The Role of Mycorrhizae in the Interactions of Phosphorus with Zinc, Copper, and Other Elements[1]

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ABSTRACT

Mycorrhizae increase the uptake of Zn and Cu by many plants, but mycorrhizal activity is suppressed by P fertilization. Soybean (*Glycine max* Mer.) and two lines of corn (*Zea mays* L.) were used to determine if this mechanism is a major cause of P-induced Zn and Cu deficiencies. Shoot dry weights and concentrations or total uptake of P, Zn, Cu, Fe, Mn, K, Ca and Mg were determined for mycorrhizal and nonmycorrhizal plants given 0, 25, 75, or 200 ppm P. Phosphorus fertilization significantly reduced Zn and Cu concentrations in mycorrhizal soybeans, but concentrations in nonmycorrhizal treatments were not affected. Concentrations of Zn and Cu in mycorrhizal and nonmycorrhizal corn were reduced by P fertilization, but the reduction for mycorrhizal plants was significantly greater than the decrease for nonmycorrhizal plants. Reductions in Zn and Cu concentrations in nonmycorrhizal corn were the result of a dilution effect and could be attributed to increased plant size rather than increased P fertility per se. The concentrations of the other analyzed elements were all affected by P level and/or mycorrhizal condition. In general, mycorrhizal and nonmycorrhizal dry weights and element concentrations converged as soil P was increased. Patterns of response to P and mycorrhizae differed slightly between corn lines, and such differences were marked for certain elements when corn was compared with soybean.

Additional Index Words: **micronutrients, mineral composition, nutrient interactions.**

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REDUCTIONS of Zn and Cu concentrations in plants by P fertilization have been recognized for many years. They occur in numerous monocots, dicots, and conifers (27, 35) although deficiency symptoms appear infrequently. The mechanisms by which P reduces the uptake or translocation of these elements are still unclear, although there is general agreement that P has its major effects within the plant rather than in the soil (27). Nevertheless, the growth medium is an important variable. In the literature reviewed by the authors, increasing P reduced concentrations of Zn and/or Cu in 41 of 45 cases if plants were grown in natural, unsterilized soil. In 18 cases where various plant species were grown in solution or sand cultures or in sterilized soil, the P effect occurred consistantly in only two cases with variable responses in five instances (1, 5, 6, 7, 9, 10, 13, 15, 19, 21, 30, 34, 36). These results suggest that a microbial factor is also involved. Nearly all instances of P-Zn or P-Cu interactions have been reported for plants which form mycorrhizae, and species such as citrus and other tree fruits, legumes, corn, etc. for which marked responses to mycorrhizae have been demonstrated, constitute the large majority of such reports. In 45 of the cases mentioned above where P reduced Zn or Cu, 41 were for plants with mycorrhizae. Of the 12 instances in which no effect was observed, in only one case were the plants mycorrhizal.

Mycorrhizae are symbiotic associations of plant roots with certain fungi. The fungal partner functions analogously to root hairs, but may extend as far as 7 cm from the root surfaces of vesicular-arbuscular mycorrhizae (29), increasing the volume of soil from which nutrients can be extracted. This function is disproportionately important for nutrients which have narrow diffusion zones around roots, particularly P, Zn, and Cu, and indeed these are the three elements whose concentrations are most consistantly increased by mycorrhizae. The benefits of mycorrhizae vary, decreasing as P fertility increases (24). Crop species range from nonmycorrhizal, to mycorrhizal but minimally benefitted, to others which are obligately myorrhizal under natural conditions. Fungal infection and/or efficiency in improving nutrient uptake are adversely affected by a number of variables, including soil fumigation, low temperatures, wet soils, and P fertilization (4, 24, 30, 32). These factors are all associated with reduced uptake of Zn and sometimes Cu (9, 14, 20, 37). As a rule, increasing the availability of P suppresses mycorrhizal colonization (16, 17, 18, 22, 23, 24, 25, 29, 30, 31, 33). Mosse (24) first suggested that this P effect might alter the performance of mycorrhizae with respect to the uptake of elements other than P, and this has been demonstrated for Cu in the data of Ross (30) and L. W. Timmer (personal communication) with soybean and citrus respectively.

This paper reports an investigation of the role mycorrhizal fungi play in the uptake of various elements. The effect of plant size on element concentrations is analyzed because plant weight may vary greatly over a range of P levels and elements may be more concentrated in smaller, stunted plants.

