

I. Weissenhorn · C. Leyval · G. Belgy · J. Berthelin

Arbuscular mycorrhizal contribution to heavy metal uptake by maize (*Zea mays* L.) in pot culture with contaminated soil

Abstract In two pot-culture experiments with maize in a silty loam (P2 soil) contaminated by atmospheric deposition from a metal smelter, root colonization with indigenous or introduced arbuscular mycorrhizal (AM) fungi and their influence on plant metal uptake (Cd, Zn, Cu, Pb, Mn) were investigated. Soil was γ -irradiated for the nonmycorrhizal control. In experiment 1, nonirradiated soil provided the mycorrhizal treatment, whereas in experiment 2 the irradiated soil was inoculated with spores of a fungal culture from P2 soil or a laboratory reference culture, *Glomus mosseae*. Light intensity was considerably higher in experiment 2 and resulted in a fourfold higher shoot and tenfold higher root biomass. Under the conditions of experiment 1, biomass was significantly higher and Cd, Cu, Zn and Mn concentrations significantly lower in the mycorrhizal plants than in the nonmycorrhizal plants, suggesting a protection against metal toxicity. In contrast, in experiment 2, biomass did not differ between treatments and only Cu root concentration was decreased with *G. mosseae*-inoculated plants, whereas Cu shoot concentration was significantly increased with the indigenous P2 fungal culture. The latter achieved a significantly higher root colonization than *G. mosseae* (31.7 and 19.1%, respectively) suggesting its higher metal tolerance. Zn shoot concentration was higher in both mycorrhizal treatments and Pb concentrations, particularly in the roots, also tended to increase with mycorrhizal colonization. Cd concentrations were not altered between treatments. Cu and Zn, but not Pb and Cd root-shoot translocation increased with mycorrhizal colonization. The results show that the influence of AM on plant metal uptake depends on plant growth conditions, on the fungal partner and on the metal, and can-

not be generalized. It is suggested that metal-tolerant mycorrhizal inoculants might be considered for soil reclamation, since under adverse conditions AM may be more important for plant metal resistance. Under the optimized conditions of normal agricultural practice, however, AM colonization even may increase plant metal absorption from polluted soils.

Key words *Glomus mosseae* · Heavy metals
Indigenous mycorrhiza · Tolerance · Transfer

Introduction

Arbuscular mycorrhizal (AM) fungi are root symbionts found in most plant species and habitats (Harley and Harley 1987). While the enhanced absorption of trace metals (Zn, Cu, Co) from deficient or nonenriched soils by AM plants has been documented (Faber et al. 1990; Killham 1985; Kothari et al. 1991; Li et al. 1991; Rogers and Williams 1986; Tinker and Gildon 1983), relatively little attention has been paid to the role of AM fungi in metal-contaminated soils. Under such conditions, Killham and Firestone (1983) found an adverse effect of AM on plant growth, which they attributed to the enhanced uptake of Cu, Ni, Pb and Zn with increasing metal supply and decreasing pH. In contrast, several other authors (El-Kherbawy et al. 1989; Leyval et al. 1991; Schüepp et al. 1987) reported that shoot concentrations of Zn, Cu, Pb and Cd decreased with AM colonization at high levels of available metals, whereas at lower levels metal uptake increased compared with nonmycorrhizal plants. Dueck et al. (1986) reported alleviation of the negative effect of Zn on the growth of two grasses by AM colonization, though Zn uptake and translocation to the shoots was not hampered.

