# Host Genotype Determines the Impact of Soil Phosphorus on Arbuscular Mycorrhizal Symbiosis in Maize (Zea mays L.)

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#### Abstract

Growth responses of maize genotypes, i.e., VL90 and VL16 of low and VL89 and HIM129 of relatively high P requirements, to inoculation with a native consortium of arbuscular mycorrhizal (AM) fungi was studied in a sandy loam soil fertilized with single super phosphate (SSP) to provide 0 (P0), 60 (P1), 90 (P2) and 120 (P3) mg P kg-1 soil. AM colonization increased vegetative plant growth significantly after 45 d at P<sub>0</sub> and P<sub>1</sub> levels for genotype VL90 and VL16, at P<sub>2</sub> and P<sub>3</sub> levels for VL89 and Po, P1, and P2 levels in HIM129. Except for VL89, a growth depression in roots and shoots of AM plants was observed at either P2 or P3 levels. This was most pronounced in VL90 and VL16. In contrast, in non-mycorrhizal plants no growth depression was observed; genotype VL90 at P3 was an exception. Root and shoot P, and shoot Zn concentrations were significantly higher in AM compared with nonmycorrhizal plants, at various P levels. However, the pattern of phosphorus and zinc uptake in mycorrhizal and non-mycorrhizal shoots was genotype specific. Alkaline phosphatase (ALPase) activity of mycorrhizal and non-mycorrhizal roots was variable with respect to genotype and soil P level. In mycorrhizal roots ALPase activity was significantly higher at P0 and P1 levels in VL90, P0, P1, P2 level in VL16, P2 and P3 levels in VL89 and at all P levels in genotype HIM129.

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Small additions of P to soil supported AM colonization, while high levels decreased it; all such responses were genotype dependent. Maximum AM colonization in genotype VL90 was observed at P0 level, while in genotype VL89, AM colonization increased with phosphorous availability with maximum at P3 level. This study shows that the impact of soil P on AM symbiosis is governed by the host at the genus as well as the genotype level.

Keywords: Arbuscular mycorrhizal fungi, genotype, phosphorus

### 1. Introduction

Symbiosis of arbuscular mycorrhizal fungi with plant roots is known to increase the uptake of phosphorus (P) (Siquiera et al., 1998), Zn (Wellings et al., 1991; Burkert and Robson, 1994) and other mineral elements (Smith and Read, 1997). This is achieved largely through external hyphae that absorb P beyond the depletion zone around root and root hairs and transport it to root tissues (Jakobsen et al., 1992). In addition, mycorrhizal roots can also acidify the rhizosphere soil with a resultant increase in the solubility of phosphorus, or by production of phosphatases, which make organically bound phosphate available to plants (Bekele et al., 1983).

However, it has been reported that high soil phosphorus levels severely limit mycorrhizal infection directly by inhibition of external hyphal growth and spread (Sanders, 1975; Graham et al., 1982) or indirectly by inducing changes in mycorrhizal infection through reduced carbohydrate supply. Wherever available phosphate is low in soil, small additions of phosphate can positively influence infection (Barea, 1991). These effects may be mediated via growth of both root and fungus. However, responses vary with plant species that differ in efficiency of uptake and utilization of nutrients, besides their inherent P requirement (Bryla and Koide, 1998). It seems that the responsiveness of the host to mycorrhizal fungus is governed by the phosphorus status of the soil relative to that required for maximum growth of the host i.e., host phosphorus requirement. However, based on detailed analysis of over one hundred genotypes of maize, we believe that it is the host rather than soil P which is a major determinant of mycorrhizal responsiveness. Furthermore, the impact of soil P on the mycorrhizal symbiosis is also governed by the host.

In studies carried out by Singh (2001), a wide variation in response to mycorrhizal colonization in maize (*Zea mays* L.) genotypes was observed. In the present study, four of these maize genotypes i.e., VL90 and VL16 (low P requirement) and VL89 and HIM129 (relatively high P requirement) based on their P response curves, were chosen to test the above assumption.

#### 2. Materials and Methods

Host

Maize (Zea mays L.) seeds were obtained from Vivekanand Research Center (ICAR), Almora. They were surface sterilized with 2% mercuric chloride for two min, followed by three rinses in sterile distilled water.

