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The Soil-Root Interface in Relation to Mineral Nutrition*

VOLKER RÖMHELD

Institut für Pflanzenernährung, Universität Hohenheim, Postfach 70 05 62, D-7000 Stuttgart 70, F.R.G.

Abstract

Plant growth is dependent in many aspects on root growth, availability of water and mineral nutrients and microbial activity at the soil-root interface, or the so-called rhizosphere. In general, with decreasing spatial and chemical availability of mineral nutrients in the bulk soil, root growth and the conditions in the rhizosphere are becoming increasingly important for plant growth.

Conditions in the rhizosphere differ in many respects from those in the bulk soil. In general, increase in rate of root exudation stimulates the microbial activity in the rhizosphere. Rhizosphere microorganisms can affect plant growth positively as well as negatively e.g. through their influence on root development, mobilization and immobilization of mineral nutrients and decomposition of root exudates.

1. Introduction

The rhizosphere is the soil-root interface and consists of a thin soil layer around the root. The extension of this soil layer (rhizocylinder) can vary between 0.1 up to a few millimeters which depends mainly on the length of the root hairs. Due to root hairs, root exudates and subsequent enhanced microbial activity, soil aggregates of the rhizosphere are heavily sticking on the root surface of soil-grown plants (Fig. 1).

The chemical and physical conditions in the rhizosphere differ considerably from those in the bulk soil which is caused by root processes such as root respiration (O_2 consumption, CO_2 release), release of protons and root exudates and nutrient and water uptake (Fig. 2). Preferential uptake of nutrients or water leads to depletion (e.g. P, K) or accumulation of certain nutrients (e.g. Ca) or other mineral elements (e.g. salts) in the rhizosphere. Depending on the ratio of cation-anion uptake and pH buffer capacity of the soil, the rhizosphere pH can differ considerably from that in the bulk

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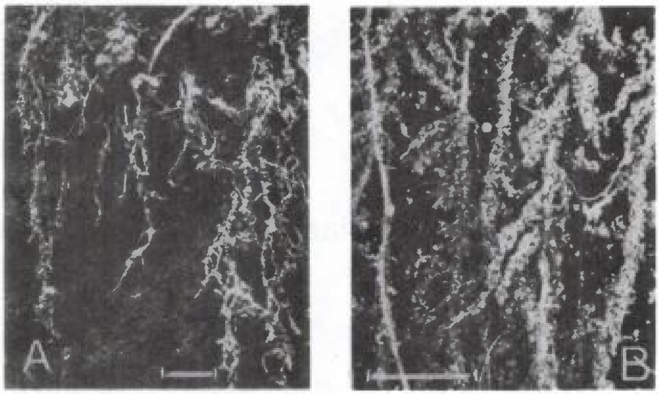

Figure 1. **Roots with adhering rhizosphere soil. A. Rape (*Brassica napus*) plants in the field; B.** Barley (*Hordeum vulgare* L.) plants from a pot experiment. (Bar = 2 cm)

