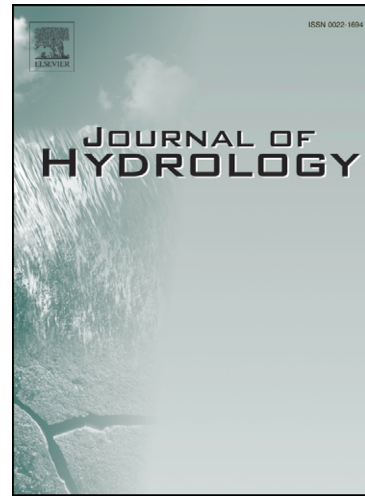

Are Preferential Flow Paths Perpetuated by Microbial Activity in the Soil Matrix? - A Review

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Are Preferential Flow Paths Perpetuated by Microbial Activity in the Soil Matrix? - A Review.

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Abstract

Recently, the interactions between soil structure and microbes have been associated with water transport, retention and preferential or column flow development. Of particular significance is the potential impact of microbial extracellular polymeric substances (EPS) on soil porosity (i.e., hydraulic conductivity reduction or bioclogging) and of exudates from biota, including bacteria, fungi, roots and earthworms on the degree of soil water repellency. These structural and surface property changes create points of wetting instability, which under certain infiltrating conditions can often result in the formation of persistent preferential flow paths. Moreover, distinct differences in physical and chemical properties between regions of water flow (preferential flow paths) and no-flow (soil

matrix) provide a unique set of environmental living conditions for adaptable microorganisms to exist. In this review, special consideration is given to: 1) the functional significance of microbial activity in the host porous medium in terms of feedback mechanisms instigated by irregular water availability, and 2) the related physical and chemical conditions that force the organization and formation of unique microbial habitats in unsaturated soils that prompt and potentially perpetuate the formation of preferential flow paths in the vadose zone.

Key Words

Preferential flow paths, finger flow, column flow, extracellular polymeric substances (EPS), bioclogging, water-repellent soils, hydrophobic compounds, fungal exudates.

1. Introduction and Background

It is widely accepted from well known field studies that preferential flow is the rule rather than the exception in a wide variety of soils (Dekker and Ritsema, 1994; Flury et al., 1994; Steenhuis et al., 1996; Ritsema, 1999). Additionally, preferential flow is a significant transport mechanism that may account for the large number of inaccuracies in water and solute transport predictions (Ritsema and Dekker, 2000). The rising concern about preferential flow (previously referred to as fingering, and recently redefined as column flow in the field) of water in soil is mainly due to the agricultural impacts of reduced soil water retention and bypass of water through the root zone; thus affecting seed emergence, plant growth, and consequently crop yield. In addition, preferential flow is directly implicated with increased risk of groundwater contamination (Bauters et al., 2000; Wang et al., 2000; Doerr et al., 2007) and general leaching of agrochemicals into the subsurface. Moreover, localized dry spots (LDS) in golf greens are a result of unwettable soil patches between soil regions that experience preferential flow, and are commonly treated with wetting agents (Kostka, 2000). The ubiquitous occurrence of preferential flow throughout the world, independent of climate type, land use, and soil type and texture (Andreini and Steenhuis, 1990; Dekker and Ritsema, 1996a; Baveye et al., 1998a; Ritsema, 1999; Doerr et al., 2006, 2007) has proven that it is a common field phenomenon.

Infiltration patterns of preferential flow of the column type are distinct as shown in the exposed trench of Figure 1. This phenomenon is most commonly attributed to the onset of flow instability at the wetting front of a porous medium, which in natural fields tends do be heterogeneous, layered, and often macroporous. The principal cause of column flow, as demonstrated in well characterized and homogeneous media laboratory experiments, is associated with saturation overshoot at the fingertip (DiCarlo, 2004). Here, the region directly behind the wetting front has a high and uniform water saturation, called the finger tip, and is followed by a second region with low and non-uniform water saturation, called the finger tail. However, saturation overshoot does not occur at very low water fluxes or fluxes near the saturated conductivity of the medium. Under field conditions column flow can be enhanced by air entrapment, soil layering (i.e., drastic changes in hydraulic conductivity layers), soil macropores, surface desaturation, and soil water repellency (Bauters et al., 2000; Wang et al., 2000; Or et al., 2007a). In addition, variable environmental factors that affect soil biological activity (e.g.. temperature, pH, precipitation) further complicate the system by stimulating certain responses that can induced localized and sporadic water repellence and alter the porosity of the soil. Both, abiotic and biological derived disturbances of the medium promote column flow. It is thus critical to recognize: how preferential flow is initiated, how the flow patterns affect the activity of the soil fauna, and how biological responses to environmental changes affect preferential flow to better understand water transport and retention in soils prone to it (Feeney et al., 2004; 2006; Doerr et al., 2007).