Soil

A sandy loam soil (pH 6.0; 2.85% organic carbon; 0.23% N; 0.16% K; 6.7 ppm Olsen's P; 2.4 ppm Fe) collected from the maize plot of Vivekanand Research Center, Almora was sieved through a 2-mm sieve, and sterilized by autoclaving thrice (121°C) for 8 h with 24 h interval between two autoclaving schedules. Phosphorus was incorporated into soil in the form of finely ground single super phosphate (SSP) to provide, 0, 60, 90 and 120 mg P kg<sup>-1</sup>; these are designated as P<sub>0</sub>, P<sub>1</sub>, P<sub>2</sub>, P<sub>3</sub>, respectively.

Soil from each P treatment was used to fill in 500-g capacity earthen pots and inoculated with 50 g of a consortium of AM fungi comprising 40 infectious propagules  $\rm g^{-1}$  of soil as spores, hyphae and infected root pieces. Inoculum was applied in a hole beneath the seed site, and two seeds were sown in each pot; they were thinned to one after one week of germination. Control pots received only 20 ml of filtered (Whatman No.1) washings of a mixture of fungal inoculants (Koide and Li, 1989). Each treatment was replicated thrice and arranged in a completely randomized design in a glasshouse providing light intensity of 2400  $\mu E/m^2$ .s at 400–700 nm and 40/37°C day/night temperature with 70–80% relative humidity. Pots were watered when required. The experiment was terminated after six weeks.

Fresh weights of shoots and roots were recorded; the tissue was dried at 68°C for 48 h and reweighed for dry weight values. P and Zn concentrations were measured by the vanadomolybdate method (Jackson, 1958) and by Atomic Absorption Spectroscopy (GBC 902, Switzerland), respectively. Root subsamples were used for measurement of fungal colonization after clearing and staining with trypan blue (Phillips and Hayman, 1970) and for detection of alkaline phosphatase activity. Infection rating was done according to McGonigle et al. (1990) and expressed as total colonization (M% - percentage of root cortex with infection) or arbuscular colonization (AC% - percentage of root cortex with arbuscules) and hyphal colonization (HC% - percentage of root cortex with hyphae). Mycorrhizal responsiveness was calculated for each genotype at various P levels, as follows: percent mycorrhizal responsiveness = {(dry weight of mycorrhizal shoot – dry weight of non-mycorrhizal shoot/dry weight of non-mycorrhizal shoot) × 100} (Hetrick et al., 1992).

### Preparation of inoculum

Indigenous mycorrhizal propagules in soil (spores/sporocarps/hyphae/root bits) served as inoculum and were multiplied on maize ( $Zea\ mays\ L.\ var.\ Naveen$ ) for four growth cycles of 45 d each. Spores were isolated by the wet sieving and decanting technique (Gerdemann and Nicolson, 1963), surface sterilized by 2% chloramine T (w/v), 0.02% streptomycin (w/v), 0.01% gentamycin (w/v) and 2 drops of Tween-20. They were subjected to mass culturing in sterilized sand, which gave a homogeneous indigenous AM inoculum (dominated by  $Acaulospora\ scrobriculata$ ,  $Gigaspora\ albida$ , and  $Glomus\ intraradices$ ) containing 40 infectious propagules  $g^{-1}$  soil as determined by the most probable number method (Porter, 1979).

### Quantitative estimation of phosphatase

After harvesting, roots were washed carefully in 4°C distilled water to remove soil debris and detached immediately for phosphatase analysis. They were cut from upper and lower portions, collected from the median part of the root after eliminating the main root of the first order. One g fresh root was homogenized in a pestle and mortar at 4°C using 0.1 M borate buffer (1:1 w/v), pH 8.0 containing 1% glutathione. The macerate was centrifuged at 20,000 rpm for 10 min and the supernatant was collected. To 0.1 ml enzyme extract, 0.5 ml of Tris citrate buffer (pH 8.5, 5.5 mM) was added followed by MgCl<sub>2</sub> (0.5 mM). An enzyme blank was prepared with borate buffer in place of enzyme extract; tubes were incubated at 37°C for 30 min. The reaction was terminated by adding 5 ml of 0.05 M NaOH and release of p-nitrophenol was measured at 405 nm.

The values were converted to  $\mu$ moles of p-nitrophenol with reference to standard curve prepared with p-nitrophenol. Enzyme activity was expressed as mU/ml of root extract where U, 1 enzyme unit, is that enzyme activity which transform 1  $\mu$ mole of substrate in 1 minute under the specific experimental conditions (Gianinazzi-Pearson and Gianinazzi, 1976).

## Statistical analysis

The data were analyzed using a three-factorial Complete Randomized design.

