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Mineral Nutrient Acquisition in Nonmycorrhizal and Mycorrhizal Plants

By

HORST MARSCHNER¹⁾

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Summary

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Both, root-induced changes in the rhizosphere and colonization of roots by mycorrhizal fungi have marked influence on mineral nutrient acquisition by plants from soils. Depending on plant species and nutritional status of the plants, root exudation of organic acids, phenolics or phytosiderophores enhances mobilization of sparingly soluble mineral nutrients in the rhizosphere. Colonization of roots by endomycorrhizae (AM) and ectomycorrhizae (ECM) is widespread in soil-grown plants and increases the spatial availability of mineral nutrients in the soil thus enhancing host plant growth particularly on nutrient-poor soils. Carbon investment into below-grown plant parts can be important for mineral nutrient acquisition, by allowing root-induced changes in the rhizosphere (e.g. organic acid exudation) which may increase flexibility and specificity of the plant responses. Mycorrhizal colonization may ensure a higher longterm stability in which protection against metal toxicity and root pathogens may also be important components.

Introduction

Key factors controlling the acquisition of mineral nutrients by plants from soils are the chemical (binding form) and spatial availability (mobility in the soil, root growth parameters) of the nutrients, root-induced changes in the rhizosphere (e.g. pH, exudates), and mycorrhizal associations (MARSCHNER 1995). Roots do not simply act as sink for mineral nutrients and water, delivered from the bulk soil by massflow and diffusion, but together with their associated microflora may strongly modify the rhizosphere. These root-induced changes are of crucial importance for mineral nutrient acquisition by plants, and tolerance to adverse chemical soil conditions such as soil acidity. In respect of root-induced changes, enhanced root

¹⁾ University of Hohenheim, Institute of Plant Nutrition (330), 70593 Stuttgart, Germany

exudation of low molecular weight organic solutes such as organic acids has attracted particular attention in the last decade. The main focus of the present paper is on root-induced changes in the rhizosphere (e.g. pH, exudates) and mycorrhizal associations, with special reference to perennial plant species.

Root-induced changes

Roots preferentially take up either particular mineral nutrients or water, thus leading to depletion or accumulation of mineral nutrients in the rhizosphere. Soil pH is an important parameter to characterize the chemical availability of mineral nutrients in soils. However, the rhizosphere pH may differ from that of the bulk soil by up to two units, depending on plant and soil factors. In plants grown in, and adapted to, acid soils, the pH of apical root zones is often considerably higher than basal zones and the bulk soil (Fig. 1). Such a pH increase might not only favour uptake rate of cations such as Mg^{2+} but also play an important role in detoxifying monomeric Al in the rhizosphere.

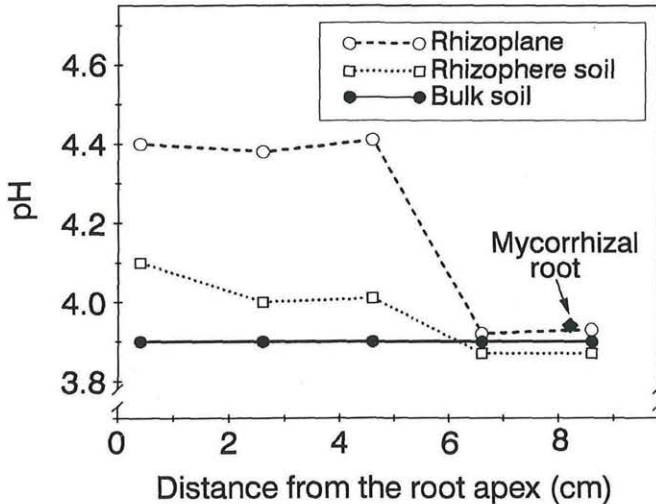


Fig. 1. pH pattern in bulk soil and the rhizosphere along the axes of nonmycorrhizal roots of 80-year-old Norway spruce; September 1986; location Heidelberg. (MARSCHNER 1991).

