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MYCORRHIZAL DEPENDENCY AND RESPONSE OF TOMATO (*LYCOPERSICON ESCULENTUM*) TO INOCULATION BY INDIGENOUS ARBUSCULAR MYCORRHIZAL FUNGI AS INFLUENCED BY AVAILABLE SOIL PHOSPHORUS LEVELS

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ABSTRACT: A pot experiment was conducted on tomato (*Lycopersicon esculentum*) to evaluate the responses of tomato to inoculation of mycorrhiza (AMF) under different levels of soil phosphorus (P) concentrations in a greenhouse study. The results showed different responses on dry matter yield, shoot phosphorus concentration, mycorrhizal colonization and mycorrhizal dependency of the tomato plant. No evidence of AM fungal colonization was noted in the uninoculated soil. *L. esculentum* responded positively to AM fungus inoculation except at the two levels of soil P concentration (0.32 ppm and 0.92 ppm). Shoot dry matter, stem diameter and P concentration of the plant increased significantly in response to inoculation at the lowest three levels of soil P concentration (0.02, 0.04 and 0.12 ppm) as compared to the negative controls. The best response in all parameters was observed at the soil P concentration levels of 0.02 and 0.04 ppm. Levels of P concentration greater than 0.12 ppm suppressed AM fungi colonization. Soil P concentration levels of 0.32 and 0.92 ppm caused negative mycorrhizal dependencies (MD). The P level 0.32 ppm was found to be the cut-off value for positive response to inoculation of AM fungi in most of the tested parameters.

Keywords/phrases: Arbuscular mycorrhizal fungi (AMF); *Lycopersicon esculentum*; Mycorrhizal colonization; Mycorrhizal dependency; P concentration levels.

INTRODUCTION

Tomato (*Lycopersicon esculentum*) is a flowering plant found in the family Solanaceae and is native to America. It is an important vegetable cultivated throughout the world (Villareal, 1980; Opeña, 1985; Talekar, 1999). It was introduced to Ethiopia where it grows as garden crop (Yosef Haile and Yayeh Zewdie, 1989), and field crop on a large-scale, both under irrigation and rain-fed conditions (Heusler and Ayelle, 1987).

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Although the total area covered by the crop in the country is not known, it is largely cultivated in the Rift valley around Melkasa, Koka, Zwai, Wondo-Genet, Guder, Bako, Wolliso and other areas mainly with irrigation and in small-scale production for fresh fruit consumption during the dry season. According to statistics of 1985, the average yield of fresh fruits in two farms was about 13 t/ha (Heusler and Ayelle, 1987) which is very low as compared to yield of 30 t/ha in China (Yang *et al*., 1989).

Phosphorus is one of the most important nutrients that limit tomato growth since most of the agricultural soils in the country are deficient in phosphorus (Berhanu Debele, 1993), and the amount of P fertilizer application in the country is very low because of its low affordability to low input agriculture. Furthermore, the fertilizer use efficiency of applied P is generally very low due to either acidity or basicity-induced phosphorus fixation with aluminum and calcium complex formation, respectively (Tekalign Mamo and Haque, 1987).

Arbuscular mycorrhizal (AM) fungi are useful microorganisms that occur in nearly all natural and agricultural soils, and colonize roots of many plant species (Smith and Read, 1997). AM fungi could play an important role in improving the plant productivity by increasing the efficiency of fertilizer uptake under tropical conditions (Medina *et al.,* 1990) and improving P translocation to shoots from unavailable phosphorus pool (Gaur *et al*., 1998).

Various mechanisms are suggested to explain the ability of AM fungi-inoculated plants to increase P uptake. The most important one is the extension of external hyphae which decreases the distance of diffusion for P ions to mycorrhizal roots. In general, mycorrhizal plants absorb more PO_4^{3-} in solution than the non-mycorrhizal ones (Owusu-Bennoah and Wild, 1980).

