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Influence of phosphorus and endomycorrhiza (*Glomus intraradices*) on gas exchange and plant growth of chile ancho pepper (*Capsicum annuum* L. cv. San Luis)

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Abstract

Seedlings of chile ancho pepper were grown in pots containing a pasteurized mixture of sand and a low phosphorus (P) sandy loam soil, and either inoculated (VAM) or not inoculated (NVAM) with the endomycorrhizal fungus *Glomus intraradices*. Long Ashton nutrient solution (LANS) was modified to supply P to the seedlings at 0, 11, and 44 g(P) m^{-3} (P_0, P_{11}, P_{44}, respectively). Low P depressed net photosynthetic rate (P_N), stomatal conductance (g_s), phosphorus use efficiency (P_N/P), and internal CO_2 concentration (C_i). The mycorrhiza alleviated low P effects by increasing P_N, g_s, P_N/P, and decreasing C_i. At P_0, C_i of NVAM plants was equal to or higher than that of VAM plants, suggesting nonstomatal inhibition of photosynthesis. Gas exchange of VAM plants at P_0 was similar to that of NVAM plants at P_{11}. Endomycorrhiza increased leaf number, leaf area, shoot, root and fruit mass at P_0 and P_{11} compared to NVAM plants. Reproductive growth was enhanced by 450 % in mycorrhizal plants at P_{44}. Root colonization (arbuscules, vesicles, internal and extraradical hyphae development) was higher at lower P concentrations, while sporulation was unaffected. The enhanced growth and gas exchange of mycorrhizal plants was in part due to greater uptake of P and greater extraradical hyphae development.

Additional key words: fruit; internal CO_2 concentration; leaf area ratio; leaf number and area; net photosynthetic rate; phosphorus use efficiency; root; shoot; stomatal conductance.

Introduction

Endomycorrhiza (VAM) can increase plant growth. This beneficial effect has frequently been attributed to higher P uptake and enhanced P nutrition of mycorrhizal

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plants (Baylis 1972, Lynch 1990, Davies and Linderman 1991, Kothari *et al.* 1991, Smith and Read 1997). The P_N of mycorrhizal plants is also increased as a result of improved plant nutritional status (Koch and Johnson 1984, Fitter 1988). However, improved P_N of mycorrhizal plants can be independent of P status (Bethlenfalvay *et al.* 1987, Davies *et al.* 1993). The benefit of mycorrhiza to native plant species is greatest at low soil P, but declines rapidly at moderate P deficiency (Jasper and Davey 1993); sporulation may be affected, although spore number is not necessarily related to the degree of colonization of the host root system (Hetrick and Bloom 1986).

The objectives of this research were: (*1*) to determine the influence of endomycorrhiza in alleviating low P effects of mycorrhizal chile ancho pepper plants based on plant growth and gas exchange characteristics, and (*2*) to evaluate the influence of P on mycorrhizal development of arbuscules, vesicles, and intraradical and extraradical hyphae formation. A long-term goal of this research is to demonstrate the usefulness of mycorrhiza for more efficient utilization of P fertilization in sustainable production systems for this important agricultural crop in Mexico.

Materials and methods

Plants: Seeds of *Capsicum annuum* L. (chile ancho cv. San Luis) were sown in a medium of pasteurized peat : perlite (1 : 1, v/v), on 25 March 1994, and transplanted five weeks later into 1 700 cm^3 pots containing coarse sand : low P sandy loam soil (1 : 1, v/v) with a textural analysis of 85 % sand, 10 % clay, and 5 % silt. The pot medium was previously steam pasteurized during two consecutive days for 5 h d^{-1} at 80 °C. Plants were irrigated during the first week, and subsequently irrigated and fertilized as needed, using 200 cm^3 per pot of modified Long Ashton nutrient solution (LANS, Hewitt 1966) to supply three phosphorus concentrations: 0, 11, and 44 g(P) m^{-3}. The mycorrhizal treatments were: *Glomus intraradices* Schenck & Smith (VAM) and the noninoculated control (NVAM). The experiment was a 2×3 factorial in a completely randomized design with two levels of VAM and three levels of P. There was one plant per pot with each pot as a single replicate. All results were analyzed using Analysis of Variance (ANOVA) (SAS Institute 1988).

For VAM colonized plants, 200 g of soil containing 6 500 spores and colonized root segments of strawberry host plants were used as inoculum. The inoculum was applied as a band in the middle of the pot. During the 52 d of the study, the environmental conditions in the greenhouse were: maximum photosynthetic photon flux (PPF) of 1100 µmol m^{-2} s^{-1}, mean day/night temperature 27/23 °C, and mean day/night relative humidity 82/92 %.

