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Interactive Effects of Mucilage and Drying and Wetting Cycles on Rhizosheath and Aggregate Development

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ABSTRACT

Aims: Mucilage is vital for rhizosheath formation, the soil adhering to plant roots after gentle shaking. We hypothesized that alternating drying-wetting cycles affect mucilage's role in rhizosheath development and soil aggregation within the rhizosphere.

Methods: To explore this, we employed flax cord as an artificial root model, subjecting it to soils with varying clay contents (22% and 32%), both sterilized and unsterilized. We moistened the model roots with 0.12% w/w (grams of dry chia seed mucilage per gram of water) and incubated them under controlled conditions. Soil moisture levels were maintained at 75% of water holding capacity (reference) and subjected to five dry–wet (DW) cycles, mimicking wet–dry fluctuations. Subsequently, we isolated the rhizosheath through gentle shaking and analyzed surrounding soil particle-size distribution and aggregate properties using laser diffraction and scanning electron microscopy (SEM).

Results: Remarkably, constant wet conditions had more pronounced impact, significantly enhancing rhizosheath development, particularly in unsterilized soil with 22% clay. Conversely, DW cycles led to a notable reduction in rhizosheath compared to the wet treatment, likely due to physical interactions affecting rhizosheath formation. Notably, there were minimal treatment effects on particle aggregation outside the rhizosheath, with an average diameter of <10 µm and limited influence from the water regime.

Conclusions: We conclude that water regime emerged as the key factor influencing mucilage's contribution to rhizosheath formation, whereas clay content and microbial activity played minor roles in this simple model that represent a complex and dynamic biological system.

1 | Introduction

Soil aggregates and their stability play a crucial role in soil health and fertility, as they are key components of soil structure, influencing water infiltration, water retention, nutrient cycling, and carbon (C) sequestration. Soil aggregates form largely through the associations between clay minerals, oxides as well as microbial substances and plant-derived organic matter (Totsche et al. 2018). Elevated soil microbial activity may both enhance the generation of binding substances like microbial exudates and hyphae (Rahman et al. 2017) but also potentially degrading them, particularly in the absence of additional C sources from plants (Amelung et al. 2023). When soils are sterilized, new bacterial populations establish that may affect aggregation but potentially

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alter root growth as well (Li et al. 2019; Wertz et al. 2007). The presence of plant roots significantly promotes aggregate formation through their physical enmeshment, alterations of water tension during growth, and excretion exudates from root tips. This leads to better developed soil aggregation in the rhizosphere compared to the adjacent bulk soil environment (Amelung et al. 2023; Li et al. 2020). Mucilage, one of the most effective plant exudates, significantly aids in soil aggregation (Galloway et al. 2020; Monnier 1965; Williams et al. 2021). Mucilage is a polymeric gel composed of high molecular weight polysaccharides and trace amounts of lipids. The specific chemical compounds of root mucilage readily attach to clay minerals, assisting in aggregate formation and stabilization (Mench et al. 1988; Morel et al. 1991; Nazari 2021; Read et al. 2003; Tosif et al. 2021; Vermeer and McCully 1982). Particularly, freshly released mucilage from maize roots aids in aggregating the rhizosheath and preventing its disintegration (Morel et al. 1991). Within the rhizosphere, mucilage functions as a bioadhesive that binds soil particles via its polysaccharide and protein constituents, thereby encouraging soil aggregation. The addition of isolated corn root cap mucilage to soil, in the presence of microbes, has been shown to form water stable aggregates in vitro (Morel et al. 1991). Microbial activity, triggered by mucilage, plays a vital role in this aggregation process by enhancing the decomposition of organic matter and producing extracellular substances that contribute to the stabilization of soil aggregates (Chenu 1993; Jones et al. 2009). Mechanistically, mucilage impacts soil structure through both biological and physical pathways. Recent studies indicate that mucilage's rheological properties, such as viscosity and elasticity, are key to its role as a bioadhesive, strengthening soil cohesion by forming a hydrated, flexible film between soil particles (Naveed et al. 2019). Several microscale effects have been identified to explain the stabilization of the soil structure by mucilage. In the wet state, stronger binding between soil particles due to a gluing effect leads to an increased cohesion of soil aggregates (Watt et al. 1993; Zhang et al. 2008). After drying and rewetting, reduction of the wetting rate, cementation, and increased polymer-particle surface contact enhance aggregate stability and reduce slaking (Buchmann et al. 2015; Orts et al. 2007). Chemical interactions between mucilage and soil particles further affect soil structural stability (Barré and Hallett 2009; Buchmann and Schaumann 2018). Furthermore, mucilage contributes to improved water retention in the rhizosphere, establishing a conducive environment for soil aggregation processes (Carminati et al. 2010; Dobbelaere et al. 2003; Naveed et al. 2017).

Beyond biological effects, aggregates also form during (dry–wet [DW]) cycles, essential for promoting aggregation, triggering nutrient cycling, and organic matter decomposition (Kemper et al. 1985; Krause et al. 2018; Mikha et al. 2005). Under dry conditions, soil particles are tightly bound due to stronger water menisci and final coagulation of particles at low distance, as suggested by the DLVO theory (Osipov 2015; Pashley and Karaman 2021). In contrast, wetting the soil not only leads to the expansion of the electric double layer and related particle dispersion but also results in a rapid incorporation of free water, trapping air in pores, causing swelling, and finally also causing inflation of soil aggregates (Kemper et al. 1985; Stewart and Hartge 1995). Microbial activity can be boosted by DW cycles due to cell death during drought and microbial reconsumption after rewetting (Bell et al. 2014; Clark et al. 2009; Placella et al. 2012). DW cycles bring particles closer together as the soil dries, allowing mucilage to enhance bonding, but wetting can disrupt some aggregates by breaking weaker bonds. Repeated cycles can either strengthen aggregate stability by reinforcing particle cohesion or weaken it if mucilage degrades over time. On the basis of this, we hypothesize that rhizosheath development, aggregate formation, sizes, and aggregate stability in the rhizosphere are influenced by DW cycles, therewith potentially modulating the role of mucilage as key bonding partner.

The study's objectives were threefold: first, to quantify the role of mucilage in rhizosheath formation, soil aggregate formation, and size distribution in bulk soil in the presence of mucilage and under constant moisture conditions for two soils with varying clay content. Second, to evaluate how soil sterilization and resultant inhibition of microbial activity affect rhizosheath formation, soil aggregate formation, and size distribution. Third, to assess to what degree the above-mentioned interactions were modulated by DW cycles. We used flax cord as a model root and chia mucilage as a model root-mucilage to investigate rhizosheath and aggregate. To characterize these interactions in detail, we employed laser diffraction and scanning electron microscopy (SEM) to analyze the structure and stability of aggregates formed.

2 | Materials and Methods

2.1 | Soil Sampling, Characteristics, and Treatment

The soils used in the study were collected from the Scheyern research station (48°29′36″ N, 11°26′15″ E) situated in the rural area outside Munich (Germany). The selected soils were sandy to loamy textured Luvisols with mean annual temperature of 7.4°C and a mean annual precipitation of 803 mm. Detailed information of the selected soils, that is, soil properties, sampling plots, and soil sampling, is given in Krause et al. (2018). Soil samples with clay contents of 22% and 32% were selected from field triplicates for subsequent experiments. As all soils were sourced from the identical experimental site, there were no variations in management across the various replicates. Illitic clay minerals were prevalent in all soil samples, which were devoid of carbonates. Additionally, Fe chlorite, kaolinite, and smectite were present as supplementary clay minerals. Furthermore, the selected soils underwent additional sterilization treatment. For this purpose, 0.5 kg soil was divided into three portions and placed in an aluminum container covered with aluminum foil. The soil was then autoclaved at 121°C under 103 kPa for 30 min and kept left in a laminar flow at room temperature in between for 3 consecutive days. The purpose of autoclaving the soils was to partially eliminate microorganisms and identify any microbial-induced effects. After those soils were oven dried at 60°C and sieved to pass through 2-mm sieve. These soils were named as sterilized soils, and the soils without autoclaving were considered as unsterilized soils.