A field study on metal-polluted plots in the close vicinity of a Pb-Zn smelter in the north of France showed abundant AM spore density and root colonization of the maize crop (Weissenhorn et al. 1994). At the same time, metal accumulation in the maize shoots was

I. Weissenhorn (✉) · C. Leyval · G. Belgy · J. Berthelin
Centre de Pédologie Biologique,
Centre National de la Recherche Scientifique,
Laboratoire Associé à l'Université de Nancy I,
BP5, F-54501 Vandoeuvre-lès-Nancy Cedex, France
Fax: (33) 83576523; e-mail: Leyval@cpb.cnrs-nancy.fr

markedly elevated above that in uncontaminated control plots. An AM fungal culture isolated from this metal-polluted soil was more tolerant to Cd than a laboratory reference strain when spore germination was tested in vitro (Weissenhorn et al. 1993). These results suggested adaptation of the indigenous AM fungi population to the elevated metal concentrations in the soil near the smelter. However, the influence of the mycorrhiza on the accumulation of heavy metals by the plants growing on this soil could not clearly be established because of the lack of nonmycorrhizal controls under field conditions.

In the present study, two pot experiments were conducted with this metal-contaminated soil, irradiated to provide a nonmycorrhizal control. Root colonization by indigenous AM fungi or a laboratory reference strain, *Glomus mosseae*, and metal uptake and translocation were investigated. Corresponding to the field study, maize was used as the experimental plant. In contrast to most other pot experiments, studying the interactions between heavy metals and AM, metals were not added as soluble salts. Instead, the more realistic approach using the contaminated soil from the smelter site was chosen, where the long-term metal deposition ensures that the heavy metals are in equilibrium with the other soil constituents.

Materials and methods

Soil and soil extractions

The soil used in the two pot experiments was collected from an agricultural field plot at 750 m distance from a Pb-Zn smelter (Métaleurope, Noyelles-Godault, France) as previously described (Weissenhorn et al. 1994). The soil is a silty loam, regularly limed with sugar house foams, and cropped in 3-year rotation with maize, wheat and sugar beet. It is contaminated with Cd, Zn and Pb due to atmospheric deposition from the smelter for more than 60 years (Table 1). Soil was sampled in June 1991, sieved to < 4 mm and air dried.

Part of the soil was then sterilized by γ -irradiation (25 kGy) several weeks before use to eliminate mycorrhizal propagules. In order to determine the influence of this soil sterilization on metal availability, both the nonirradiated and the irradiated soils were subjected to single extractions with two different extractants, (a) 1 M $\text{CH}_3\text{CHOONH}_4$ -0.1 M EDTA and (b) 0.1 N $\text{Ca}(\text{NO}_3)_2$. Triplicate aliquots of 5 g (NH_4OAc -EDTA) or 10 g [$\text{Ca}(\text{NO}_3)_2$] of soil were shaken in plastic flasks with 50 ml of extractant for 2 h at 20°C. Then extracts were filtered through ash-free paper and the calcium nitrate extracts were acidified with 14 N nitric acid (1 ml) to prevent metal adsorption on the glass flasks. All solutions were kept at 4°C until analysis. Concentrations of metals (Cd, Zn, Pb, Cu, Mn) were determined by inductively coupled

Table 2 Plan of experiments (*Gm* *Glomus mosseae*, *M* mycorrhizal, *NM* nonmycorrhizal, *P2* P2 culture)

Experiment	Treatment	Substrate	Mycorrhizal inoculum
1	NM	Irradiated soil	None
	M	Nonirradiated soil	Indigenous
2	NM	Irradiated soil	None
	Gm	Irradiated soil	<i>G. mosseae</i> (100 spores/plant)
	P2	Irradiated soil	P2 culture (100 spores/plant)

plasma atomic emission spectrometry (ICP-AES) (Jobin Yvon 32) or inductively coupled plasma mass spectrometry (VG Plasma-Quad PQ2+) according to the metal concentration. Each solution was analysed in triplicate using standards in a similar matrix. Blanks were analysed in the same way. Available P in the soil before and after irradiation was assessed by extraction with 0.5 M NaHCO_3 (Olsen et al. 1954). The P concentration in the solution was measured by ICP-AES (Jobin Yvon 32).