Coating of water-repellent compounds on some soil minerals or soil aggregate surfaces is a result of the slow accumulation of potentially hydrophobic organic compounds produced by plant root exudates, subsurface waxes from plant leaves, and fungal and microbial by-products (Hallett and Young, 1999; Doerr et al., 2000; White et al., 2000; Mainwaring et al., 2004). Furthermore, the soil grain's surface texture has been shown by McHale et al. (2005) to promote the water repellency of soil grains with hydrophobic surface chemistries into super-hydrophobicity by allowing water drops to roll off (i.e., Casey-Baxter 'slippy' conditions) of the dry and rough soil surface. As Dekker and Ritsema (1994) indicate, soils typically display greater water repellency during the summer (rather than during winter or fall) when they are susceptible to fall below a 'critical water content.' Thus, maintaining a minimum moisture content in the soil might prevent this enhanced water-repellency condition from occurring. Recently, irrigation of agricultural lands with wastewater (Wallach et al., 2005), greywater (Shafran et al., 2005), or application of sewage sludge to fields (Hurrass and Schaumann, 2006) as a means to conserve water in water-scarce areas has been found to be responsible for the development of soil water repellency and column flow in arid regions.

Although considerable advances have been made to elucidate the abiotic interrelationships between the soil's physical properties, wetting/drying cycles, water repellency, and column flow, several biological feedback mechanisms that support life in such unpredictable soil environments also contribute to the chemical and physical characteristics known to promote column flow in the first place. In this review, the functional significance of microbial activity on the host porous medium, and the related physical and chemical conditions that force the organization and formation of unique microbial habitats in the vadose zone are considered. A brief description of the physical mechanisms behind column flow is first provided, followed by a discussion on three biological factors that promote this type of flow by directly or indirectly inducing soil water repellency or changing the medium's hydraulic conductivity. These include: 1) self-organization of microbial organisms at or near column flow regions; 2) the secretion of bacterial compounds that induce soil water repellency, reduce soil porosity, and decrease the soil's hydraulic conductivity; and 3) fungal contributions to soil water-repellency from surface active hydrophobins.

2.1 Physics of Column Flow

Early studies of preferential flow ascribed the phenomenon to macropores in the soil medium (Beven and Germann, 1982), but more recent findings have shown that unstable infiltration often produce similar flow patterns (Parlange and Hill, 1976; Bauters et al., 2000; Rooij et al., 2000; Wang et al., 2000; Bundt et al., 2001). Similarly, water repellent soils are well known to have distinct preferential flow patterns (Van Ommen et al., 1988; Dekker and Jungerius, 1990; Bauters et al., 2000) with water moving into the deep soil in columns and dry soil volumes in between, but the physics of this phenomenon is not completely understood.

For soils prone to column flow, a typical preferential solute model divides the soil profile into a distribution soil layer near the soil surface that typically appears saturated, and below, a conveyance zone where preferential flow paths form (Steenhuis et al., 1994; Kim et al., 2005). The distribution zone follows uniform Richards type infiltration, and conducts water and its solutes into preferential flow paths in the conveyance zone (Figure 2). The thickness of the distribution zone in tilled soils can be the depth of the plowed soil (Kim et al., 2005), while in structured, sandy and water repellent soils it can be limited to 3 to 5 centimeters in depth (Darnault et al., 2004).

Several identified factors or conditions that trigger wetting front instability either individually or in combination are:

1. An increase of soil hydraulic conductivity with depth, such that coarse-textured soil is overlain by fine-textured soil (Hill and Parlange, 1972; Parlange and Hill, 1976)
2. Soil water repellency (Raats, 1973; Dekker and Jungerius, 1990; Ritsema et al., 1998)
3. Air entrapment (Raats, 1973; Hillel, 1987)
4. Non-ponding rainfall/irrigation (Selker et al., 1992; Wang et al., 2000)

Here, condition 1 indicates that a sharp increase in hydraulic conductivity will increase the velocity of the imbibing water, causing the wetting front to break up into fingers. For condition 2, ‘subcritical’ water repellency in soils, a concept introduced by Tillman et al. (1989), explains how water infiltration is impeded by repellency despite the appearance of readily wetting soil in the distribution zone because fingers are formed in the conveyance zone below. A study from Bauters et al. (1998) indicates that a ratio as small as 3.13% of hydrophobically treated soil grains to non-repellent grains will make the medium slightly water repellent, and an increase of the ratio to 5% will render the soil extremely water repellent. This evidence clearly indicates that small additions of hydrophobic compounds to the medium are not trivial and could clearly induce column flow. In condition 3, large fluxes of infiltrating water lead to air entrapment, where water moves downward in columns, and eventually, compressed air will move upward. Lastly, condition 4 indicates that for density driven displacements, such as non-ponding rainfall/irrigation, the front becomes unstable when the flux, q, is smaller than the soil's conductivity at the maximum water content, $K(\theta_{max})$, close to the wetting front (Parlange and Hill, 1976):