2.2 | Extraction of Chia Seed Mucilage

We used chia seed (*Salvia hispanica* L.) mucilage as a model for root exudates due to its well-characterized and reproducible composition, ease of harvest in sufficient quantities, and similar physical properties to plant-derived mucilage. Although it lacks the full biochemical complexity of natural root exudates, chia mucilage mimics key functional traits such as gel formation, high viscosity, and adhesive behavior. Its chemical composition, including glucose, xylose, and uronic acids, closely resembles that of maize root mucilage (Naveed et al. 2019; Zickenrott et al. 2016). Previous studies have demonstrated comparable effects of chia and natural mucilage on soil hydraulic properties and gas diffusivity (Benard et al. 2019; Kroener et al. 2018), supporting its use as a standardized model for studying mucilage soil interactions. The extraction of chia seed mucilage followed the method outlined by Ahmed et al. (2014). In short, 5 g of chia seeds were mixed in 50 g of deionized water and left to swell for 2 min under stirring using a magnetic stirrer. The mixture was then kept at room temperature for 2 h. Subsequently, the chia seed-water mixture was sieved using a syringe that was cut at the one end, whereas vacuum pressure was applied through a vacuum pump and the chia seed gel was obtained. The harvested chia seed gel was freeze-dried and was subsequently pulverized using a ball mill into powder form. The freeze-dried chia seed mucilage powder was mixed with deionized water to prepare a 0.12% (w/w) hydrated mucilage (g mucilage per g of water), following our previous study where this concentration resulted in strong rhizosheath formation (Rahim et al. 2024). This value lies within the range reported for mucilage concentrations in the rhizosphere (Ahmed et al. 2016; Chaboud 1983; Holz, Zarebanadkouki, et al. 2018). Although chia mucilage does not dissolve fully in water, it swells to form a colloidal gel due to its high-molecular-weight polysaccharides (Naveed et al. 2019). Magnetic stirring was used to disperse aggregates and obtain a stable, homogeneous suspension (Benard et al. 2019; Kroener et al. 2018).

2.3 | Aggregation Experiment

We used flax cord having diameter of 3 mm as a model plant root (Rahim et al. 2024) as it has similar thickness and is also hairy, as at least some roots in soil. The advantage of using a model compound was that it did not change during the experiment. Aluminum containers used as sample holders measuring 16.6 cm in length, 6.5 cm in height, and 3 cm in width were used. First, a total of 40 g of dry soil was used. Initially, 20 g of soil was added to the container, and the flax cord was placed horizontally at the center of the soil layer. After that, 2 g of chia seed mucilage (0.12% w/w gram of dry chia seed mucilage per gram in water) (Rahim et al. 2024) was injected from the top onto each flax cord. The volume of mucilage applied was calculated on the basis of the formula:

$$V = \pi \times r^2 \times L \tag{1}$$

Resulting in 0.495 mL of mucilage applied to each cord, which was compared to the total volume of the cord (0.0495 mL). The ratio of cord volume to mucilage applied a reasonable ratio for real root systems, as supported by previous studies (Ahmed et al. 2014, 2016; Naveed et al. 2017). Mucilage production in plant roots can form a hydrated mucilage layer around the root, extending beyond the root surface (Chaboud 1983; Holz, Leue, et al. 2018). The remaining 20 g of soil was then added to cover the flax cord. At the end of the setup phase, distilled water was sprayed to adjust the soil to 75% of its water holding capacity (WHC) for the reference (control) treatment, which remained at this moisture level throughout the experiment. The (DW) treatment consisted of five cycles over a 20-day period. In each cycle, soil was allowed to dry from 75% to 15% WHC, followed by rewetting to 75% WHC on the afternoon of Days 4 at 25°C. This cycle was repeated four times. After the final drying phase on Days 20, flax cords were removed, and rhizosheath mass was recorded. As soils with different clay contents were used, the drying rates varied. Therefore, soils were not rewetted simultaneously but only once they had reached the target dryness level (15% WHC). To monitor soil moisture accurately, all samples were weighed daily. Evaporative losses were compensated for by carefully adding deionized water with a syringe to maintain target WHC levels. The control treatment received water only to maintain constant 75% WHC and did not undergo any drying cycles. At the end of the DW cycles, rhizosheath formation was determined by weight. The flax cords were extracted, and their weights were recorded when the soil reached to 15% of their WHC.

WHC was calculated before the start of the experiment using the capillary rise method. Perforated aluminum sample holders lined with filter paper were filled with soil and saturated by submersion in deionized water. After saturation (100% WHC), the filter paper was removed, water leakage was checked, and the weight was recorded. Soils were then dried to 75% WHC for treatment application. The maximum WHC was 0.314 mL g^{-1} for soils with 22% clay and 0.35 mL g^{-1} for soils with 32% clay (both sterilized and unsterilized).

2.4 | Particle-Size Distribution and Stability

Due to limited rhizosheath mass, particle-size distribution and stability analyses were not possible. Hence, we characterized individual aggregates of the rhizosheath using SEM and applied general techniques for assessing particle-size distribution and stability to the remaining mucilage affected rhizosphere soil, which had also received the mucilage and the DW cycles but which did not stick to the model roots. For particle-size distribution and stability tests, the remaining air-dried bulk soil samples were analyzed using a laser diffraction particle analyzer (Horiba LA960, Kyoto, Japan) as described in Krause et al. (2018) and Tang et al. (2022). This approach involved analyzing the volume-based particle size distribution in an aqueous suspension· Software algorithm based on the Mie theory converts scattered light data into volume-based size distribution. Additionally, particle-size distribution was also qualitatively analyzed using SEM. Dried-bulk soil and rhizosheath were prepared for SEM analysis by gently spreading them onto a double-sided C-tape and mounting onto a sample holder. The microstructural analysis was obtained using SEM (Hitachi SU–8000) at 2 keV.

The soil stability was tested using the same particle analyzer method described by others (Kowalenko and Babuin 2013; Mason et al. 2011; Siebers et al. 2024). Aggregates were agitated and subjected to continuous mechanical force, whereas their stability was assessed by measuring particle size distribution repeatedly over a 40-min period. Measurements were taken every 40 s for the first 10 min and then every 3 min for the remaining 30 min. The particle sizes collected were used to calculate the shift in median volume-based diameter (Dv50).

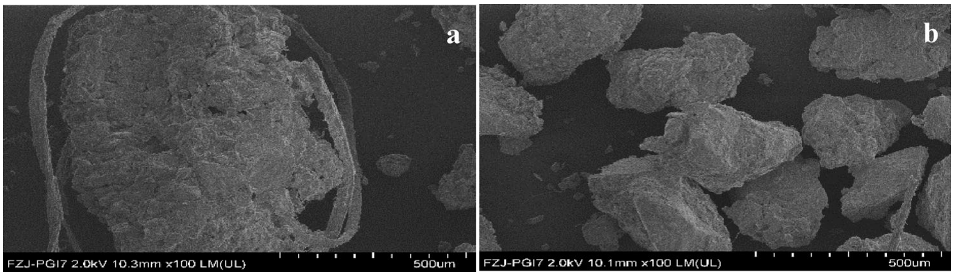

FIGURE 1 | Images of aggregates from rhizosheath soil by scanning electron microscope; (a) aggregates from composite samples of rhizosheath of steri soil 32% clay in wet conditions and (b) aggregates from composite samples of rhizosheath of unsteri soil 22% clay in wet conditions.

