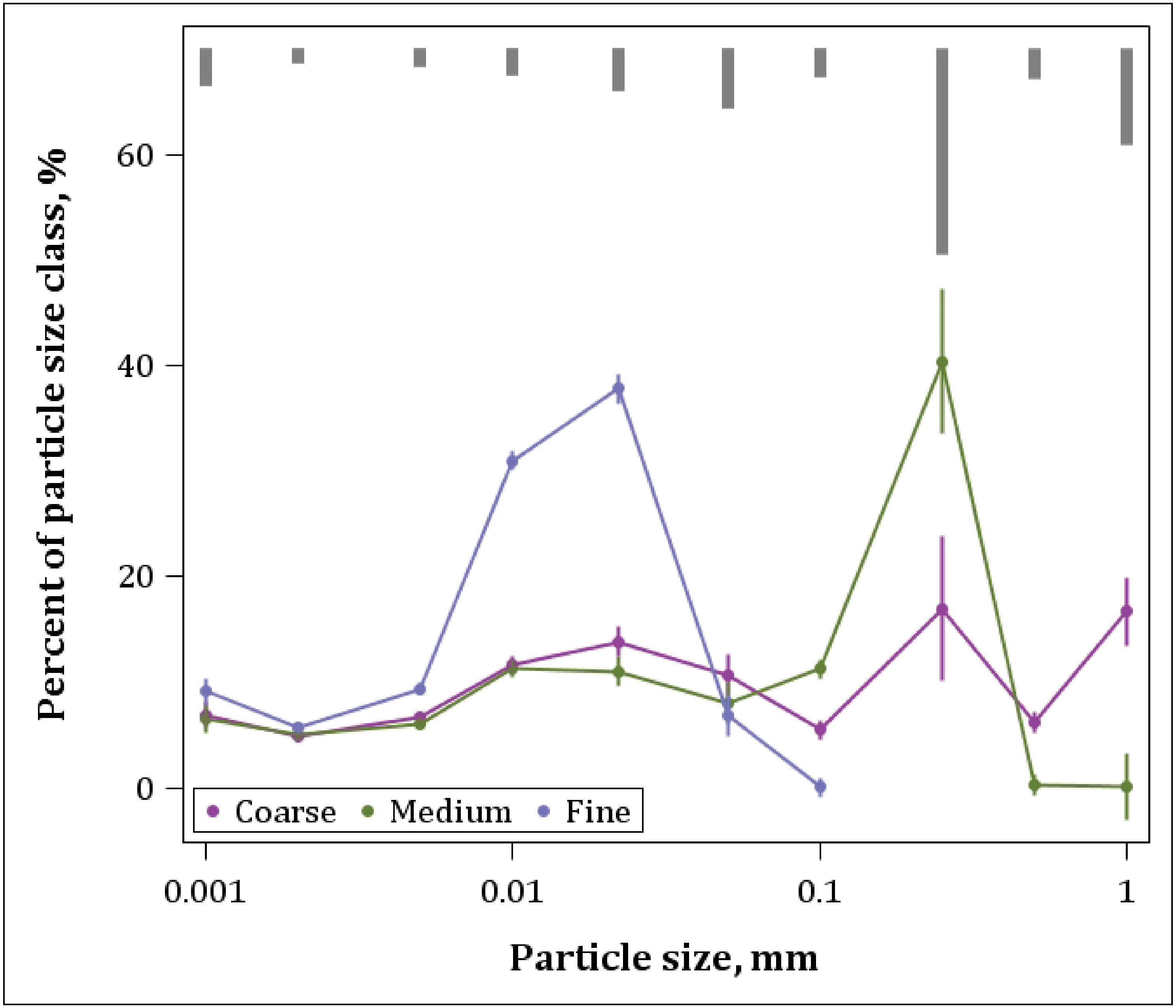
Figure 3. Relationships between soil and leaf water contents for soybean (a) and corn (b) leaves in fine (0.01 – 0.05 mm), medium (0.1 – 0.5 mm) and coarse (1 – 2 mm) fractions. Solid lines are cubic regression models fitted to the data in the course of ANCOVA. Grey bars represent least significant difference values for comparing plants and fractions ($p<0.05$) at selected soil water content levels.