### 3. Results

### Plant growth

Mycorrhizal inoculation had a positive effect on vegetative plant growth at

 $P_0$  and  $P_1$  levels; at higher P levels ( $P_2$  and  $P_3$ ) both negative and positive growth responses were observed. Genotypes VL90 and VL16 responded positively to mycorrhizal inoculation only at  $P_0$  and  $P_1$  levels; for genotype VL89, this response occurred at the  $P_2$  and  $P_3$  level. Genotype HIM129 achieved maximum shoot dry weight through AM inoculation at  $P_2$  level. Mycorrhizal plants of all genotypes except VL89 showed growth depression at  $P_3$  level, while the response of non-mycorrhizal plants was positive to fertilizer application even at the highest level i.e.,  $P_3$ ; VL90 was an exception. Irrespective of mycorrhizal inoculation, phosphorus levels  $P_2$  and  $P_3$  were optimum for growth of maize plants with the most shoot dry weight accumulation (Table 1). Genotype VL89 could benefit from mycorrhizal inoculation only at  $P_2$  and  $P_3$  levels; however at  $P_0$  and  $P_1$  level, the difference between mycorrhizal and non-mycorrhizal shoot biomass was non-significant.

The pattern for root biomass accumulation was similar to that of shoot growth. The detrimental effect of P at P<sub>3</sub> level was more evident on root growth of mycorrhizal plants; in non-mycorrhizal plants, such an effect was limited to genotype VL90 at P<sub>3</sub> level. Irrespective of phosphorus treatment, mycorrhizal inoculation significantly increased root growth of all genotypes except VL89, where results were non-significant compared with non-mycorrhizal plants (Table 2).

### Phosphorus concentration and uptake

In all four genotypes, plants colonized by mycorrhizal fungi had more phosphorus in shoot than uncolonized plants at all phosphorus levels. It is noteworthy that in these genotypes shoot phosphorus concentration in mycorrhizal plants at  $P_0$  level was significantly higher than that achieved in non-mycorrhizal plants at  $P_3$  level (Table 3). Irrespective of the phosphorus level, in non-mycorrhizal treatments, maximum shoot P concentration was recorded in genotype HIM129 followed by VL89, VL16 and VL90. Phosphorus uptake pattern was quite different in these genotypes, but uptake was significantly higher in mycorrhizal plants compared to non-mycorrhizal plants at all phosphorus levels, except for HIM129 at the  $P_3$  level. However, when calculated on the basis of percent increase over control, P optima i.e., the level at which a genotype could best benefit from the AM symbiosis, was  $P_1$  for VL90,  $P_3$  for VL89, and  $P_2$  for VL16 and Him129 (Fig. 1).

## Zinc concentration and uptake

Mycorrhizal inoculation resulted in improved zinc concentration in shoots of all the genotypes at various phosphorus levels; genotype HIM129 at P<sub>3</sub> level

Shoot dry weights of four maize genotypes grown at different soil P levels with or without AM inoculation Table 1.

Genotype	$P_0$			$P_1$			$P_2$			P3			Myco	rrhiza	Aycorrhiza vs. genotype
	M	NM	Mean	Z	NM	Mean	M	NN	Mean	Σ	NM	Mean	M	NM	Mean
VL90	1.32		1.15	1.57	1.32	1.45	1.48	1.96	1.72	1.4	1.8	1.6	1.44	1.51	1.48
VL16	1.64		1.40	1.71	1.30	1.51	1.63	1.86	1.75	1.6	2.0	1.8	1.65	1.57	1.61
VL89	1.32	1.34	1.33	1.69	1.68	1.69	1.91	1.73	1.82	2.53	1.73	2.13	1.86	1.62	1.74
HIM129	1.77		1.38	1.83	1.19	1.51	2.55	1.46	2.01	1.27	1.98	1.63	1.86	1.41	1.63
Mean	1.51		1.31	1.7	1.37	1.54	1.89	1.75	1.82	1.7	1.88	1.79	1.7	1.53	
CD at 5%	Genot 0.04	Genotype (I)		Phosph 0.04	phorus (J)	<u> </u>	Myco 0.03	Mycorrhiza 0.03	(K)		1J 0.08	IK 0.06	9	JK 0.06	IJK 0.12

Data are presented after three factorial analyses and P0, P1, P2, and P3 represent four soil P levels where SSP was supplemented to provide 0, 60, 90 and 120 mg P kg<sup>-1</sup> soil. M = mycorrhizal, NM = non-mycorrhizal.