Gas exchange: P_N, g_s, and C_i were measured with a *LiCor 6200* Portable Photosynthesis System (*LiCor*, Lincoln, NE, USA) at 15 and 50 d after transplanting from 09:00-11:00 h to assess gas exchange on five plants per treatment from two newly matured leaves per plant ($n = 10$). Measurements were made with ambient

CO_2 concentration of about 360 cm^3 m^{-3} under 1000 μmol m^{-2} s^{-1} of PPF supplied from a 400 W high pressure sodium vapor lamp filtered through 5 cm of water enclosed in a plexiglas box. The efficiency of PPF per unit of leaf P concentration, phosphorus use efficiency (PUE), was calculated as P_N/P.

Plant growth and development and leaf tissue elemental analysis: Final growth measurements of fifteen plants per treatment ($n = 15$) were taken at day 52 after transplanting, and included leaf area, leaf number, fruit and root dry mass, shoot dry mass (stem, leaves, fruit dry mass), root/shoot ratio, and leaf area ratio (LAR). Leaves were analyzed for phosphorus with an inductively coupled atomic emission spectrophotometer (*3510 ICP, W.R. Grace & Co.*, Fogelsville, PA, USA). From fifteen plants per treatment, newly matured leaves from 3 plants were pooled into a single sample for analysis ($n = 5$).

Mycorrhizal development: Soil aggregation, as a measure for extraradical hyphae development, was assessed by allowing the soil of five potted plants from each treatment to dry at room temperature (25 °C), extracting the root system, and shaking it gently in order to obtain pieces of soil attached to roots and bound by fungal hyphae (Graham *et al.* 1982, Kough and Linderman 1986). The attached soil was then removed by washing the roots, collecting the remnant soil, and drying it in a forced air oven. The soil dry mass divided by root dry mass was utilized to calculate the extraradical hyphae index (ERH index).

For spore counts, 100 g samples of soil from five plants per treatment ($n = 5$) were processed through glycerol flotation and spore extraction methods (Furlan and Fortin 1975, Schenck 1982). The supernatant was resuspended in 20 cm^3 of distilled water, and three replicates of 1.0 cm^3 were taken for spore counts.

For VAM analysis of roots, 1-cm root segments from 15 plants per treatment were sampled at harvest and pooled to assess colonization percentage through clearing and staining of the root samples (Phillips and Hayman 1970). Ten 1-cm stained root pieces were placed on each slide and three microscopic observations per 1-cm root piece at 40× were made at the top, middle, and bottom of each root piece. There were 15 slides per treatment (450 observations per treatment). The presence of arbuscules, vesicles, and hyphae were recorded and the values obtained were statistically analyzed using Chi-square analysis with a 2-test pair separation.

Results

Gas exchange: Low P depressed P_N, g_s, phosphorus use efficiency (P_N/P), and C_i (Fig. 1). Endomycorrhiza helped alleviate low P effects at days 15 and 50, increasing P_N, g_s, and P_N/P, while decreasing C_i (Fig. 1). At P_0, C_i of NVAM plants was equal to or higher than VAM, suggesting nonstomatal inhibition of photosynthesis (Fig. 1*E,F*). Gas exchange of VAM plants at P_0 was similar to that of NVAM plants at P_{11} (Fig. 1), as was tissue P concentration (Table 2). VAM plants tended to have higher P_N and g_s than NVAM plants across the range of P supplied (Fig. 1). At P_0, VAM plants had higher P_N/P than NVAM plants, whereas at P_{11} and P_{44}, P_N/P of the VAM plants was lower than that of the NVAM plants (Fig. 1*G,H*).