Experiment 1

In experiment 1, the effect of the indigenous mycorrhizal population on plant metal uptake and translocation was studied (Table 2). Maize (*Zea mays* L.) was grown in 1-l plastic pots containing 1.2 kg of either nonirradiated (mycorrhizal treatment) or irradiated (nonmycorrhizal treatment) soil. The irradiated soil was re-inoculated with the autochthonous microflora by adding a suspension of the nonsterile soil (10 g in 90 ml sterile distilled water) filtered at 5 μm to exclude mycorrhizal propagules. Each pot received 10 ml of the filtered suspension. Total microbial population was estimated at the end of the experiment by most probable number according to Alexander (1982). The numbers of colony-forming units (CFU) were of the same order for both the nonirradiated and the irradiated, re-inoculated soil (2×10^6 CFU g dry soil). Maize seeds were disinfected with 30% H_2O_2 for 30 min and rinsed with sterile distilled water three times. One seed per pot was placed about 2 cm below the soil surface. There were five pots per treatment randomly arranged in a growth chamber (L'aurore S.A.) with 24°C day/20°C night, 12 h photoperiod, 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photon flux density and around 70% relative humidity. The pots were watered with distilled water and received once a week 100 ml of the following nutrient solution: 100 mg l^{-1} NH_4NO_3 , 75 mg l^{-1} KNO_3 , 25 mg l^{-1} KH_2PO_4 . Plants were grown for 9 weeks and had reached tasseling stage when they were harvested.

Experiment 2

Experiment 2 was designed to compare an AM fungal culture (P2) from the metal-polluted soil, identified as *Glomus mosseae* (Weissenhorn et al. 1993), with a laboratory reference culture, *Glomus mosseae* (Nicol. & Gerd.) Gerd. & Trappe (provided by

Table 1 Soil characteristics. Data refer to soil dry matter (105°C). Total soil metals were obtained according to extraction by fusion with lithium metaborate followed by acid (HCl) dissolution. (OM organic matter, CEC cation exchange capacity)

pH (H ₂ O)	OM (g kg ⁻¹)	CaCO ₃ (g kg ⁻¹)	CEC (cmol kg ⁻¹)	Cd (mg kg ⁻¹)	Zn (mg kg ⁻¹)	Pb (mg kg ⁻¹)	Cu (mg kg ⁻¹)	Mn (mg kg ⁻¹)
7.5	28.7	16.3	16.4	17.7	1220	895	45	310

Table 3 Mycorrhizal colonization, dry matter and phosphorus content of plants from experiment 1. Values as means \pm SE of five replicates within one column followed by different

letters are significantly different ($P < 0.05$; t -test) (*M* mycorrhizal, *NM* nonmycorrhizal)

	Mycorrhizal colonization (%)	Dry matter (g/plant)		Phosphorus			
		Root	Shoot	Root		Shoot	
				mg/dry wt.	mg/plant	mg/dry wt.	mg/plant
NM	0.0 \pm 0.0 a	0.32 \pm 0.02 a	4.7 \pm 0.3 a	2.9 \pm 0.1 a	0.92 \pm 0.07 a	4.4 \pm 0.2 b	20.7 \pm 1.5 a
M	24.5 \pm 3.7 b	0.41 \pm 0.01 b	6.4 \pm 0.6 b	2.2 \pm 0.1 b	0.88 \pm 0.03 a	3.3 \pm 0.1 b	21.0 \pm 1.6 a

V. Gianinazzi-Pearson, INRA, Dijon), with regard to their colonization capacity in the polluted soil and their effect on metal transfer to the plant. A nonmycorrhizal treatment served as control (Table 2).