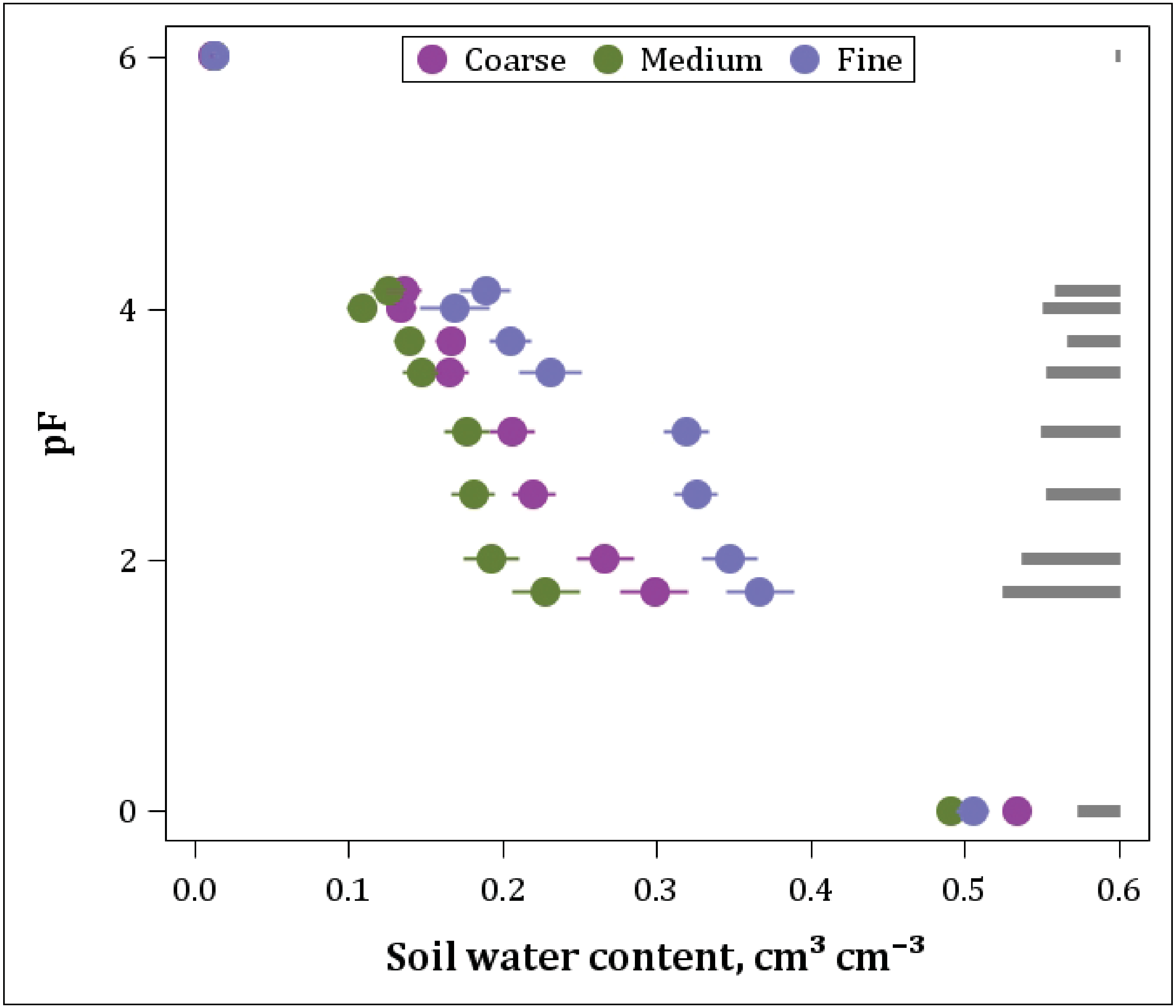
Figure 4. Relationships between pF and leaf water contents for soybean (a) and corn (b) leaves in fine (0.01 – 0.05 mm), medium (0.1 – 0.5 mm) and coarse (1 – 2 mm) fractions.

Figure 5. Swelling of soybean leaves in fine (0.01 – 0.05 mm), medium (0.1 – 0.5 mm) and coarse (1 – 2 mm) soil fractions at three levels of soil water content along with soybean leaf swelling after saturation in water. Dash lines mark air-dry leaf (100%) and water-saturated leaf (166%).

