Water Dynamics of the Root Zone: Rhizosphere Biophysics and Its Control on Soil Hydrology

Approximately 40% of total terrestrial precipitation transits the tiny volume of rhizosphere soil around plant roots before being transpired, making it one of the most hydrologically active regions of the biosphere. This study considers several findings at the root–soil interface that affect our understanding of water retention and flow in the root zone and hence the water relations of all vegetated soil profiles. Imaging methods, including neutron radiography and light transmission, are illuminating the dynamics of water content around plant root systems. These methods, together with studies on samples of mucilage and mucilage-compound-amended soils, have provided increasing evidence that rhizosphere hydraulic properties differ from those of bulk soil. Changes in soil structure due to root growth, rhizodeposition, and repeated drying cycles change the pore size distribution and coat soil particles with organic compounds. Some of these compounds exhibit hydrophobic or hydrophilic behavior, depending on the soil water content, giving rise to the hysteretic-like behavior in the rhizosphere that has been observed in dynamic image sequences. Data from studies that consider the water retention properties of maize (*Zea mays L.*) mucilage from primary and nodal roots together with polymer gels are compared to consider the likely impact of mucilage on soil water release. Roots often generate and are intimately associated with flow paths for water and solutes in the soil, and vegetation is well known to exert a major influence on catchment hydrology. The potential use of vegetation to manage hydrologic processes at field scale is considered briefly as a way of influencing water outflow rates and engineering soils for particular purposes.

Plant roots contribute enormously to the terrestrial cycling of water, to the maintenance of the soil biophysical matrix, and to soil ecosystem function. Evapotranspiration represents approximately 59% of terrestrial precipitation (Oki and Kanae, 2006), so the transpiration component is probably about 40% of terrestrial precipitation. This transpired water will pass through the rhizosphere with a probable mean residence time of hours to days (e.g., 100 cm root cm\(^{-2}\) vegetated surface, root diameter 0.2 mm, 1-mm rhizosphere, 0.3 cm\(^{-1}\) transpiration rate, 0.2 cm\(^{3}\) cm\(^{-3}\) soil water content, would give a rhizosphere residence time of 2 d). Plant roots continually and efficiently till the soil, with the work done on the soil during root extension of perhaps 10 MJ ha\(^{-1}\) yr\(^{-1}\) for a cereal field (e.g., 0.4-mm-diameter roots, 0.2-MPa growth pressure, 300 cm cm\(^{-2}\) annual root extension, giving 8 MJ ha\(^{-1}\) yr\(^{-1}\)). This seems a remarkably efficient process when compared with the hundredfold greater 1 GJ ha\(^{-1}\) required for plowing using farm machinery (Arvidsson, 2010). The nature of the soil deformation and failure caused by plant roots is physically very different from that caused by a plow, with the length, diameter, and continuity of individual macropores created by roots often being distinct (Jassogne et al., 2007; White and Kirkegaard, 2010).

Roots ramify throughout the surface horizons of soils globally at densities of up to 30 cm cm\(^{-3}\) (Pierret et al., 2005), and yet our understanding of their effects on soil hydraulic properties is still relatively poor. Indeed, roots may often be considered an annoyance in making soil coring more difficult and increasing the heterogeneity of samples. It is important to consider what fraction of the soil volume is influenced by roots and that can be thought of as rhizosphere soil (Gregory, 2006). The typical maximum root length density attained below a temperate cereal crop may be up to 10 cm cm\(^{-3}\) in the tilled surface of an agricultural soil. In this region, the volume of root tissue might only amount to 2% of the soil volume, while the volume of rhizosphere soil represents about half of the soil volume (47%, assuming cylindrical roots of 0.5-mm diameter in the rhizosphere extending 1 mm from the root surface and neglecting overlap between neighboring roots).
length densities often decrease approximately exponentially with depth (Gerwitz and Page, 1974; Schenk, 2008), and so in deeper soil horizons the proportion of soil that can be considered rhizosphere will be much smaller. Deep roots are rarely studied in detail, and their occurrence may be underestimated by the usual root distribution functions (Mulia and Dupraz, 2006), although such roots will frequently be associated with, and often responsible for generating, important pathways for water movement (Christina et al., 2011).