$$q < K(\theta_{\max}) \tag{1}$$

This condition mechanistically justifies the constriction of water flow during irrigation events, leading to the inevitable formation of fingers that drain out the excess water. The different causes for unstable wetting fronts indicate that the velocity of a wetting front increases with depth, making the front unstable. All the above listed factors can contribute to the small perturbations required to de-stabilize the initially uniform wetting front, and break up the infiltrating water into preferential flow paths.

Initially in the distribution zone, the wetting front is dominated by capillarity, but as irregularities are encountered in the media, gravity becomes the dominant infiltrating force (Rooij, 2000). Continual drainage cycles of infiltration and desaturation in soils that experience preferential flow is caused by hysteresis at the finger or column core (Glass et al., 1989; Liu et al., 1995; Wang et al., 2000). As a result, the patterns of preferential flow paths do not move around much, and generally actively conduct water for long periods of time (Rooij, 2000; Bundt et al., 2001). As Rooij (2000) explains, once the supply of infiltrating water ceases, the wetted column cores begin drying and water is slowly lost to the surrounding dry soil as a combination of vapor diffusion and liquid water transport until equilibrium is reached. As Liu et al. (1995) point out, the soil in the region of water flow (i.e., preferential flow paths) will remain wetter than the soil in the region of no water flow (i.e., the rest of the soil matrix); thus, subsequent infiltration events will follow old flow paths where the conductivity is higher. Moreover, following the initial wetting and after the columns have stopped expanding laterally, moisture differences between the wet column and the dry soil matrix will be maintained because the matric potential will have also reached equilibrium (DiCarlo et al., 1999). This indicates that from a soil water characteristic curve standpoint, column cores are on a drying curve and are considerably wetter at an equal pressure as that of the surrounding dry areas, which are on a wetting curve. For such cases, the non-uniform saturation is an effect of hysteresis that allows pressures to equalize between flow and no flow regions with different saturation levels. These conditions will remain fixed if the wetting/drying cycle is frequent enough to prevent complete soil desiccation or complete saturation that would erase the spatially fragmented soil-moisture hysteresis.

Of the above processes that drive column flow, changes in hydraulic conductivity, water-repellency of certain soil grains, and hysteresis of already formed preferential flow paths are crucial for initiating and maintaining preferential flow in soils with active microfauna. First, condition 1 is conceived where active microorganisms reduce the effective porosity of the soil due to biofilm formation near the surface, such that in coarse textured soils the top soil layer has a lower hydraulic conductivity (from bioclogged pores) than the soil beneath it. Second, condition 2 is created by the secretion of hydrophobic substances by the microfauna during periods of water stress (to reduce localized evaporation from neighboring dry soil), causing preferential flow in any type of soil, independent of particle size. Lastly, hysteresis will ensure that columns form repeatedly in the same location and persist for extended periods of time. Thus, soil conditions produced by preferential flow impact the growth and activity of microorganisms in the soil, and soil microbial activity accentuates the conditions that trigger preferential flow (Figure 3). In essence, the physical processes necessary for preferential flow are strengthened by microbial activity of organisms, and the types of microbial activity are responses to the environmental conditions established by preferential flow, such that the physical and biological processes strengthen each other and perpetuate preferential flow.

2.2 Preferential Flow Paths as Biological 'Hot Spots'

The distinct physico-chemical properties of spatially separated soil compartments, particularly at regions of water flow, stimulate deliberate organization of "hot spots" or zones of elevated biological activity in the soil (Lee, 1985; Pivetz and Steenhuis, 1995; Bundt et al., 2001). The different environmental living conditions that support highly active microbial zones are predominantly affected by the greater amount of oxygen, moisture and nutrient availability in the preferential flow paths than in the rest of the soil matrix, which explains why certain soils experience enhanced degradation of organic compounds transported through preferential flow paths (Pivetz and Steenhuis, 1995). Advective transport of dissolved substrate in preferential pathways is thus a prominent mechanism that supports such highly active microbial zones. Since the distances traversed by migrating microbes are comparable in scale to the separation between individual preferential flow paths, the investment to relocate to a better suited microenvironment is a feasible and worthwhile operation for microorganisms.

