

Influence of arbuscular mycorrhizal fungi on uptake of Zn and P by two contrasting rice genotypes

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ABSTRACT

There is little experimental evidence about the functional significance of arbuscular mycorrhizal fungi (AMF) colonization in providing nutrients for lowland rice. This study was undertaken to examine whether growth and nutrient deficiencies may affect plants benefit from AMF inoculation. Two contrasting rice (*Oryza sativa* L.) genotypes and two AMF species (*Glomus mosseae* and *G. intraradices*) were used in this experiment. Under P starvation, P uptake in the genotype tolerant to P deficiency (Fajr), declined significantly up to 36% ($P < 0.05$) in response to AMF inoculation, while it enhanced by about 70% ($P < 0.01$) in susceptible genotype (Shafagh). Under Zn starvation, Zn uptake of Zn-efficient genotype (Shafagh) increased by about 2 fold ($P < 0.01$), but a reduction of 52% ($P < 0.05$) was observed in the Zn-inefficient genotype (Fajr) upon mycorrhization. Greater genotypic differences were observed for –P–Zn plants. Our results imply that genotypic difference in responsiveness to inoculation with AMF is attributable to different contribution of mechanisms for increased nutrient uptake in mycorrhizal plants depending on nutrient, nutritional status and nutrient efficiency of genotypes.

Keywords: arbuscular mycorrhizal fungi; *Glomus mosseae*; *Glomus intraradices*; *Oryza sativa*; rice genotypes

Colonization of roots with arbuscular mycorrhizal fungi (AMF) often improves the phosphorus nutrition of host plants growing on soils with sparingly soluble P forms (Shenoy and Kalagudi 2005). Increased absorption surface and lower threshold concentration for P uptake in mycorrhizal root systems are contributing factors (Peterson and Massicotte 2004). Recent evidences suggest that AMF can provide the dominant route for plant P supply, even when overall growth or P uptake remains unaffected (Smith et al. 2003). Improved uptake of other mineral elements by mycorrhizal roots has also been demonstrated for nitrogen, potassium (George et al. 1995) and for micronutrients such as Zn, Cu, Fe and Mn (Azcón et al. 2003, Ortas and Akpinar 2006). It is well known that the Zn bioavailability is limited by low Zn mobility in the soil solution and then by spatial availability. Accordingly, absorption area is important parameter influencing bioavailability of Zn (Hacisalihoglu and Kochian 2003). Therefore, an increased absorption surface as a result of arbuscular mycorrhizal colonization may be of particular importance for Zn uptake compared to other micronutrients.

In contrast to other crop species, there is little experimental evidence about the role of mycorrhizal colonization in lowland rice plants (Solaiman and Harita 1996, Purakayastha and Chhonkar 2001). In a previous work, we showed a large variation in Zn efficiency among Iranian lowland rice genotypes (Hajiboland and Salehi 2006). However, there is no information on P efficiency trait of these genotypes. In the present study, in addition of characterization of P efficiency in two selected genotypes, we investigate whether inoculation of these genotypes with AMF could further increase P and Zn uptake. Here we test if there is a variation in mycorrhizal responsiveness between two contrasting rice genotypes, and how this difference is related to P and Zn efficiency in the nonmycorrhizal condition. Moreover, we test the following hypotheses: (i) mycorrhizal responsiveness is related not only to the nutritional status of plants (e.g. nutrient requirement), but also to plants nutrient efficiency, (ii) high mycorrhizal responsiveness based on plant growth is not necessarily associated with higher mycorrhizal responsiveness based on P or Zn uptake.

MATERIAL AND METHODS

Fungal inoculum, plant materials, nursery cultivation and transplantation. Two mycorrhizal fungi species including *Glomus mosseae* (Nicol and Gerd) Gerdemann and Trappe or *G. intraradices* Schenck and Smith (Soil Biology Laboratory, Faculty of Agriculture, University of Tabriz) were propagated 4 months on sorghum plants in a greenhouse. Pot contents, including sand, root segments, hyphae and spores were used as inoculum. Number of spores in the inoculum was 33–35 per g for both mycorrhizae species and root colonization was 74.8 and 78.8% for *G. mosseae* and *G. intraradices*, respectively.