MATERIALS AND METHODS

A Philo silt loam (Fluvaquentic Dystrocrept) was used which had, prior to treatment, a pH of 6.1, 8 ppm Bray no. 1 P, a cation exchange capacity (CEC) of 13.8 meq/100 g, K, Mg, and Ca saturations of 1.6, 5.6, and 63.4% respectively, and DTPA (diethylenetriaminepentaacetic acid) extractable (2) concentrations of 1.9 ppm Cu, 1.8 ppm Zn, 93 ppm Mn, and 88 ppm Fe. This soil was pasteurized with aerated steam for 30 min at 76°C to kill indigenous mycorrhizal fungi. Phosphorus was added as ground calcium monophosphate at rates of 0, 25, 75, and 200 ppm. Potassium sulfate, magnesium sulfate, and calcium hydroxide were added to attain 5, 20, and 75% saturations of the exchange capacity with K, Mg, and Ca respectively and 100 ppm N was added as NH_4NO_3. At the end of the experiment, the pH of a composite soil sample was 7.1, and micronutrient concentrations were 0.8 ppm Cu, 0.9 ppm Zn, 22 ppm Mn, and 20 ppm Fe. Soybean was inoculated with *Rhizobium japonicum* and not given fertilizer N. Mycorrhizal inoculum was prepared by wet-sieving soil from the root systems of sudangrass [*Sorghum bicolor* (L.) Moench] infected with the mycorrhizal fungus *Gigaspora gigantea* [(Nicol. & Gerd.) Gerdemann

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Table 1—Dry weight, mycorrhizal colonization, and shoot element analyses for mycorrhizal and nonmycorrhizal soybean and corn.

	Added soil P	Shoot dry weight	P	Zn	Cu	Fe	Mn	K	Ca	Mg	Mycorrhizal colonization
	ppm	g	%	ppm				%			
						Soybean					
NMR†	0	1.06 d‡	0.070 g	16.4 d	5.5 bc	55 d	62 d	2.16 bc	1.70 bc	0.58 cd	
	25	0.98 d	0.078 g	15.8 d	6.2 b	62 cd	71 c	2.30 bc	1.65 bc	0.59 bc	
	75	2.21 b	0.118 f	14.2 d	5.7 bc	71 abc	88 a	2.04 c	1.84 a	0.64 ab	
	200	2.81 a	0.236 c	17.6 d	5.2 c	80 ab	92 a	3.08 a	1.73 bc	0.64 a	
MR	0	1.72 c	0.142 e	56.5 a	8.2 a	67 bc	73 bc	2.40 b	1.80 ab	0.54 d	86 a
	25	2.44 ab	0.181 d	35.7 b	7.4 a	76 ab	73 bc	3.03 a	1.56 c	0.57 cd	81 ab
	75	2.64 a	0.271 b	28.5 c	6.0 b	73 abc	75 bc	3.13 a	1.61 c	0.56 cd	79 ab
	200	2.67 a	0.359 a	28.4 c	6.2 b	83 a	81 b	3.28 a	1.59 c	0.57 cd	75 b
						Corn 884P × 94					
NMR	0	0.94 h	0.080 f	30.0 c	7.4 c	85 ab	76 b	6.30 bc	1.23 b	0.46 a	
	25	2.80 f	0.107 cde	17.3 ef	4.5 e	58 c	57 de	6.26 bc	0.98 d	0.36 cd	
	75	6.13 bc	0.117 cd	19.1 de	4.8 e	43 efg	43 g	4.06 d	0.74 efg	0.32 de	
200	200	8.64 a	0.202 a	11.5 f	4.1 e	43 efg	51 ef	2.78 f	0.60 i	0.39 bc	
MR	0	1.41 g	0.096 e	65.5 a	10.1 a	87 a	71 bc	6.92 b	1.11 c	0.45 a	66 a
	25	4.98 cd	0.120 bc	34.7 bc	6.2 d	54 cd	48 fg	4.04 d	0.70 fgh	0.36 cd	64 a
	75	7.27 ab	0.144 b	24.4 d	4.8 e	40 fg	44 g	3.12 ef	0.57 i	0.36 cd	50 ab
	200	8.08 ab	0.202 a	14.9 ef	4.4 e	41 fg	51 ef	2.84 f	0.56 i	0.39 bc	21 c
						Corn 70 × 94					
NMR	0	0.83 h	0.084 f	30.8 c	7.3 c	59 a	86 a	6.76 b	1.41 a	0.40 bc	
	25	3.70 ef	0.110 cde	19.2 de	4.2 e	47 def	68 c	6.82 b	1.07 c	0.32 de	
	75	6.75 abc	0.113 cde	16.9 ef	4.4 e	44 efg	60 d	3.88 de	0.76 ef	0.29 e	
	200	8.98 a	0.189 a	12.6 f	4.0 e	42 fg	59 d	2.76 f	0.62 hi	0.33 de	
MR	0	1.06 h	0.110 de	64.1 a	8.7 b	83 ab	88 a	7.96 a	1.41 a	0.41 ab	41 b
	25	4.17 de	0.145 b	38.0 b	5.8 d	50 de	61 d	5.78 c	0.83 e	0.35 cd	59 a
	75	7.41 ab	0.125 bc	20.8 de	4.3 e	37 g	52 ef	3.06 e	0.63 hi	0.32 de	49 ab
	200	6.84 abc	0.199 a	15.9 ef	4.8 e	46 ef	70 bc	3.08 e	0.65 ghi	0.38 bc	10 c