In this brief selective review, I consider how recent biophysical studies of rhizosphere properties demonstrate that roots may exert a major controlling influence on soil hydraulic properties and hence the water balance and dynamics of the vadose zone. The effects of roots on soil physical properties are considered first with respect to their effects on water-release characteristics and on the soil water regime in the rhizosphere. The role that roots have in determining flow paths through the soil is then considered in relation to soil hydraulic conductivity and the importance of root-sized macropores in controlling larger scale hydrologic processes. Finally, I consider the extent to which targeted management of vegetation is a potential way to engineer soils for particular purposes.

**Imaging Water Content around Growing Roots**

Given the consistent interest in plant physiology and water uptake in the literature during the last century, it is surprising that we are only now starting to understand the detailed water dynamics of the rhizosphere. A particularly promising approach to unraveling the dynamics of water content changes in situ is the imaging of the water content in the soil around growing root systems. Visible light and neutron imaging have both been used to quantitatively track the changes in water content around a developing root system (Carminati et al., 2010; Garrigues et al., 2006; Moradi et al., 2011). Visible light transmission through a thin (<10-mm) layer of translucent sand increases with increasing water content. This provides a relatively cheap and accessible way to quantify water content changes around a developing root system and has shown the way a drying front progresses around the roots of lupin (*Lupinus angustifolius* L.) (Fig. 1a). Similar dynamic information on water content changes in rhizosphere and bulk soil have been obtained recently using neutron imaging, although this technique requires specialist facilities available only in certain countries (Fig. 1b). The rhizosphere of lupin retained a greater water content than expected as the soil dried but was slower to rewet after watering. Such hysteretic behavior is probably due to changes in the rhizosphere water retention characteristics. These changes are associated with physical changes in the soil structure as well as with exudates released by the roots and associated microbes and are discussed below.

**How Roots Influence Rhizosphere Physical Properties**

Roots change the size distribution and connectivity of soil pores. In pushing through soil, they compress the matrix of soil pores around them to accommodate their own volume; the soil immediately adjacent to the root surface may contain 23% less pore space than the bulk soil (Bruand et al., 1996). Roots release a complex mixture of organic compounds into the soil, including sugars, amino acids, organic acids, phospholipids, and pectin-like polysaccharides. Much of the material is released from the root cap and serves to lubricate the penetration of soil by the root tip, in addition to the production of border cells from the root cap that may completely coat the surface of root tips growing in compacted soils and cushion the root proper from the abrasive soil particles (Iijima et al., 2003). Root hairs, typically 10 μm diameter, emerge from the epidermis behind the elongation zone and persist for a period of days or weeks, typically penetrating the rhizosphere to a distance of up to several millimeters. The root hairs increase the radial distance from which roots extract water and nutrients from the rhizosphere soil and provide an added source of C from root hair exudates and senescing root hair tissue. These hairs are also largely responsible for the soil rhizosheath that forms around excavated root systems; a rhizosheath is almost completely absent in root mutants that lack root hairs (Fig. 2), while rhizosheath mass
per unit length increases with root hair length (Haling et al., 2010). Soil in the rhizosphere and rhizosphere may well have properties significantly different from those of the bulk soil due to the close proximity of the root as a source of exudates and a sink for water and nutrients (Hinsinger et al., 2009).

Changes in the water retention properties of the rhizosphere have been studied recently using several different approaches, each with its own advantages and limitations. These include adding particular root exudate compounds to soil (Read et al., 2003), testing soil aggregates collected from adjacent to the root surface (Whalley et al., 2005), and in situ imaging of the soil water content around roots (Carminati et al., 2010). The advantage of adding compounds to soil is that the effects of each exudate component can be quantified and understood separately. Adding lecithin to soil and sand resulted in the rhizosphere retaining relatively less water as the suction increased (Fig. 3a). The effect was greater for sand than for sandy loam soil and for relatively small suctions (e.g., 2–15 kPa), probably because the surfactant had to be present in sufficient quantity to cover the menisci in water-filled pores.