Surface sterilized seeds of two genotypes (Fajr, Shafagh) of rice (*Oryza sativa* L.) (provided by Rice Research Center, Guilan, Iran) were germinated in the dark on filter paper soaked with saturated CaSO_4 solution. In a preliminary experiment, Zn deficiency tolerance was determined in the order of Shafagh > Fajr, and P deficiency tolerance was determined in the order of Fajr > Shafagh. Germinated seeds were transferred to 5 l nursery containers including three treatments (without AMF inoculation, inoculation with *G. mosseae* or *G. intraradices*) with three independent replications per treatment. Nursery containers were filled with sterilized sand mixed with ~300 mg inoculum, then 30 young seedlings were transferred to each container and plants were grown for three weeks. Non-inoculated containers received the same amount of sterilized inoculum. Containers were irrigated with distilled water daily to maintain moisture at field capacity and were fed each week with half strength nutrient solution (Yoshida et al. 1972) without P, but $\text{Ca}_3(\text{PO}_4)_2$ was added at 4 g/Kg to each container. At the end of nursery culture, colonization of seedling roots was tested by random sampling (Phillips and Hayman 1970).

The used AMF isolates were isolated from the Tabriz Plain and identified according to the Schenck and Perez (1988). Also, the isolates were confirmed by Professor J. Morton at the West Virginia University (USA).

Treatments and experimental design. Five colonized plants were transplanted to the 3 l pots that were filled with quartz sand (~1 mm diameter) after washing, sterilization and weighing. Roots were carefully separated from rhizosphere soils and were washed with distilled water for removing soil particles before transplanting. Three mycorrhizal treatments (–AMF, inoculation with *G. mosseae* or *G. intraradices*), two levels of Zn

(without and with $0.5\mu\text{M}$ Zn) and P (without and with 0.3mM KH_2PO_4) were applied (Yoshida et al. 1972). The plants were grown under flooded conditions realized by 0.5 cm water above the sand. Plants were grown for two months under controlled environmental conditions with a temperature regime of $25^\circ\text{C}/18^\circ\text{C}$ day/night, 14/10 h light/dark period, a relative humidity of 70/80% and at a photon flux density of about $300\text{--}400\mu\text{mol}/\text{m}^2/\text{s}$. Plants were daily irrigated by double-distilled water or nutrient solution (Yoshida et al. 1972) after determination of nutrients depletion by measuring N and P concentrations in the pots.

Harvest and analyses. Before harvest, plant height was measured and the relative amount of chlorophyll was determined with a chlorophyll meter (SPAD-502, Minolta). Harvested plants were firstly rinsed with tap water and then with distilled water. The mycorrhizal colonization percentage was evaluated by the grid line intercept method (Phillips and Hayman 1970). After determination of dry weight, oven-dried samples were ashed in a muffle furnace at 550°C for 8 h, then were resuspended in 10% HCl and made up to volume by double distilled water. Concentration of P was determined by the ammonium-vanadate-molybdate method (Gericke and Kurmies 1952), and of K by flame photometry. Zn and Fe were determined by atomic absorption spectrophotometer (AA 6300, Shimadzu, Japan). Nutrient uptake was calculated for each pot as the sum of nutrient content of shoots and roots for 5 plants.

P and Zn efficiency (E) of two tested genotypes were calculated based on the following formulae (Osborne and Rengel 2002): $E = (\text{Shoot dw at low nutrient supply}/\text{shoot dw at adequate nutrient supply}) \times 100$. Mycorrhizal responsiveness (MR) was calculated as: $\text{MR} = [(\text{Plant dw}_{+\text{AMF}} - \text{Plant dw}_{-\text{AMF}})/\text{Plant dw}_{-\text{AMF}}] \times 100$ (Hetrick et al. 1992). Mycorrhizal nutrients responsiveness (MNR) was calculated similarly: $\text{MNR} = [(\text{Nutrients uptake}_{+\text{AMF}} - \text{Nutrients uptake}_{-\text{AMF}})/\text{Nutrients uptake}_{-\text{AMF}}] \times 100$ (Gao et al. 2007).

Experiments were conducted in a randomized complete block design using three independent replications. Statistical analyses of data were carried out by ANOVA test (Tukey test at $P < 0.05$).

RESULTS

AMF colonization was not observed in the non-inoculated plants. The highest colonization rate occurred in the absence of both P and Zn.

Application of P lowered colonization significantly from 25–27% to only 13–15% and addition of both Zn and P to the pots decreased AMF colonization from 25–27% to 7–11%. Root colonization between two AMF species was significantly different only in –P –Zn and +P +Zn treatments.

As expected, P deficiency caused a reduction of growth in both experiments, however, genotypes differed in the susceptibility to P deficiency. Reduction of shoot dw was 29% in Fajr but 72% in Shafagh. Calculated P efficiency for Fajr and Shafagh was 72 and 29 respectively, therefore, a clear contrasting response was observed between Fajr and Shafagh in tolerance to P deficiency.