Root dry weights of four maize genotypes grown at different soil P levels with or without AM inoculation Table 2.

Genotype	$^{P_0}$			P <sub>1</sub>			P <sub>2</sub>			P3			Myco	rrhiza	Mycorrhiza vs. genotype
	Σ	NM	Mean	M	NM	Mean	M	NM	Mean	Σ	NM	Mean	Σ	NM	Mean
VL90	2.29	1.65	1.97	3.53	1.89	2.62	2.75	F.9	2.33	1.28	1.14	1.21	2.42	1.65	2.03
VL16	2.4	1.27	1.83	3.12	1.56	2.34	3.1	1.64	2.37	1.5	1.68	1.59	2.53	1.54	2.03
VL89	1.03	1.19	1.11	1.3	1.45	1.38	1.36	1.35	1.36	1.46	1.3	1.38	1.29	1.32	1.31
HIM129	1.2	0.67	0.94	1.25	0.77	1.01	1.37	98.0	1.12	1.10	0.87	1.01	1.23	0.79	1.01
Mean	1.73	1.19	1.46	2.26	1.42	1.84	2.15	1.44	1.79	1.34	1.25	1.29	1.87	1.32	
CD at 5%	Genotype (1 0.04	ype (I)		Phosph 0.04	horus (	<u> </u>	Myco 0.03	Mycorrhiza 0.03	(K)		0.08	IK 0.05	2	JK 0.05	IJK 0.11

Data are presented after three factorial analyses and P0, P1, P2, and P3 represent four soil P levels where SSP was supplemented to provide 0, 60, 90 and 120 mg P kg<sup>-1</sup> soil. M = mycorrhizal, NM = non-mycorrhizal.

Table 3 Shoot P concentrations of four maize genotypes grown at different soil P levels with or without AM inoculation

M         NM         Mean         M         Mean           VL90         1475         719         1097         1825         744         1284.5           VL16         1431         644         1037.5         1838         675         1256.5           VL16         1450         585         1017.5         1550         769         159.5           HIM129         1531         744         1137.5         1594         1000         1297           Mean         1471.75         673         1072.38         1701.75         797         1249.38           Genotype         Mycorrhiza vs. genotype         M         Mean           VL90         806.25         830.58         1318.42           VL16         1859.25         883.0         1371.13           VL89         1551.17         903.25         1227.21           HIM129         1637.17         1034.0         1336.04           Mean         1034.0         1336.04	$P_1$		$P_2$			$F_3$		
1475 719 1097 1825 744 1431 644 1037.5 1838 675 1450 585 1017.5 1550 769 1531 744 1137.5 1594 1000 1471.75 673 1072.38 1701.75 797  Mycorthiza vs. genotype  M NM Mean  806.25 830.58 1318.42 1859.25 883.0 1371.13 1551.17 903.25 1227.21 1637.17 1034.0 1336.04	M	Mean	M	NM	Mean	M	NM	Mean
1431 644 1037.5 1838 675 1450 585 1017.5 1550 769 1531 744 1137.5 1594 1000 1471.75 673 1072.38 1701.75 797  Mycorrhiza vs. genotype  M NM Mean  806.25 830.58 1318.42 1859.25 883.0 1371.13 1551.17 903.25 1227.21 1637.17 1034.0 1336.04	1825	1284.5	1925	0.906	1415.5	2000.0	953.33	1476.67
1450 585 1017.5 1550 769 1531 744 1137.5 1594 1000 1471.75 673 1072.38 1701.75 797  Mycorrhiza vs. genotype  M NM Mean  806.25 830.58 1318.42 1859.25 883.0 1371.13 1551.17 903.25 1227.21 1637.17 1034.0 1336.04	1838	1256.5	2137	1138.0	1637.67	2030.67	1075.0	1552.83
1531 744 1137.5 1594 1000 1471.75 673 1072.38 1701.75 797 Mycorrhiza vs. genotype  M NM Mean  806.25 830.58 1318.42 1859.25 883.0 1371.13 1551.17 903.25 1227.21 1637.17 1034.0 1336.04	1550	1159.5	1575	1009.0	1292.0	1629.0	1250.0	1439.83
1471.75 673 1072.38 1701.75 797  Mycorrhiza vs. genotype  M NM Mean  806.25 830.58 1318.42 1859.25 883.0 1371.13 1551.17 903.25 1227.21 1637.17 1034.0 1336.04	1594	1297	1705	1158	1431	1718.0	1237.67	1477.83
Mycorrhiza vs. genotype  M NM  806.25 830.58 1859.25 883.0 1551.17 903.25 1637.17 1034.0	1701.75	1249.38	1835.75	1052.75	1444.25	1844.58	1129.0	1486.79
806.25 830.58 1859.25 883.0 1551.17 903.25 1637.17 1034.0	genotype							
806.25 830.58 1859.25 883.0 1551.17 903.25 1637.17 1034.0								
1859.25     883.0       1551.17     903.25       1637.17     1034.0       1637.17     1034.0								
1551.17 903.25 1637.17 1034.0 1637.17 1034.0								
1637.17 1034.0 1 1637.17 1034.0								
1637.17								
	1034.0							