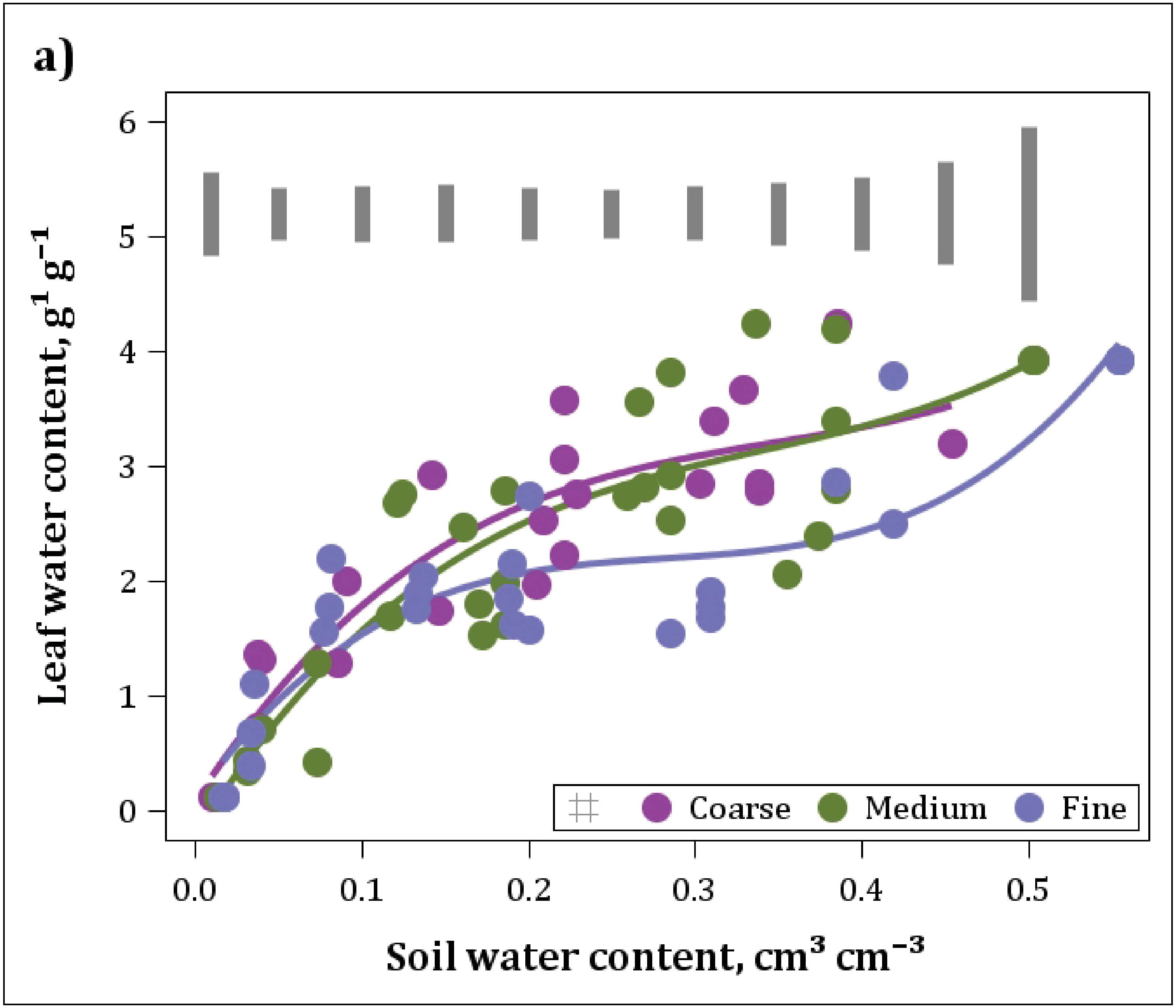
Figure 6. X-ray CT images of (a) fine (0.01 – 0.05 mm), medium (0.1 – 0.5 mm) and coarse (1 – 2 mm) fractions of the dry (?) Kalamazoo soil. Dark areas on the images denote pore space, while bright areas denote the solids.

Figure 7. Examples of spatial distributions of iodine solution in the soybean leaves and three soil fractions at three levels of soil saturation. Colors identify air (white), solids (black) and iodine solution (blue).