Root and shoot dw and plants height decreased significantly by low Zn supply. In addition, genotypic differences were observed, Fajr demonstrated a high susceptibility with up to 33% reduction of shoot dw in –Zn treatments, compared to Shafagh with only 3% reduction of shoot dry matter. Zinc efficiency calculated for Fajr and Shafagh was 67 and 97, respectively.

Effect of inoculation on chlorophyll content and growth of plants

Shoot and root dry matter of non-mycorrhizal plants was greater than those of mycorrhizal ones. Plants height and chlorophyll content responded

similarly to AMF colonization and were decreased up to 33% (Table 1). Reduction of plants growth due to AMF inoculation was similar between –P and +P plants. Growth of Zn deficient inoculated plants (by *G. intraradices*) was decreased up to 73% in shoot and 77% in roots, while this reduction in Zn sufficient plants was only 15% in shoot and 16% in roots. The effect of AMF species was different and the difference between responses of Zn deficient and sufficient plants to inoculation was greater in plants inoculated with *G. intraradices* than in those inoculated with *G. mosseae* (Table 1). In contrast to Fajr, for Shafagh, significant growth stimulation was observed in inoculated plants (Table 2). Interestingly, in Shafagh, a Zn-efficient genotype, inoculation by AMF stimulated particularly root growth of Zn deficient plants, while inhibited that in Zn sufficient ones. Similarly with Fajr, the effect of inoculation with *G. intraradices* was more prominent than inoculation with *G. mosseae*. However, such an effect was less expressed in shoot (Table 2).

Nutrients uptake under inoculation and non-inoculation conditions

Phosphorus uptake in Fajr declined in response to AMF inoculation in P deficient plants either significantly (in plants inoculated with *G. mosseae*) or in tendency (in plants inoculated with

Table 1. Leaf chlorophyll content, shoot and root dry weight (mg dw/pot) of rice (*Oryza sativa* L. cv. Fajr) without (–AMF) and with inoculation by *Glomus mosseae* (*G. m.*) or *Glomus intraradices* (*G. in.*) at different phosphorus and zinc levels

| P | Zn | AMF | Root colonization (%) | Chlorophyll (relative) | Plant height (cm) | Shoot dw (mg/pot) | Root dw (mg/pot) |
|----|-----|---------------|-----------------------|------------------------|-----------------------|-------------------------|-------------------------|
| –P | | –AMF | 0 ^g | 54 ± 9 ^{bc} | 21 ± 3.4 ^b | 2132 ± 221 ^c | 898 ± 221 ^c |
| | –Zn | <i>G. m.</i> | 25 ± 0.6 ^b | 36 ± 2 ^c | 14 ± 0.6 ^b | 945 ± 112 ^d | 341 ± 101 ^d |
| | | <i>G. in.</i> | 27 ± 1 ^a | 41 ± 6 ^c | 16 ± 2.5 ^b | 824 ± 199 ^d | 323 ± 98 ^d |
| | | –AMF | 0 ^g | 84 ± 5 ^a | 33 ± 1.9 ^a | 3657 ± 321 ^b | 1547 ± 198 ^b |
| | +Zn | <i>G. m.</i> | 19 ± 0.8 ^c | 59 ± 12 ^{bc} | 23 ± 4.7 ^b | 1959 ± 151 ^c | 784 ± 187 ^{cd} |
| | | <i>G. in.</i> | 20 ± 0.6 ^c | 77 ± 19 ^{ab} | 30 ± 7.5 ^a | 2658 ± 254 ^c | 1025 ± 98 ^{bc} |
| +P | | –AMF | 0 ^g | 82 ± 13 ^{ab} | 32 ± 5.4 ^a | 3468 ± 553 ^b | 1798 ± 102 ^b |
| | –Zn | <i>G. m.</i> | 13 ± 1 ^d | 59 ± 2 ^{bc} | 23 ± 0.7 ^b | 1359 ± 158 ^d | 421 ± 78 ^d |
| | | <i>G. in.</i> | 14 ± 0.6 ^d | 56 ± 16 ^{bc} | 22 ± 6.2 ^b | 1124 ± 268 ^d | 412 ± 31 ^d |
| | | –AMF | 0 ^g | 100 ± 1 ^a | 39 ± 0.3 ^a | 5167 ± 131 ^a | 2341 ± 278 ^a |
| | +Zn | <i>G. m.</i> | 8 ± 1 ^e | 82 ± 8 ^{ab} | 32 ± 3.1 ^a | 3347 ± 152 ^b | 1368 ± 98 ^b |
| | | <i>G. in.</i> | 11 ± 1 ^f | 92 ± 6 ^a | 36 ± 2.2 ^a | 4389 ± 98 ^a | 1953 ± 101 ^b |