Maize seeds were disinfected (see experiment 1) and pregerminated on water agar (5%) in 50-ml tubes at 24°C. After 1 week, one seedling was planted in each pot containing 1.2 kg of irradiated reinoculated (see experiment 1) soil. The two mycorrhizal treatments (Gm and P2) received 100 spores per plant, which were inoculated directly onto the roots with a Pasteur pipette prior to planting. The spores were rinsed three times in sterile distilled water but not disinfected. There were five pots per treatment arranged randomly in a growth chamber (Conviron PGR15) with 24°C day/20°C night, 16 h photoperiod, 980 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photon flux density and around 60% relative humidity. Plants were watered with distilled water during the first 3 weeks, with a 2.5 mM KNO_3 solution during the following 2 weeks, and a half-strength Hoagland solution (Hoagland and Arnon 1950) with reduced P concentration (20 μM) during the last 2 weeks of the experiment (100 ml per day). After 7 weeks, plants were harvested at tasseling stage.

Plant analysis

Plant metal and P concentrations were determined after wet-digesting of the dried and ground plant material with HNO_3 (Weissenhorn et al. 1994) in the same way as the soil extracts. Percentage of mycorrhizal root cortex was evaluated after staining with trypan blue using a five-class system according to Trouvelot et al. (1986) as previously described in detail (Weissenhorn et al. 1994).

Data analysis

All concentrations refer to soil or plant dry matter determined at 105°C. Means and standard errors were calculated for five replicate values. Means were compared by t -test (experiment 1) or Tukey's multiple range test (experiment 2) at a significance level of $P < 0.05$. When variances were too heterogeneous to achieve significant ANOVA results, means were compared by t -test based on separate variances (SYSTAT: Wilkinson 1989).

Results

Experiment 1

Mycorrhizal root colonization by indigenous AM propagules in the nonirradiated soil reached 24.5% (Table 3). Shoot and root dry matter of the mycorrhizal maize was significantly higher than that of the nonmycorrhizal plants grown in the irradiated soil. Both tissue concentrations and total uptake of Cd by plants were significantly lower for mycorrhizal than for nonmycorrhizal plants (Fig. 1; Table 4). Cu, Zn and Mn concentrations were also significantly lower in the mycorrhizal plants, whereas their total contents did not differ between mycorrhizal and nonmycorrhizal plants. For Pb, by contrast, no differences in plant tissue concentrations were observed between treatments, and total Pb uptake tended to be higher for mycorrhizal plants, though this was not statistically significant.

Fig. 1 Metal concentrations of plants from experiment 1 as means \pm SE of five replicates. A significant difference ($P < 0.05$; t -test) between treatments is indicated by different letters above columns separately for each metal (*M* mycorrhizal, *NM* nonmycorrhizal)

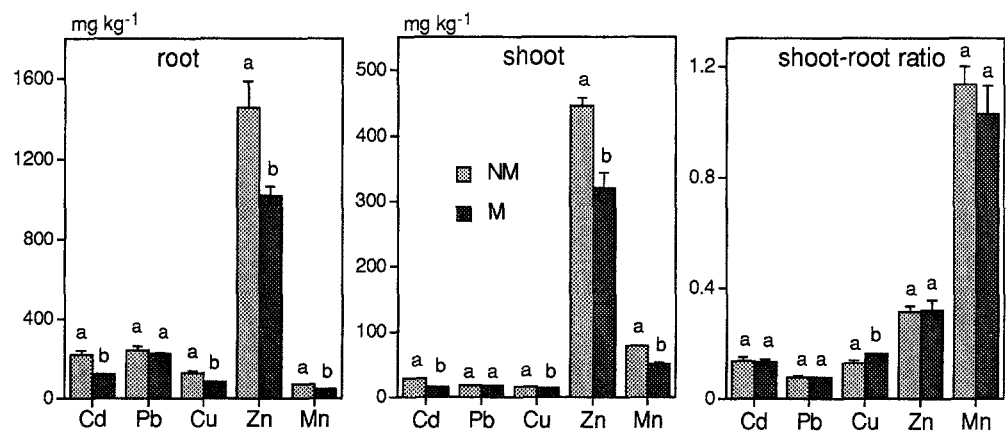


Table 4 Metal contents ($\mu\text{g}/\text{plant}$) of plants from experiment 1 as the means \pm SE of five replicates. A significant difference ($P < 0.05$; t -test) between treatments (NM, M) is indicated by different letters. * Significance was tested without the assumption of equal variances (separate variances t -test) (M mycorrhizal, NM nonmycorrhizal)