Many prokaryotes and fungi are able to sense gradients of certain compounds (e.g., nutrient and toxic substances) by chemotaxis or quorum sensing, and decide to consequently move/grow towards or away from the source of the compound. Dispersion, and thus colonization of new surfaces with better habitat conditions may be achieved by bacteria that actively use pili or flagella, are transported by interception with flowing water, or are carried away by sorption to another living organism. This ability to relocate can contribute greatly to the altered distribution of organic matter in soils. As the year long study by Bundt et al. (2001) reported, carbon (C) concentrations in preferential flow paths were 10 to 70% greater than in the matrix of a forest soil after measuring temporal and spatial variations between flow and no-flow regions from freshly exposed trenches. Similarly, organic nitrogen (N) concentrations, effective cation exchange capacity (CEC) and base saturation levels were observed to hold similar elevated levels in the preferential flow paths. The high organic matter content in the preferential flow paths was attributed to three main sources: greater proportion of living or decayed roots in flow paths than in the matrix, preferential input of dissolved organic matter from the surface, and enhanced release of microbial biomass C from rewetting of relatively dry soil.

Even with the ability of microorganisms to relocate toward more favorable conditions, the transport mechanisms that allow exuded enzymes to be intercepted by flowing water and carry decomposition products away from the microorganisms' cells are largely dependent on the abrupt water fluxes at and near preferential flow paths. In this way, irregular and non-homogeneous infiltration patterns can result in devastating scenarios for soil biota if soluble exo-enzymes and other catalytic products are too quickly swept away by convection, thus destroying the return on energy invested in making them. Inversely, toxic decomposition products may not get carried off fast enough from the vicinity of the microbial propagules (Ekschmitt et al., 2005) and can otherwise result in self-intoxication. For these reasons, it appears that only resilient microorganisms with the ability to cope with extreme environmental fluctuations and the capacity to keep their cells protected, anchored, and hydrated will be fit enough to survive in soils prone to finger flow.

It is clear that favorable conditions for microbial activity in the soil depend on the balanced combination of substrate and moisture availability, allowance for gas exchange with the atmosphere, and a moderate rate of transport of excreted/exuded toxic compounds around the cell. Because of these preferences, enhanced microbial activity tends to exaggerate differences in habitat quality between regions where these necessities are met (typically at or near preferential flow regions) and where they are not (in the soil matrix). Furthermore, the enhanced activity and colonization patterns have been contentiously coined as either stochastic or forced organization events by various studies (Ekschmitt et al., 2005; Doerr et al., 2007; Or et al., 2007b), depending on the quality of substrate available intrinsically in the soil or delivered freshly by the fingers. In either case, it is sensible to catalog preferential flow paths as biological 'hot spots' from reported evidence of increased biological activity in locations where columns form. Although this clearly indicates that a set of complex feedback mechanisms must exist for microorganisms to cope with harsh environmental stresses (Doerr et al., 2007), the specific responses from bacteria experiencing fluctuations associated preferential flow is an area that has been under-explored.

2.3 Impact of Bacterial Compounds on Porous Media

The vadose zone is characterized by its spatial fragmentation and highly dynamic hydration conditions, ranging from complete saturation to wilting point soil moisture. Accordingly, microorganisms must respond to unpredictable and harsh environmental conditions near the soil surface in order to remain viable. A typical adaptation for microbes to cope with soil dehydration and rapid chemical fluctuations of the flowing soil water is through physiological adjustments, such as biosynthesis of extracellular polymeric substances (EPS) (Or et al., 2007b). From experimental and theoretical evidence, it is commonly accepted that biofilm surface attachment with EPS is the prevailing lifestyle of bacterial colonies in soil (Fenchel, 2002; Chang and Halverson, 2003; Young and Crawford, 2004). The EPS structure buffers microcolonies from abrupt hydrating or dehydrating conditions, dampens rapid fluctuations of aqueous temperature, controls the diffusional pathways that deliver resources to the colony, and anchors the cells to soil surfaces (Or et al., 2007a; 2007b). However, the synthesized EPS can and often modify physical and chemical characteristics of the soil that cause preferential flow by reducing the effective soil porosity (i.e., pore clogging) when the EPS is hydrated, or by making certain portions of the soil hydrophobic when the EPS dries up.

2.3.1 Bioclogging

Microbes modify their microenvironment by synthesizing and excreting EPS in order to shelter themselves from temporal variations of the variable porous media they reside in (Or et al., 2007b). However, because there is a lack of consensus regarding the spatial distribution and properties of biofilms and microbial aggregates in unsaturated and fragmented conditions, calculations on physical and hydrological processes typically ignore the impact of microbial activity on the porous medium characteristics. Undoubtedly, soil structural properties are affected by EPS synthesis; particularly in terms of altered pore geometry as a result of bioclogging. These two factors can significantly reduce the porosity and hydraulic conductivity (up to 96 and 98% respectively) (Cunningham et al., 1991) between soil layers and consequently promote conditions that can support preferential flow (Thullner et al., 2002).