Data are presented after three factorial analyses and P<sub>0</sub>, P<sub>1</sub>, P<sub>2</sub>, and P<sub>3</sub> represent four soil P levels where SSP was supplemented to provide 0, 60, 90 and 120 mg P kg<sup>-1</sup> soil. M = mycorrhizal, NM = non-mycorrhizal.

IJK 79.02

JK 39.51

IK 39.51

IJ 55.88

Mycorrhiza (K)

19.76

Phosphorus (J) 27.94

Genotype (I) 27.94

CD at 5%

was an exception (data not shown). Zinc uptake in mycorrhizal shoots was significantly higher compared to non-mycorrhizal control plants but only up to  $P_2$  level; the differences at  $P_3$  level were non-significant between mycorrhizal and non-mycorrhizal shoots, viz., VL90 and VL16 or uptake was significantly lower i.e., HIM129. With the exception of genotype VL89, in non-mycorrhizal treatments, zinc uptake increased with change in phosphorus level; however the increase was non-significant between  $P_2$  and  $P_3$  levels in genotypes VL16 and VL90 (Fig. 2).

### Mycorrhizal colonization and responsiveness

As judged by total, arbuscular and hyphal components, mycorrhizal colonization varied considerably among the genotypes and also at different phosphorus levels. Addition of P decreased AM colonization (total as well as arbuscular) in genotype VL90, while the reverse was true for genotype VL89. Maximum total and arbuscular colonization at  $P_2$  level was observed in HIM129, however increase in total colonization was non-significant between  $P_0$  and  $P_1$  levels. For genotype VL16,  $P_1$  level was best suited for mycorrhizal proliferation. Hyphal colonization appeared to be inversely affected by P application in genotypes VL90 and VL16; in HIM129, it increased with P concentration in soil (Fig. 3). Parallel to mycorrhizal colonization, fertilizer application consistently decreased the mycorrhizal responsiveness (based on shoot dry weight) in genotype VL90 and VL16. In genotype HIM129, highest response to AM inoculation was observed at  $P_0$  and  $P_2$  levels; for genotype VL89 it was at  $P_3$  (Fig. 4).

## Alkaline phosphatase

Irrespective of available phosphorus, alkaline phosphatase (ALPase) activity of maize roots was increased significantly in these genotypes as a result of mycorrhization. The increase was most noticeable at  $P_0$  and  $P_1$  levels in genotype VL90;  $P_0$ ,  $P_1$ , and  $P_2$  levels in genotype VL16;  $P_2$  and  $P_3$  in genotype VL89 and at all four levels in genotype HIM129. ALPase activity of non-mycorrhizal roots remained either unaffected by soil  $P_1$  level, i.e., genotype VL89 and HIM129, or increased with increase in phosphorus level, i.e., VL90. In genotype VL16, an increase in ALPase activity was observed at  $P_1$  compared to  $P_0$  followed by a sharp decrease at  $P_2$  and  $P_3$  levels (Fig. 5).

#### 4. Discussion

The AM fungal consortium used in this study increased significantly the

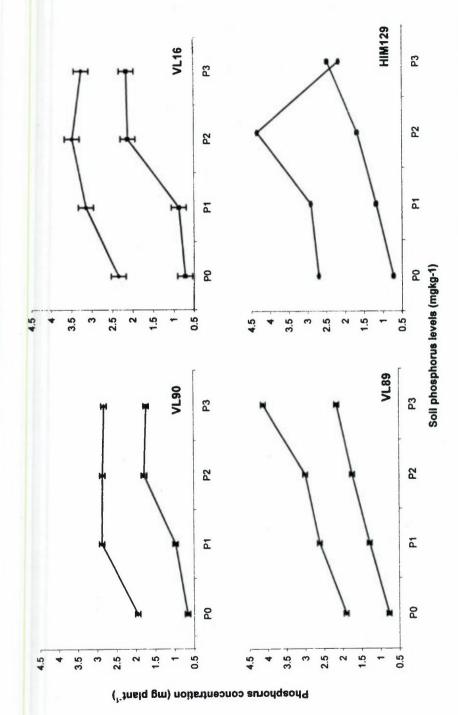


Figure 1. Phosphorus concentration in mycorrhizal (♦) and non-mycorrhizal (■) shoots of maize (Zea mays L.) genotypes at four soil phosphorus levels.