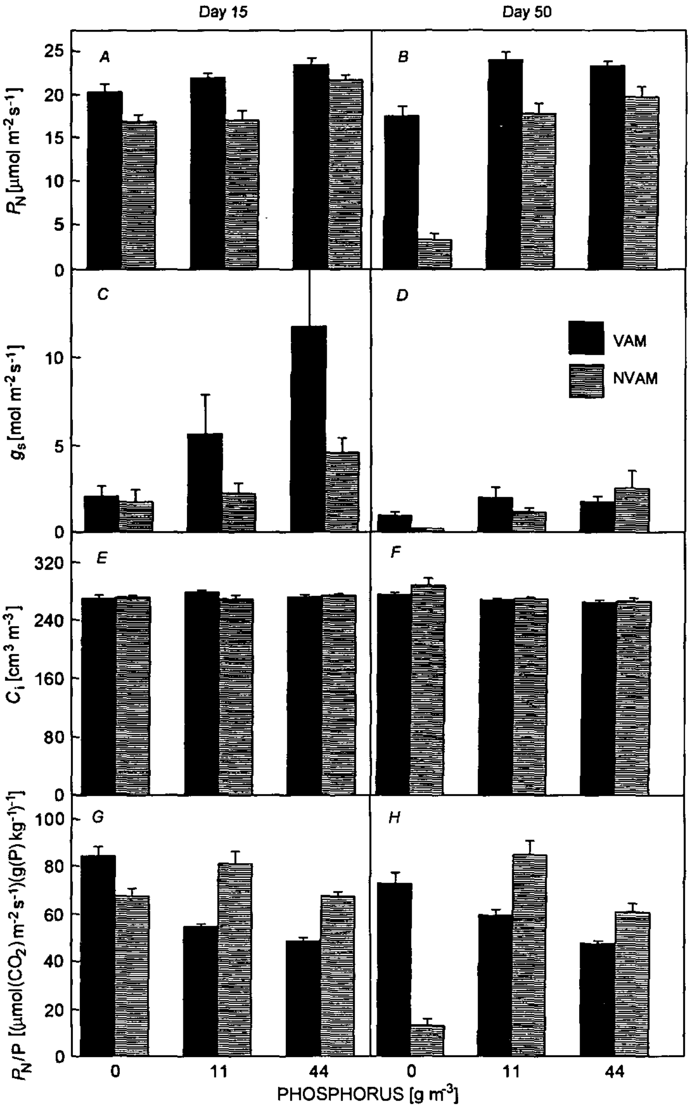

Fig. 1. Net photosynthetic rate (P_N), stomatal conductance (g_s), internal CO_2 concentration (C_i), and phosphorus use efficiency (P_N/P) of mycorrhizal (VAM) and noncolonized (NVAM) chile ancho pepper plants ferilized with 0, 11, and 44 g(P) m^{-3}. Plants were analyzed at days 15 and 50 after transplanting. Means ± SE, $p<0.05$, n = 10. Solid black histograms are VAM, while histograms with horizontal lines are NVAM treatments.

Plant growth: Greatest growth reduction occurred with NVAM plants at P_0, as reflected by decreased leaf number and area, root, shoot, and fruit dry mass, and the LAR, and an increased root/shoot ratio at P_0 (Table 1). At P_0, endomycorrhiza increased all growth parameters including leaf size (11.7 *versus* 4.0 cm^2) and decreased the root/shoot ratio compared to noncolonized plants. At P_{11}, VAM also increased all growth parameters, except fruit dry mass and the root/shoot ratio. At P_{44}, reproductive growth was 450 % greater in VAM plants, even though vegetative

Table 1. Effect of the endomycorrhizal (VAM) fungus (*Glomus intraradices*) and three phosphorus levels (indices of P in g m^{-3}) on the growth and development of Chile pepper (*Capsicum annuum* L. cv. San Luis). Means with standard error and ANOVA; $n = 15$. NS = nonsignificant, * = significant at 5 % level, ** = significant at 1 % level, *** = significant at 0.1 % level. d.m. = dry mass.

	P	Leaf number	Leaf area [cm^2]	Fruit d.m. [g]	Root d.m. [g]	Shoot d.m. [g]	LAR [m^2 kg^{-1}]	Root/shoot [kg kg^{-1}]
VAM	P_0	37±2	435±37	0.3±0.2	1.7±0.1	5.3±0.2	6.2±0.4	0.3±0
	P_{11}	60±2	761±30	0.3±0.2	2.7±0.1	8.9±0.4	6.6±0.2	0.3±0
	P_{44}	88±2	1390±23	0.9±0.3	4.5±0.1	17.8±0.3	6.2±0.1	0.3±0
NVAM	P_0	15±1	61±7	0.0±0.0	0.7±0.0	0.9±0.1	3.8±0.3	0.8±0
	P_{11}	54±2	607±16	0.1±0.0	1.9±0.1	6.4±0.2	7.3±0.2	0.3±0
	P_{44}	86±1	1414±37	0.2±0.1	4.4±0.2	17.3±0.3	6.5±0.1	0.3±0
Signif.:								
VAM		***	***	*	***	***	**	***
P		***	***	NS	***	***	***	***
VAM×P		***	***	NS	***	***	***	***

growth was similar to NVAM plants. The LAR (leaf area/root and shoot mass), that relates total plant dry matter production with the leaf area as an index of photosynthetic capacity, did not differ among colonized plants, but was lowest at the P_0 NVAM treatment which also had the greatest growth suppression.