† NMR = nonmycorrhizal, MR = mycorrhizal.
‡ Means followed by the same letter do not differ significantly at the 5% level. All corn data analyzed together.

and Trappe] to obtain fungal spores falling in the 0.05–0.25 mm range. This intermediate fraction was added to sand (for bulk) and mixed into the soil of mycorrhizal treatments. A portion of the filtrate, which did not contain mycorrhizal spores, was added to both mycorrhizal and nonmycorrhizal treatments. One-liter pots of soil were planted with pregerminated seeds of either Chippewa 64 soybean or the single cross corn hybrids Pa 70 × Pa 94 and Pa 884P × Pa 94 (33). The soybean experiment was replicated 10 times and the corn experiment was replicated 5 times in a 4 P level × +/− mycorrhizae factorial design with 8 treatments.

After 40 days in the greenhouse, all plants were harvested and the shoot dry weights were recorded. Root samples were stained with lactophenol-Trypan Blue (28) to determine the extent of mycorrhizal colonization. Percentage colonization was calculated as the number of 1.2 mm-wide microscope fields per 100 containing any mycorrhizal fungus structure. Percentage colonization is not a quantitative indicator of mycorrhizal activity, but colonization figures are included to demonstrate the adverse effects of P on fungal growth in the roots.

Plant tops were dry-ashed and analyzed by atomic absorption or emission for Zn, Cu, Fe, Mn, K, Ca, and Mg concentrations. Phosphorus was determined colorimetrically with a molybdenum-vanadate reagent.

In addition to standard analyses of variance, all element concentration data were submitted to regression analysis with either: (i) each of the eight individual treatments analyzed spearately with the dry weight of each replicate as an independent variable; (ii) each of the four P levels analyzed separately with dry weight and +/− mycorrhizal inoculation as the independent variables; (iii) all data within each of the two inoculation treatments analyzed together with P level as the independent variable; and (iv) all data within each of the two inoculation treatments analyzed with both P level and dry weight as independent variables.

These methods of analysis were used (*a*) to determine if concentrations of elements were inversely associated with plant size (weight), indicating that some variation in concentration resulted from a growth dilution effect; (*b*) to determine differences in element concentrations due directly or indirectly to mycorrhizae with the appropriate corrections for dry weight; (*c*) to determine if element concentrations were significantly affected by the level of P in the mycorrhizal and nonmycorrhizal treatments without corrections for plant size; and (*d*) to determine if element concentration was still a function of P level if corrections were made for any growth dilution effect.

The fourth type of analysis (iv) presents statistical problems since the independent variables (P level and dry weight) are not truely independent. To determine the reliability of results from this analysis, the regression equations generated by the first analysis method (i) were used to correct element concentrations to the expected values for plants of an arbitrary standard weight (2 g for soybean, 5 g for corn). In cases where the dry weight variable was not statistically significant, the original data were used. The tendency of these individual element concentration means to increase or decrease as a function of the level of P was then compared to the response of element concentrations to P as determined by method (iv), in which the data for all four levels of P were analyzed together. Any lack of correspondence between the two methods were noted. In a fifth analysis, the independent variables foliar P concentration and shoot dry weight were regressed on Zn and Cu concentrations. For all regression analyses, data for the two corn lines were combined to provide ten replicates, and an additional variable (line) was added to regression models. Total uptakes of the eight elements were also analyzed for differences between means and significance of factors and factor interactions.