Data in each column followed by the same letter are not different significantly ($P < 0.05$)

Table 2. Leaf chlorophyll content, shoot and root dry weight (mg dw/pot) of rice (*Oryza sativa* L. cv. Shafagh) without (–AMF) and with inoculation by *Glomus mosseae* (*G. m.*) or *Glomus intraradices* (*G. in.*) at different phosphorus and zinc levels

| P | Zn | AMF | Root colonization (%) | Chlorophyll (relative) | Plant height (cm) | Shoot dw (mg/pot) | Root dw (mg/pot) |
|----|-----|---------------|-----------------------|------------------------|-----------------------|-------------------------|-------------------------|
| –P | | –AMF | 0 ⁱ | 59 ± 9 ^b | 24 ± 1 ^b | 845 ± 46 ^{de} | 569 ± 74 ^f |
| | –Zn | <i>G. m.</i> | 25 ± 0.6 ^b | 65 ± 10 ^b | 26 ± 1.5 ^b | 1178 ± 63 ^d | 929 ± 91 ^d |
| | | <i>G. in.</i> | 27 ± 0.6 ^a | 58 ± 10 ^b | 26 ± 5.5 ^b | 1152 ± 54 ^d | 718 ± 59 ^e |
| | | –AMF | 0 ⁱ | 65 ± 10 ^b | 27 ± 3.9 ^b | 1058 ± 74 ^d | 687 ± 68 ^e |
| | +Zn | <i>G. m.</i> | 19 ± 1 ^d | 56 ± 8 ^b | 26 ± 0.6 ^b | 897 ± 97 ^d | 529 ± 98 ^e |
| | | <i>G. in.</i> | 22 ± 1 ^c | 63 ± 7 ^{ab} | 20 ± 4.3 ^b | 608 ± 101 ^e | 579 ± 39 ^e |
| +P | | –AMF | 0 ⁱ | 86 ± 13 ^{ab} | 38 ± 1.5 ^a | 3598 ± 98 ^b | 968 ± 102 ^{de} |
| | –Zn | <i>G. m.</i> | 13 ± 0.6 ^f | 89 ± 11 ^{ab} | 39 ± 4.5 ^a | 2574 ± 103 ^c | 1279 ± 116 ^d |
| | | <i>G. in.</i> | 15 ± 0.6 ^e | 108 ± 11 ^a | 43 ± 1.1 ^a | 4068 ± 448 ^a | 3398 ± 258 ^b |
| | | –AMF | 0 ⁱ | 100 ± 11 ^a | 40 ± 3.3 ^a | 3698 ± 358 ^b | 4238 ± 259 ^a |
| | +Zn | <i>G. m.</i> | 7 ± 0.8 ^h | 91 ± 10 ^a | 38 ± 2.4 ^a | 2867 ± 305 ^c | 1201 ± 98 ^d |
| | | <i>G. in.</i> | 10 ± 0.6 ^g | 94 ± 9 ^a | 44 ± 1.5 ^a | 4928 ± 321 ^a | 2341 ± 128 ^c |

Data in each column followed by the same letter are not different significantly ($P < 0.05$)