Depending on the soil chemical and physical conditions, species, age and nutritional status of plants, a varied proportion of photosynthetic carbon is released into the rhizosphere ("rhizodeposition"). Of this carbon the low molecular weight fraction is of particular importance for mineral nutrient acquisition as this fraction contains compounds as, for example, organic acids, phenolics or phytosiderophores which are directly able to mobilize sparingly soluble mineral nutrients in the rhizosphere. In many instances root exudation of these low molecular weight solutes is strongly enhanced under mineral nutrient deficiency, phosphorus, iron and zinc in particular. Typically, these deficiency-induced enhanced exudation rates

are confined to certain root zones, increasing the effectivity of the exudates in mineral nutrient mobilization (RÖMHELD 1990). This principle of high exudation rates is nearly perfectly realized in plants forming root clusters, bottlebrush - like rootlets with determined growth which form on lateral roots (DINKELAKER & al. 1995). Many woody species of the families *Proteaceae* and *Casuarinaceae* belong to this group. The root clusters are induced mainly by phosphorus deficiency and for a few days excrete large amounts of organic acids (DINKELAKER & al. 1995) as well as phenolics (Fig. 2). A small soil volume is thereby intensively extracted not only for phosphorus but also for other macro- and micronutrients, which thus become available to the plant roots. As a rule, in plant species which form root clusters, mycorrhizal associations are absent.

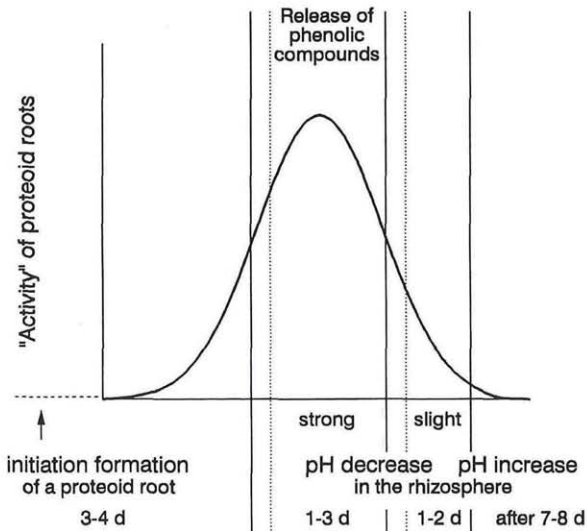


Fig. 2. Distribution and function of proteoid roots and other root clusters. (DINKELAKER & al. 1995).

Mycorrhizal associations

On a global basis, about 80% of the plants are mycorrhizal, including most of our forest trees. There are two major mycorrhizal groups, Endomycorrhizas (vesicular-arbuscular VAM, or arbuscular AM) and Ectomycorrhizas. In both groups, the external hyphae (mycelium) are crucial for the mineral nutrient acquisition of mycorrhizal plants as these hyphae enlarge the surface area and the volume of soil delivering nutrients to the plant (Fig. 3). In tree species of Central Europe, both types of mycorrhizas occur, in some like *Abies*, *Pinus* or *Larix* species only ECM, in others like *Populus*, *Salix* or *Acer* species both, ECM and AM. Formation and maintenance of mycorrhizas requires considerable amounts of photosynthates and mycorrhiza strongly compete with roots for photosynthates. As

a rule, in mycorrhizal plants, shoot growth is more enhanced than root growth. Root growth can even be depressed by mycorrhizal colonization, and root longevity reduced (HOOKER & al. 1995).

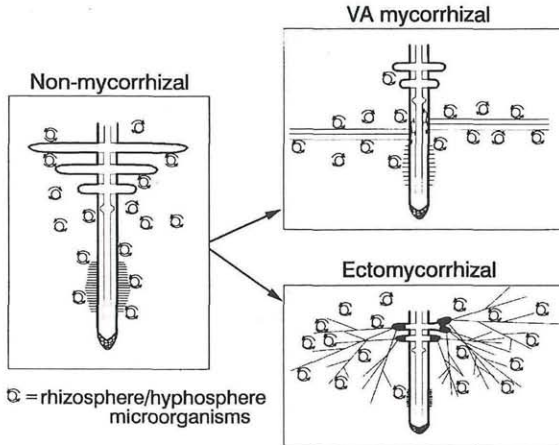


Fig. 3. Schematic presentation of the effects of mycorrhizal colonization on root morphology and non-infecting rhizosphere microorganisms. (MARSCHNER 1995).

In mycorrhizal plants the soil-root interface is altered and a "mycorrhizosphere" is formed, which is an ill-defined compartment, difficult to evaluate in its importance for mineral nutrient acquisition of soil-grown plants. There are some techniques available which allow at least separation of the hyphal from the root compartment. Such model system can be established easily in annual species colonized with AM and allow quantification of the mineral nutrients delivered by the external hyphae to the host plant. The results demonstrate that this delivery can account for a considerable proportion of the host plant's demand of phosphorus, zinc and copper (MARSCHNER & DELL 1994). The same principle of technique can be applied for ECM and tree seedlings (READ 1991).