Although mycorrhization of plants is widespread in nature, the response of different plant species to different groups of mycorrhiza and different levels of nutrients (especially phosphorus) is variable (Gerdemann, 1975; Liu and Wang, 2003). This leads to the coining of the term, mycorrhizal dependency, which refers to the dependence of plant species on the mycorrhizal condition for maximum growth at a given level of P content in the soil (Gerdemann, 1975). The magnitude of response is known to vary both between and within species and is mainly attributed to the ability of different species to absorb P from soils low in available P (Plenchette *et al.*, 1983).

AM fungal trap cultures are very helpful in unveiling fungal community members that are undetected in initial extraction of spores from field soil (Morton *et al*., 1995). Tomato is one of those appropriate plants (maize, alfalfa, tobacco and white clover) used for AM fungi trap cultures. However, there is no information whether tomato (a recently introduced plant in Ethiopia) is forming associations with indigenous AM fungi, and continues to be a competent plant for trap culture.

Therefore, the objective of this study was to demonstrate the response of tomato (as exotic species) to indigenous AM fungi, and to determine the mycorrhizal dependency of tomato, an important vegetable in Ethiopia, under different levels of soil P concentrations.

MATERIALS AND METHODS

A pot experiment was conducted on tomato in a greenhouse at Addis Ababa University (08°57′53.4″N and 038°40′18.8″E). The mean minimum and maximum daily temperatures were 22°C and 28°C, respectively. The experiment was conducted at five different levels of soil P concentrations (0.02 ppm, 0.04 ppm, 0.123 ppm, 0.32 ppm and 0.92 ppm). Potassium dihydrogen phosphate (KH_2PO_4) was used as P source to adjust different levels of available P. Phosphorus was extracted from the soil by bicarbonate solution at pH 8.5. Extractable P was determined by the bicarbonate (Olsen) method and quantified colorimetrically using the phosphomolybdate complex as outlined by Van Reeuwijk (1993). Each phosphorus level was evaluated with and without AM fungi inoculation. The pH of all leveled soils was adjusted to be 5.4 (1:2 soil to water).

Forest soil was mixed with sand (60:40) to improve drainage and was steam sterilized twice for 2 hours at 121°C and filled into surface sterilized plastic pots of 3 kg capacities. Arbuscular mycorrhizal fungi inocula (50 gm) consisting of spores, colonized soil, extrametrical mycelia and AM fungi colonized root segments were collected from pot cultures of trap plants, tobacco (*Nicotiana tabacum* L.) which had been grown for three months after being inoculated with mycorrhiza fungi of the dominant type (*Glomus spp*.) (Tadesse Chanie, 2006) and mixed thoroughly with the soil in each pot. Controls received a similar amount of autoclaved inoculum.

Seeds of *L. esculentum* were surface disinfected with 0.01% (w/v) $HgCl_2$ for 2 minutes and washed several (3–4) times with sterilized distilled water. After germinating seeds on Petri dishes for 4-5 days, three germinating seeds of uniform appearance were transplanted in each pot. After

establishment, the number of seedlings was thinned out to one per pot.

Watering alternated between distilled water and phosphorus free nutrient solution (100 ml per pot of one fifth Rorison's nutrient solution) (Merryweather, 2004). Pots were arranged in a completely randomized design on a bench with pot position changed weekly and with three replicates per treatment. The experiment was undertaken from Jaunary 22 to April 4, 2006. Roots were cleared in 10% KOH as indicated in Kormanik and McGraw (1982); Brundrett *et al*. (1994). Cleared roots were stained in trypan blue (0.05% in 14:1:1 lactic acid: glycerol: water). Proportional colonization was estimated using a magnified intersection method, at 200x magnification under the compound microscope (McGonigle *et al*., 1990). At each intersection there were six possible mutually exclusive outcomes. The line might intersect at **p**, **q**, **r,** **s**, **t** and **u** where: **G** is (**p+q+r+s+t+u**) intersections inspected, **p** is no fungal structures, **q** is arbuscules, **r** is mycorrhizal vesicles, **s** is arbuscules and mycorrhizal vesicles, **t** is mycorrhizal hyphae but no arbuscules or mycorrhizal vesicles and **u** is hyphae not seen to be connected to arbuscules or mycorrhizal vesicles.