The determination of soil stability was performed with the same particle analyzer following the method described by others (Kowalenko and Babuin 2013; Mason et al. 2011; Siebers et al. 2024). During the test, aggregates were agitated and circulated under a continuous mechanical force. We recorded particle size distribution every 40 s for the first 10 min and then every 3 min for the remaining 30 min, over a total of 40 min. The data collected allowed us to calculate changes in the median volume-based diameter (Dv50).

2.5 | Statistical Tests

For data analysis and plotting, we used Microsoft Excel (Excel 2016, Microsoft Corporation, Washington, USA) and Origin (OriginPro 2018b, Originlab). To test the rhizosheath formation under both wet conditions and DW cycle, we performed paired sample *t*-test ($p < 0.05$). To compare the stability of the soil aggregates between treatments, we performed one way ANOVA ($p < 0.05$). If significant differences occurred, we used the least significant differences (LSD) to perform a post hoc separation of means ($\alpha = 0.05$), as proposed by Webster (2007) for soil experiments.

3 | Results

3.1 | Rhizosheath

In general, under continuously wet conditions, significantly larger rhizosheath formation was observed across treatments. Maximum development was found in unsterilized soil with 22% clay, reaching 1.4 ± 0.3 g cm^{-1} root length. In contrast, sterilization led to visibly less compact aggregate structures in the 32% clay soil (Figure 1a), which also showed significantly lower rhizosheath mass (0.6 ± 0.1 g cm^{-1}) compared to its unsterilized counterpart (1.3 ± 0.3 g cm^{-1}). SEM revealed well-developed and densely packed aggregates in this treatment (Figure 1b)

Under DW cycles, rhizosheath formation was markedly reduced in all treatments, irrespective of soil type or sterilization (Figure 2). Rhizosheath mass remained around 0.2 g cm^{-1} root length for all conditions: sterilized 22% clay (0.2 ± 0.0), unsterilized 22% clay (0.2 ± 1.4), sterilized 32% clay (0.2 ± 0.1), and unsterilized 32% clay (0.2 ± 0.0), indicating that repeated drying limited rhizosheath development.

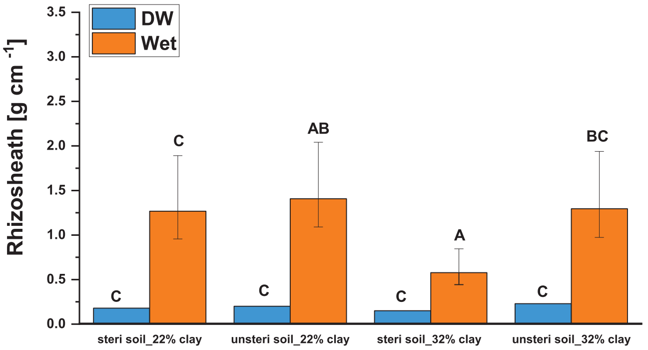

FIGURE 2 | Rhizosheath formation in sterilized and unsterilized soils with 22% and 32% clay under dry–wet (DW) and constant wet cycles. Mean values ± SD, $n = 4$. Different uppercase letters indicate significant differences between treatments and clay contents ($p < 0.05$).

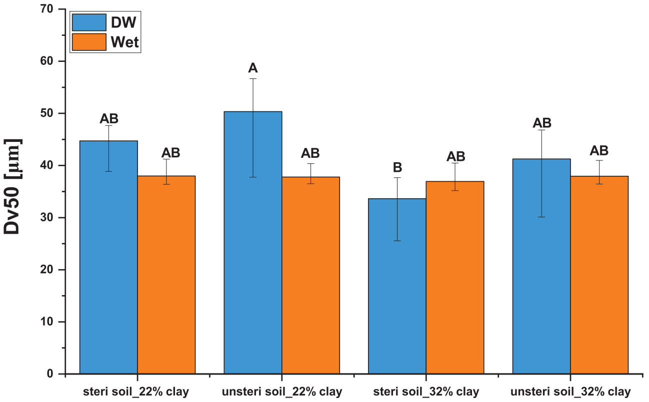

FIGURE 3 | Average median diameter (Dv50) of aggregated particles in the soils exposed to dry–wet (DW) cycles or constant wet conditions. Mean values ± SD, $n = 4$. Different capital letters indicate significant differences between treatments and clay content ($p < 0.05$).

3.2 | Particle Size Distribution

The DW cycles tended to shift the median diameter (Dv50) to larger sizes (50.3 µm) compared to the wet treatments (37.9 µm), but the difference was not significant ($p = 0.05$) (Figure 3). The only significant difference was found between sterilized soil with 22% clay and the unsterilized soil with 32% clay. Conversely, a consistent particle size distribution was observed for microaggregates with a median diameter (Dv50) in soils subjected to the wet treatment, regardless of the clay content or the imposition

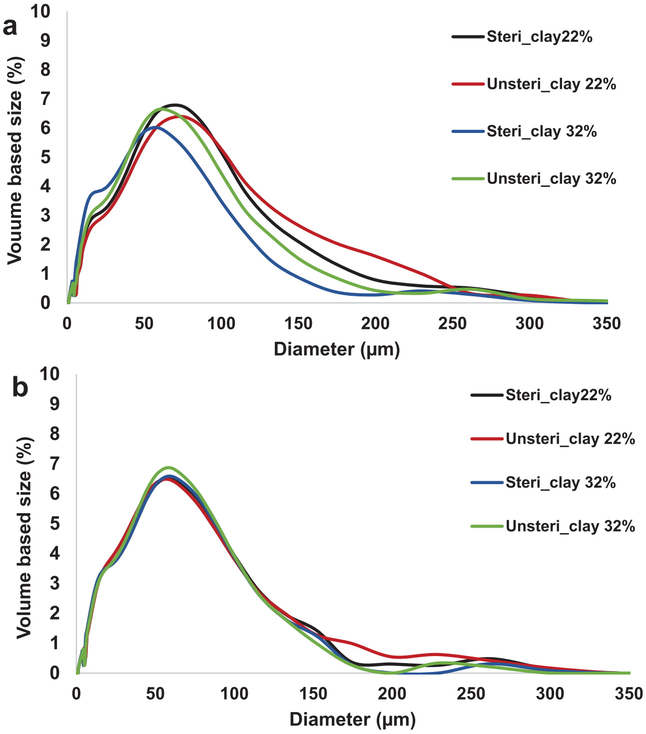

FIGURE 4 | Particle size distribution of sterile and unsterile soils under (a) dry–wet (DW) cycles and (b) when exposed to constant wet conditions at 75% water holding capacity.

of sterile conditions. Hence, and in line with our hypothesis, DW cycles increased aggregation but without increase of rhizosheath quantities (Figure 3).