Leaf P elemental analysis: At P_0, VAM plants had similar P content as NVAM plants (Table 2). However, P at P_{11} and P_{44} was greater with VAM than NVAM plants.

Table 2. Arbuscule, vesicle, and hyphae formation of the endomycorrhizal (VAM) fungus *Glomus intraradices* with chile ancho peppper (*Capsicum annuum* L. cv. San Luis) at three levels of phosphorus (indices of P in g m^{-3}). $^{x}n = 5$. $^{y}n = 5$ (100 g samples of soil). ^{z}Means with standard error and ANOVA; $n = 450$ observations of 1-cm root segment per treatment. Values statistically analyzed using Chi-square analysis with a 2-pair test separation. NS = nonsignificant, * = significant at 5 % level, ** = significant at 1 % level, *** = significant at 0.1 % level. ERH = extraradical hyphae index.

	P	Leaf tissue P^{x} [%]	Arbuscules^{x,z} [%]	Vesicles^{x,z} [%]	Hyphae^{x,z} [%]	Spores^{y}	ERH [kg kg^{-1}]
VAM	P_0	0.24±0.02	96^{a}	65^{a}	98^{a}	441±78	43±8
	P_{11}	0.40±0.03	94^{a}	59^{a}	96^{a}	435±37	33±6
	P_{44}	0.48±0.03	96^{b}	44^{b}	75^{b}	345±23	17±2
NVAM	P_0	0.25±0.01	0	0	0	140±16	18±4
	P_{11}	0.21±0.02	0	0	0	153±12	25±4
	P_{44}	0.32±0.03	0	0	0	148±21	10±1
Signif.:							
VAM		***				***	***
P		***				NS	**
VAM×P		**				NS	NS

Mycorrhizal development: Root colonization (arbuscules, vesicles, internal and extraradical hyphae development) was higher at P_0 and P_{11} than at P_{44} (Table 2). The high percentage of arbuscules (71 to 96 %) observed in the root cortex of VAM plants indicates that a very active symbiosis occurred, even at full strength LANS (P_{44}). Increased soil aggregation (macroaggregates) was observed in mycorrhizal plants, as indicated by the higher extraradical hyphae index (ERH index). High P depressed extraradical hyphae development. Among VAM plants there were no differences in mycorrhizal development between P_0 and P_{11}. The quantity of spores recovered in soil was independent of P treatments. Spores observed in the nonmycorrhizal treatments were principally due to nonviable remnant spores from the original soil used to establish the experiment. None of the controls were colonized by VAM.

Discussion

This paper characterizes the ability of an endomycorrhiza, *Glomus intraradices*, to overcome low P supply in chile ancho 'San Luis'. The benefit of VAM on gas exchange occurred as early as 15 d after colonization when plants were still in a vegetative phase. The enhanced growth, development, and gas exchange of mycorrhizal plants were in part due to greater uptake of P and increased extraradical growth. P_N of mycorrhizal plants can increase as a result of improved plant nutritional status (Koch and Johnson 1984, Fitter 1988). However, under drought stress, improved P_N of mycorrhizal plants can also occur independent of P status (Bethlenfalvay *et al.* 1987, Davies *et al.* 1993). While tissue P was similar at P_0, plant biomass of VAM plants was greater than NVAM plants, so there was greater total plant acquisition of P. Mycorrhizal plants grown at P_{44} had a 450 % increase in reproductive growth, which also suggests the growth benefit of this symbiont under non-P limitation.

Greatest P-stress occurred with P_0 with dramatic reductions in gas exchange, vegetative and reproductive growth. Low P depressed P_N, g_s, and P_N/P, and increased C_i. Nonstomatal inhibition of photosynthesis occurred with NVAM plants since their C_i was higher or equal to VAM plants. Mycorrhizae affect phytohormone production which can also indirectly affect plant gas exchange (Duan *et al.* 1996, Harley and Smith 1983, Smith and Read 1997). With NVAM plants under low P, there was greater saccharide partitioning to the root system (higher root/shoot ratio) and a lower LAR. Greater carbon allocation to the root system allows for more extensive root development (relative to shoot growth). The P-stress induced reduction in photosynthesis limits carbon production which accounts for the lower LAR, *i.e.*, less transpiring and photosynthesizing surface per total plant mass (Hunt 1982).

Endomycorrhiza helped alleviate P-stress of chile ancho, increasing P_N, g_s, P_N/P, and decreasing C_i. Gas exchange of VAM plants at P_0 was similar to NVAM plants at P_{11} (plants from both treatments had the same tissue P). P nutrition may be central to mycorrhizal enhancement of plant growth and its subsequent application to low input sustainable agricultural systems (Bethlenfalvay and Linderman 1992).