As Or et al. (2007a) point out, at the onset of drying conditions microbial colonies respond by enhanced production of EPS if enough free C is readily available. Two key benefits of EPS synthesis during periods of limited water availability are its high water holding capacity and desiccation tolerance. The biopolymer responds to its immediate environmental hydration status by altering its morphology. Under electron microscopy (Figure 4) these structural changes are obvious and range from soft and spongy under wet conditions, to stiff and flat when dried (Roberson and Firestone, 1992). In certain types of soils, like those with high clay content, the open EPS structure can enhance soil transport properties (Czarnes et al., 2000) by physically separating mineral particles from each other (Baveye et al., 1998b). While the presence of EPS typically enhances the soil's water holding capacity, in certain cases, hydrated EPS layer can also reduce available pore spaces for flow if the microbes inhabit naturally well-drained soils (Nevo and Mitchell, 1967; Cunningham et al., 1991; Vandevivere and Baveye, 1992; Seki et al., 1998; Kim and Fogler, 2000).

The reduction of effective soil porosity is due to a combined effect of biomass accumulation, microbially-induced mineral precipitation, and biogenic air bubble formation (Baveye et al., 1998b), although most published studies focus on biomass accumulation to explain pore occlusion with conventional mathematical models (e.g. Hagen-Poiseulle equation and the Kozeny-Carmen equation). In addition to soil bioclogging from biomass growth, it is important to note that microbial populations can produce biofilm layers that are unsustainably thick so nutrients may not diffused quickly enough to sustain the cells located in the deepest regions. It is suspected that soil bioclogging from microorganism overgrowth may be attributed to surface inputs of the substrate rich irrigation water. The shear force from flowing soil water often enhances biomass sloughing from such regions undergoing endogenous decay. At times, however, partial removal of built up biofilm occurs spontaneously without any change in the flow rate or quality of the applied solution. Although the sloughed material can facilitate permeability recovery at the source, the biofilm fragments may congest other pores in deeper soil layers (Metcalf & Eddy, 2002).

It is apparent that microbial activity near the soil surface can clog the topsoil by EPS overproduction in nutrient rich soils. Thus, a layer of reduced hydraulically conductive soil will be formed near the surface overlaying more conductive soil beneath (similar to the effect observed by Hill and Parlange, [1972]), promoting points of instability for imbibing water fronts to break up into columns. It is also sensible to assume that colonies that settle near preferential flow paths (because of substrate supply and moisture availability) must experience mechanical limitations for biofilm growth from the shear forces of the flowing water. Even so, the successful colonization of areas where substrate and moisture abound (i.e. at or near fingers) could potentially change the soil's distribution of conductive pores significantly to fix the location where fingers repeatedly form, and therefore perpetuate preferential flow.

2.3.2 Hydrophobic soil particle surfaces

Typical field trends show that water repellent compounds and soil water repellency (as measured by the Water Drop Penetration Test) are a main cause of preferential flow (Jamison, 1945; Bond, 1964). Soil water repellency has been reported to be common among soils characterized by large particles and in soils of shallow depth (Bundt et al., 2001; Bauters et al., 2000; Ekschmitt et al., 2005). Partial coating of hydrophobic EPS on soil minerals can modify significantly the matric potential of the medium by increasing the soil-water contact angle and the water head entry value (Bauters et al., 2000), which consequently lead to preferential flow. This phenomenon may not be obvious in fields that appear to take up water readily, but localized partially-hydrophobic soil particles impede the rate of infiltration and trigger finger formation between unwettable soil patches (Or et al., 2007b).

Studies on the role of bacterial extracellular polymeric substances in soil water repellence development, such as the one by Schaumann et al. (2007), report that changes to soil wettability after being coated with specific biofilms depend on the bacterial strain producing it. Other studies have focused on the ability of exopolysaccharides to act as biosurfactants in order to increase the solubility of hydrophobic substances in the soil and make them available for the cells embedded in the EPS matrix (Ekschmitt et al., 2005). In addition, reports on wax-degrading bacteria state that such organisms may change the water-repellency of soils through biosurfactant production and direct consumption of hydrophobic waxes (Roper, 2005). Furthermore, the solubilization of hydrophobic substances by (bio)surfactants may facilitate their distribution throughout the soil, which even in small quantities can exacerbate the soil's water-repellency to a great degree and produce preferential flow.