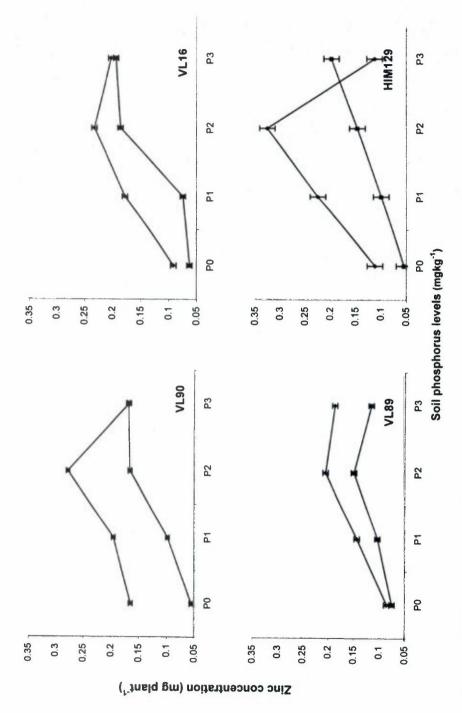


Figure 2. Zinc concentration in mycorrhizal (�) and non-mycorrhizal (■) shoots of maize (Zea mays L.) genotypes at four soil phosphorus levels.

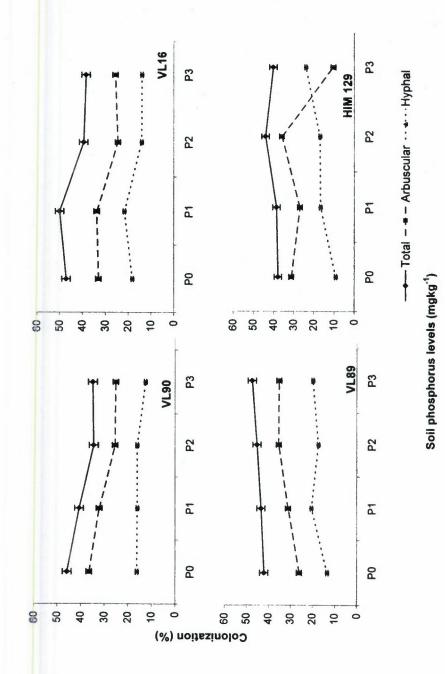


Figure 3. AM colonization of maize genotypes at different soil P levels.

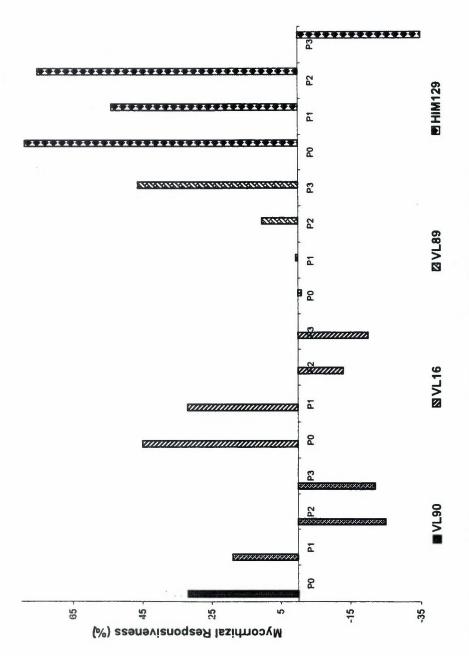


Figure 4. Mycorrhizal responsiveness of maize genotypes at four soil phosphorus levels.