The DW cycles and continuous wet conditions (reference treatment constantly maintained at 75% WHC) had minimal impact on the size distribution of the aggregated particles, which ranged between 0.1 and 35 µm. The average size of isolated soil particles peaked at 6.7 µm (Figure 4), constituting between 64% and 68% of soil microaggregates in the sterilized and unsterilized soil with 22% clay, respectively. In the finer textured soil with 32% clay, this peak was shifted to 5.8 µm, with a slightly narrower overall diameter range of 0.1–26 µm. Evidently, higher clay content appeared to shift particle size distribution toward smaller sizes under DW cycles, with larger amounts of aggregates in the size range >1 µm being visible in a small shoulder in the particle size distribution (Figure 4a). The pattern of particle size distribution under wet conditions was like that under DW cycles; yet with even smaller differences among treatments. The size range of particles was between 0.2 and 26 µm, peaking at 5.8 µm for all treated soils, with highest percentage 68% for unsteri soil_clay 32% and 64% distribution was noticed for both steri and unsteri soil_clay 22% contents. Noteworthy, in the sterilized treatments, we also noticed a re-aggregation to larger particles ranging from 16 to 26 µm (Figure 4b).

3.3 | Soil Stability

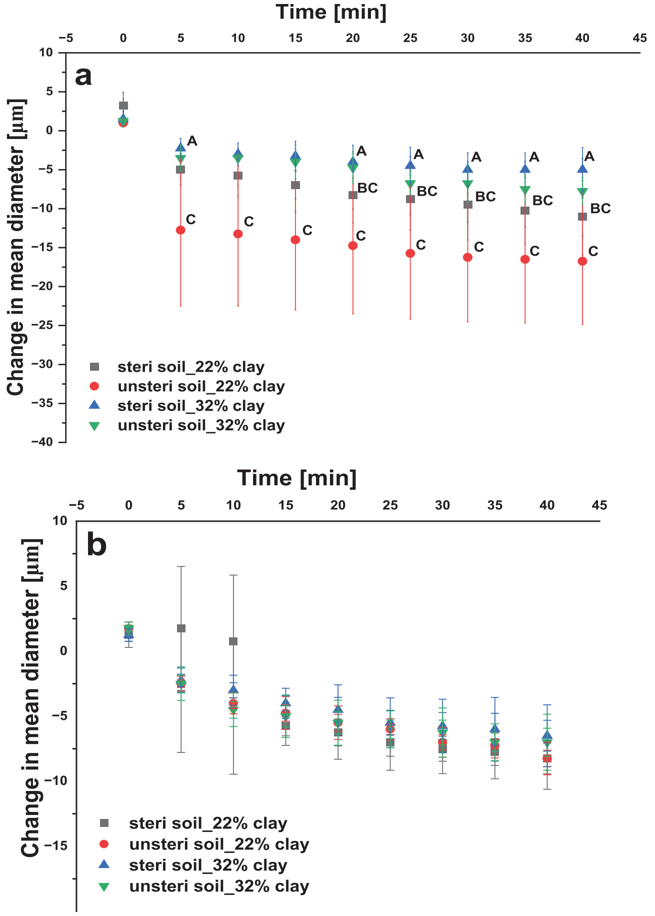

FIGURE 5 | Aggregate stability of soil particles as indicated by changes in median diameter with time under (a) dry–wet (DW) cycles and (b) constant wet conditions. The capital letters indicate significant differences between treatments but within time point ($p < 0.05$).

During the drying-wetting cycles, the median diameter of aggregates exhibited a more pronounced decrease in samples containing 22% clay compared to those with 32%. Moreover, this reduction was more significant in unsterilized samples (Figure 5a). Conversely, under consistently wet conditions, the median diameter decreased over time for all soils in a comparable fashion (Figure 5b), with no significant differences observed between soils of varying clay content. Total losses in median diameter averaged −5 µm but did not reach the −15 µm as in the soils with DW cycles. In summary, constant wet conditions promoted, thus, the formation of rhizosheath, but it did not promote aggregation, neither in size nor stability. It was rather the other way round that the better aggregated bulk soil in the DW cycles coincided with less rhizosheath, as if the formation of aggregates in the surrounding bulk soil interfered with rhizosheath formation by mucilage near the root tips.

4 | Discussion

4.1 | Mucilage Effects Under Constant Moisture and DW Cycles

In this study, the development of rhizosheaths was significantly enhanced under wetter conditions compared to DW cycles in an artificial root model system. Excessive moisture tended to reduce the cohesion of soil particles, making them more prone to detachment and subsequent adherence to the roots (Bates and Lynch 2001), thereby enhancing rhizosheath formation. This is primarily attributed to the bioadhesive properties of mucilage, which acts as a polymeric gel that binds soil particles to the root surface. The high molecular weight polysaccharides in mucilage interact with soil particles through van der Waals forces, hydrogen bonding, and ionic interactions (Ahmed et al. 2014; Naveed et al. 2019). Additionally, mucilage's polysaccharides interact with calcium ions (Ca^{2+}) to form gel-like structures that stabilize soil aggregates by creating cross-linked networks, with divalent cations like Ca^{2+} acting as bridges (Czarnes et al. 2000; de Kerchove and Elimelech 2007). These physicochemical interactions likely enhance rhizosheath formation under steady moisture, while being disrupted during drying events.

In natural environments, several factors contribute to this phenomenon. Ample moisture promotes enhanced root growth, resulting in a larger root surface area and increased exudate release (Abdul-Jabbar et al. 1984; Barber and Mackay 1985). These exudates act as a binding agent, facilitating rhizosheath formation (Aslam et al. 2022). However, it's important to emphasize that in our study, we exclusively utilized model roots, and thus, this aspect of natural root growth does not directly apply to our experimental setup. The structure of the rhizosheath creates an ecological niche with favorable microclimatic conditions, promoting microbial growth, including nitrogen-fixing bacteria (Bergmann et al. 2009; Othman et al. 2003), and the production of microbial gluing agents (Davinic et al. 2012; Six et al. 2004). In contrast, aggregate stability reflects broader soil cohesion mechanisms influenced by clay content, mucilage bonding, and microbial byproducts. Although rhizosheath formation involves localized interactions, aggregate stability is a bulk soil property. Constant moisture minimizes soil drying and cracking, ensuring continuous accumulation of the rhizosheath around the roots.

Rhizosheath formation was significantly reduced during DW cycles across all treatments, irrespective of soil type (Figure 2). This suggests that repeated drying and rewetting events limit mucilage's ability to form strong rhizosheaths, likely due to the disruption of microbial adhesive agents during drying. Although mucilage remains effective under steady moisture, drying may hinder its diffusion into the surrounding soil, reducing particle attachment and rhizosheath formation. This aligns with our observed reduction in rhizosheath mass, though it contrasts with earlier findings (Rahim et al. 2024) that suggest mucilage can form cohesive films even during drying. In our study, drying likely caused mucilage to coagulate, impeding its spread and reducing rhizosheath development. Moisture fluctuations in DW cycles may also cause soil cracking and shrinkage, disrupting rhizosheath continuity and promoting detachment. Rewetting can wash away accumulated rhizosheaths. Similar effects occur in natural soils, where drying induces root desiccation and microbial shifts (Hinsinger et al. 2009). DW cycles may restrict available carbon, limiting microbial decomposition (Fierer and Schimel 2002; Mikha et al. 2005; Sommers et al. 1981), though rewetting often triggers a CO_2 flush due to renewed microbial activity (Birch 1958; Franzluebbers et al. 1994; Zhang, Yu et al. 2020).