P_N/P is an index relevant to studies of this nature because P_N is a key growth parameter, and P deficiency limits crop productivity. High P_N/P values were found in mycorrhizal plants (Braun and Bethlenfalvay 1988, Davies *et al.* 1993). Plants with optimum P concentration should be more vigorous with higher P_N and g_s than plants with limiting P (Radin 1984, Dietz and Foyer 1986, Radin and Eidenbock 1986, Hensen *et al.* 1988). Low P can also reduce the concentration and activity of ribulose-1,5-bisphosphate carboxylase/oxygenase, and slow the regeneration of intermediate substances in the Calvin cycle (Lauer *et al.* 1989). Highest P_N/P occurred with VAM chile ancho plants at the lowest P level, whereas P_N/P was higher in noncolonized plants at P_{11} and P_{44}. This was because VAM chile ancho plants have higher P_N than noncolonized plants regardless of P fertility, and the uptake of P by VAM plants (0.40 and 0.48 % tissue P, respectively) is higher compared to NVAM plants at P_{11} and P_{44} (0.21 and 0.32 % tissue P, respectively). In another study with nonmycorrhizal *C. annuum* comparing a bell-pepper type with chile ancho, P_N/P was greatest at P_{11} across a gradient of P treatments that ranged from P_0 to P_{88} (Davies *et al.* 1999). In that study, P_N did not increase when P-supply was above P_{44} (tissue P of 0.22 and 0.23 % for bell pepper and chile ancho, respectively). Apparently there is a threshold level of around 0.20 to 0.25 % leaf tissue P where P_N is highest and P_N/P begins to decline. This also corresponds to commercially recommended levels for producing nutrient sufficient pepper plants (Maynard and Hochmuth 1997).

Mycorrhizal enhancement of plant growth and development at P_0 was not due to increased leaf tissue P (0.24 *versus* 0.25 % P for VAM and NVAM, respectively). However, the fact that P concentration was similar between VAM and NVAM plants at P_0 does not necessarily mean that P was not involved in growth enhancement. Sometimes leaves are very conservative in their P concentrations. When more P becomes available, they make more leaf area and keep the concentration the same (Smith and Read 1997). This is further reinforced by the greatly reduced leaf area and LAR of NVAM plants at P_0.

Greater extraradical hyphae development can in part explain the greater growth and gas exchange of VAM plants at P_0. Mycorrhiza can increase lateral root formation, which can indirectly increase cytokinin production which enhances P_N (Davies *et al.* 1996). Content of abscisic acid tends to be lower in xylem sap of mycorrhizal plants which in part explains the higher g_s frequently reported in VAM plants (Duan *et al.* 1996). Extraradical hyphae enhance the water status of bell peppers (Davies *et al.* 1992), and increase nutrient uptake in other crops (Bethlenfalvay and Linderman 1992). Mycorrhizal fungi explore the soil volume in a manner analogous to increasing root density. Extraradical hyphae bridge gaps between the soil and roots as well as binding soil particles to each other and to roots. This can be beneficial for enhancing nutrient uptake and minimizing water loss with diurnal fluctuations in soil water and subsequent soil shrinkage and gaps in the soil-root interface and between soil particles.

Not only does this mycorrhizal symbiont alleviate P-stress, but reproductive growth was enhanced 450 % in mycorrhizal plants at P_{44} compared to NVAM plants. P_N and tissue P were also highest with VAM plants at P_{44}. Maintaining high P_N is important during the reproductive stage to support greater sink demand for photosynthates. While colonization levels were somewhat reduced at P_{44} compared to low P, colonization was still sufficiently high: 71 % arbuscule formation, 44 % vesicles, and 75 % hyphae formation. The high percentage of arbuscule formation in the root cortex indicates that a very active symbiosis occurred. There was no P effect on VAM sporulation, *i.e.*, 4410 *versus* 3450 spores per kg media. However, *G. intraradices* is a species that sporulates inside the roots, hence the quantity of spores in soil may increase over time as plant roots senescence.

In summary, the commercial implication of this study is that *G. intraradices* can potentially be incorporated into chile ancho seedling transplant systems under protected culture at higher P fertility without sufficient depression in colonization and then outplanted into commercial production fields in Mexico and other areas with sustainable agricultural systems where low or unavailable soil P must be managed. With bell pepper types, which are very mycorrhiza dependent, the utilization of other endomycorrhizae isolates to overcome low soil-P in the field has been documented (Haas *et al.* 1986).

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