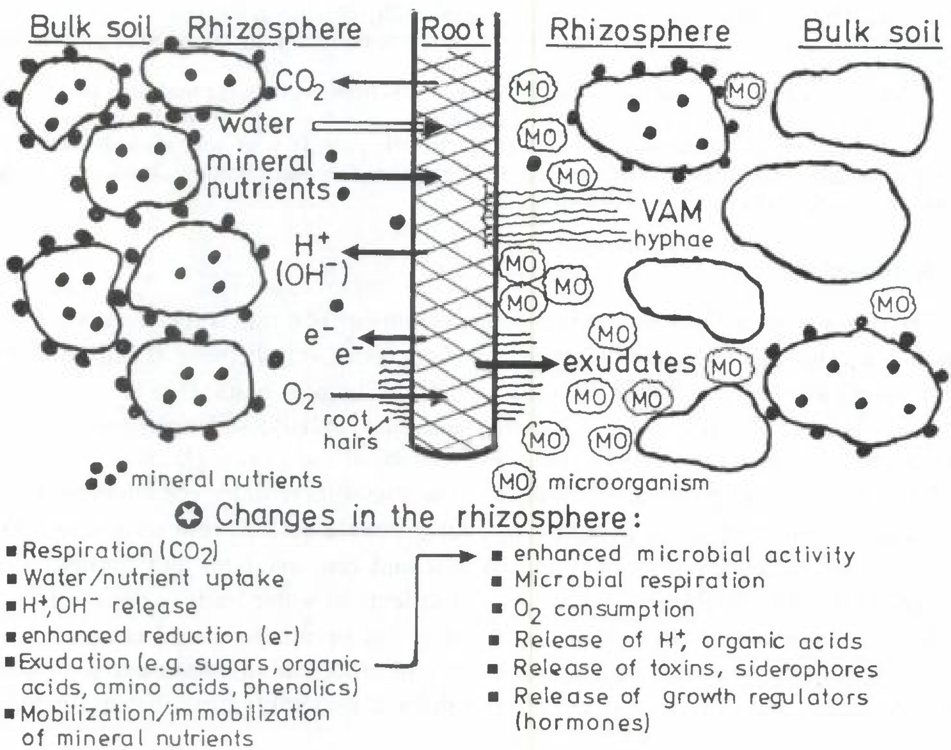

Figure 2. Processes and changes in the rhizosphere induced by plant roots.

soil (Marschner and Römheld 1983). Root exudation leads to a manyfold increased microbial activity in the rhizosphere which will result in further changes in the rhizosphere such as accumulation of growth regulators, siderophores and toxins (Schönwitz and Ziegler 1989).

Changes in rhizosphere pH and redox potential and release of reducing and chelating compounds are of particular importance for chemical availability (mobilization, immobilization) of mineral nutrients, and also of beneficial mineral elements such as Si and of toxic elements (e.g. Al, Cd, Cr). In many instances, in response to low nutrient availability in the soil specific morphological and physiological changes of roots occur which may enhance mobilization of mineral nutrients in the rhizosphere and acquisition by plants. Plant species and even cultivars can differ in this adaptive changes which can be used for improvement of nutrient acquisition in particular and of plant productivity in general by plant breeding.

2. Root-Induced Changes in the Rhizosphere as Affected by Mineral Nutrition

Root morphology

For mineral nutrients with a low mobility such as P and K typical depletion zones around roots can be observed (Jungk and Claassen 1989). Root growth and root surface area are, therefore, of decisive importance for the availability of these nutrients. In general, with decreasing chemical availability of mineral nutrients in the soil root growth is relatively or even absolutely enhanced (Fig. 3). Such a compensation of low chemical availability of mineral nutrients by increased

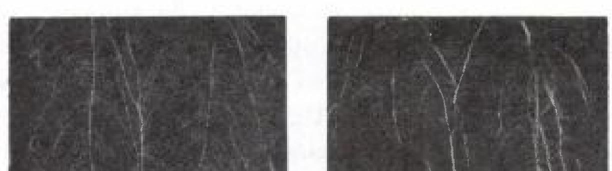

Figure 3. Effect of nitrogen supply on root growth of bean (***Phaseolus vulgaris*** L.) plants grown in flat soil boxes for 14 days (without and with 16.6 mg N $100\,g^{-1}$ soil as $Ca(NO_3)_2$). (Bar = 2 cm)

spatial availability is also reflected in an enhanced density and length of root hairs under P and Fe deficiency (Jungk and Claassen 1989; Marschner et al. 1989).

Rhizosphere pH

The pH in the rhizosphere may differ markedly from that of the bulk soil. The root-induced pH changes are mainly caused by active proton efflux coupled with nutrient uptake and release of organic acids (Marschner and Römheld 1983). The most prominent pH changes are caused by the form of nitrogen supply. Usually nitrate supply is correlated with preferential anion uptake and thus higher net excretion of HCO_3^- or OH^- over H^+ with a corresponding increase in rhizosphere pH, and ammonium supply causes the reverse. N_2 fixation facilitates relatively the uptake of cations and thus decreases rhizosphere pH.

A particular case of differences in rhizosphere pH within a root system can be observed in various phosphorus efficient plant species such as white lupin, rape and buckwheat, which decrease the rhizosphere pH of apical root zones under conditions of low P availability. At least a part of this acidification is due to release of organic acids which in turn enhance the mobilization of P and also of micronutrients (Dinkelaker et al., 1989; Hoffland et al., 1989).