	Root	Shoot	Whole plant	Shoot/root ratio
Cadmium				
NM	89 \pm 14 a*	135 \pm 8.7 a	224 \pm 19 a	1.71 \pm 0.28 a
M	49 \pm 1.5 b	100 \pm 7.3 b	149 \pm 8 b	2.05 \pm 0.14 a
Lead				
NM	77 \pm 7.1 a	86 \pm 7 a	163 \pm 13 a	1.13 \pm 0.05 a
M	91 \pm 4.0 a	109 \pm 11 a	200 \pm 11 a	1.21 \pm 0.16 a
Copper				
NM	40 \pm 3.2 a	74 \pm 6 a	114 \pm 8 a	1.90 \pm 0.17 a
M	34 \pm 0.8 a	86 \pm 10 a	120 \pm 10 a	2.54 \pm 0.34 a
Zinc				
NM	469 \pm 67 a	2112 \pm 163 a	2581 \pm 225 a	4.67 \pm 0.29 a
M	414 \pm 20 a	2005 \pm 109 a	2419 \pm 96 a	4.90 \pm 0.47 a
Manganese				
NM	23 \pm 2.1 a	375 \pm 25 a	398 \pm 27 a	16.80 \pm 0.60 a
M	21 \pm 1.3 a	326 \pm 41 a	347 \pm 41 a	16.20 \pm 2.50 a

Experiment 2

Maize root colonization by the AM fungal culture originating from the polluted soil (P2) was significantly higher than with the laboratory *Glomus mosseae* culture (Table 5). According to in vitro spore germination

tests (Weissenhorn et al. 1993), P2 culture is more tolerant to Cd than the reference *Glomus mosseae*. The present results seem to confirm this tolerance at the root colonization level. They are also in accordance with the abundant AM resting spores and root colonization found in the field plot (Weissenhorn et al. 1994).

In contrast to experiment 1, dry matter yield and plant P did not differ between the nonmycorrhizal and the two mycorrhizal treatments (Table 5), despite the difference in colonization level. The considerable higher dry matter yield of experiment 2 compared to experiment 1 must be attributed to the better growth conditions, i.e. higher light intensity and longer photoperiod.

Contrary to experiment 1, maize Cd concentrations did not differ significantly between treatments (Fig. 2). Zn root concentrations were also similar for all three treatments, but shoot Zn increased with mycorrhizal colonization. Due to the high variances, particularly for the two mycorrhizal treatments, a significant difference could not be established between the three treatments, but only between the nonmycorrhizal and the pooled mycorrhizal (Gm plus P2) treatments. For Cu, differences, between treatments were not consistently related to the degree of root colonization (Fig. 2). Plants inoculated with *G. mosseae* had significantly lower root Cu concentrations than in the two other treatments. However, inoculation with the P2 culture significantly increased shoot Cu concentrations, which reached phytotoxic levels (Sauerbeck 1982), though soil Cu concen-

Table 5 Mycorrhizal colonization, dry matter and phosphorus content of plants from experiment 2 as the means \pm SE of five replicates. Values within one column followed by different

letters are significantly different at $P < 0.01$ (Tukey) (*Gm* *Glomus mosseae*, *NM* nonmycorrhizal, *P2* P2 culture)