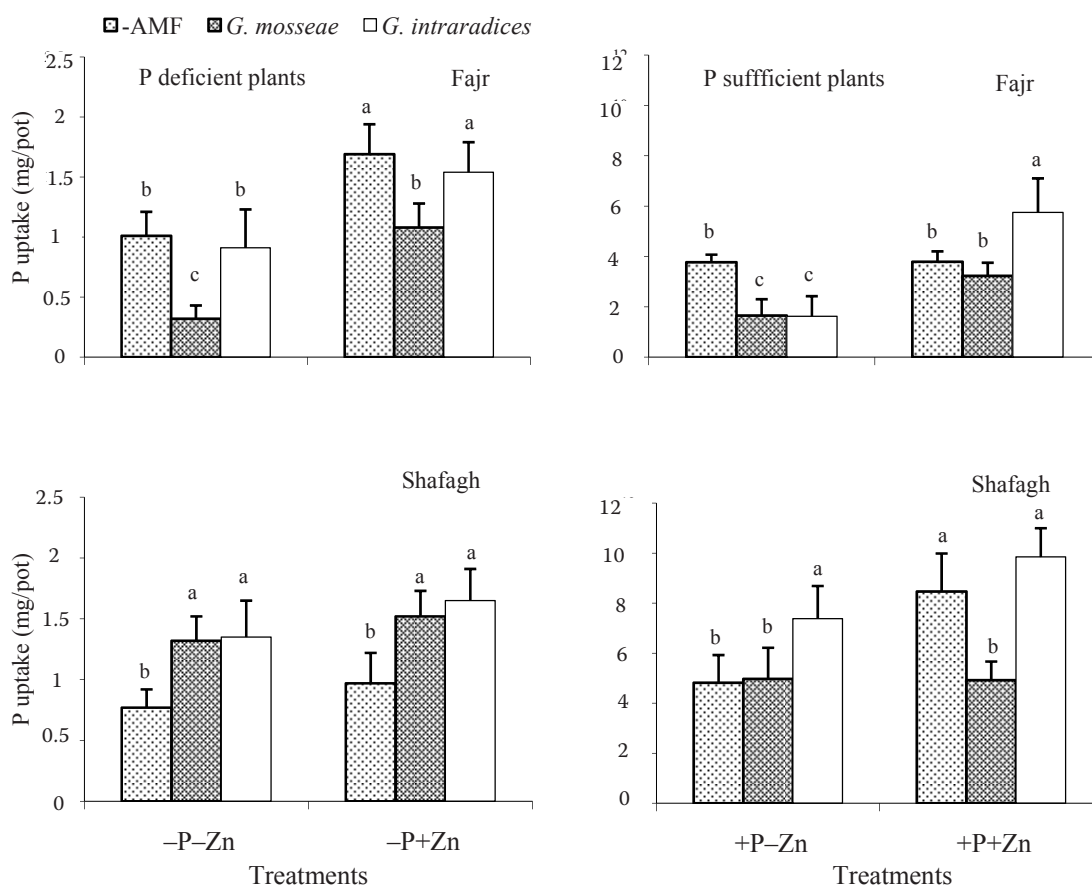


Figure 1. Uptake of P by rice (*Oryza sativa* L. cv. Fajr and Shafagh) without (–AMF) and with inoculation by *Glomus mosseae* or *Glomus intraradices* at different phosphorus nutritional status. Columns indicated by the same letter are not different significantly ($P < 0.05$)

G. intraradices). In this genotype, P sufficient plants had lower P uptake under inoculation conditions with both AMF species under low but not adequate Zn supply. In P and Zn sufficient plants (+P +Zn), a significant improvement of P uptake was observed in plants inoculated with *G. intraradices*. In contrast to Fajr, in Shafagh, AMF inoculation showed a positive effect on P uptake either in tendency or significant, in both P deficient and sufficient plants with the exception of +P +Zn plants inoculated with *G. mosseae* (Figure 1).

Zn uptake was affected by AMF inoculation differently depending on genotypes. Inoculation with AMF resulted in a reduction of Zn uptake in Fajr. In contrast, AMF inoculation enhanced Zn uptake in Shafagh. Phosphorous nutritional status did not affect the responses of Zn uptake to inoculation, however, P sufficient plants showed higher Zn uptake than P deficient ones (Figure 2).

Potassium uptake tended to decrease by inoculation. Although these changes were mainly non-significant, the reduction was obviously higher in Fajr than in Shafagh (Table 3).

Similarly with the effect of AMF inoculation on Zn uptake in Fajr, Fe uptake was decreased in inoculated plants in all treatments. In contrast, Fe uptake was increased significantly by AMF inoculation in Shafagh particularly in P and Zn sufficient plants inoculated with *G. intraradices*. However, the effect of AMF inoculation on Fe uptake in both genotypes was much less prominent than that of Zn uptake. AMF inoculation increased Zn uptake up to 4 fold (309%), while this stimulation for Fe uptake was only 59% for the same genotype and treatment (-P -Zn Shafagh) (Table 3).