4.2 | Impact of Sterilization

Microbial activity in unsterilized soils typically contributes to adhesion by producing extracellular polymeric substances (EPS), which enhance particle cohesion Zhang, Du, et al. (2020). The addition of maize root mucilage to agricultural soil enhances microbial carbon levels and increases cultivable bacteria abundance, altering the community's metabolic structure and improving its catabolic potential for carbohydrates (Benizri et al. 2007). Studies have shown that artificial root exudates can change bacterial community structure (Baudoin et al. 2003; Griffiths et al. 1998). Rhizosphere bacteria exhibit variability in their ability to utilize mucilage (Knee et al. 2001), with those better suited to mucilage utilization experiencing significant growth in its presence. However, some studies showed that mucilage's effects on microbial communities can vary. Although mucilage can enhance growth and alter the structure of specific bacterial groups, its effects may differ across microbes (López-Gutiérrez et al. 2005; Mounier et al. 2004). It is particularly notable that mucilage significantly influences carbon utilization, especially under drought conditions, enhancing uptake in certain groups, such as fungi and certain Gram-negative bacteria (Ahmed et al. 2018). Our study observed similar trends in rhizosheath development, with unsterilized soils showing enhanced rhizosheath formation, which aligns with (Zhang, Du et al. 2020), who observed increased rhizosheath formation in rice plants grown in non-sterilized soils. Microbial gluing agents may have outcompeted mucilage decomposition, although we did not directly measure microbial activity or mucilage degradation in this study. We also observed significantly higher rhizosheath formation in unsterilized soil with lower clay content (22%).

Sterilization enhanced aggregate stability (Figure 4a) by shifting the reliance toward abiotic factors like clay minerals and cation bridging. These differences were also visible in the SEM images. Larger aggregates were observed in sterilized soils with higher clay content (32%), which also showed reduced rhizosheath formation (Figure 1a). In contrast, smaller aggregates possibly coated with organic matter were present in rhizosheaths formed under wet conditions, particularly in unsterilized soils with lower clay content (22%), which exhibited higher rhizosheath mass (Figure 1b). These observations highlight the cohesive nature of clayey soils and the substantial role of abiotic factors such as clay minerals and cation bridging in aggregate formation under sterilized conditions. They also support the idea that mucilage contributes to particle cohesion in coarser soils, where lower clay content and the presence of microbial activity favor the formation of smaller, mucilage-bound aggregates. Further support for these observations comes from the particle size distribution data. The median diameter of soil microaggregates, as measured by laser diffraction, was <10 µm, aligning with previous studies Krause et al. (2018). Larger aggregates (>10 µm) likely included organic carbon fractions and inorganic components like clay minerals and Fe/Al (oxyhydr)oxides (Churchman 2018). Soil with higher clay content exhibited better aggregate stability (Figures 1a and 5), as clay particles have a high surface area and electrostatic charges that aid in aggregation through cation bridging and organic gluing agents (Bronick and Lal 2005; Krause et al. 2018; Tisdall and Oades 1982; Totsche et al. 2018).

This is consistent with the concept that in less clayey soils, larger particles tend to form more open aggregates (Tisdall and Oades 1982), whereas in clay-rich soils, compact aggregates dominate due to the fine texture and higher surface area. The interplay between biotic (EPS, microorganisms) and abiotic factors (clay minerals, oxides) is critical for soil aggregate formation Clarholm and Skyllberg (2013). Additional structural components such as organic matter coatings, microbial byproducts, and porosity further influence aggregate stability (Roosch et al. 2024). Pedogenic oxides, such as Fe (oxyhydr)oxides, also contribute to aggregate stability by cementing particles together (Siebers et al. 2024). Sandy soils typically exhibit larger rhizosheaths due to lower porosity and limited root-soil contact. However, our study found that rhizosheath formation was facilitated at lower clay content, in agreement with other studies (Bailey and Scholes 1997; Leistner 1967; Oppenheimer 1960). Two factors may explain this: (1) better diffusion of mucilage in soils with less clay (Ahmed et al. 2014; Carminati et al. 2010; Rahim et al. 2024), and (2) less aggregation of coarser soils, allowing easier attachment of particles to the (model) plant root.

Nevertheless, when organic matter becomes depleted or in conditions of sterilization, aggregates may disintegrate due to the loss of the organic "glue" that binds them together (Siebers et al. 2024). This disintegration can lead to the emergence of smaller particles or aggregates that exhibit higher stability, primarily driven by the increased prevalence of abiotic components such as clay minerals and oxides. These abiotic factors, especially electrostatic interactions and cation-bridging, provoke robust forces of attraction between soil particles, resulting in enhanced aggregate cohesion and overall stability (Brady and Weil 2008; Rengasamy 2006).

5 | Conclusions

This study advances the mechanistic understanding of how root mucilage, microbial activity, and moisture dynamics influence rhizosheath and soil aggregation processes. First, our findings confirm that mucilage plays a crucial role in rhizosheath formation under constant wet conditions, where it supports adhesion between soil particles and the root surface. Second, the inhibition of microbial activity through soil sterilization reduced rhizosheath development, indicating that microbial-derived compounds contribute significantly to binding in the rhizosheath. Third, DW cycles modulated these interactions by reducing rhizosheath formation but promoting bulk soil aggregation, indicating that physical restructuring and moisture-driven changes in mucilage functionality outweigh mucilage-root binding effects in these conditions. Together, these outcomes support our initial hypotheses: root mucilage contributes to both rhizosheath and aggregate formation, but its function is strongly conditioned by environmental factors. Specifically, rhizosheath formation depends on microbial activity and continuous moisture, whereas aggregate formation in bulk soil is favored by DW cycles. The inverse relationship observed between rhizosheath formation and aggregate development under varying moisture regimes suggests a functional decoupling of these processes.

Importantly, our results propose that DW cycles promote aggregate formation in the bulk soil by inducing physical restructuring and capillary forces among particles, thereby enhancing interparticle cohesion more effectively than at the root–soil interface. Using a simplified model system, this work disentangles key drivers of root–soil interactions and provides a foundation for further research under more complex field conditions, particularly to evaluate the scaling of these mechanisms across soil textures and land management systems.

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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.

References

Abdul-Jabbar, A. S., D. G. Lugg, T. W. Sammis, and L. W. Gay. 1984. "A Field Study of Plant Resistance to Water Flow in Alfalfa." *Agronomy Journal* 76, no. 5: 765–769. https://doi.org/10.2134/agronj1984.00021962007600050014x.

Ahmed, M. A., C. C. Banfield, M. Sanaullah, A. Gunina, and M. A. Dippold. 2018. "Utilisation of Mucilage C by Microbial Communities Under Drought." *Biology and Fertility of Soils* 54, no. 1: 83–94. https://doi.org/10.1007/s00374-017-1237-6.

Ahmed, M. A., E. Kroener, P. Benard, M. Zarebanadkouki, A. Kaestner, and A. Carminati. 2016. "Drying of Mucilage Causes Water Repellency in the Rhizosphere of Maize: Measurements and Modelling." *Plant and Soil* 407, no. 1: 161–171. https://doi.org/10.1007/s11104-015-2749-1.

Ahmed, M. A., E. Kroener, M. Holz, M. Zarebanadkouki, and A. Carminati. 2014. "Mucilage Exudation Facilitates Root Water Uptake in Dry Soils." *Functional Plant Biology* 41, no. 11: 1129–1137. https://doi.org/10.1071/FP13330.

Amelung, W., N. Meyer, A. Rodionov, et al. 2023. "Process Sequence of Soil Aggregate Formation Disentangled Through Multi-Isotope Labelling." *Geoderma* 429: 116226. https://doi.org/10.1016/j.geoderma.2022.116226.