A reasonable estimate of percentage of root length colonization (% RLC) was done from 100 or more intersections for each root sample. Where a total of **G = (p+q+r+s+t+u)** were inspected, the percentage of root length colonized by mycorrhizal hyphae was calculated as: **MHC=100 [(q+r+s+t)/G]**.The percentage of root length colonized by arbuscules, and the percentage of root length colonized by mycorrhizal vesicles were calculated as: arbuscular colonization **(AC) = 100 (q+s/G)** and vesicular colonization **(VC) = 100 (r+s/G)**.

The plants were cut at the soil level after 72 days of transplanting. Stem diameters were measured right at the soil level using calipers. The dry matter yield of shoot was determined after drying at 70°C for 72 hours and the dependency ratio was calculated. The mycorrhizal dependency (MD) of *L. esculentum* was calculated based on the plant dry matter yield (Plenchette *et al*., 1983).

$$MD = \frac{\text{Mycorrhizal dry matter yield} - \text{Non-mycorrhizal dry matter yield}}{\text{Mycorrhizal dry matter yield}}$$

Phosphorus concentration in shoot samples was determined by the phospho-molybdate method (Murphy and Riley, 1962) after dry-ashing 0.1 g portion of oven dried and ground plant samples in a muffle furnace at 500°C for four hours.

Statistical analyses were performed using the program SPSS V.12.0 package (SPSS Inc., Chicago, IL., USA). One way analysis of variance (ANOVA) was used and means were compared by Duncan's Multiple Range Test at $P \leq 0.05$. Plots were done using Microcal Origin 6.0.

RESULTS

Dry matter yield and shoot P content

Mycorrhizal inoculation significantly increased the shoot dry weight of *L. esculentum* at soil P levels of 0.04 ppm and 0.12 ppm (Fig. 1). Non-inoculated plants reached their maximum shoot dry matter yield at a P level of 0.32 ppm at which they grew better than inoculated plants.

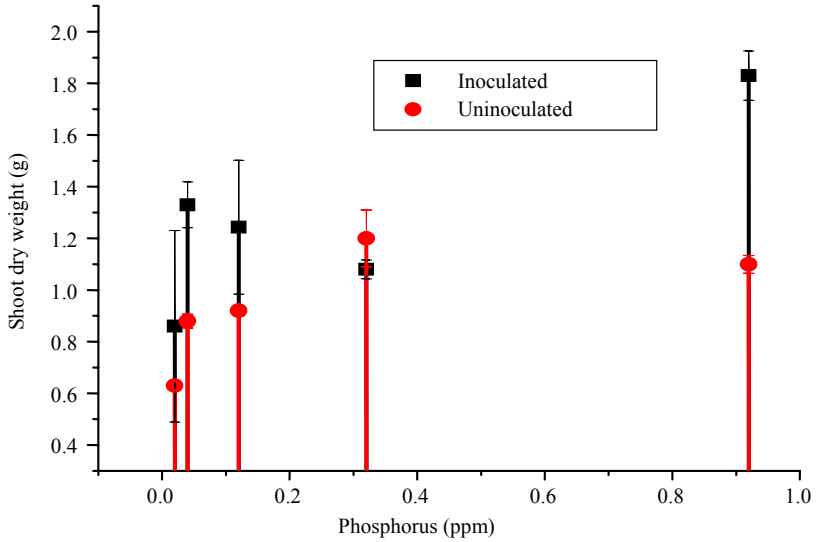

Fig. 1. Changes in shoot dry weight of *L. esculentum* in response to available soil P levels and mycorrhizal inoculation. The vertical error bars represent the standard error of means.