Undoubtedly, the morphological and surface chemical adjustments of EPS alter the characteristics of the soil matrix and the hydrological processes within it in such ways that the potential of a soil type to experience enhanced preferential flow is increased. Two main means by which this occurs are: 1. a decrease the porosity, and thus the hydraulic conductivity, of coarse soils that would otherwise drain well, and 2. induced soil water repellency when EPS dries out and becomes hydrophobic. Both these changes impede water infiltration and consequently create points of instability where columns can form in soils of any particle size.

2.4 Influence of Fungal Compounds on Soil Water-repellency

Fungi have long been suspected to be implicated in the development of soil water repellency (Bond and Harris, 1964; Savage et al., 1969; White et al., 2000; Feeney et al., 2004; 2006). They are known to produce highly surface active hydrophobins as a protection mechanism against desiccation stress (Hakanpaa et al., 2004), and in addition use them as a surfactant to lower the pore water surface tension and aid hyphae breach the surface of the soil water and grow into air filled voids (Wessels, 2000). In addition to helping the organism survive dry spells, fungal exudates may also be used as a future food source and as a protective coating that creates harsh microenvironments to keep competitors at bay. Soil fungi have various survival mechanisms to resort to if environmental stresses are high, and highly resilient fungi have the ability to restore repellency levels in their microenvironment within a couple of weeks of being physically disturbed by soil management practices such as tillage (Hallett et al., 2005).

As Wessels (2000) and Hallett (2007) point out, these fungal exudates are commonly amphiphilic in nature. The dual surface hydrophobicity is further complicated by the amount of available moisture in the surrounding region. As Hallett (2007) explains, exudates tend to be strongly hydrophilic when wet, but below a critical moisture threshold the hydrophilic surfaces bond strongly with each other and with soil particles leaving an exposed hydrophobic surface as illustrated in Figure 5. Therefore, if fungi-containing soil dries beyond this critical water content, the soil behavior can shift abruptly from wettable to non-wettable; yielding soil patches where wetting fronts become unstable and the conditions for finger formation are again satisfied. Although prolonged wetting and field saturation can allow soils to regain wettability, inevitable draining and the occurrence of successive and prolonged drying periods can resume soil water repellency (Doerr et al., 2000; Kostka, 2000; McHale et al., 2005).

As in the case of bacteria induced water repellency, the effect that fungal hydrophobins have on the porous medium will depend on the proportion of soil particles coated with the hydrophobic surfaces. The fraction of the soil surface area affected,

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which varies considerably with soil texture, will also determine the magnitude of the effect. Sandy soils have the lowest surface area to volume ratio, so a hydrophobic coating will alter a larger proportion of the particles than for a loamy or clayey soil with a surface area that is several orders of magnitude greater, thus making the sandy porous medium more prone to experience finger flow infiltration.

Various agricultural and woodland soil studies have found a strong correlation between fungal biomass (measured as ergosterol concentrations) and the level of repellency within agricultural soils (Fenney et al., 2006). Soils with fairy ring symptoms have been reported to have characteristic of hydrophobic hyphal surfaces and depressed grass growth (Dekker and Ritsema, 1996b). A study by Fidanza et al. (2007) found significantly higher water repellence and reduced soil moisture in necrotic zones that were clearly infested with basydiomycete fungi, but the levels of pH, total nitrogen, magnesium, calcium, cation exchange capacity, and organic matter were not consistently different between the necrotic and healthy turfgrass zones. Few studies are available on specific fungal compounds that may be responsible for the observed increase in soil water repellency. Nonetheless, Fenney et al. (2004) studied the correlation between glomalin (a specific arbuscular mycorrhizal-fungal exudate) and potting soil repellency. Although inconclusive, this study has not disproved the suspicion that glomalin may be somehow implicated in soil water repellency due to its particularly high adhesive and hydrophobic properties (Wright and Upadhyaya, 1998).

3. Conclusion

Undoubtedly, both bacteria and fungi have the potential to greatly affect the porous media by altering soil water retention and its natural physical properties. Reduced effective porosity can arise from the high concentration of microbes in areas where basic survival requirements are met (such as in the vicinity of preferential flow paths), which can lead to: abundant production of extracellular polymers by highly active microbial cells; sloughing events of this polymeric material caused by overgrowth, starvation or shearing; and release of gaseous byproducts of decomposition and endogenous decay. Heightened soil water repellence may be caused by exuded compounds from fungi and bacteria that are either intrinsically hydrophobic, change their surface properties to become hydrophobic when desiccated, or liberate with biosurfactants existing hydrophobic compounds in the soil. Whichever combination of the above phenomena may be present in the soil, their activation is brought about mainly as a response to recurring water stress. And as indicated in the section describing the physics behind finger flow, the effects of such activities contribute in theory to the physical and chemical conditions that generate preferential flow in soils. In any case, more basic work is still needed before the feedback mechanisms between soil microorganisms and the ever changing environmental conditions in the vadose zone are fully understood. Special attention should be given to soil flora responses to the hasty environmental changes experienced in soils prone to preferential flow.

