Review

Rhizosphere interactions between microorganisms and plants govern iron and phosphorus acquisition along the root axis – model and research methods

Petra Marschner [a,*], David Crowley [b], Zed Rengel [c]

[a] School of Agriculture, Food and Wine, Faculty of Sciences, University of Adelaide, Adelaide, Australia
[b] Department of Environmental Sciences, University of California, Riverside, CA, USA
[c] Soil Science and Plant Nutrition, School of Earth and Environment, The University of Western Australia, Australia

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ABSTRACT

Iron and phosphorus availability is low in many soils; hence, microorganisms and plants have evolved mechanisms to acquire these nutrients by altering the chemical conditions that affect their solubility. In plants, this includes exudation of organic acid anions and acidification of the rhizosphere by release of protons in response to iron and phosphorus deficiency. Grasses (family *Poaceae*) and microorganisms further respond to Fe deficiency by production and release of specific chelators (phytosiderophores and siderophores, respectively) that complex Fe to enhance its diffusion to the cell surface. In the rhizosphere, the mutual demand for Fe and P results in competition between plants and microorganisms with the latter being more competitive due to their ability to decompose plant-derived chelators and their proximity to the root surface; however microbial competitiveness is strongly affected by carbon availability. On the other hand, plants are able to avoid direct competition with microorganisms due to the spatial and temporal variability in the amount and composition of exudates they release into the rhizosphere. In this review, we present a model of the interactions that occur between microorganisms and roots along the root axis, and discuss advantages and limitations of methods that can be used to study these interactions at nanometre to centimetre scales. Our analysis suggests mechanisms such as increasing turnover of microbial biomass or enhanced nutrient uptake capacity of mature root zones that may enhance plant competitiveness could be used to develop plant genotypes with enhanced efficiency in nutrient acquisition. Our model of interactions between plants and microorganisms in the rhizosphere will be useful for understanding the biogeochemistry of P and Fe and for enhancing the effectiveness of fertilization.

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1. Introduction

In this review, we focus on the interactions between plant roots and microorganisms in relation to acquisition of iron and phosphorus; both of which are poorly available in most soils. A better understanding of these interactions could not only provide important information about the biogeochemistry of these nutrients, but also guide plant breeders to enhance the plant competiveness and increase the effectiveness of management options such as fertilization or plant species/cultivar choice for agriculture and restoration.

Plants and microbes have developed similar mechanisms for mobilization and uptake of Fe and P. In the rhizosphere, Fe and P are mobilized by plant- or microbe-derived compounds, and there is intense competition for uptake. Microbes appear to be more competitive than plants, because they are not only able to take up nutrients bound to plant-derived compounds, but can also decompose these plant-derived compounds and immobilize nutrients in the biomass before they reach the root surface (Fig. 1).

After a brief overview of microbial ecology of the rhizosphere and the mechanisms of Fe and P mobilization, we present a conceptual model that takes into account the spatial and temporal variability of plant–microbe interactions in the rhizosphere along the root axis. Although there is some evidence for this model, we currently lack data to support it conclusively. However, we now have the tools to investigate the interactions between plants and microbes in the rhizosphere at the relevant scales, i.e. nanometre to centimetre; some of these are discussed in terms of their advantages and limitations to encourage researchers to use them for rhizosphere studies related to nutrient acquisition. Lastly, we
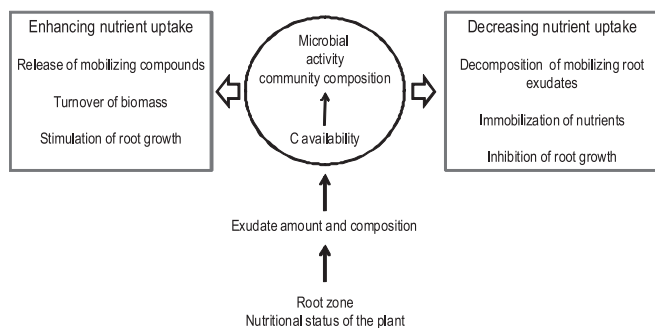
Fig. 1. Mechanism by which microorganisms in the rhizosphere enhance or decrease nutrient availability to plants and some of the factors influencing the relative magnitude of the mechanisms.

suggest mechanisms that could enhance the ability of plants to acquire Fe and P that may eventually be used for plant breeding and selection of nutrient-efficient cultivars.

2. Microbial ecology of the rhizosphere

Microorganisms play a key role in nutrient cycling by decomposing and mineralizing organic material and releasing as well as transforming inorganic nutrients. When microorganisms are subjected to specific nutrient deficiencies, they can further influence nutrient availability by solubilization, chelation and oxidation/reduction. Bacteria and fungi store nutrients in, and release nutrients from, their biomass as they undergo turnover, or are fed upon by protozoa. Additionally, microorganisms can affect plant growth and nutrient uptake by release of growth-stimulating or -inhibiting substances that influence root physiology and root system architecture (Ryu et al., 2005; Govindasamy et al., 2009).