	Mycorrhizal colonization (%)	Dry matter (g/plant)		Phosphorus			
		Root	Shoot	Root		Shoot	
				mg/dry wt.	mg/plant	mg/g dry wt.	mg/plant
NM	0.0 \pm 0.0 a	3.9 \pm 0.2 a	20.8 \pm 0.6 a	1.84 \pm 0.04 a	7.2 \pm 0.5 a	2.5 \pm 0.1 a	51.5 \pm 2.7 a
Gm	19.1 \pm 2.3 b	4.0 \pm 0.3 a	20.9 \pm 0.8 a	1.77 \pm 0.09 a	7.1 \pm 0.5 a	2.3 \pm 0.2 a	48.5 \pm 2.3 a
P2	31.7 \pm 2.1 c	4.4 \pm 0.2 a	21.4 \pm 0.6 a	1.77 \pm 0.06 a	7.8 \pm 0.6 a	2.3 \pm 0.1 a	49.5 \pm 1.5 a

Fig. 2 Metal concentrations of plants from experiment 2 as means \pm SE of five replicates. A significant difference ($P < 0.05$; Tukey) between treatments is indicated by different letters above columns separately for each metal. A bold letter indicates a significant ($P < 0.05$) difference between the respective treatment and the two other treatments pooled (separate variances t -test) (*Gm* *Glomus mosseae*, *NM* nonmycorrhizal, *P2* P2 culture)

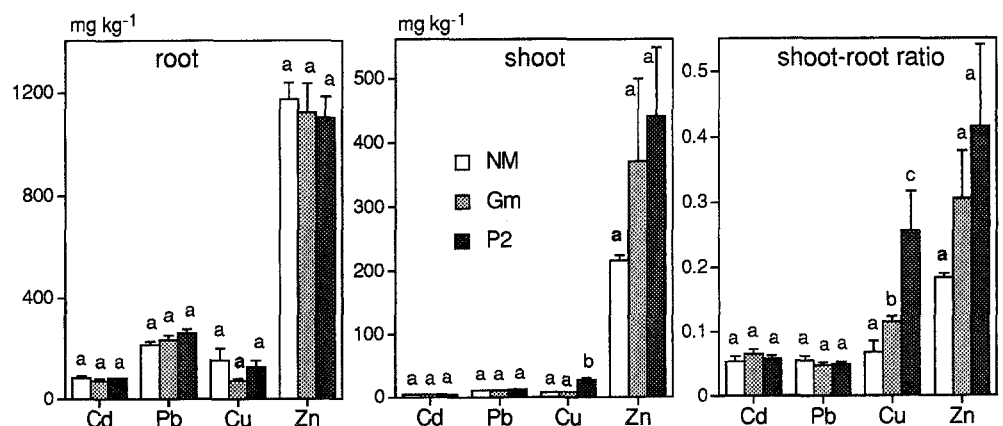


Table 6 Extractable soil metal and phosphorus concentrations (mg kg^{-1}). Letters indicate a significant difference ($P < 0.05$; t -test) between nonirradiated and irradiated soil for each extraction (OAc acetate)

Metal	Non-irradiated soil		Irradiated soil	
	EDTA-NH ₄ OAc	Ca(NO ₃) ₂	EDTA-NH ₄ OAc	Ca(NO ₃) ₂
Cd	12.8 ± 0.2 a	0.42 ± 0.01 a	13.1 ± 0.1 a	0.46 ± 0.03 a
Zn	305.3 ± 2.4 a	4.52 ± 0.04 a	318.0 ± 3.6 a	5.01 ± 0.07 b
Pb	536.3 ± 2.2 a	0.22 ± 0.03 a	551.6 ± 3.5 a	0.26 ± 0.02 a
Cu	11.0 ± 0.1 a	0.08 ± 0.01 a	11.6 ± 0.2 a	0.08 ± 0.01 a
Mn	9.5 ± 0.2 a	1.81 ± 0.04 a	13.5 ± 0.3 b	3.29 ± 0.04 b
P (NaHCO ₃)	89 ± 1.3a		88 ± 2.1a	
pH (H ₂ O)	7.50		7.51	

tration, in contrast to the other investigated metals, did not exceed current European Union limit values of 50–140 mg kg^{-1} dry wt. (CED 1986). Similar to experiment 1, the concentrations of Pb in root and shoot did not differ significantly between treatments though a rising trend was notable along with colonization level (Fig. 2).