AM fungi inoculation significantly increased the stem diameter of *L. esculentum* at soil P levels of 0.02, 0.04 and 0.12 ppm (Fig. 2). Non-inoculated plants reached their maximum diameter at a P level of 0.92 ppm (Fig. 2). Non-inoculated plants started increasing stem diameter after P level of 0.04 ppm (Fig. 2).

Fast maturation of *L. esculentum* (flowering and fruiting) was observed on inoculated plants as compared to non-inoculated ones. Flowering and fruiting was observed on inoculated plants at 55-60 days after planting while

none was seen on non-inoculated ones during this period.

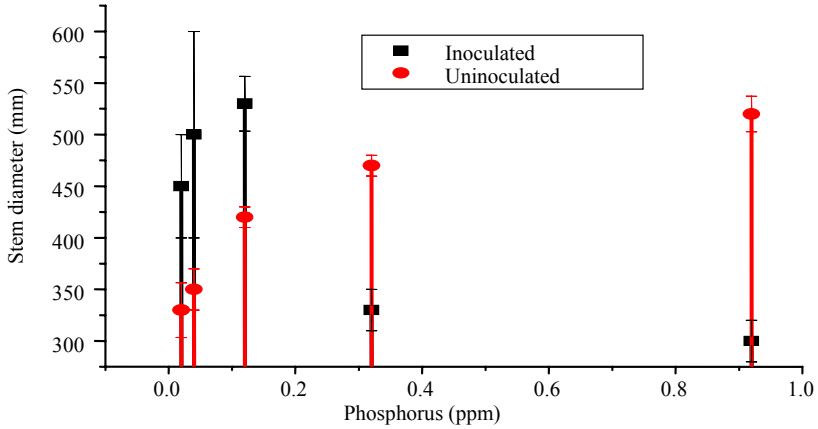

Fig. 2. Changes in stem diameter of *L. esculentum* in response to available soil P levels and mycorrhizal inoculation. The vertical error bars represent the standard error of means.

The shoot P concentration of inoculated plants of *L. esculentum* was significantly greater ($p \leq 0.05$) compared to non-inoculated plants at lower levels of soil P tested (Fig. 3). As P level increased in the soil solution to 0.12 ppm, the concentration of shoot P increased (Fig. 3). At higher level (0.92 ppm), mycorrhizal inoculation did not enhance the P concentration over their non-inoculated counterparts (Fig. 3).

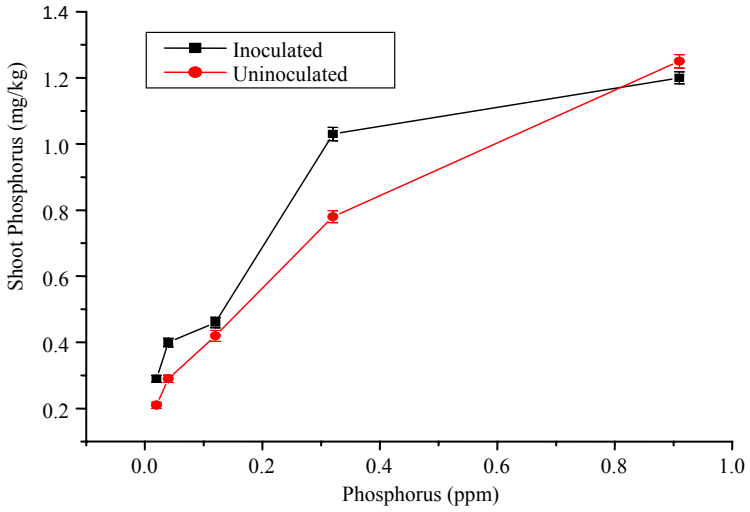

Fig. 3. Shoot P status of mycorrhizal and non-mycorrhizal *L. esculentum* in response to available soil P levels. The vertical error bars represent the standard error of means.