Aslam, M. M., J. K. Karanja, I. C. Dodd, M. Waseem, and X. Weifeng. 2022. "Rhizosheath: an Adaptive Root Trait to Improve Plant Tolerance to Phosphorus and Water Deficits?" *Plant, Cell and Environment* 45, no. 10: 2861–2874. https://doi.org/10.1111/pce.14395.

Bailey, C., and M. Scholes. 1997. "Rhizosheath Occurrence in South African Grasses." *South African Journal of Botany* 63, no. 6: 484–490. https://doi.org/10.1016/S0254-6299(15)30803-6.

Barber, S. A., and A. D. Mackay. 1985. "Sensitivity Analysis of the Parameters of a Mechanistic Mathematical Model Affected by Changing Soil Moisture." *Agronomy Journal* 77, no. 4: 528–531. https://doi.org/10.2134/agronj1985.00021962007700040006x.

Barré, P., and P. D. Hallett. 2009. "Rheological Stabilization of Wet Soils by Model Root and Fungal Exudates Depends on Clay Mineralogy." *European Journal of Soil Science* 60, no. 4: 525–538. https://doi.org/10.1111/j.1365-2389.2009.01151.x.

Bates, T. R., and J. P. Lynch. 2001. "Root Hairs Confer a Competitive Advantage Under Low Phosphorus Availability." *Plant and Soil* 236: 243–250. https://doi.org/10.1023/A:1012791706800.

Baudoin, E., E. Benizri, and A. Guckert. 2003. "Impact of Artificial Root Exudates on the Bacterial Community Structure in Bulk Soil and Maize Rhizosphere." *Soil Biology and Biochemistry* 35, no. 9: 1183–1192. https://doi.org/10.1016/S0038-0717(03)00179-2.

Bell, C. W., D. T. Tissue, M. E. Loik, et al. 2014. "Soil Microbial and Nutrient Responses to 7 Years of Seasonally Altered Precipitation in a Chihuahuan Desert Grassland." *Global Change Biology* 20, no. 5: 1657–1673. https://doi.org/10.1111/gcb.12418.

Benard, P., M. Zarebanadkouki, M. Brax, et al. 2019. "Microhydrological Niches in Soils: How Mucilage and EPS Alter the Biophysical Properties of the Rhizosphere and Other Biological Hotspots." *Vadose Zone Journal* 18, no. 1: 1–10. https://doi.org/10.2136/vzj2018.12.0211.

Benizri, E., C. Nguyen, S. Piutti, S. Slezack-Deschaumes, and L. Philippot. 2007. "Additions of Maize Root Mucilage to Soil Changed the Structure of the Bacterial Community." *Soil Biology and Biochemistry* 39, no. 5: 1230–1233. https://doi.org/10.1016/j.soilbio.2006.12.026.

Bergmann, D., M. Zehfus, L. Zierer, B. Smith, and M. Gabel. 2009. "Grass Rhizosheaths: Associated Bacterial Communities and Potential for Nitrogen Fixation." *Western North American Naturalist* 69, no. 1: 105–114. https://doi.org/10.3398/064.069.0102.

Birch, H. F. 1958. "The Effect of Soil Drying on Humus Decomposition and Nitrogen Availability." *Plant and Soil* 10: 9–31. https://doi.org/10.1007/BF01343734.

Brady, N. C., and R. R. Weil. 2008. *The Nature and Properties of Soils*. Prentice Hall.

Bronick, C. J., and R. Lal. 2005. "Manuring and Rotation Effects on Soil Organic Carbon Concentration for Different Aggregate Size Fractions on Two Soils in Northeastern Ohio, USA." *Soil and Tillage Research* 81, no. 2: 239–252. https://doi.org/10.1016/j.still.2004.09.011.

Buchmann, C., M. Meyer, and G. E. Schaumann. 2015. "Characterization of Wet Aggregate Stability of Soils by H-NMR Relaxometry." *Magnetic Resonance in Chemistry* 53, no. 9: 694–703. https://doi.org/10.1002/mrc.4147.

Buchmann, C., and G. E. Schaumann. 2018. "The Contribution of Various Organic Matter Fractions to Soil–Water Interactions and Structural Stability of an Agriculturally Cultivated Soil." *Journal of Plant Nutrition and Soil Science* 181, no. 4: 586–599. https://doi.org/10.1002/jpln.201700437.

Carminati, A., A. B. Moradi, D. Vetterlein, et al. 2010. "Dynamics of Soil Water Content in the Rhizosphere." *Plant and Soil* 332: 163–176. https://doi.org/10.1007/s11104-010-0283-8.

Chaboud, A. 1983. "Isolation, Purification and Chemical Composition of Maize Root Cap Slime." *Plant and Soil* 73: 395–402. https://doi.org/10.1007/BF02184316.

Chenu, C. 1993. "Clay—or Sand—Polysaccharide Associations as Models for the Interface Between Micro-Organisms and Soil: Water Related Properties and Microstructure." In *Soil Structure/Soil Biota Interrelationships*, edited by L. Brussaard and M. J. Kooistra, 143–156. Elsevier.

Churchman, G. J. 2018. "Game Changer in Soil Science. Functional Role of Clay Minerals in Soil." *Journal of Plant Nutrition and Soil Science* 181, no. 1: 99–103. https://doi.org/10.1002/jpln.201700605.

Clarholm, M., and U. Skyllberg. 2013. "Translocation of Metals by Trees and Fungi Regulates pH, Soil Organic Matter Turnover and Nitrogen Availability in Acidic Forest Soils." *Soil Biology and Biochemistry* 63: 142–153. https://doi.org/10.1016/j.soilbio.2013.03.019.

Clark, J. S., J. H. Campbell, H. Grizzle, V. Acosta-Martìnez, and J. C. Zak. 2009. "Soil Microbial Community Response to Drought and Precipitation Variability in the Chihuahuan Desert." *Microbial Ecology* 57: 248–260. https://doi.org/10.1007/s00248-008-9475-7.

Czarnes, S., P. D. Hallett, A. G. Bengough, and I. M. Young. 2000. "Root-and Microbial-Derived Mucilages Affect Soil Structure and Water Transport." *European Journal of Soil Science* 51, no. 3: 435–443. https://doi.org/10.1046/j.1365-2389.2000.00327.x.

Davinic, M., L. M. Fultz, V. Acosta-Martinez, et al. 2012. "Pyrosequencing and Mid-Infrared Spectroscopy Reveal Distinct Aggregate Stratification of Soil Bacterial Communities and Organic Matter Composition." *Soil Biology and Biochemistry* 46: 63–72. https://doi.org/10.1016/j.soilbio.2011.11.012.

de Kerchove, A. J., and M. Elimelech. 2007. "Formation of Polysaccharide Gel Layers in the Presence of Ca^{2+} and K^+ Ions: Measurements and Mechanisms." *Biomacromolecules* 8, no. 1: 113–121. https://doi.org/10.1021/bm060670i.

Dobbelaere, S., J. Vanderleyden, and Y. Okon. 2003. "Plant Growth-Promoting Effects of Diazotrophs in the Rhizosphere." *Critical Reviews in Plant Sciences* 22, no. 2: 107–149. https://doi.org/10.1080/713610853.

Fierer, N., and J. P. Schimel. 2002. "Effects of Drying–Rewetting Frequency on Soil Carbon and Nitrogen Transformations." *Soil Biology and Biochemistry* 34, no. 6: 777–787. https://doi.org/10.1016/S0038-0717(02)00007-X.