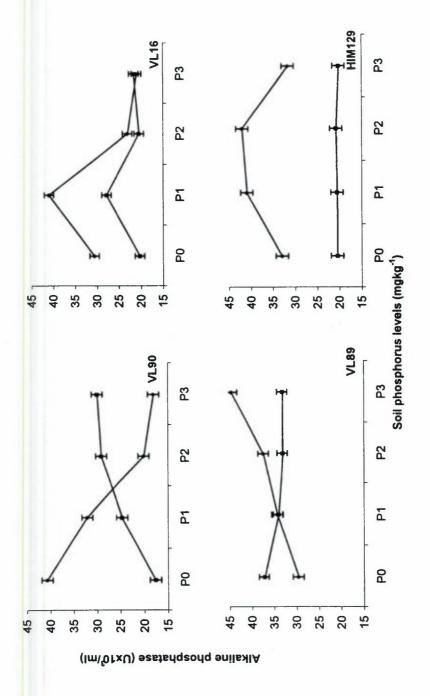


Figure 5. Alkaline phosphatase activity in mycorrhizal (�) and non-mycorrhizal (■) roots of maize (Zea mays L.) genotypes at four soil phosphorus levels.

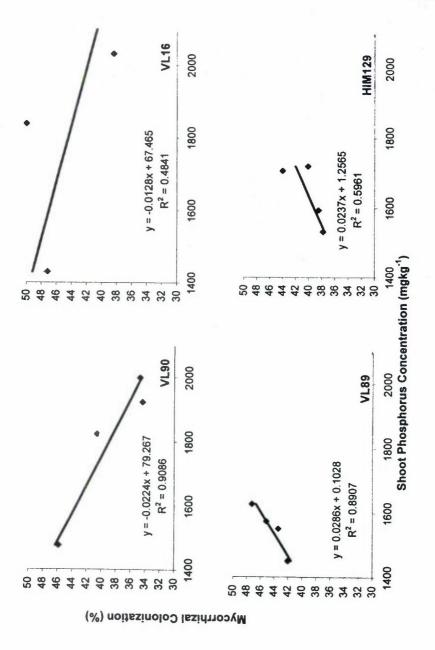


Figure 6. Correlation between mycorrhizal colonization and shoot phosphorus concentration in different genotypes of maize (Zea mays L.).

vegetative plant growth (root and shoot, dry weights) of all the four maize genotypes. Since mycorrhizal infection usually results in increased allocation of C to the root, it implies increased root and mycelial biomass; that would explore more area for nutrients and consequently result in higher uptake rates (Jakobsen, 1995). However, such a mycorrhizal growth response was observed only at P<sub>0</sub> and P<sub>1</sub> levels for genotype VL90 and VL16; P<sub>2</sub> and P<sub>3</sub> levels for genotype VL89 and P<sub>0</sub>, P<sub>1</sub> and P<sub>2</sub> levels for genotype HIM129. This suggested that each genotype responded in a characteristic manner to fertilizer application and mycorrhizal inoculation. This may be due to inherent differences in their ability to acquire and utilize phosphorus besides their inherent requirement (Bryla and Koide, 1998). Omar (1995), has reported increased dry matter yield in maize plants inoculated with *G. constrictum* at P levels of up to 30 and/or 60 mg kg<sup>-1</sup> soil; above this level, the dry matter yield began to decrease.

In our study, all genotypes except VL89, exhibited growth depression in shoots and roots of AM plants at either 90 mg kg<sup>-1</sup> or 120 mg kg<sup>-1</sup> P level, possibly as a consequence of P toxicity (Antunes and Cardoso, 1991). These observations receive support from the available data on AM-induced growth depression at high P in other plant systems (Graham and Eissenstat, 1992). It would appear that the cost of maintenance of mycorrhizal fungus exceeds the benefit to the host (Koide, 1991). This negative impact was more pronounced in genotypes VL90 and VL16, since they had a low phosphorus requirement and were therefore more sensitive to excess phosphorus.

In contrast, in non-mycorrhizal plants, no growth depression was observed except in genotype VL90 at P<sub>3</sub> level. This positive response to phosphate in non-mycorrhizal plants appears to reduce the overall mycorrhizal growth effect (Guillemin et al., 1995). Genotype VL89 is of special interest, since it responded to mycorrhizal inoculation only at higher phosphorus levels, i.e., 90 mg kg<sup>-1</sup> or 120 mg kg<sup>-1</sup> soil; these levels were toxic to other maize genotypes. It can be speculated that this genotype has a rather high P demand.