Redox potential

O_2 consumption by respiration of roots and microorganisms can result in a decline of the redox potential in the rhizosphere or at least in microsites (Fig. 2). In addition, release of reducing root exudates and reductase activity on the root surface will further decrease the redox potential in the rhizosphere. As consequence, an enhanced mobilization and uptake of nutrients and other mineral elements with easy change of valency (e.g. Fe, Mn) can be expected. Also, higher rates of denitrification take place in the rhizosphere than in the bulk soil. Under certain conditions such as Fe and P deficiency release of reductants and reductase activity of the root are enhanced (Fig. 4; Marschner et al., 1986, 1989) which improve mobilization of Fe and Mn. Thus in various Fe deficient plant species (mainly dicots) an enhanced acquisition of Fe and also of Mn from MnO_2 and even Mn toxicity can be observed on certain calcareous soils (Marschner et al., 1986).

Under anaerobic conditions adapted plant species such as rice can build up an oxidation zone around the root surface by oxygen transport from the shoot to the roots and rhizosphere via aerenchyma to avoid water-logging injury.

Root exudates

Up to 25% of the photosynthates can be released as root exudates into the rhizosphere. This release depends on various internal and external factors such as energetic and nutritional status of the plant, mechanical impedance, anaerobiosis, rhizosphere pH and microorganisms. Under nutrient deficiency (e.g. K, Zn, Fe) the

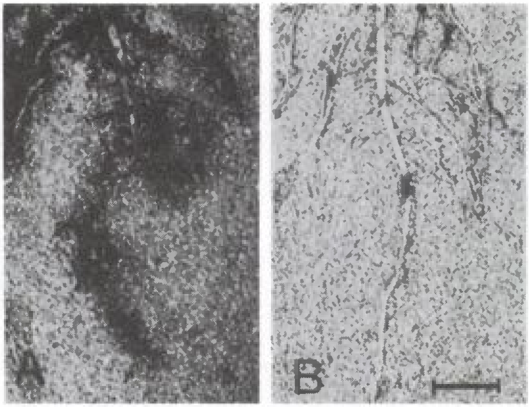

Figure 4. Fe III reduction in the rhizosphere of peanut plants (*Arachis hypogeae* L.) grown in a calcareous soil as affected by the Fe nutritional status (A. without, B. with foliar Fe application). Fe III reduction is indicated by the formation of the red coloured Fe II $(BPDS)_3$ (black in the photo). (For more details see Marschner and Römheld 1983; Marschner et al., 1986). (Bar = 2 cm)

release of low-molecular-weight (LMW) exudates such as sugars, organic and amino acids are enhanced (Marschner et al., 1986; Cakmak and Marschner 1988; Zhang et al., 1989; Trolldenier 1989). In general also rhizosphere microorganisms increase the rate of root exudation (Gardner et al., 1983).

For mobilization of mineral nutrients in the rhizosphere the LMW components with reducing and chelating properties (e.g. phenolics, organic acids) are of particular importance. Various dicots release organic acids in response to P deficiency which results in enhanced P acquisition (Dinkelaker et al. 1989; Hoffland et al., 1989). In white lupin grown on a P deficient calcareous soil the release of citric acid comes up to such high values (up to 20% of the total dry weight of the plant) that precipitation as Ca citrate particles in the rhizosphere becoms visible (Fig. 5; Dinkelaker et al., 1989). Due to the release of citric acid and formation of Ca citrate or Fe/Al citrate phosphate gets available for plants from Ca and Fe/Al phosphates, respectively.

In dicots and non-graminaceous monocots as response to Fe deficiency an enhanced release of reductants such as caffeic acid results in an increased Fe aquisition (Brown and Jolley 1989). The efficiency of such Fe mobilizing reductants is, however, strongly pH dependent (Marschner et al., 1989). In graminaceous species as response to Fe and Zn deficiency the release of chelating compounds; so-called phytosiderophores (PS) is increased (Takagi et al., 1984; Zhang et al., 1989). The efficiency of PS in mobilization of Fe and Zn is much less pH dependent than the reductants of dicots under Fe deficiency. The rate of release of PS are correlated with the Fe chlorosis resistance of the various graminaceous genotypes on calcareous soils (Brown and Jolley 1989; Marschner et al., 1989).