Discussion

In the first experiment, the lower Cu, Zn, Mn and especially Cd uptake by plants grown in the untreated soil (Fig. 1; Table 4) might be ascribed to the mycorrhizal colonization. A decrease of shoot concentrations of these metals in mycorrhizal compared to nonmycorrhizal plants on soils with high metal availability has been reported (Bethlenfalvai and Franson 1989; El-Kherbawy et al. 1989; Leyval et al. 1991; Schüepp et al. 1987).

The results of this first experiment should, however, be interpreted with caution. The higher metal concentrations in the nonmycorrhizal plants were strongly related to their significantly lower biomasses (Table 3). P root and shoot concentrations were also higher in the smaller nonmycorrhizal plants, but there was no significant difference in total P uptake between the two treatments (Table 3). Therefore, the better plant growth in the untreated soil cannot be attributed to mycorrhizal-enhanced P uptake. However, the mycorrhizal symbiosis can play an important role in generally improving plant viability (Perrin 1990; Schönbeck and Dehne 1981). Inversely, the lower plant dry matter in the sterilized soil could be due to an inhibitory effect. γ -irradiation of soil can increase Mn availability, though to a lesser extent than other soil sterilization treatments (Bowen and Cawse 1964; McGee 1987). Though there was no significant difference in Cd, Cu and Pb extractability before and after irradiation, the availability of Zn and particularly Mn according to the extraction with Ca(NO₃)₂ was higher in the irradiated soil (Table 6). Plant Mn concentrations were higher on irradiated than on untreated soil (Fig. 1). However, they did not exceed normal values (Marschner 1986). Thus, Mn phyto-

toxicity seems not likely. It is not excluded that microbial degradation of organic matter was stimulated in the irradiated soil after reinoculation and that higher amounts of metals were released during the 9 weeks of pot culture.

The significantly lower metal concentrations and the bigger size of mycorrhizal plants in experiment 1 were not observed in experiment 2, where AM significantly modified neither plant growth nor metal accumulation compared with the nonmycorrhizal control. This is apparently due to the difference in experimental conditions, particularly the higher light intensity in experiment 2, which allowed a tenfold higher root and fourfold higher shoot biomass (Tables 3, 5). Leyval and Berthelin (1982) also observed a mycorrhizal growth effect on maize only under suboptimal growth conditions. Therefore, the decreased metal concentration in the mycorrhizal plants of experiment 1 is likely to be due to a biomass dilution effect. A general mycorrhizal increase of plant viability and biomass dilution effect were also involved in the alleviation of Zn, Cd and Cu toxicity of mycorrhizal *Calluna vulgaris*, *Festuca*, *Calamagrostis* and white clover (Bradley et al. 1982; Dueck et al. 1986; Gildon and Tinker 1983).

However, direct mechanisms such as retention of metals at hyphal level, as suggested for ericoid mycorrhiza by Bradley et al. (1982) cannot be excluded, especially for Cd, of which in experiment 1 both concentration and total uptake were significantly decreased in mycorrhizal plants. Schüepp et al. (1987) reported a significant decrease of Cd in shoots of mycorrhizal maize and lettuce, though AM colonization had no influence on plant dry matter. These results support the hypothesis of a direct involvement of AM fungi in either reducing metal uptake or root-shoot translocation. The sequestration of metals by polyphosphate granules in fungal vacuoles was suggested as one possible mechanism by Turnau et al. (1993). These authors also found that the cytoplasm of the AM fungus contained more Cd, Ti and Ba than that of the host (*Pteridium aquilinum*) cells.