Franzluebbers, K., R. W. Weaver, A. S. R. Juo, and A. J. Franzluebbers. 1994. "Carbon and Nitrogen Mineralization From Cowpea Plants Part Decomposing in Moist and in Repeatedly Dried and Wetted Soil." *Soil Biology and Biochemistry* 26, no. 10: 1379–1387. https://doi.org/10.1016/0038-0717(94)90221-6.

Galloway, A. F., P. Knox, and K. Krause. 2020. "Sticky Mucilages and Exudates of Plants: Putative Microenvironmental Design Elements With Biotechnological Value." *New Phytologist* 225, no. 4: 1461–1469. https://doi.org/10.1111/nph.16144.

Griffiths, B. S., K. Ritz, N. Ebblewhite, and G. Dobson. 1998. "Soil Microbial Community Structure: Effects of Substrate Loading Rates." *Soil Biology and Biochemistry* 31, no. 1: 145–153. https://doi.org/10.1016/S0038-0717(98)00117-5.

Hinsinger, P., A. G. Bengough, D. Vetterlein, and I. M. Young. 2009. "Rhizosphere: Biophysics, Biogeochemistry and Ecological Relevance." *Plant and Soil* 321, no. 1–2: 117–152. https://doi.org/10.1007/s11104-008-9885-9.

Holz, M., M. Leue, M. A. Ahmed, P. Benard, H. H. Gerke, and A. Carminati. 2018. "Spatial Distribution of Mucilage in the Rhizosphere Measured With Infrared Spectroscopy." *Frontiers in Environmental Science* 6: 87. https://doi.org/10.3389/fenvs.2018.00087.

Holz, M., M. Zarebanadkouki, Y. Kuzyakov, J. Pausch, and A. Carminati. 2018. "Root Hairs Increase Rhizosphere Extension and Carbon Input to Soil." *Annals of Botany* 121, no. 1: 61–69. https://doi.org/10.1093/aob/mcx127.

Jones, D. L., C. Nguyen, and R. D. Finlay. 2009. *Carbon Flow in the Rhizosphere: Carbon Trading at the Soil–Root Interface*. Springer.

Kemper, W. D., R. Rosenau, and S. Nelson. 1985. "Gas Displacement and Aggregate Stability of Soils." *Soil Science Society of America Journal* 49, no. 1: 25–28. https://doi.org/10.2136/sssaj1985.03615995004900010004x.

Knee, E. M., F.-C. Gong, M. Gao, et al. 2001. "Root Mucilage From Pea and Its Utilization by Rhizosphere Bacteria as a Sole Carbon Source." *Molecular Plant-Microbe Interactions* 14, no. 6: 775–784. https://doi.org/10.1094/MPMI.2001.14.6.775.

Kowalenko, C. G., and D. Babuin. 2013. "Inherent Factors Limiting the Use of Laser Diffraction for Determining Particle Size Distributions of Soil and Related Samples." *Geoderma* 193: 22–28. https://doi.org/10.1016/j.geoderma.2012.09.006.

Krause, L., A. Rodionov, S. A. Schweizer, et al. 2018. "Microaggregate Stability and Storage of Organic Carbon Is Affected by Clay Content in Arable Luvisols." *Soil and Tillage Research* 182: 123–129. https://doi.org/10.1016/j.still.2018.05.003.

Kroener, E., M. Holz, M. Zarebanadkouki, M. Ahmed, and A. Carminati. 2018. "Effects of Mucilage on Rhizosphere Hydraulic Functions Depend on Soil Particle Size." *Vadose Zone Journal* 17, no. 1: 1–11. https://doi.org/10.2136/vzj2017.03.0056.

Leistner, O. A. 1967. *The Plant Ecology of the Southern Kalahari. Botanical Survey Memoir No 38. Department of Agriculture Technical Services*. Government Printer.

Li, J., X. Yuan, L. Ge, et al. 2020. "Rhizosphere Effects Promote Soil Aggregate Stability and Associated Organic Carbon Sequestration in Rocky Areas of Desertification." *Agriculture, Ecosystems and Environment* 304: 107126. https://doi.org/10.1016/j.agee.2020.107126.

Li, K., M. J. DiLegge, I. S. Minas, A. Hamm, D. Manter, and J. M. Vivanco. 2019. "Soil Sterilization Leads to Re-Colonization of a Healthier Rhizosphere Microbiome." *Rhizosphere* 12: 100176. https://doi.org/10.1016/j.rhisph.2019.100176.

López-Gutiérrez, J. C., L. Philippot, and F. Martin-Laurent. 2005. "Impact of Maize Mucilage on Atrazine Mineralization and atzC Abundance." *Pest Management Science: Formerly Pesticide Science* 61, no. 9: 838–844. https://doi.org/10.1002/ps.1078.

Mason, J. A., R. S. B. Greene, and R. M. Joeckel. 2011. "Laser Diffraction Analysis of the Disintegration of Aeolian Sedimentary Aggregates in Water." *Catena* 87, no. 1: 107–118. https://doi.org/10.1016/j.catena.2011.05.015.

Mench, M., J. L. Morel, A. Guckert, and B. Guillet. 1988. "Metal Binding With Root Exudates of Low Molecular Weight." *Journal of Soil Science* 39, no. 4: 521–527. https://doi.org/10.1111/j.1365-2389.1988.tb01236.x.

Mikha, M. M., C. W. Rice, and G. A. Milliken. 2005. "Carbon and Nitrogen Mineralization as Affected by Drying and Wetting Cycles." *Soil Biology and Biochemistry* 37, no. 2: 339–347. https://doi.org/10.1016/j.soilbio.2004.08.003.

Monnier, G. 1965. "Action Des Matieres Organiques Sur La Stabilite Structurale Du Sol." *Sols Africains* 10, no. 1: 5–42. https://coilink.org/20.500.12592/34r5fe8.

Morel, J. L., L. Habib, S. Plantureux, and A. Guckert. 1991. "Influence of Maize Root Mucilage on Soil Aggregate Stability." *Plant and Soil* 136, no. 1: 111–119. https://doi.org/10.1007/BF02465226.

Mounier, E., S. Hallet, D. Chèneby, et al. 2004. "Influence of Maize Mucilage on the Diversity and Activity of the Denitrifying Community." *Environmental Microbiology* 6, no. 3: 301–312. https://doi.org/10.1111/j.1462-2920.2004.00571.x.

Naveed, M., M. A. Ahmed, P. Benard, et al. 2019. "Surface Tension, Rheology and Hydrophobicity of Rhizodeposits and Seed Mucilage Influence Soil Water Retention and Hysteresis." *Plant and Soil* 437: 65–81. https://doi.org/10.1007/s11104-019-03939-9.

Naveed, M., L. K. Brown, A. C. Raffan, et al. 2017. "Plant Exudates May Stabilize or Weaken Soil Depending on Species, Origin and Time." *European Journal of Soil Science* 68, no. 6: 806–816. https://doi.org/10.1111/ejss.12487.

Nazari, M. 2021. "Plant Mucilage Components and Their Functions in the Rhizosphere." *Rhizosphere* 18: 100344. https://doi.org/10.1016/j.rhisph.2021.100344.

Oppenheimer, H. R. 1960. "Adaptation to Drought: Xerophytism." In *Plant-Water Relationships in Arid and Semi-Arid Conditions: Reviews of Research*, edited by UNESCO., 105–132. Bucher.

Orts, W. J., A. Roa-Espinosa, R. E. Sojka, et al. 2007. "Use of Synthetic Polymers and Biopolymers for Soil Stabilization in Agricultural, Construction, and Military Applications." *Journal of Materials in Civil Engineering* 19, no. 1: 58–66. https://doi.org/10.1061/(ASCE)0899-1561(2007)19:1(58).