The water-release properties of mucilage drops exuded by the primary and nodal roots of maize were studied by Read and Gregory (1997) and by McCully and Boyer (1997). In both studies, the water potential of the mucilage was measured as a function of mucilage water content per unit dry matter using a psychrometer. It is possible to convert the results of both studies to the same scale (Fig. 3b) and make a direct comparison between the data. The potentials measured for the nodal root mucilage were for smaller mucilage water contents than for the primary root mucilage (drops of mucigel in differently hydrated states are shown in Fig. 4a, 4b, and 4c). The water potentials measured for the nodal root mucilage ranged to more negative values than for the primary root mucilage but, in both cases, the water potential appeared to be initially a power-law function of mucilage water content. Under air-dry conditions, a potential of −11 MPa was measured for nodal root mucilage, corresponding to a water content of 0.04 g g⁻¹; this data point diverges substantially from the original line for the nodal root mucilage and may indicate that more than one process is responsible for generating water potential during drying (although it is interesting to note that the point lies on an extrapolation of the line fitted to the Read and Gregory data; Fig. 3b).

The explanation for the strong dependence of mucilage water potential on water content must lie in the combination of matric and osmotic potentials that together give rise to the water potential measured by a psychrometer. These component potentials have been considered for agar gel media by Beruto et al. (1995), who measured the water potential in washed and unwashed gels. The matric potential was estimated as between −3.7 and −9.9 kPa for
The more negative water potential measured for the nodal maize Fig. 3b suggests that the water potential measured is similar to that process and so change its matric potential at a given water content. It is also possible that the nodal root mucilage may have a different structure than that of the primary root, which may affect the shrink–swell process and so change its matric potential at a given water content. Possible explanations for the more negative potentials at lower water contents are due to an increased concentration of solutes giving rise to negative osmotic potentials or to the spacing between polymer chains in the very negative potentials of mucilage at smaller water contents. Two gel media (0.8% concentration) in double-distilled water, were contained within the pores of the dense, structured subsoil of this soil. The rewetting of soil around roots may be changed, in a manner that depends on the plant species, due to these organic deposits on the soil particle surfaces (Hallett et al., 2003). This hydrophobicity of the organic coatings will depend on the soil water content, with hydrophobicity greatest in dry soil and surfactant-like behavior possible in wet soil (Hallett et al., 2003; Read et al., 2003). This is a potential source of hysteretic behavior for water content–matric potential relations in the soil of macropore

Fig. 4. Mucilage from (a) primary root of maize grown in solution culture, (b) nodal roots of maize in glasshouse, (c) wheat primary roots after freeze drying; (d) schematic representation of a droplet of mucilage (polymer network in black) containing solutes (yellow circles) and silt and clay soil particles before (left) and after (right) drying. As the mucigel dries, polymer strands become closer together and any solutes present increase in concentration. Scale bars in (a–c) are approximately 1 mm, and 1 μm in (d).

More experimental work, together with an improved theoretical framework for understanding, is needed to properly unravel this fascinating and important observation.

Roots, Holes, Flow Paths, and Scaling Up

It has long been recognized that vegetation exerts a major influence on catchment hydrology through paired catchment studies typically involving changes in vegetation presence or type, such as afforestation or deforestation (Brown et al., 2005). Replacing grass with trees decreases water yield due to greater evapotranspiration and decreases the duration of faster flow events, probably due to slower water movement through the soil and increased storage capacity for water within the soil (Brown et al., 2005). Such consequences of changes in vegetation type may take 5 to 10 yr to establish during tree growth, although responses to deforestation are generally more rapid (Lacombe et al., 2010).

Changes in hydrologic processes result from the continuous network of branched roots that permeate the soil, with new roots being continually formed as old ones decay. Root turnover rates vary from a period of days for very fine, unbranched roots of grasses, to years for thick structural roots of trees; even between tree species, half a cohort of apple (Malus domestica Borkh.) tree roots only survived a period of 30 d, compared with >300 d for the roots of citrus trees (Eissenstat et al., 2000). The cumulative effect of root turnover is the generation of continuous flow paths through the soil, the walls of which are coated with organic remains of root material and associated microbial populations (Jassogne et al., 2007). These channels provide pathways of small mechanical resistance for future root growth, especially in hard soils, and are of importance for the roots of annual crops. White and Kirkegaard (2010) found that >85% of wheat (Triticum aestivum L.) roots were contained within the pores of the dense, structured subsoil of an Australian Kandosol. Although nearly all of the roots they found were growing within biopores larger than the root diameter, they observed that only 5% of the soil pores at >0.6-m depth were occupied by roots, compared with about one-third of soil pores in horizons closer to the surface.