RESULTS AND DISCUSSION

Dry Weight

The response of soybeans to P was parabolic for mycorrhizal plants and sigmoidal for nonmycorrhizal plants (Table 1). Corn yields differed from soybean yields in two major respects. The range of dry weights over the four levels of P was much greater for corn than for soybean, and the response of corn to mycorrhizae was poorer. Only the line having Pa 884P as a maternal parent demonstrated a yield response to mycorrhizae, despite the fact that P, Zn, and Cu concentrations were increased by mycorrhizae in both lines (Table 1). Yield differences might have been greater if the plants had developed for a longer time (26), although Hall (16) reports similar variation in yield responses to mycorrhizae among corn lines after 12 weeks growth.

Within the 128 data cells for each of the eight element/eight treatment/two species combinations, plant dry weights and element concentrations were inversely related in 86% of all cases, significantly so in 39% of the total. Of the 14% of cases where the relationship was positive, the association was statistically significant in only one instance.

Table 2—Statistical significance ($P = 0.05$) of differences between element concentrations of mycorrhizal and nonmycorrhizal soybean and corn when corrections are made for plant size.

P added to soil	Element							
	P	Zn	Cu	Fe	Mn	K	Ca	Mg
ppm								
			Soybean					
0	+†	+	+	+	+	+	+	NS
25	+	+	+	+	NS	+	+	+
75	+	+	+	+	NS	+	NS	NS
200	+	+	+	NS	−	NS	−	−
			Corn					
0	+	+	+	+	NS	+	NS	+
25	+	+	+	NS	−	−	−	NS
75	+	+	NS	NS	NS	−	−	+
200	NS	+	NS	NS	NS	NS	NS	NS

† +, NS, and − indicate that the element concentration in the mycorrhizal treatment is either higher, not significantly different, or lower than that of the corresponding nonmycorrhizal treatment.

Colonization

Mycorrhizal colonization decreased as P availability increased. The exception to this trend was in the low P level for Pa 70 × Pa 94 where infection was poorer than in the next two higher P levels (Table 1).

Phosphorus

Concentration of P in mycorrhizal soybeans were approximately twice those of the nonmycorrhizal treatments, and these differences were significant at all levels of added P. As with yield, the P concentration of the nonmycorrhizal soybean plants was not increased by the first increment of fertilizer P (Table 1). In corn, mycorrhizae significantly increased P concentrations at the three lower levels of P (Table 2). These results differ from those of Hall (16) and Jackson et al. (18), who in most cases did not find increased P concentrations in corn whose yields were increased by mycorrhizae. Mycorrhizal inoculation × P level (MR × P) interactions were significant for both crops and for the total P uptakes of soybean and Pa 70 × Pa 94 corn. Mycorrhizae increased the total uptake of P in soybean and both lines of corn ($P = 0.01$ as determined by analysis of variance). Mycorrhizal P uptake was higher at three of the four levels of P in Pa 884P × Pa 94, but was not significant at any level for the other line ($P = .05$ by Duncan's Modified LSD test) (Table 3).

Zinc and Copper

Zinc concentrations were higher in all mycorrhizal treatments and Cu concentrations were greater in all mycorrhizal treatments excepting the two highest levels

Table 3—Shoot element content of mycorrhizal and nonmycorrhizal soybean and corn.