Osipov, V. I. 2015. *Physicochemical Theory of Effective Stress in Soils*. Springer.

Othman, A., M. Shawky, W. Amer, M. Fayez, M. Monib, and N. Hegazi. 2003. "Biodiversity of Microorganisms in Semi-Arid Soils of North Sinai Deserts." *Archives of Agronomy and Soil Science* 49, no. 3: 241–260. https://doi.org/10.1080/0365034031000112083.

Pashley, R. M., and M. E. Karaman. 2021. *Applied Colloid and Surface Chemistry*. John Wiley and Sons.

Placella, S. A., E. L. Brodie, and M. K. Firestone. 2012. "Rainfall-Induced Carbon Dioxide Pulses Result From Sequential Resuscitation of Phylogenetically Clustered Microbial Groups." *Proceedings of the National Academy of Sciences* 109, no. 27: 10931–10936. https://doi.org/10.1073/pnas.1204306109.

Rahim, R., O. E. Jahromi, W. Amelung, and E. Kroener. 2024. "Rhizosheath Formation Depends on Mucilage Concentration and Water Content." *Plant and Soil* 495, no. 1: 649–661. https://doi.org/10.1007/s11104-023-06353-4.

Rahman, M. T., Q. H. Zhu, Z. B. Zhang, H. Zhou, and X. Peng. 2017. "The Roles of Organic Amendments and Microbial Community in the Improvement of Soil Structure of a Vertisol." *Applied Soil Ecology* 111: 84–93. https://doi.org/10.1016/j.apsoil.2016.11.018.

Read, D. B., A. G. Bengough, P. J. Gregory, et al. 2003. "Plant Roots Release Phospholipid Surfactants That Modify the Physical and Chemical Properties of Soil." *New Phytologist* 157, no. 2: 315–326. https://doi.org/10.1046/j.1469-8137.2003.00665.x.

Rengasamy, P. 2006. "World Salinization With Emphasis on Australia." *Journal of Experimental Botany* 57, no. 5: 1017–1023. https://doi.org/10.1093/jxb/erj108.

Roosch, S., V. J. Felde, D. Uteau, and S. Peth. 2024. "Exploring the Mechanisms of Diverging Mechanical and Water Stability in Macro-and Microaggregates." *Journal of Plant Nutrition and Soil Science* 187, no. 1: 104–117. https://doi.org/10.1002/jpln.202300245.

Siebers, N., E. Voggenreiter, P. Joshi, J. Rethemeyer, and L. Wang. 2024. "Synergistic Relationships Between the Age of Soil Organic Matter, Fe Speciation, and Aggregate Stability in an Arable Luvisol." *Journal of Plant Nutrition and Soil Science* 187, no. 1: 77–88. https://doi.org/10.1002/jpln.202300020.

Six, J., H. Bossuyt, S. Degryze, and K. Denef. 2004. "A History of Research on the Link Between (Micro) Aggregates, Soil Biota, and Soil Organic Matter Dynamics." *Soil and Tillage Research* 79, no. 1: 7–31. https://doi.org/10.1016/j.still.2004.03.008.

Sommers, L. E., C. M. Gilmour, R. E. Wildung, and S. M. Beck. 1981. "The Effect of Water Potential on Decomposition Processes in Soils." *Water Potential Relations in Soil Microbiology* 9: 97–117. https://doi.org/10.2136/sssaspecpub9.c3.

Stewart, B. A., and K. H. Hartge. 1995. *Soil Structure: Its Development and Function*. CRC Press.

Tang, N., N. Siebers, P. Leinweber, et al. 2022. "Implications of Free and Occluded Fine Colloids for Organic Matter Preservation in Arable Soils." *Environmental Science and Technology* 56, no. 19: 14133–14145. https://doi.org/10.1021/acs.est.2c01973.

Tisdall, J. M., and J. M. Oades. 1982. "Organic Matter and Water-Stable Aggregates in Soils." *Journal of Soil Science* 33, no. 2: 141–163. https://doi.org/10.1111/j.1365-2389.1982.tb01755.x.

Tosif, M. M., A. Najda, A. Bains, et al. 2021. "A Comprehensive Review on Plant-Derived Mucilage: Characterization, Functional Properties, Applications, and Its Utilization for Nanocarrier Fabrication." *Polymers* 13, no. 7: 1066. https://doi.org/10.3390/polym13071066.

Totsche, K. U., W. Amelung, M. H. Gerzabek, et al. 2018. "Microaggregates in Soils." *Journal of Plant Nutrition and Soil Science* 181, no. 1: 104–136. https://doi.org/10.1002/jpln.201600451.

Vermeer, J., and M. E. McCully. 1982. "The Rhizosphere in *Zea*: New Insight Into Its Structure and Development." *Planta* 156, no. 1: 45–61. https://doi.org/10.1007/BF00393442.

Watt, M., M. E. McCully, and C. E. Jeffree. 1993. "Plant and Bacterial Mucilages of the Maize Rhizosphere: Comparison of Their Soil Binding Properties and Histochemistry in a Model System." *Plant and Soil* 151, no. 2: 151–165. https://doi.org/10.1007/BF00016280.

Webster, R. 2007. "Analysis of Variance, Inference, Multiple Comparisons and Sampling Effects in Soil Research." *European Journal of Soil Science* 58, no. 1: 74–82. https://doi.org/10.1111/j.1365-2389.2006.00801.x.

Wertz, S., S. Czarnes, F. Bartoli, et al. 2007. "Early-Stage Bacterial Colonization Between a Sterilized Remoulded Soil Clod and Natural Soil Aggregates of the Same Soil." *Soil Biology and Biochemistry* 39, no. 12: 3127–3137. https://doi.org/10.1016/j.soilbio.2007.07.005.

Williams, K. A., S. A. Ruiz, C. Petroselli, et al. 2021. "Physical Characterisation of Chia Mucilage Polymeric Gel and Its Implications on Rhizosphere Science-Integrating Imaging, MRI, and Modelling to Gain Insights Into Plant and Microbial Amended Soils." *Soil Biology and Biochemistry* 162: 108404. https://doi.org/10.1016/j.soilbio.2021.108404.

Zhang, B., P. D. Hallett, and G. Zhang. 2008. "Increase in the Fracture Toughness and Bond Energy of Clay by a Root Exudate." *European Journal of Soil Science* 59, no. 5: 855–862. https://doi.org/10.1111/j.1365-2389.2008.01045.x.

Zhang, S., Z. Yu, J. Lin, and B. Zhu. 2020. "Responses of Soil Carbon Decomposition to Drying-Rewetting Cycles: A Meta-Analysis." *Geoderma* 361: 114069. https://doi.org/10.1016/j.geoderma.2019.114069.

Zhang, Y., H. Du, F. Xu, et al. 2020. "Root-Bacteria Associations Boost Rhizosheath Formation in Moderately Dry Soil Through Ethylene Responses." *Plant Physiology* 183, no. 2: 780–792. https://doi.org/10.1104/pp.19.01020.

Zickenrott, I. M., S. K. Woche, J. Bachmann, M. A. Ahmed, and D. Vetterlein. 2016. "An Efficient Method for the Collection of Root Mucilage From Different Plant Species—A Case Study on the Effect of Mucilage on Soil Water Repellency." *Journal of Plant Nutrition and Soil Science* 179, no. 2: 294–302. https://doi.org/10.1002/jpln.201500511.