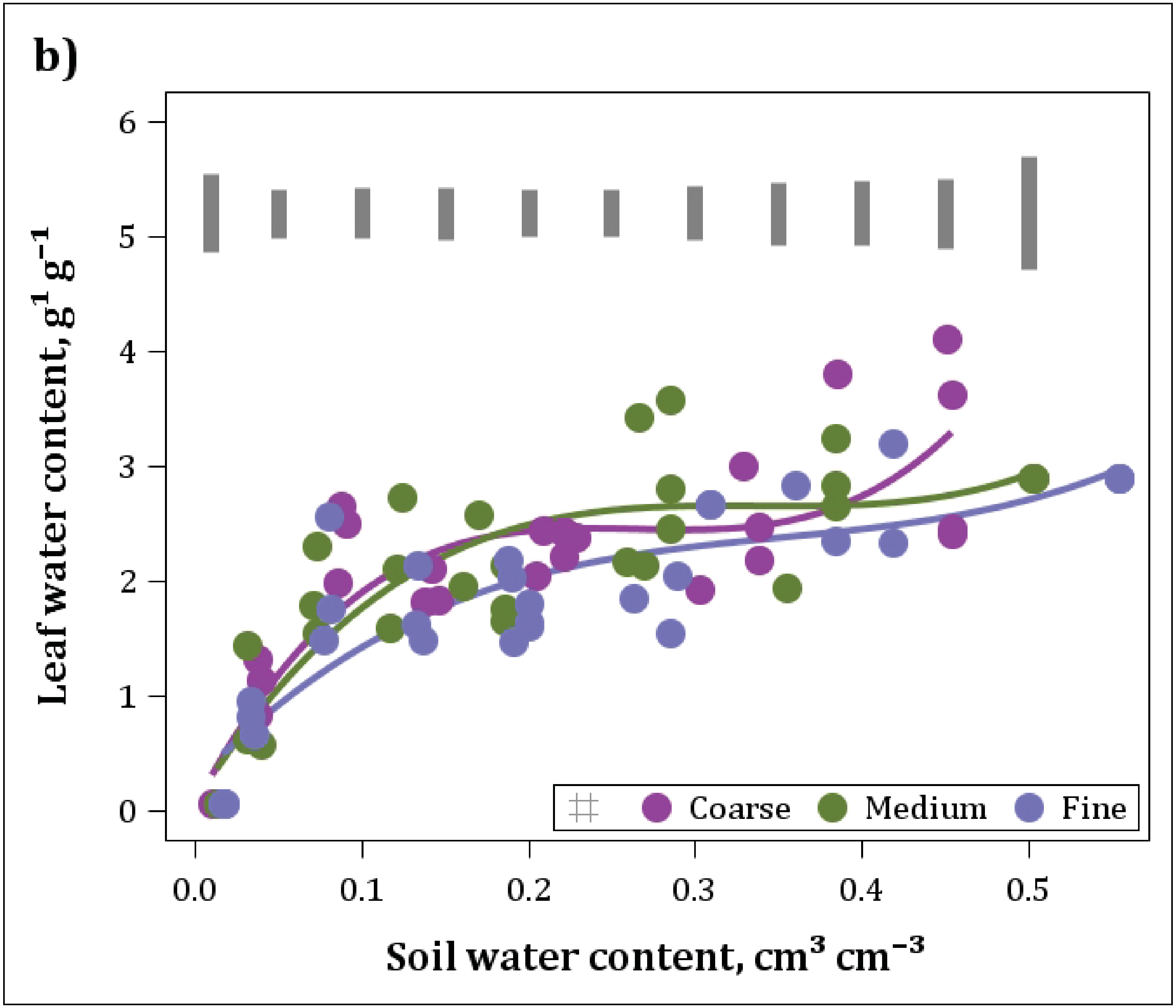

Percent of particle size class, %
60
40
20
0
Coarse
Medium
Fine
0.001
0.01
0.1
1
Particle size, mm