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Figure Captions

Figure 1. Preferential flow paths in water repellent dune sand visualized by using dyestuff staining, from Dekker and Ritsema, 2000.

Figure 2. Schematic diagram of the flow process in the soil with preferential flow paths, from Kim et al. 2005.

Figure 3. Schematic diagram of the feedback mechanisms between microbial activity and preferential flow paths.

Figure 4. Morphological changes of bacterial extracellular polymeric substance on desiccation and on rehydration, from Roberson and Firestone, 1992.

Figure 5. The transient nature of water repellency caused by hydrophilic-hydrophobic and hydrophilic-surface bonding during drying, from Hallett, 2007.

1 

2 **FIGURE 1.**

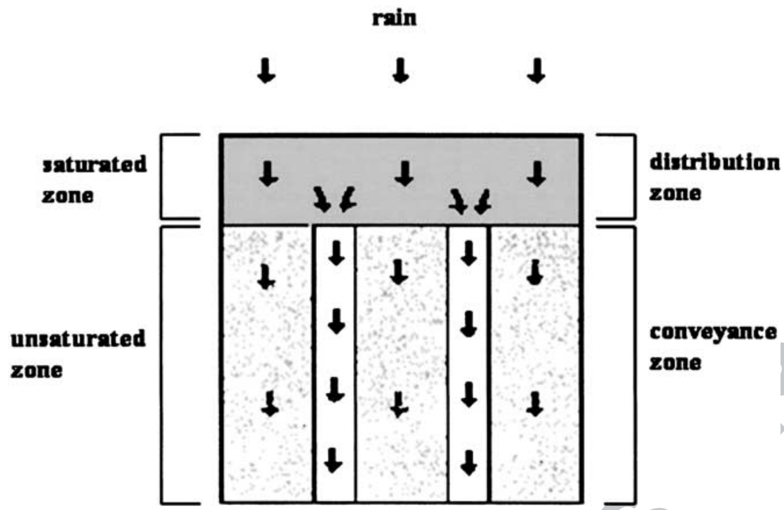
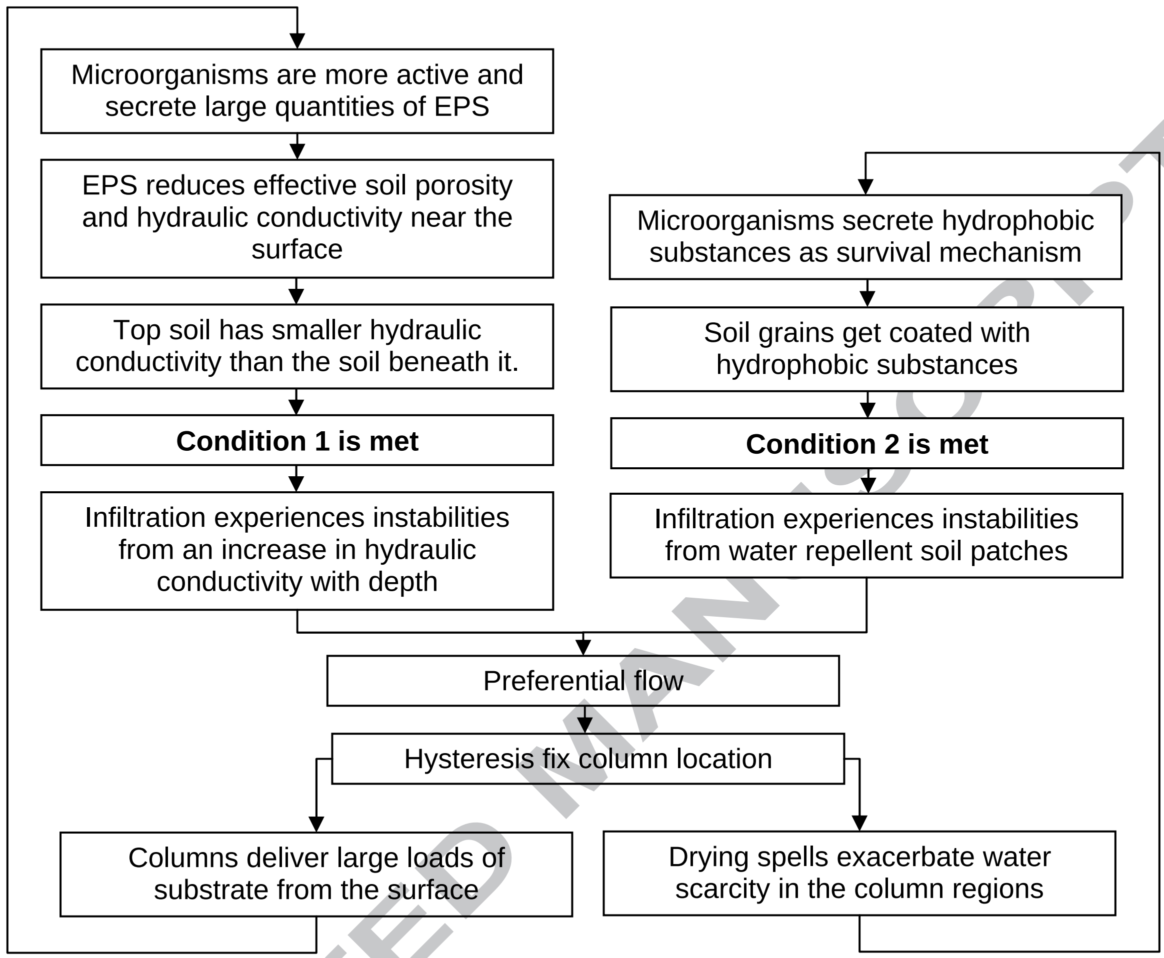