In many soils, most of the soil bacterial and fungal population is found within 1 to 3 mm of the macropore channel (Pankhurst et al., 2002). The combination of rhizodeposits and microbial exudates coating the pore walls is likely to influence the rate of wetting of this soil. The rewetting of soil around roots may be changed, in a manner that depends on the plant species, due to these organic deposits on the soil particle surfaces (Hallett et al., 2003). This hydrophobicity of the organic coatings will depend on the soil water content, with hydrophobicity greatest in dry soil and surfactant-like behavior possible in wet soil (Hallett et al., 2003; Read et al., 2003). This is a potential source of hysteretic behavior for water content–matric potential relations in the soil of macropore
walls. Such hysteresis would be analogous to that recently observed in the rhizosphere and could have substantial influence on flow dynamics in macropore channels.

Continuous root-sized pores constitute much of the porosity that controls saturated flow in soil. Figure 5a shows a power-law relation between the saturated conductivity of soils with a range of textures and the volume of pores that drain between saturation and a suction of 33 kPa (Ahuja et al., 2010). The equivalent pore diameter corresponding to a suction of 33 kPa is approximately 10 μm—the diameter of a typical root hair. Thus, saturated flow depends strongly on pores of sizes corresponding to the dimensions of plant roots and especially the presence of continuous pores.

It still remains difficult to establish the three-dimensional geometry of continuous macropores in soil. X-ray tomographs of undisturbed soil columns (80 by 7.7 cm) showed that most pore network lengths were <8 cm long under quackgrass [Elymus repens (L.) Gould ssp. repens], white clover (Trifolium repens L.), and wild oat (Avena fatua L.) (Perret et al., 1999). Macropore networks had an average hydraulic radius (pore volume divided by pore wall area) of 0.13 mm, which is of an order similar to the grass root diameter: thicker pore networks tended to be longer, with the pore length being approximately 15% longer than the distance between endpoints due to tortuosity. The branched pore networks illustrated by Perret et al. (1999) bear at least superficial resemblance to a branched root system structure, with the angular distribution of pore orientation predominantly between vertical and 55° from the vertical. Potassium iodide solution was used to study transport through macropore networks in an intact soil column from an un till ed maize–soybean [Glycine max (L.) Merr.]–alfalfa (Medicago sativa L.) arable rotation (Luo et al., 2008). Transport through the macropores was complex, with no macropores being continuous from top to bottom of the soil core, although the core was relatively narrow (10-cm diameter) in relation to its 30-cm length. Air entrapment and pore discontinuities played a major role in determining flow through the core, with the greatest flow occurring through the most continuous root- and earthworm-formed macropores in the subsoil (Luo et al., 2008).

Much of the above information is consistent with plant roots playing a major role in pore network formation and hence in determining major flow paths in soils. At still larger scales, water discharge rates in an upland subcatchment were found to depend strongly on the presence of root-sized pores as soil water content increased (Deeks et al., 2004). The discharge rate remained relatively constant until pores >50 μm (equivalent diameter) were water filled (Fig. 5b). At water contents greater than this, catchment discharge increased greatly due to rapid transport from the soil volume immediately adjacent to the stream.

The crucial role of root-sized pores was again indicated in tracer experiments in California forested riparian wetlands (Elci and Molz, 2009). Particle travel speeds were 152 times greater than the measured soil matrix conductivity values, and this was substantially attributed to the presence of dead root macropore channels forming part of a preferential pipe-flow network. Such root channels form a relatively stable, though spatially variable, pore network for water infiltration in no-till agricultural systems (Schwen et al., 2011).

Conclusions

Vegetation and particularly the root systems of plants have a major role in determining soil hydraulic properties at scales ranging from the rhizosphere of individual roots, through the development of macropore structures in soil, to the drainage of whole catchments. While the role of vegetation in soil genesis has long been recognized, it is only recently that biophysical techniques have enabled us to start unraveling the dynamics of water content variation in rooted soils. This promises to result in rapid advances in understanding during
the next decade. There is also an increasing interest in using vegetation to manage catchment hydrology. For example, the choice of grass species may affect soil conductivity via effects on pore structure in both the short and long term (Gregory et al., 2010). There is increasing interest in environmentally sustainable drainage systems, the importance of flood prevention, and the potential effects of changing rainfall patterns. A major challenge to the scientific community is to use our understanding at a range of scales to better use vegetation in land management. There are great opportunities, and many important practical problems, at the scientific interface between plant biology, soil physics, and landscape engineering, but progress will require substantial collaborative effort to bridge the gaps between traditional disciplines.

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