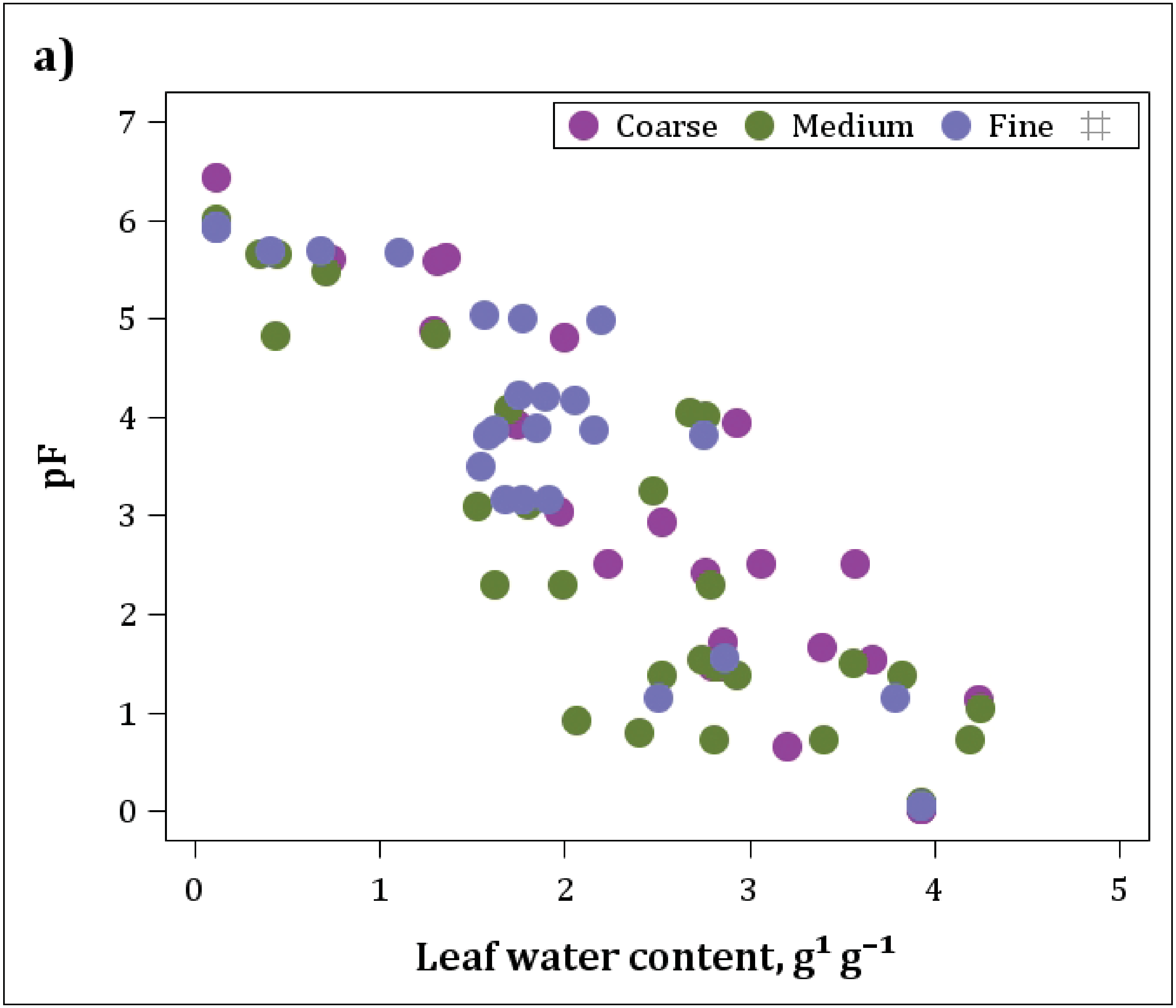


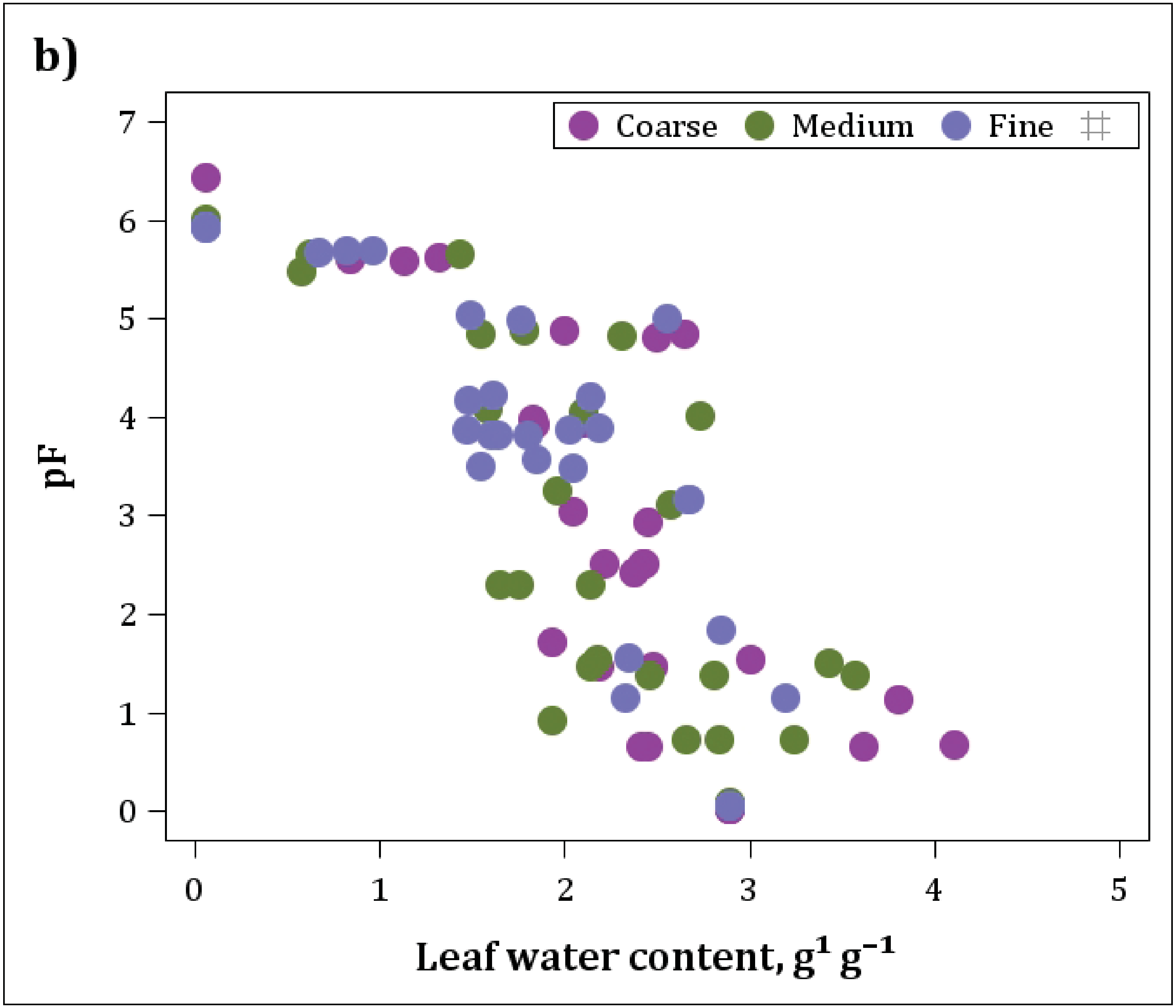
Coarse
Medium
Fine
pF
6
4
2
0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Soil water content, cm³ cm⁻³