Growth and activity of soil microorganisms are mainly limited by carbon availability (De Nobili et al., 2001; Demoling et al., 2007) because of the complex nature and thus poor decomposability of the soil organic matter. In contrast, root exudates are generally of low molecular weight and thus easily decomposable. Hence, the release of exudates by roots results in higher microbial density and metabolic activity in the rhizosphere than the bulk soil (Norton and Firestone, 1991; Soderberg and Bååth, 1998).

The structure of rhizosphere communities differs from that in the bulk soil (Foster, 1986; Marilley and Aragno, 1999; Gomes et al., 2001; Berg et al., 2002), which reflects the selective enrichment of different populations depending on amount and composition of root exudates. Exudate amount and composition vary among plant species and along the root axis, and are further modified in response to plant phenology, nutrient status, environmental stresses and diseases (Neumann, 2007).

To examine how microorganisms and plants interact during root growth in soil, it is useful to consider the processes that occur as roots elongate. The root tip is pushed through the soil by cell division and elongation of apical cells. The new root surface just behind the meristematic tissue is first colonized by microorganisms that move to the root surface by chemotaxis or are swept along with the border cells of the root cap. Under nutrient deficiency, root exudates such as sugars, organic acid anions and amino acids are released primarily in the zone immediately behind the root tip and in the distal elongation zone (Hoffland et al., 1989; Roemheld, 1991; Marschner et al., 1997a,b), which are also the site where microorganisms are least abundant but most active (Von Wiren et al., 1993; Nguyen and Guckert, 2001). However, the abundance of root exudates stimulates microbial growth and attracts more soil microorganisms to the root surface. Microorganisms may also be

carried with the mucilage that is secreted by the border cells of the root cap, which further selects for specific root-colonizing bacteria (Humphris et al., 2005). Further from the root tip, in the root hair zone and adjacent zone, root exudation is lower, and the release of secondary metabolites leads to lower microbial growth rates, with an increasing fraction of the biomass entering the stationary growth phase (Blumer and Haas, 2000; Nguyen and Guckert, 2001; Trivedi et al., 2008). Along the more mature root parts where exudation is low, the primary substrates for microbial growth include cellulose and other recalcitrant cell wall materials from sloughed-off root cortex tissue. Consequently, microbial growth rates and activity are lower along more mature root parts than in the proximal elongation zone (Nguyen and Guckert, 2001). The differences in type and quantity of carbon available in different root zones not only influence microbial growth, but also lead to distinct rhizosphere community structures (Yang and Crowley, 2000; Baudoin et al., 2001; Marschner et al., 2001). The differential microbial density and activity along the root axis play an important role in the interactions between roots and microorganisms in the rhizosphere for P and Fe because they determine microbial nutrient demand and competitiveness (see also Fig. 2).

Due to their rapid mineralization by microorganisms, root exudates are ephemeral, but can temporarily accumulate at sites where the microbial cell density is low. These microsites occur mainly behind the root tip where root growth temporarily outpaces the rate of microbial colonization. It should be noted that although microbial density in the rhizosphere is higher than in the bulk soil, microorganisms do not form a continuous layer on the root surface; indeed, only between 5 and 20% of the root surface is covered by bacteria. They are assumed to form rapidly growing micro-colonies and biofilms only in locations with high exudation rates such as the axial grooves between epidermal cells (Briones et al., 2003; Schoenwitz and Ziegler, 1989; Watt et al., 2003).

3. Interactions between microorganisms and plants influencing iron acquisition

The total Fe content in soil typically ranges from 2 to 4% (w/w), but in aerated soils its availability to organisms is limited by the low solubility of Fe(III) hydrolysis species and the slow dissolution of iron minerals. Hence, plants and microorganisms have developed mechanisms to increase Fe availability (Neilands, 1984; Marschner, 1995). Plants have two different strategies for responding to Fe deficiency (Marschner, 1995). Strategy I plants (dicots and non-graminaceous monocots) increase iron availability by releasing protons that lower the soil pH and organic acid anions. Organic acid anions can complex Fe^{3+} and hold it in a soluble form that can diffuse to the root surface. Iron solubility is also enhanced by an increased reducing capacity of the roots; converting the poorly soluble Fe^{3+} hydrolysis species into more soluble Fe^{2+}. The reductase in the root cell plasma membrane may also release iron from Fe^{3+} chelators. Other responses to iron deficiency in Strategy I plants can include changes in root morphology and histology (root tip swelling, increased root branching, more root hairs, formation of rhizodermal transfer cells, etc.) (Marschner, 1995). In contrast to dicotyledonous plants, Strategy II plants (*Poaceae*) release phyto-siderophores, which are non-proteinogenic amino acid derivatives such as mugineic acid (Takagi, 1976; Marschner, 1995). These chelators preferentially bind Fe, but can also bind Zn or Cu. Iron is taken up into the root cells in the chelated form as Fe-phytosider-ophore (Roemheld, 1991; Von Wiren et al., 1993). Phytosiderophore release by roots is spatially concentrated and shows a distinct diurnal rhythm, with maximal release occurring in the zone of elongation for a few hours after onset of light (Roemheld, 1991).