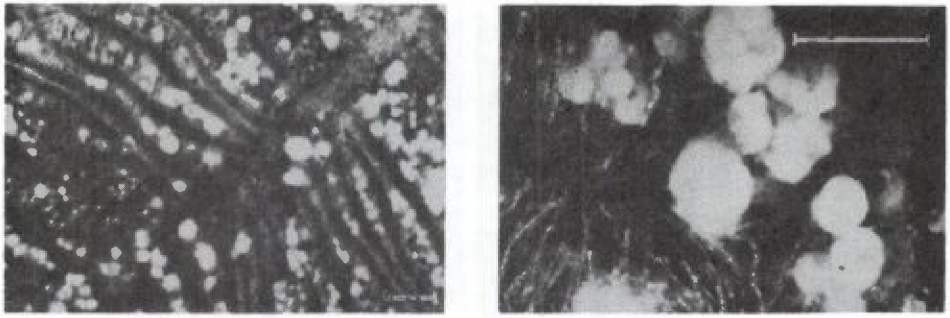

Figure 5. **Precipitation of calcium citrate in the rhizosphere of white lupin (*Lupinus albus* L.)** grown in a calcareous soil low in P availability. (For more details see Dinkelaker et al., 1989). (Bar = 1 mm)

Rhizosphere microorganisms. In general as consequence of root exudates the microbial activity is 5 to 50 times higher in the rhizosphere than in the bulk soil. This enhanced microbial population density is shown as foot print in Fig. 6. In many respects plant nutritional status affects microbial activity which in turn can influence plant growth. Nutrient deficiency (e.g. K, Fe) and nitrogen supply as NH_4 compared to NO_3 increase the number of total bacteria in the rhizosphere (Trolldenier 1989).

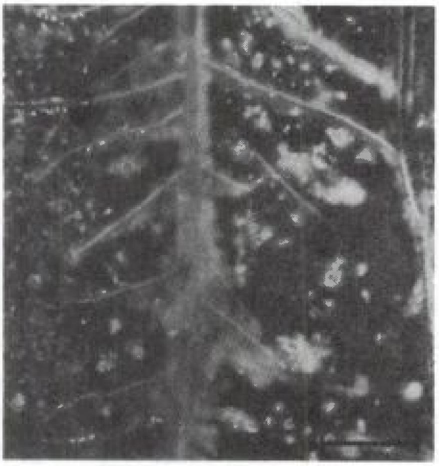

Figure 6. Foot print of the microorganisms in the rhizosphere of maize **plants** (*Zea mays* L.) on an agar sheet. The agar sheet (photo) with a microbiological culture media has been in contact with the soil/root surface for 10 minutes and was afterwards kept at 25°C for propagation of the microorganisms. (For details of the agar technique see Marschner et al., 1986). (Bar = 1 cm).

The conditions of the rhizosphere in general and the rhizosphere pH in particular have a distinct effect on the composition and activity of rhizosphere microorganisms. For example NH_4 supply has a strong suppressive effect on the pathogen *Gaeumannomyces graminis* (take-all) via the effect on the rhizosphere pH (Fig. 7). A decrease of