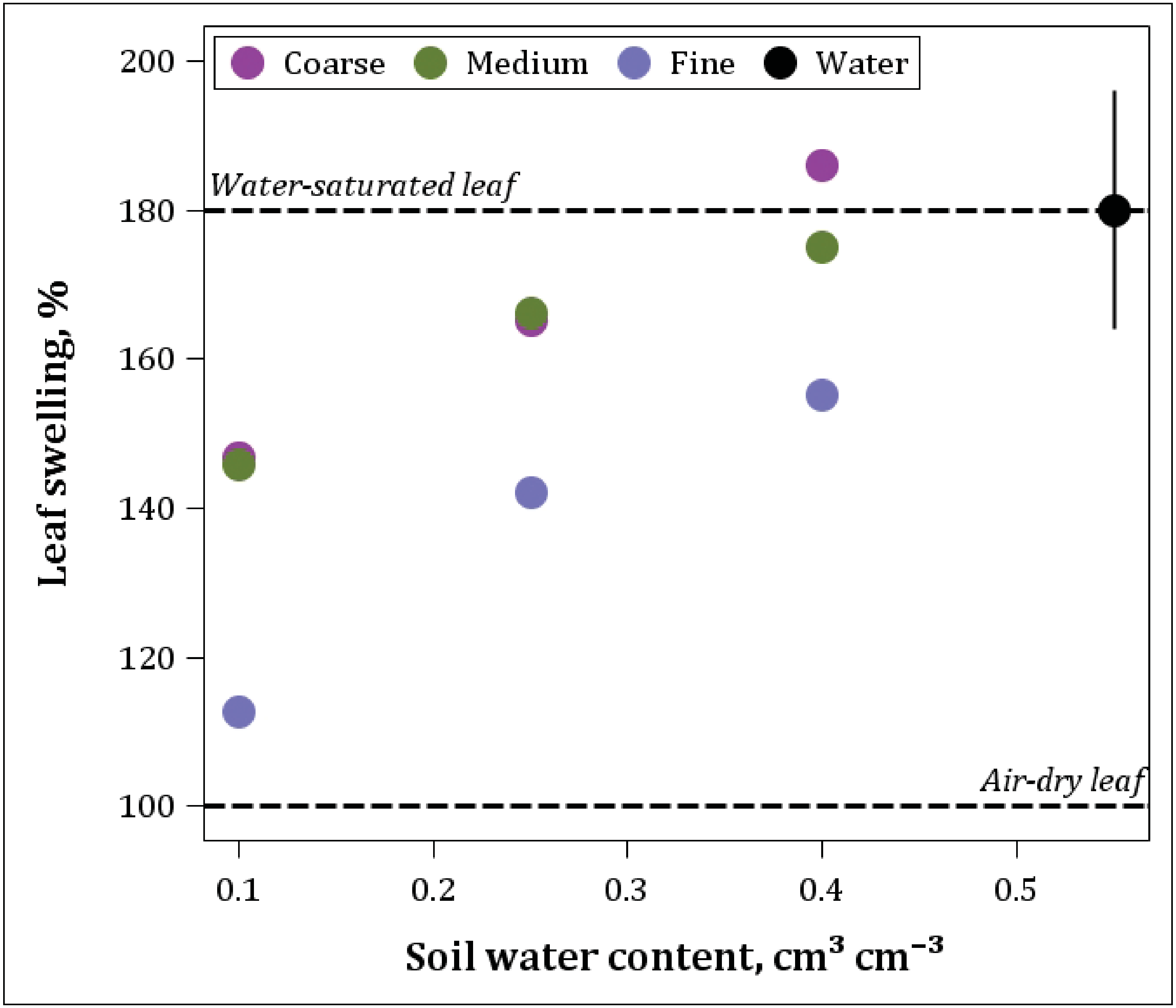


a)
Leaf water content, g1 g−1
0
1
2
3
4
5
6
0.0
0.1
0.2
0.3
0.4
0.5
Soil water content, cm3 cm−3
Coarse
Medium
Fine