AM inoculation increased shoot and root phosphorus, and shoot zinc concentration significantly at all phosphorus levels, although improved growth responses were observed only at low soil P levels in VL90 and VL16. Present data are in agreement with the observations of Smith and Gianinazzi-Pearson (1988), who reported that at low soil nutrient level/status, a marked growth response to mycorrhizal infection could be expected; this may not be apparent when nutrients are readily available, although other effects on the physiology of plants such as increased P uptake and concentration in tissue may still take place. In non-mycorrhizal plants, on the other hand, P content increased with phosphorus levels in soil with a maximum at P<sub>3</sub>.

However, it apparently was not sufficient to meet the P demand of the host. This is borne out by the observation that maximum P content in non-mycorrhizal

plants at  $P_3$  level was still lower than the phosphorus content of mycorrhizal plants at  $P_0$  level. Therefore, the actual response to mycorrhizal infection is predicted to be a function of the increase in phosphorus uptake due to mycorrhizal infection and the phosphorus utilization efficiency of the plant (Bryla and Koide, 1998).

In addition, critical analysis of data shows that maize genotypes (VL89 and Him129) with comparatively greater responsiveness to AM had higher shoot P concentration in the absence of a fungal symbiont, while the less responsive ones (VL90 and VL16) had lower shoot P concentration. Comparatively more responsive maize genotypes seem to have greater phosphorus requirement and consequently rely more on the symbiotic association to satisfy these requirements (Adjoud et al., 1996). The patterns of P and Zn uptake in shoot appeared to be genotype-specific and were somehow related to their phosphorus requirements.

Alkaline phosphatase activity was significantly higher in mycorrhizal compared to non-mycorrhizal plants at those phosphorus levels where mycorrhizal growth responses were positive. Reduced ALPase activity in mycorrhizal roots of soybean by phosphate fertilization has been reported (Gianinazzi-Pearson and Gianinazzi, 1983); in a parallel fashion, decrease in ALPase activity was observed at higher P levels (Guillemin et al., 1995). Contrary to the previous reports, our results show that small addition of P to soil increased the ALPase activity in both mycorrhizal and non-mycorrhizal plants. All such responses were, however, genotype dependent.

The intensity of AM colonization in the four genotypes was different (Graham et al., 1981; Graham and Eissenstat, 1992). This supports the previous hypothesis that mycorrhizal development is under host genetic control (Hetrick et al., 1996). Available evidence based on trypan blue staining suggests that high concentrations of soil P result in reduced AM infection (Mosse, 1973; Graham et al., 1981; Trouvelot et al., 1986; Amijee et al., 1989; DeMiranda et al., 1989; Braunberger et al., 1991); such an effect was also observed in maize roots. In the present experiments, small P addition to soil supported AM infection, while higher P levels decreased it.

But all such responses were variable with respect to genotype, e.g., genotype VL90 had maximum root colonization at P<sub>0</sub> level, while in genotype VL89, AM colonization was increased with phosphorus levels reaching a maximum at P<sub>3</sub> level. These data receive support from the observation that the response to phosphate fertilization varies with the plant viz., in some high soil P may effectively eliminate infection, whereas in others infection level is maintained over a range of soil phosphorus concentrations (Baon et al., 1992; Bolan et al., 1987). There was a strong negative linear correlation between shoot P concentration and total AM colonization in genotype VL90 and VL16 (Fig. 6). Shoot and root P concentrations have often been reported to exhibit this

relationship with AM colonization (Lu et al., 1994; Ryan, 1998). This is in consonance with the impact of P being mediated through the effect of phospholipid content on root cell membrane permeability and exudation of carbohydrates on which the fungi are dependent for energy (Graham et al., 1981); this correlation was positive for genotypes VL89 and HIM129 which is a reflection of difference in physiological interactions between AM fungi and the maize genotypes.

In the present study, no definite relationship was observed between mycorrhizal (total/arbuscular) colonization and responsiveness (data not shown). This supports the previous hypothesis that colonization is not a good indicator of AM efficiency for plant growth (Schubert and Hayman, 1986; Vierheilig and Ocampo, 1989). The external phase of infection needs to be considered for better understanding of host-mycorrhiza interaction at the physiological level. Graham et al. (1982) had suggested that the amount of external mycelium was indicative of the efficiency of AM infection.

In conclusion, the present observations show that high and low soil P levels are not likely to be inhibitory or stimulatory for AM symbiosis but, it is rather the host, that determines the impact of soil P on symbiosis. This is true not only at the genus level, but also at the genotype level and appears to be related to their P requirement. AMF are an integral component of the majority of plant systems and therefore, their natural association during the cropping practices requires critical balancing to sustain better plant growth and soil fertility status.

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