Mineral nutrient uptake in nonmycorrhizal roots of Norway spruce: In ECM plants, too, not all roots are colonized by the fungus. This is true in particular for the long roots, e.g. of Norway spruce. These roots have a high growth rate and can be readily recovered from the soil and used directly for in vivo studies of ion and water uptake (HÄUSSLING & al. 1988). Data from such studies suggest a high potential of these non-mycorrhizal roots to contribute to the acquisition of mineral nutrients like potassium, calcium, magnesium and nitrate-N, of trees in forest stands (MARSCHNER & al. 1991). When supplied at equimolar concentrations, in these roots maximal uptake rate of NH_4^+ is about 3-4 times higher than that of NO_3^- (Table 1). Uptake of NH_4^+ is associated with an approximate equimolar net release of H^+ , i.e. acidification, and uptake of NO_3^- with more than equimolar net

consumption of H^+ , i.e. pH increase. Temperature has no effect on this preference for NH_4^+ . Lowering root zone temperature only decreases uptake rates of both, NH_4^+ and NO_3^- . The strong preference for NH_4^+ uptake is also indicated by the much lower C_{min} values, i.e. the minimum external concentrations where net uptake becomes zero.

Tab. 1. Maximal rates of NH_4^+ and NO_3^- uptake, H^+ production and H^+ consumption, and C_{min} concentrations in nonmycorrhizal roots of Norway spruce at different root zone temperatures. (MARSCHNER & al. 1991).

Root zone temperature (°C)	Rates (mol $10^{-14} mm^{-2} s^{-1}$)		C_{min}
	NH_4^+ uptake	H^+ production	$\mu M NH_4^+$
20	6.0	6.7	1.5
15	5.6	5.3	2.5
10	3.0	3.4	15.0
5	2.5	2.6	30.0
	NO_3^- uptake	H^+ consumption	$\mu M NO_3^-$
20	1.4	2.3	22
15	0.7	1.4	30
10	0.6	1.2	40
5	0.5	1.0	54

Uptake rates based on the concentration ranges of 150-100 $\mu M NH_4^+$ and 150-100 $\mu M NO_3^-$ + <10 $\mu M NH_4^+$

Despite this preference for NH_4^+ compared with NO_3^- , the rhizosphere pH of nonmycorrhizal long roots grown in acid soils is usually higher than the bulk soil pH (Fig. 1; MARSCHNER & al. 1991), reflecting the much higher mobility of NO_3^- compared with NH_4^+ in soils and, thus, delivery to the roots.

Utilization of organic phosphorus

In most soils, organic P (P_{org}) comprises a high proportion of the total P, particularly in the humus horizon and upper 0-5 cm of the mineral soil. Hydrolysis of P_{org} by root-borne and microbial acid phosphatase ectoenzymes is therefore of key importance for P acquisition of forest trees, particularly growing on acid soils (HÄUSSLING & MARSCHNER 1989). Along the axes of nonmycorrhizal roots, acid phosphatase activity is particularly high at the root apex (DINKELAKER & MARSCHNER 1992) and activity is markedly enhanced under P deficiency (Fig. 4).

Compared with the bulk soil, in the rhizosphere soil the activity of acid phosphatases is usually much higher. In agreement with this, of the total depletion of P, more than 50% is accounted for by the P_{org} fraction, and in the rhizosphere of

Norway spruce (Fig. 5) the depletion of P was even confined to the P_{org} fraction and closely correlated with the acid phosphatase activity. In this case of ECM tree root systems, phosphatase activity might derive from both, roots and fungal mycelium. Although the specific activity of the acid phosphatase per unit fresh weight is usually much lower in hyphae as compared with roots, the surface area of the external mycelium is much larger than of the roots, and thus, also the spatial accessibility to P_{org} in soils. Accordingly in substrates with low bulk density like peat, ECM seedlings of Norway spruce utilize P_{org} much better than nonmycorrhizal seedlings (ELTROP 1993).

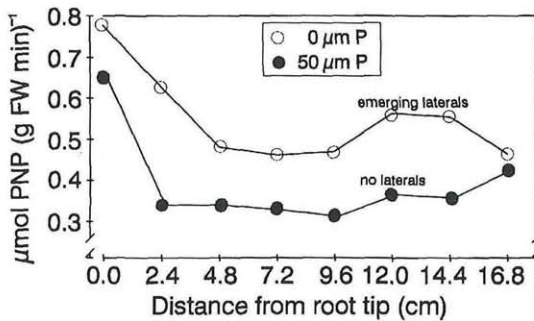


Fig. 4. Surface phosphatase activity (pNPPase) along a white, non-suberized long root of Norway spruce seedlings from nutrient solution culture and with two levels of P supply. (ELTROP, Ph.D. Thesis, 1993).