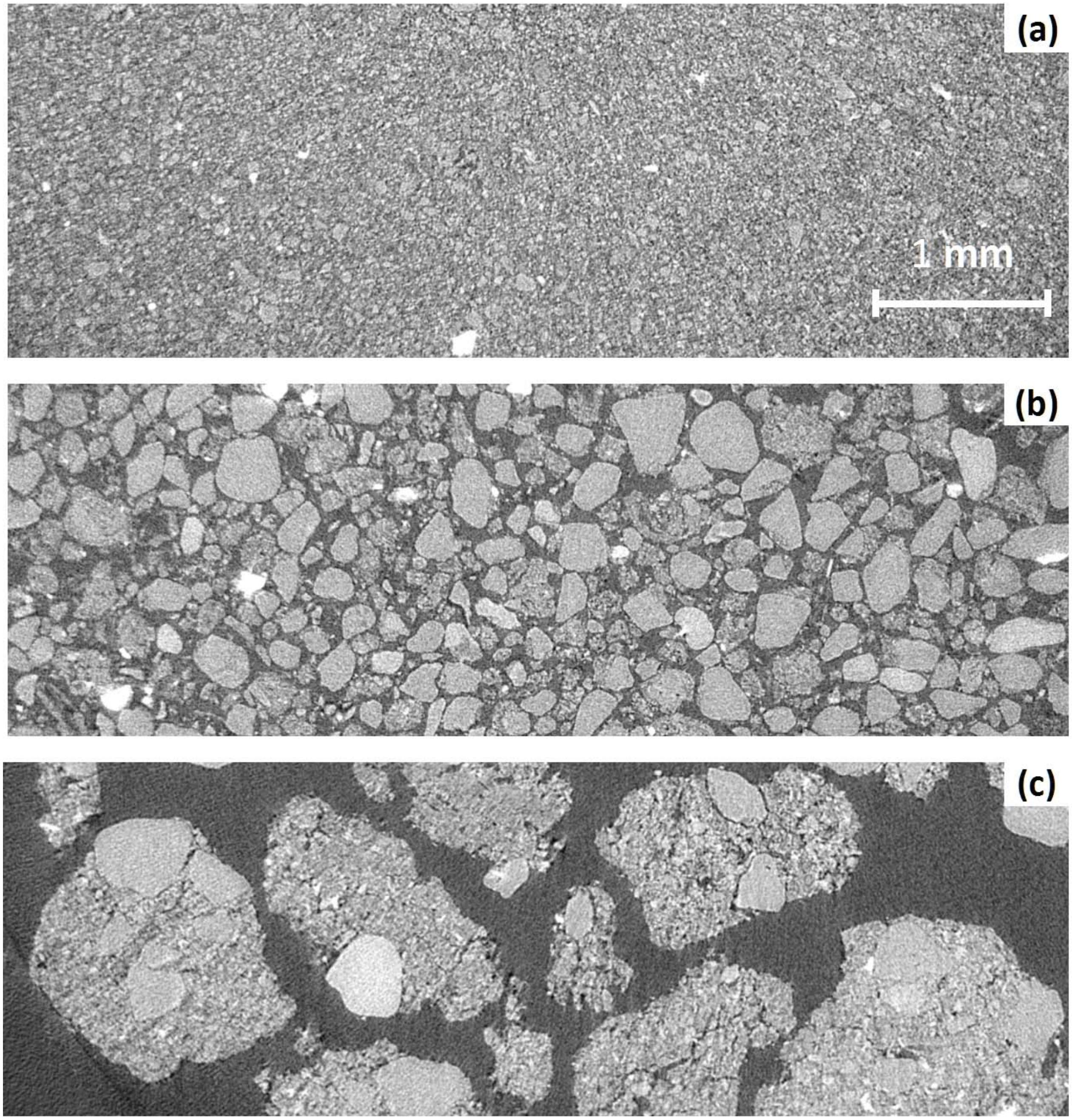

b)
Leaf water content, g1 g−1
6
5
4
3
2
1
0
0.0
0.1
0.2
0.3
0.4
0.5
Soil water content, cm3 cm−3
Coarse
Medium
Fine