DISCUSSION

Growth stimulation by inoculation with AMF was not ubiquitous for all tested genotypes and under all applied treatments. The establishment and maintenance of mycorrhizal symbiosis is linked to a flow of carbon from the host plant to the fungus (Marschner 1995). Depression of plant yield in response to AMF colonization in

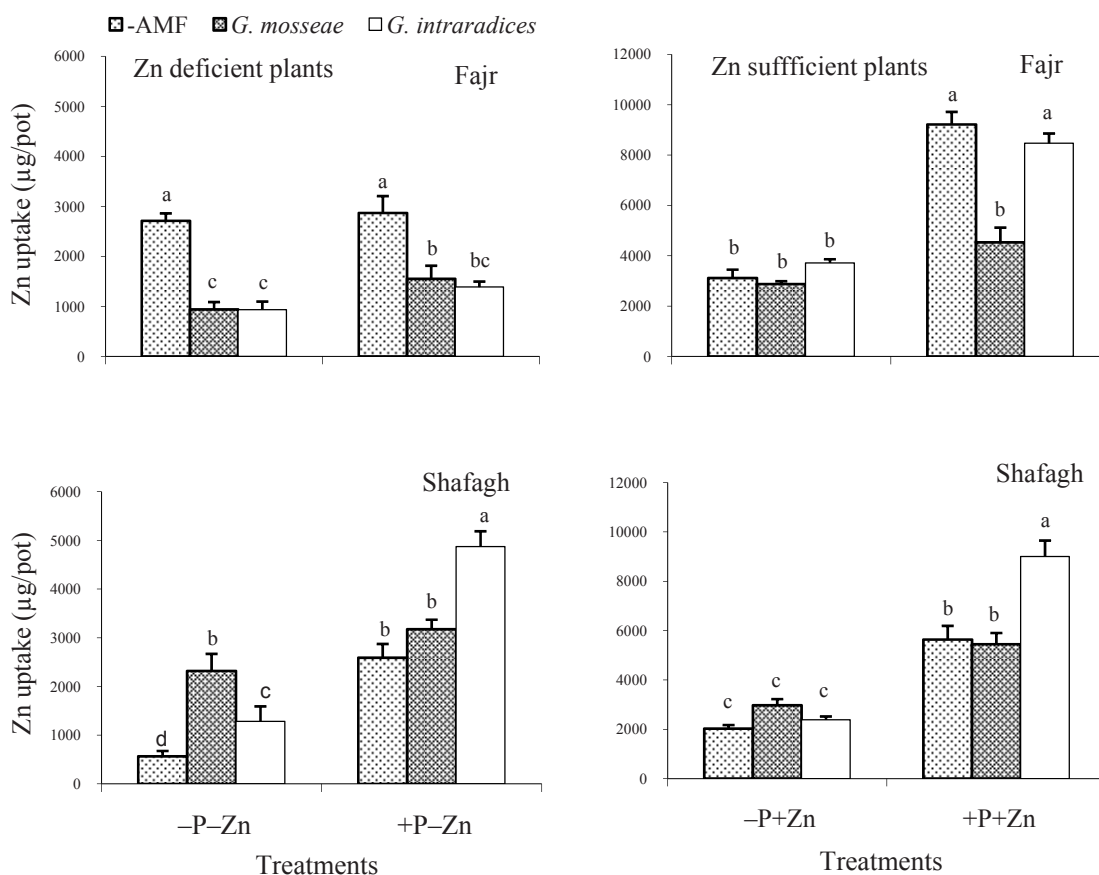


Figure 2. Uptake of Zn by rice (*Oryza sativa* L. cv. Fajr and Shafagh) without (-AMF) and with inoculation by *Glomus mosseae* or *Glomus intraradices* at different Zn nutritional status. Columns indicated by the same letter are not different significantly ($P < 0.05$)

Table 3. Uptake of K and Fe by rice (*Oryza sativa* L. cv. Fajr and Shafagh) without (–AMF) and with inoculation of roots by *Glomus mosseae* (*G. m.*) or *Glomus intraradices* (*G. in.*) at different phosphorus and zinc levels

