



Spatial distribution of rhizodeposits provides built-in water potential gradient in the rhizosphere



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ABSTRACT

Plant roots alter soil properties at an expensive physiological cost by releasing large quantities of organic carbon (rhizodeposition). The role of rhizodeposits in enhancing beneficial microbial activity and biogeochemical nutrient mobilization is widely appreciated. But the role of rhizodeposits in water uptake has started gaining modest attention only recently. In this study we present a single root model, which demonstrates the possibility for rhizodeposits to create built-in water potential gradient. The conceptual basis for this model rests on three premises: (a) rhizodeposits are distributed in declining profile with distance from the root surface, (b) considerable fraction of rhizodeposits are strongly adhered to soil particles, and (c) rhizodeposits have the ability to retain water. Thus, variable concentration of affixed rhizodeposits results in a gradient of water potential without commensurate decline in water content with proximity to root surface. To corroborate premises (b) and (c), we conducted experiments using synthetic analog of rhizodeposits (Polygalacturonic Acid, PGA) and glass-bead and sand media. Environmental scanning electron microscopy was utilized to show affixation of PGA on glass beads during drying as well as pore-scale enhanced water retention. Macroscopic enhancement of water retention was characterized by dew-point potentiometry. We simulated water uptake by a root at constant potential transpiration rates representing high atmospheric demand and considered three distinct spatial distribution patterns of rhizodeposits as well as a control (without rhizodeposition). The model simulations indicate that the benefit of such variable distribution of exudates is more pronounced when (a) the potential water uptake rate is high or (b) the rhizodeposits are constrained to a narrow volume of rhizosphere soil.

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1. Introduction

Plant roots develop in an environment, the soil, where their mobility is severely restricted and resources such as water, nutrients and air, are frequently scarce and patchy (Hinsinger et al., 2009). Therefore, one of the major adaptation strategies employed by plants is to modify their immediate environment to their benefit. The rhizosphere—a small volume of soil that surrounds each individual root—is particularly influenced and modified by the action of plant roots including exudation and enhanced wetting-drying cycles (Walker et al., 2003). The importance of the rhizosphere to healthy functioning and resilience of a plant cannot be overstated considering that it is (a) the passage for almost all water and nutrients utilized by plants, (b) a medium for efficient gas exchange during root respiration, and (c) a locus of beneficial association

between plants and soil microorganisms (Gregory, 2006; Hallett et al., 2003; Raven and Edwards, 2001). It has been extensively reported that plants invest a large portion of their photosynthetic carbon in the development and maintenance of the rhizosphere (Czarnes et al., 2000b; de León-González et al., 2006; Nambiar, 1976; Sprent, 1975; Watt et al., 1994), which likely improves their ability to optimally exploit water and nutrient distributions in the soil (Gao et al., 2011; Marschner, 2012; Morgan et al., 2005).

However, the exact mechanism by which the rhizosphere aids water and nutrient uptake by plant roots is not fully understood. Hydrodynamic considerations indicate that water potential must decline sharply in the vicinity of roots to create the necessary gradient that propels water from the bulk soil to root wall (Gardner, 1960). A decrease in soil water potential also implies commensurate drop in soil water content. The steepness of the gradient increases with proximity to root wall in order to compensate for declining permeability as well as narrowing radial cross-sectional area available for flow. Moreover, the gradient becomes steeper with increasing dryness of the bulk soil. Declining wetness in the vicinity of active roots limits water and nutrient uptake by plants

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in at least two major ways. First, hydraulic connectivity between exceedingly dry rhizosphere soil and the root walls is weakened. Second, diffusivity of nutrients is severely restricted (Carminati et al., 2010). This limitation is especially pronounced in coarse-grained soils that get drained significantly at modest suction levels. From the foregoing discussions, it appears that rhizosphere modification is particularly important aspect of plant adaptation to water and/or nutrient limited environments.

The overarching goal of this paper is to demonstrate that root rhizodeposition can mitigate the intrinsic limitations of water potential gradient in the rhizosphere by providing conditions that weaken, or even reverse, water content gradient in the rhizosphere. This hypothesis is founded on three basic premises. First, there is ample experimental evidence that shows that rhizodeposit distribution is highly localized within the rhizosphere and that it exhibits sharp decline over short distance (Gao et al., 2011; Kuzyakov et al., 2003; Li et al., 1997). The second premise is that rhizodeposits tend to get affixed to soil particles during drying. A remarkable evidence of attachment between exudates and soil particles is the formation of rhizosheath—aggregated soil zone that remains attached to the root when removed from soil (de León-González et al., 2006; Watt et al., 1994). Recently, we have shown that the primary mechanism of rhizosheath formation is deposition of exudates at inter-particle contacts during drying (Albalasmeh and Ghezzehei, 2014). The third premise is that rhizodeposits have inherent ability to retain moisture by exerting suction. It has been shown that the rhizosphere soil is generally wetter than the surrounding bulk soil (Carminati et al., 2010; Carminati and Vetterlein, 2012; Moradi et al., 2011; Watt et al., 1994), which may be attributed to the additional water retention by exudates. Carminati et al. (2011) developed a model that reproduced their experimental observations by considering rhizosphere hydraulic properties that result higher water holding capacity than the bulk soil.