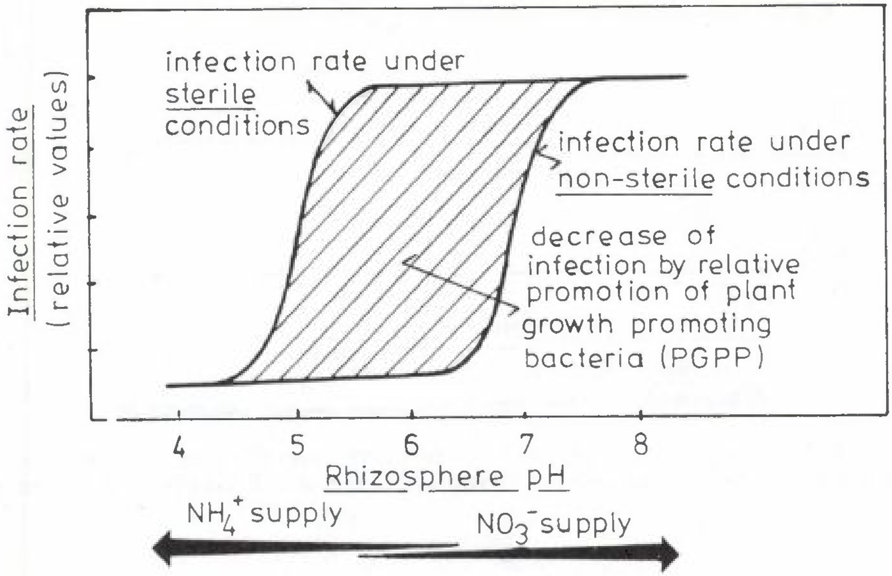

Figure 7. Relationship between infection of wheat (*Triticum aestivum* L.) with *Gaeumannomyces graminis* and rhizosphere pH as affected by form of N supply. (Based on Smiley and Cook, 1973; schematical presentation).

pH with NO_3 supply suppress growth of the pathogen either directly by inhibited hyphae growth or indirectly by a relatively promotion of certain growth promoting bacteria over the pathogen. A decreased rhizosphere pH as consequence of NH_4 supply can also increase resistance of plants to certain fungal diseases such as powdery mildew (*Erysiphe graminis*) by an enhanced mobilization and uptake of silicon (Fig. 8).

On the other hand, rhizosphere microorganisms can promote plant growth by improved nutrient availability for higher plants. This is in particular the case with symbionts like *Rhizobium* and mycorrhizal fungi. Further, microorganisms can affect plant growth by release of growth regulators, siderophores and toxins (Fig. 2). The increase in root length, number of lateral roots and density and length of root hairs by auxin producing *Azospirillum* is an example how microorganisms can affect mineral nutrition indirectly by increased root surface area (Marschner et al., 1986).

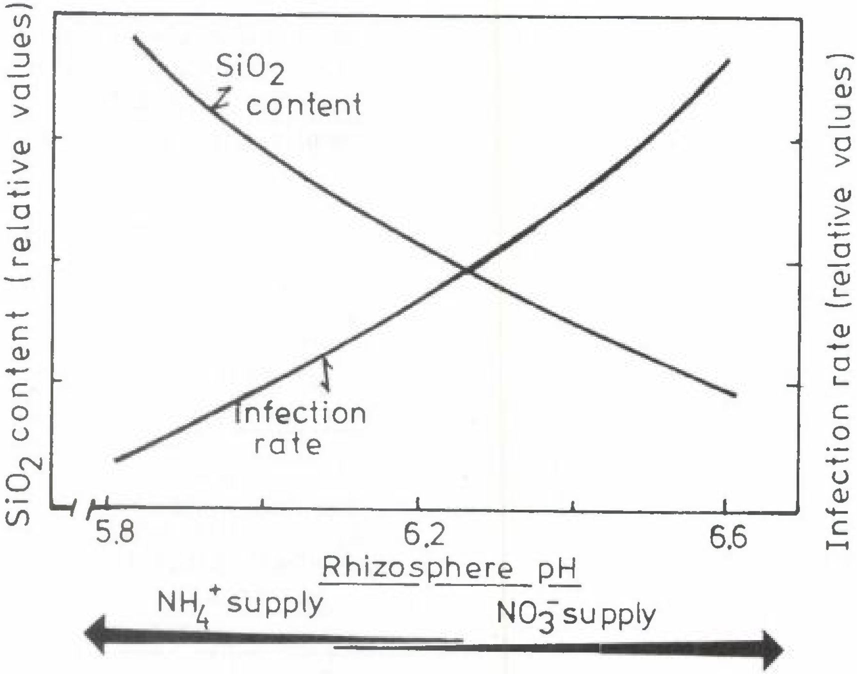

Figure 8. Effect of rhizosphere pH on SiO_2 content in leaves of wheat (*Triticum aestivum* L.) and infection with *Erysiphe graminis*. (Based on Leusch and Buchenauer 1988; schematical presentation).

3. Conclusion

During the last decade the knowledge on the various rhizosphere processes and their interrelationships is grown up rapidly. Manipulation of rhizosphere conditions for better nutrient acquisition, improvement of symbiosis and plant growth promoters, and suppression of pathogens will help in future to increase plant productivity.

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