Plants exhibited metal concentrations clearly above normal values (Sauerbeck 1982) yet without obvious symptoms of toxicity. As shown by the low root-shoot

translocation factors, the metals, particularly Cd and Pb, were relatively strongly retained at the root level in mycorrhizal as well as in nonmycorrhizal plants (Figs. 1, 2). This indicates that plants have their own protection mechanisms against metal toxicity, such as metal accumulation in plastids of root cells or on transfer cell wall ingrowths (Turnau et al. 1993) or sequestration by inducible low-molecular-weight metal-binding proteins (phytochelatins, metallothioneins) as shown for maize roots (Rausser and Glover 1984). Root mucilages and high molecular weight soluble root exudates from maize have also been shown to bind Cd (Mench et al. 1987; Morel et al. 1986). Under abiotic and biotic stress conditions, qualitatively and quantitatively modified exudation (Krafczyk et al. 1984; Laheurte and Berthelin 1988; Rovira and Davey 1974) and mycorrhizae may provide additional metal-binding capacity.

In the present study, Zn and particularly Cu root-shoot translocation significantly increased with mycorrhizal colonization (Figs. 1, 2), whereas Pb and Cd shoot-root ratios did not differ between treatments, suggesting metal-specific mechanisms. For Zn and Cu, hyphal uptake and translocation are known to be similar to P transport (Cooper and Tinker 1978; Tinker and Gildon 1983) and considerable hyphal contribution to plant Zn and Cu supply has been demonstrated in compartment studies (Kothari et al. 1991; Li et al. 1991).

The difference between the two fungal cultures in experiment 2 also suggests AM fungi-specific mechanisms. Direct hyphal uptake and translocation, and indirect mycorrhizal effects on root morphology and exudation and rhizosphere microorganisms (Kothari et al. 1990) may play different roles. The higher root colonization by P2 fungi is likely to proliferate a more intense network of external hyphae (Sanders et al. 1977) increasing the total uptake surface compared with the Gm treatment. In addition, external hyphal development of the metal-sensitive Gm fungi might have been impeded due to metal toxicity (Graham et al. 1986). Gildon and Tinker (1983) demonstrated the higher capacity for mitigating Zn toxicity to plants of a Zn-tolerant AM fungal partner than a Zn-sensitive one. This seemed to be mainly a biomass dilution effect due to the higher mycorrhizal potential of the tolerant strain at elevated Zn concentrations. In contrast, under the favourable growth conditions in experiment 2 the higher mycorrhizal colonization by the tolerant P2 fungi did not lead to a better plant growth but enhanced metal (Cu, Zn) absorption and translocation. These results demonstrate the delicate balance between mycorrhizal effects on plant growth and trace metal acquisition.

Conclusions

The results of this pot-culture study, complementary to a preceding field study on the same soil (Weissenhorn et al. 1994), indicate that the indigenous AM fungi population is adapted to the elevated metal concentrations

in the polluted soil. Therefore, metal-tolerant mycorrhizal inocula might be considered for soil reclamation to improve growth and viability of plants and their metal resistance, particularly under adverse conditions, as on acid P-deficient metal-contaminated heath lands (Bradley et al. 1982). However, mycorrhizal abundance in a polluted soil does not necessarily mean that mycorrhizal efficiency, e.g. in terms of P uptake, is not affected. Also, the role of AM in plant resistance to metal stress and in the protection of the food chain should not be overestimated. Under the optimized conditions of normal agricultural practice (fertilization, liming), a substantial influence of AM on metal assimilation seems rather unlikely. In the metal-polluted P2 soil in both field (Weissenhorn et al. 1994) and the present growth chamber study, AM colonization did not prevent plant metal concentrations far above normal values. On the other hand, AM also did not increase metal uptake compared to nonmycorrhizal plants to an alarming extent. It is, however, not excluded that under more acid soil conditions (without liming) their effects might be more pronounced (Killham and Firestone 1983; El-Kherbawy et al. 1989).

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