| P | Zn | AMF | Fajr | | Shafagh | | |
|------|-----|------------------------|------------------------|-------------------------|--------------------------|--------------------------|-------------------------|
| | | | K uptake (mg/pot) | Fe uptake (µg/pot) | K uptake (mg/pot) | Fe uptake (µg/pot) | |
| –P | –Zn | –AMF | 74 ± 12 ^b | 870 ± 168 ^{ab} | 82 ± 26 ^e | 876 ± 152 ^f | |
| | | <i>G. m.</i> | 32 ± 4 ^b | 187 ± 43 ^c | 87 ± 12 ^c | 1398 ± 112 ^e | |
| | | <i>G. in.</i> | 27 ± 9 ^b | 228 ± 98 ^c | 85 ± 27 ^{de} | 923 ± 198 ^{fg} | |
| | +Zn | –AMF | 128 ± 17 ^{ab} | 1101 ± 330 ^a | 91 ± 66 ^{cd} | 1649 ± 52 ^{fg} | |
| | | <i>G. m.</i> | 55 ± 11 ^b | 417 ± 92 ^c | 64 ± 8 ^c | 1532 ± 59 ^e | |
| | | | <i>G. in.</i> | 90 ± 15 ^b | 258 ± 46 ^c | 45 ± 26 ^c | 1765 ± 116 ^e |
| –AMF | | 151 ± 51 ^{ab} | 990 ± 167 ^a | 130 ± 41 ^c | 3213 ± 389 ^{cd} | | |
| +P | –Zn | <i>G. m.</i> | 60 ± 13 ^b | 269 ± 56 ^c | 139 ± 45 ^c | 2431 ± 312 ^d | |
| | | <i>G. in.</i> | 52 ± 30 ^b | 438 ± 65 ^c | 326 ± 108 ^b | 6998 ± 395 ^a | |
| | +Zn | –AMF | 188 ± 23 ^a | 1103 ± 127 ^a | 257 ± 172 ^b | 4478 ± 197 ^c | |
| | | <i>G. m.</i> | 118 ± 23 ^a | 814 ± 160 ^a | 138 ± 19 ^b | 5477 ± 660 ^b | |
| | | | <i>G. in.</i> | 166 ± 53 ^a | 1068 ± 150 ^a | 284 ± 33 ^b | 6041 ± 575 ^b |
| | | –AMF | 151 ± 51 ^{ab} | 990 ± 167 ^a | 130 ± 41 ^c | 3213 ± 389 ^{cd} | |

Data in each column followed by the same letter are not different significantly ($P < 0.05$)

this work might be explained by competition of fungus with plants for photosynthesis products, likely because of a low photosynthesis rate due to a low light intensity in growth chamber (300–400 µmol/m²/s) compared with open field conditions (1700–2000 µmol/m²/s).

It is well established that colonization of roots and establishment of mycorrhizae are significantly reduced at high P levels in soil and plant (Shenoy and Kalagudi 2005). However, there is no experimental evidence related to the dependence of root colonization on Zn level in soil. In this work, colonization of roots was affected not only by P but also by Zn supply level, deficiency conditions induced colonization in both genotypes and AMF species.

Effect of AMF inoculation on nutrient uptake

AMF colonization had a significant effect on uptake of P and Zn. Root colonization by AMF improves P (Smith et al. 2003) and Zn (Gao et al. 2007) uptake per unit of root length due to the enhancement of root surface area by hyphal growth and providing an extra route for P uptake as mycorrhizal pathway. In this work, growth response of root to AMF is possibly another important cause of increased P and Zn uptake by inoculation as well as genotypic differences. Root dry weight was increased in Shafagh up to 63% (e.g. in –P –Zn

plants inoculated with *G. mosseae*) which was associated by a 4-fold increase in P uptake per plant. Conversely, root length was inhibited by inoculation in Fajr up to 62% concomitant with reduction of P uptake up to 69%. Reduction of Zn uptake in Fajr and its enhancement in Shafagh in inoculated plants were also associated with inhibition and stimulation of root growth, respectively. An obvious genotypic difference in AMF-induced changes in the root/shoot ratio (dry weight base, data not shown) of +P –Zn plants further confirms this conclusion. This ratio reduced from 0.52 to 0.37 in Fajr upon mycorrhization (*G. intraradices*), while increased from 0.26 to 0.83 in Shafagh. A general tendency in reduction of K uptake in Fajr could be the result of an overall growth reduction, particularly root growth and surface area in AMF inoculated plants.

Effect of AMF colonization in dependence of AMF species and of plant genotype

Though a similar colonization rate, mycorrhizal species were different in their effect on growth and nutrient uptake. *G. intraradices* affected positively growth and nutrient uptake more than *G. mosseae*. A poor effectivity of *G. mosseae* might be related to poor development and activity of the external hyphae, low hyphal transport rates, and poor

solute interchange at the arbuscule-host root cell interface (Marschner 1995).

The positive effect of AMF inoculation, which was observed only in Shafagh with concomitant enhancement in root growth, suggests a considerable role for response of root in determination of response of nutrient uptake in AMF plants. However, the contribution of root growth in increased nutrients acquisition should not be overestimated. Root length and spatial availability are of high importance for nutrients such as P, Zn and K (Marschner 1995), but Fe uptake does not seem to be related highly to root growth. In our experiment, beside expected increased uptake of nutrients such as P and Zn, Fe uptake was also affected in parallel with root growth response and unexpectedly, improvement of root growth did not affect K uptake.