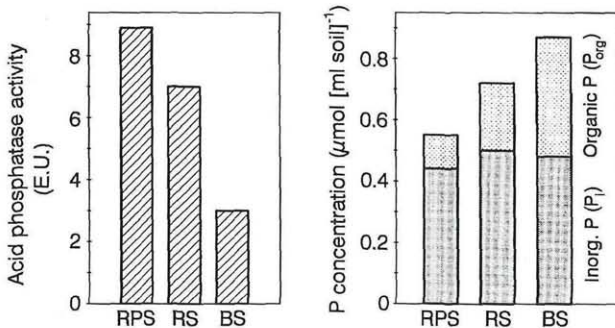


Fig. 5. Acid phosphatase activity and P concentration (P_i ; P_{org}) in the H_2O extractable fraction of rhizoplane (RPS) and rhizosphere (RS) soil of bulk soil (BS) in 80-year-old Norway spruce. (HÄUBLING & MARSCHNER 1989)

Role of AM and ECM in mineral nutrient acquisition

As a rule, mycorrhizal colonization of roots enhances mineral nutrient acquisition of the host plant mainly by increasing the surface area and, thus, the spatial availability of mineral nutrients (Fig. 6). Therefore, in plants with a coarse root system growing in a nutrient-poor substrate, particularly with low bulk density

(e.g. peat, litter layer of forest soils), growth enhancement effects are most evident. In general the mycorrhizal contribution to host plant nutrition is high for mineral nutrients of low mobility in the soil compared with plant demand. This is true for P and some micronutrients, but not for Ca or Mg, for example (Fig. 6). There is good evidence that not only ECM but also AM can substantially contribute to the N nutrition of host plants (GEORGE & al. 1992). Some ericoid and ECM fungi release acid proteinases as ectoenzymes and thereby hydrolyse proteins and provide access for the host plant to this resource (ABUZINADAH & al. 1986). Some ECM fungi release large amounts of oxalic acid which dissolves sparingly soluble calcium phosphates, and presumably other mineral nutrients are also mobilized by acidification (LAPEYRIE & al. 1990).

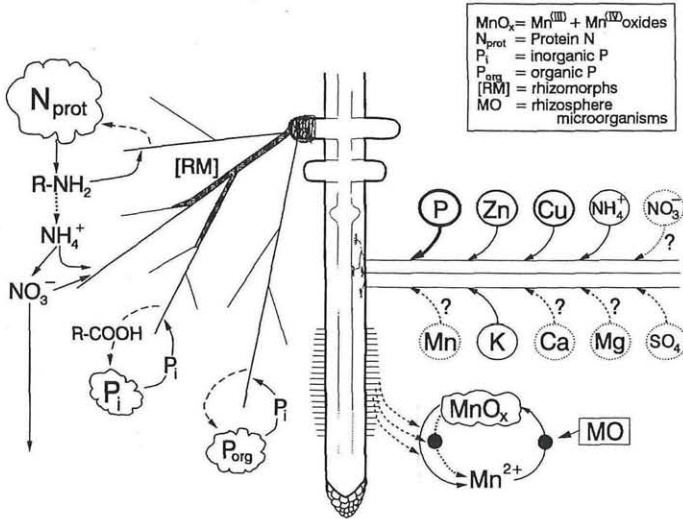


Fig. 6. Schematic presentation of components of the nutrient dynamics in and acquisition from the "hyphosphere" of endo- (VA-) mycorrhizal roots and of additional components found in ectomycorrhizal roots. (MARSCHNER 1995).

Indirect effects of AM and ECM on mineral nutrient acquisition: Mycorrhization can also enhance nutrient acquisition and host plant growth indirectly by increasing the tolerance of the host plant to high concentrations of heavy metals (e.g. zinc) or aluminium, or by suppressing root pathogens. In both instances, mycorrhization has a protective effect on the host roots and, thus, enhances root growth and the capacity of the host root system to acquire mineral nutrients.

So far, however, the only well documented ECM protective effects are for heavy metals like Zn (COLPAERT & VAN ASSCHE 1992) or for Al (CUMMING & WEINSTEIN 1990). In most instances, protection is brought about by a high retention capacity of the fungal mycelium or its exudates for heavy metals or Al, thereby reducing accumulation of toxic concentrations in the host plant tissue.

There is a long list of examples on suppression of soil-borne fungal and bacterial root pathogens brought about by inoculation with mycorrhizae, AM in particular. In some instances of ECM, this suppression is achieved by production of

oxalic acid and other compounds by the fungus. In most other instances, increase in resistance of the host plant against pathogens is achieved by changes in root exudation, host root anatomy, and enhanced defence reactions of the host roots, i.e. induced resistance.

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