	Added soil P	P	Zn	Cu	Fe	Mn	K	Ca	Mg
	ppm	mg	μg				mg		
				Soybean					
NMR†	0	0.72 e‡	17 d	5.9 d	59 d	66 e	2.3 c	1.8 e	0.62 d
	25	0.75 e	15 d	5.9 d	59 d	67 e	2.2 c	1.6 e	0.57 d
	75	2.11 d	26 c	10.2 c	143 c	153 cd	3.6 b	3.5 cd	1.43 c
	200	6.62 b	44 c	14.5 b	222 a	258 a	8.6 a	4.9 a	2.22 a
MR	0	2.44 d	97 a	14.0 b	115 c	127 d	4.2 b	3.1 d	1.15 c
	25	4.35 c	86 ab	17.9 a	187 b	175 bc	7.3 a	3.9 bc	1.87 b
	75	7.21 b	76 b	15.9 ab	192 ab	199 b	8.4 a	4.3 ab	1.92 ab
	200	9.51 a	74 b	16.4 b	212 ab	214 ab	8.6 a	4.2 ab	2.12 ab
				Corn 884P × 94					
NMR	0	0.75 e	28 d	6.9 c	80 e	72 e	6.0 c	1.2 d	0.43 f
	25	2.97 d	48 d	12.4 b	161 d	159 d	17.5 b	2.7 c	0.99 d
	75	6.86 c	112 bc	28.3 a	259 c	258 bc	23.6 a	4.3 ab	1.88 bc
	200	13.95 a	84 c	33.4 a	362 a	373 a	21.0 ab	4.6 a	2.69 a
MR	0	1.34 d	95 bc	14.1 b	147 d	101 de	9.7 c	1.6 d	0.63 e
	25	5.91 c	169 a	30.1 a	277 bc	238 c	19.9 ab	3.5 bc	1.75 c
	75	9.99 b	169 a	33.6 a	288 bc	308 b	21.8 a	4.1 ab	2.48 ab
	200	16.08 a	118 b	35.0 a	312 b	406 a	22.6 a	4.5 ab	3.13 a
				Corn 70 × 94					
NMR	0	0.69 d	25 d	5.8 d	64 e	71 d	5.7 c	1.2 d	0.32 d
	25	3.82 c	70 c	14.8 c	174 d	249 c	24.8 ab	4.0 bc	1.11 c
	75	7.41 b	108 c	24.1 b	288 bc	396 b	25.4 a	5.1 ab	1.93 b
	200	16.77 a	112 b	35.5 a	872 a	530 a	24.7 ab	5.6 a	2.89 a
MR	0	1.03 d	68 c	8.9 d	85 e	93 d	8.3 c	1.5 d	0.43 d
	25	5.73 c	160 a	23.1 c	198 d	253 c	22.5 ab	3.5 c	1.42 c
	75	9.24 b	153 a	31.9 ab	264 c	386 b	22.6 ab	4.6 abc	2.36 ab
	200	13.35 a	105 b	32.5 a	333 ab	466 a	20.5 b	4.4 bc	2.55 a

† NMR = nonmycorrhizal, MR = mycorrhizal.
‡ Means followed by the same letter do not differ significantly at the 5% level. Corn lines analyzed separately.

of P in corn (Table 2). With no correction for differences in plant size, an increase in soil P significantly decreased Zn and Cu in mycorrhizal soybeans but not in nonmycorrhizal plants (Table 4). In corn, concentrations of these elements were reduced in mycorrhizal and nonmycorrhizal treatments as soil P was increased. With corrections for differences in plant size, P significantly decreased mycorrhizal soybean Cu and Zn concentrations but increased nonmycorrhizal Cu and Zn (Table 4). Because no attempt was made to correct for any decrease in soil pH resulting from the addition of calcium monophosphate, it is possible that the significant increase in Zn, Cu, and other elements may have resulted from an increased availability at lower pH's rather than a direct effect of improved P nutrition. In corn, with compensation for variation in plant size, P decreased Zn only in mycorrhizal plants and Cu concentrations were not affected by increasing P. These results indicate that mycorrhizae are an important component in the uptake of Zn and Cu and that the major causes of the effects of P on Zn and Cu occurred for the same reason, i.e. a P-induced suppression of uptake by mycorrhizal fungi. In some cases, as with corn, the apparent antagonism of Zn and Cu by P results from a growth dilution effect and is a function of plant size rather than P fertility per se. In this regard, foliar P concentrations were correlated with both Cu and Zn concentrations in all four mycorrhizal soybean treatments but were unrelated in the nonmycorrhizal treatments. In corn, which did not respond well to mycorrhizae, P and Zn were correlated in only two of the mycorrhizal treatments, and P and Cu were not correlated in any treatments. This positive correlation of P with Zn and Cu is consistent with random variability in the quantity or efficiency of element uptake

Table 4—Regression analysis of the significance ($P = 0.05$) of the level of soil P for shoot concentrations of several elements with or without corrections for difference in plant size.