The objective of this study is to integrate the above three premises in to a modeling framework that relies on a simplified representation of a single active root similar to that of Carminati et al. (2011). Ultimately, the modeling framework is intended to demonstrate that a declining distribution of physically attached rhizodeposits can result in the development of built-in water potential gradient without commensurate gradient in water content. In real soils, these phenomena are intertwined with many other complicating factors including continuous multifaceted changes as well as physical and biogeochemical heterogeneities. To overcome these complexities, this study follows a reductionist approach that aims the address the essential processes in isolation. For this purpose, experimental evidence of rhizodeposit attachment and water retention enhancement are developed using synthetic exudate compounds and idealized porous materials.

The remainder of this paper is organized as follows. In Section 2, we present empirical basis and mathematical representation for rapidly declining exudate profile in the rhizosphere. Then, in Section 3 we briefly describe the restricted mobility of exudates due to physical attachment with the mineral matrix and provide visual illustration of this phenomenon using synthetic rhizodeposit constituent (Polygalacturonic Acid, PGA) and glass-beads. In Section 4, we present microscopic visualization and macroscopic characterization of enhanced water retention in the presence of synthetic constituent of rhizodeposition (PGA). This section culminates in modified water retention curve model that incorporates spatial variability of exudate concentration. In Section 5, we incorporated the above three aspects of the rhizosphere in a hydrodynamic model of the rhizosphere. The model considers an idealized single root in an axi-symmetric geometry. The hydrodynamic role of exudates is illustrated in Section 6 using a few example exudate distributions.

2. Nature and distribution of rhizodeposits

The sources of rhizodeposits can be grouped in to three main types: (a) sloughing off of root cells, (b) secretion of mucilage, and (c) excretion of exudates (Nguyen, 2009). The mucilaginous material released by the root tips of many plants is mainly composed of polymerized sugars and up to 6% protein (Nguyen, 2009). The carboxylic groups of mucilage often form cation bridges with clays and result in formation and stabilization of aggregates (Czarnes et al., 2000b). When fully hydrated, fresh mucilage can hold up to 450% of water by weight. However, most of this water is drained when the soil is dried below 0.1 MPa (McCully and Boyer, 1997). In addition, roots exude low-molecular weight organic compounds that are released either by passive diffusion or active excretion. Exudates consist of sugars, amino acids and organic acids Neumann and Römheld (2007). The controlled release of particular exudates in response to sensed environmental stimuli is assumed to be a major mechanism that allow plant to face unfavorable rhizosphere conditions (Nguyen, 2009).

For the purpose of this study, the important aspect of rhizodeposition is the spatial distribution of the organic compounds in the vicinity of roots. A few studies have carried out high-resolution spatial sampling of root exudates. Gao et al. (2011) sampled rhizosphere soil close to the root surface of ryegrass (*Lolium multiflorum Lam.*). They subdivided the rhizosphere soil (0–8 mm) into three concentric zones: the rhizoplane (≈ 1 mm from the root wall) as well as strongly and loosely adhering soil (at ≈ 4 and 8 mm from the root wall, respectively). Their measurements of soluble organic carbon concentration at 40 and 50 days from sowing shown in Fig. 1a exhibit declining profiles. Similarly, Li et al. (1997) investigated the distribution of organic acids near the roots of lupin (*Lupinus sp.*). They used rhizobox that allowed partitioning the rhizosphere soil into ten 0.5-mm wide compartments on both sides of a 1-mm wide root compartment. Fig. 1b depicts the distribution of citric, malic and oxalic acids collected at various distances. The rhizodeposit distribution observed by Li et al. (1997) is restricted to much smaller soil volume compared to that of Gao et al. (2011).

The distribution of exudates in the rhizosphere is controlled by exudation intensity, uptake of exudates by roots, diffusion from the root surface, and microbial utilization (Kuzyakov et al., 2003). The mechanism of exudate diffusion has been studied by means of $^{14}\text{CO}_2$ labeling of shoots and subsequent analysis of ^{14}C in thin compartments of the rhizosphere (Darrah, 1991a,b,c; Kuzyakov et al., 2003). The diffusion coefficient calculated by fitting Fickian diffusion model to experimentally determined ^{14}C profiles range from 10^{-7} to 10^{-4} cm^2/s . Higher coefficients correspond to non-adsorbing substances such as glucose or sucrose. While substances that are strongly adsorbed by soil such as citric or glutamic acids are characterized by lower diffusion coefficients.

A model of enhanced water uptake that will be developed later in this paper depends on this declining distribution of rhizodeposits. In the remainder of this paper, the spatial distribution of rhizodeposits at any given time will be denoted mathematically by

$$X_{OM}(r) = \frac{\xi X_o}{1 + (\xi - 1) e^{\beta(r-R)}} \quad (1)$$

where X_o (kg/kg) is the organic matter mass fraction at the root-soil interface, $X_{OM}(r)$ (kg/kg) is the spatial distribution of organic matter mass fraction, R (m) is the radius of the root, r (m) is radial distance from the center of the root, and ξ and β (1/m) are shape factors. The best fit of Eq. (1) to experimental data of Gao et al. (2011) and Li et al. (1997) are shown as solid lines in Fig. 1. The best-fit parameters are reported in Table 1. It is important to note here that rhizodeposit distribution is non-stationary. The evolution of the distribution depends on a number of factors including age

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