rain
saturated zone
distribution zone
unsaturated zone
conveyance zone

FIGURE 2.

7


Microorganisms are more active and secrete large quantities of EPS
EPS reduces effective soil porosity and hydraulic conductivity near the surface
Top soil has smaller hydraulic conductivity than the soil beneath it.
Condition 1 is met
Infiltration experiences instabilities from an increase in hydraulic conductivity with depth
Microorganisms secrete hydrophobic substances as survival mechanism
Soil grains get coated with hydrophobic substances
Condition 2 is met
Infiltration experiences instabilities from water repellent soil patches
Preferential flow
Hysteresis fix column location
Columns deliver large loads of substrate from the surface
Drying spells exacerbate water scarcity in the column regions

8

9 **FIGURE 3.**

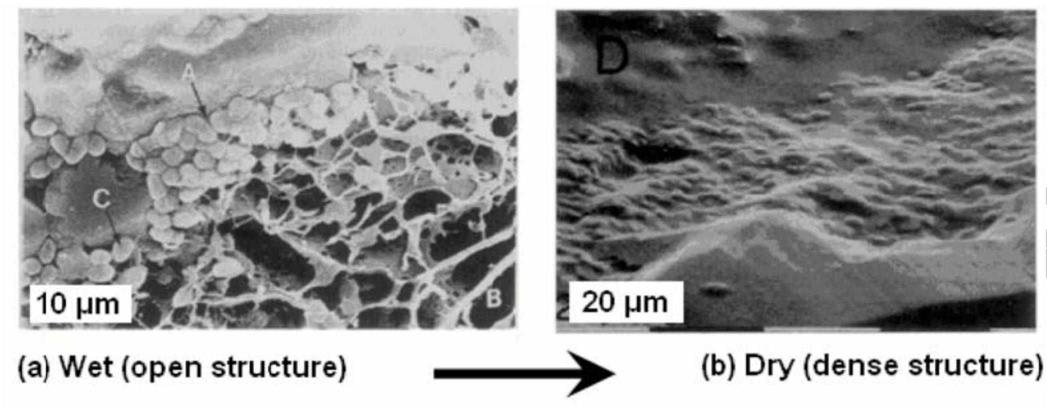
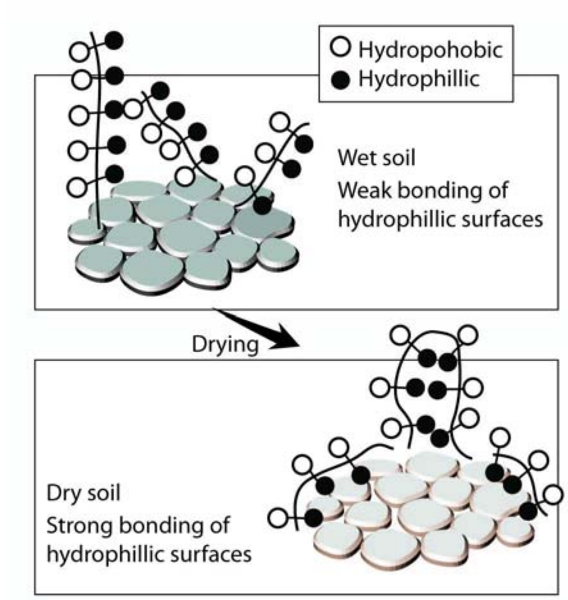


FIGURE 4.

13



14

15 **FIGURE 5**.

16