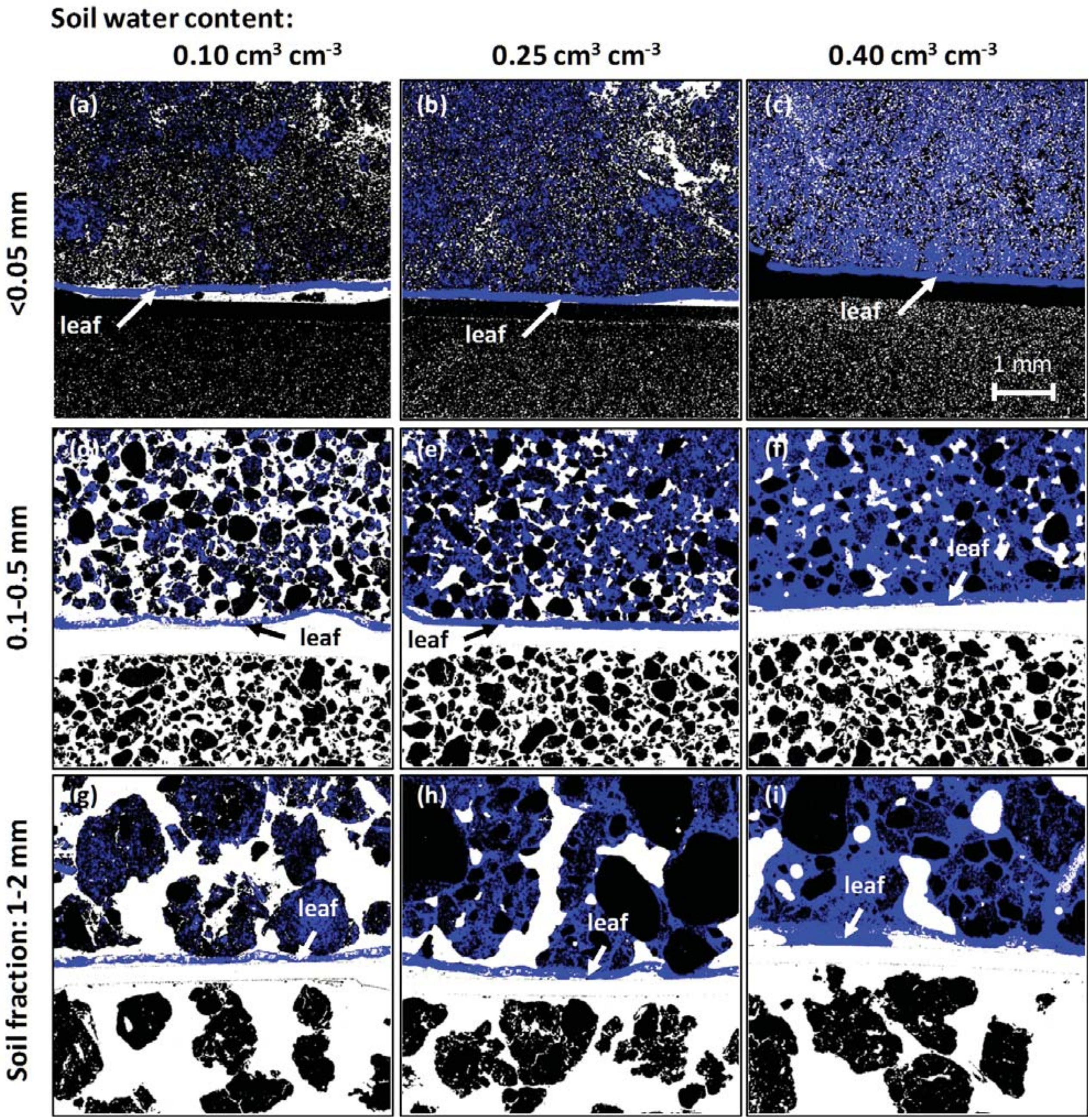

a)
Coarse
Medium
Fine
pF
7
6
5
4
3
2
1
0
0
1
2
3
4
5
Leaf water content, g1 g-1


b)
Coarse
Medium
Fine
pF
0
1
2
3
4
5
6
7
0
1
2
3
4
5
Leaf water content, g1 g−1



Coarse
Medium
Fine
Water
Water-saturated leaf
Air-dry leaf
Leaf swelling, %
200
180
160
140
120
100
0.1
0.2
0.3
0.4
0.5
Soil water content, cm³ cm⁻³


(a)
1 mm
(b)
(c)



Soil water content:
0.10 cm³ cm⁻³
0.25 cm³ cm⁻³
0.40 cm³ cm⁻³
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
leaf
1 mm
<0.05 mm
0.1-0.5 mm
Soil fraction: 1-2 mm

Table 1. Thickness and porosity of the corn and soybean leaves used in the study. The porosity is calculated assuming cellulose density of 1.5 g cm^{-3}. Means ± standard deviation are shown (n = 4). Letters indicated statistically significant differences between corn and soybean means ($P < 0.05$).

Plant	Air-dry		Water-saturated	
	thickness	porosity	thickness	porosity
	μm	cm^3 cm^{-3}	μm	cm^3 cm^{-3}
Soybean	78.1 ± 2.1a	0.522 ± 0.060a	140.6 ± 4.1a	0.735 ± 0.030a
Corn	46.7 ± 2.4b	0.341 ± 0.044b	104.7 ± 13.0b	0.705 ± 0.024a