Crop/ element	Without dry weight as an independent variable: Significance of soil P level		With dry weight as an independent variable: Significance of soil P level		Significance of plant size	
	NMR†	MR	NMR	MR	NMR	MR
Soybean/						
P	+‡	+	+	+	NS	–
Zn	NS	–	+	–	–	–
Cu	NS	–	+	–	–	–
Fe	+	+	+	+	NS	NS
Mn	+	NS	+	NS	–	NS
K	+	+	+	+	–	NS
Ca	NS	–	+	NS	–	–
Mg	+	NS	+	NS	–	NS
Corn/						
P	+	+	+	+	–	–
Zn	–	–	NS	–	–	–
Cu	–	–	NS	NS	–	–
Fe	–	–	–	NS	NS	–
Mn	–	–	(NS)	(+)	–	–
K	–	–	–	–	NS	–
Ca	–	–	–	(NS)	NS	–
Mg	–	NS	(+)	(+)	–	–

† NMR = nonmycorrhizal, MR = mycorrhizal.
‡ +, NS, – indicate that element concentrations either increase, are not significantly different at the 5% level, or decrease with increasing soil P or plant size (dry weight). Parentheses indicate that these results, based on four combined levels of P, do not correspond to trends determined from regression analyses for individual levels of soil P.

by mycorrhizae. In terms of total uptake per plant, all MR × P interactions were significant ($P = 0.05$) as were the main effects of mycorrhizal inoculation alone.

Iron, Manganese, Potassium, Calcium, and Magnesium

Iron and potassium were the two elements, other than P, Zn, and Cu whose concentrations were generally higher in mycorrhizal soybean shoots (Table 2). These elements were also the only two, other than P itself, to be increased by P fertilization in both mycorrhizal and nonmycorrhizal soybean (Table 4). Therefore, it is not possible to differentiate increased uptake of Fe and K by mycorrhizae from increased uptake or translocation as a result of improved P nutrition for this species. Higher Fe (12, 23) and K (23) concentrations in mycorrhizal plants have been reported in a few instances, but the effects of mycorrhizae on the uptake of these elements and on Mn, Ca, and Mg are not straightforward. Mycorrhizae usually increase P uptake, which requires some charge compensation by the major cations. Differences in plant size resulting from differences in P nutrition may also be accompanied by the growth dilution effect. A mycorrhizal condition can favor the uptake of K relative to Ca and Mg, which diffuse more rapidly in soil than K. This occurred with soybean (Table 1) but was less evident in corn. Mycorrhizal infection dramatically alters the lipid composition of the root (11), and mycorrhizal infection, either directly or by improving P nutrition, has been reported to increase root amino acids (3). These effects could also alter cation requirements. Improved P nutrition, the primary effect of mycorrhizae, alters the plant in various ways, increasing the amount of vascular tissue (8) and altering the composition of soluble molecules (19). Presumably, the cations required to balance these bound or soluble charged species are also affected. The ratio of neutral dry matter (e.g. cellulose) to charged dry matter might also be changed by P fertilization. The uptake and translocation of Fe and Mn can be antagonized by P, Cu, and Zn (27), whose concentrations are increased by mycorrhizae, but this is more likely if the amounts of these three elements are excessive. Within-treatment analyses of the corn and soybean data do not indicate any consistent inverse relationship between P, Cu, and Zn with Fe and Mn.

CONCLUSIONS

These experiments indicate two mechanisms for P-induced reductions in Cu and Zn concentrations, (i) the suppression of mycorrhizal uptake of these elements, and (ii) a dilution effect in which the larger, P-sufficient plants do not concentrate elements as much as smaller, deficient plants. These two mechanisms operate for both Cu and Zn. Increasing P decreased mycorrhizal root colonization, further indicating the adverse effects of P on mycorrhizae. The P level × mycorrhizal inoculation interaction was significant for dry weight, P, Cu, Zn, and Mn concentrations, but not for Fe concentrations. There were interactions for Ca, Mg, and K in one but not both crop species. In general, differences between mycorrhizal and nonmycorrhizal treatments decreased as P nutrition was increased.

Mycorrhizal infection is the natural condition of most plant species (24), and many crops benefit from mycorrhizae even at moderate to high levels of P. The use of nonmycorrhizal plants for nutrition experiments often may not be appropriate, particularly if P, Zn, and Cu are being studied or if P is a variable. Because large proportions of these elements may be taken up through mycorrhizal fungi, mycorrhizae must be considered as a component in the analysis of environmental or nutritional effects on P, Cu, or Zn uptake.

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