Benefit from AMF was observed in the genotype (Shafagh) that showed a higher sensitivity to P deficiency simultaneously with higher tolerance to Zn deficiency. A significant improvement of plant growth under inoculation conditions may be considered the main cause of positive response of Shafagh to AMF regarding P and Zn uptake. To test this hypothesis, we calculated mycorrhizal responsiveness (MR) and mycorrhizal nutrient responsiveness (MNR) for four tested nutrients as well as correlation coefficient between the two parameters (Table 4). Variation in responsiveness can be partitioned into dependence and non-dependence components, dependence variation

relates to plant performance under stress but non-dependence variation describes differences in the interaction between plant and fungus (Sawers et al. 2008). A significant correlation between mycorrhizal responsiveness and mycorrhizal P and Zn responsiveness in Fajr suggests an important contribution of growth response to P and Zn acquisition of mycorrhizal plants in this genotype, i.e. greater amount for dependence component of responsiveness.

In contrast, the lack of such correlation in Shafagh indicates that mechanisms which are not directly related to the growth response to AMF, e.g. variation in nutrient acquisition properties and/or delivery into the host plant, are responsible for higher MNR in this genotype. Characterization of P transporters in rice and study of their expression under

–AMF and +AMF conditions suggest that there is a switch from one pattern of gene expression to another. Thus the genetic determinants of performance in –AMF and +AMF plants vary independently (Paszkowski et al. 2002).

Accordingly, greater MNR for P in Shafagh could be explained by higher expression level of AMF-specific P transporters and/or their greater efficiency in the P delivery to the host plant, i.e. greater amount for non-dependence component of responsiveness. However, molecular base and the cause of greater MNR for Zn in this genotype (with greater Zn-efficiency in the absence of AMF), remains unknown. In contrast to P and Zn, Fe and K uptake in

Table 4. Mycorrhizal responsiveness (MR) and mycorrhizal nutrients responsiveness (MNR) calculated for P, Zn, Fe and K and correlation coefficient (*R*) between them in rice genotypes (*Oryza sativa* L. cv. Fajr and Shafagh) inoculated with *Glomus mosseae* (*G. m.*) or *Glomus intraradices* (*G. in.*) at different P and Zn levels

| Treatments | MR | | MNR | | | | | | | | | |
|------------|--------------|---------------|--------------|--------------------|--------------|--------------------|--------------|---------------|---------------------|---------------|--------------------|-----|
| | | | P | | Zn | | Fe | | K | | | |
| | <i>G. m.</i> | <i>G. in.</i> | <i>G. m.</i> | <i>G. in.</i> | <i>G. m.</i> | <i>G. in.</i> | <i>G. m.</i> | <i>G. in.</i> | <i>G. m.</i> | <i>G. in.</i> | | |
| Fajr | –P | –Zn | –58 | –11 | –68 | –1 | –65 | –66 | –79 | –74 | –57 | –64 |
| | | +Zn | 30 | 34 | –36 | –9 | –8 | 19 | –62 | –77 | –57 | –30 |
| | +P | –Zn | –66 | –14 | –56 | –57 | –46 | –52 | 6 | 151 | –60 | –66 |
| | | +Zn | –37 | 35 | –15 | 52 | –51 | –8 | –26 | –3 | –37 | –12 |
| | <i>R</i> | | | | 0.66* | | 0.81** | | –0.11 ^{ns} | | 0.53 ^{ns} | |
| | Shafagh | –P | –Zn | 49 | –11 | 71 | 75 | 309 | 126 | 60 | 5 | 6 |
| +Zn | | | –18 | –17 | 57 | 70 | 47 | 17 | –7 | 7 | –30 | –50 |
| +P | | –Zn | –16 | 94 | 3 | 53 | 23 | 88 | –24 | 118 | 7 | 151 |
| | | +Zn | –49 | 79 | –42 | 16 | –3 | 60 | 22 | 35 | –46 | –11 |
| <i>R</i> | | | | 0.29 ^{ns} | | 0.44 ^{ns} | | 0.79** | | 0.71* | | |

** significant at 0.01, * significant at 0.05, ^{ns} not significant ($P < 0.05$)

mycorrhizal plants appeared to be determined by plant growth in Shafagh but not in Fajr. Our results imply a different contribution of mechanisms for an increased nutrient uptake in mycorrhizal plants depending on nutrient and plant genotype.

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