Root length mycorrhizal colonization

The percent root length of *L. esculentum* colonized by AM fungi decreased significantly with increasing levels of soil P (Fig. 4). Percentage of root length colonized with mycorrhizal hyphal colonization (MHC) and arbuscular colonization (AC) was highest at 0.02 ppm but declined as soil P level increased from 0.12 ppm to 0.32 ppm (Fig. 4). Vesicular colonization (VC) was not affected by soil P levels (Fig. 4).

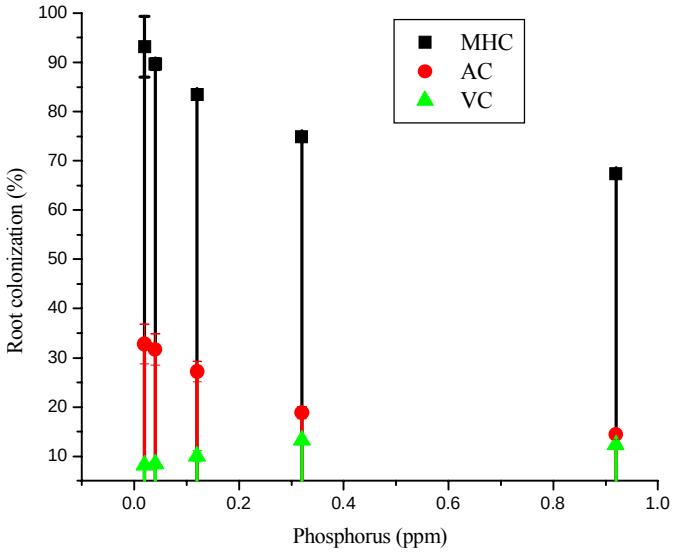

Fig. 4. Effects of available soil P levels on percent root colonized by AMF of *L. esculentum*. The vertical error bars represent the standard error of means.

Mycorrhizal dependency

Maximum mycorrhizal dependency (33.8%) of *L. esculentum* was observed at 0.04 ppm soil P, the second lowest P level. The MD values started declining above soil P levels of 0.04 ppm (Fig. 5). Negative values for MD were observed at 0.32 and 0.92 ppm.

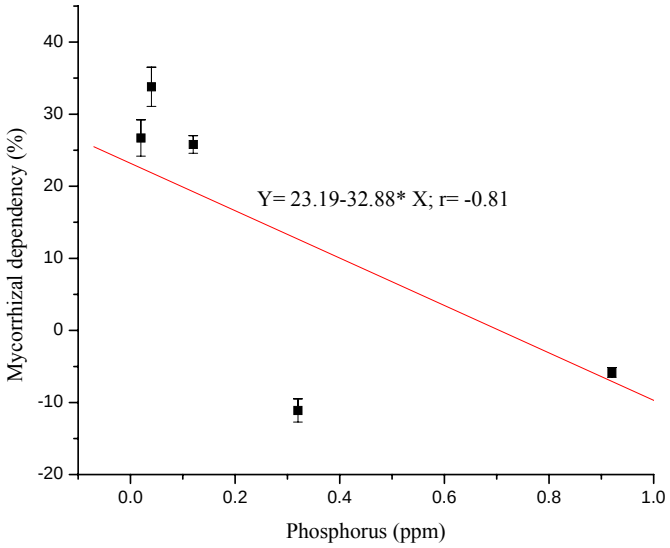

Fig. 5. Changes in the AM fungi dependency of *L. esculentum* in response to changes in available P levels. The vertical error bars represent the standard error of means.

DISCUSSION

Uncertainties arise when trying to draw conclusions from the literature partly because most investigations are based on the amount of P added to soils rather than on the resulting available P (Mitiku Habte and Manjunath, 1987). Such experiments are bound to demonstrate variable effects of soil P on the AM symbiosis because soils differ in the extent to which they retain the added P in forms that are not accessible to plants (Linderman and Hendrix, 1982). In the present study, varying levels of available soil P were achieved. Hence, a clear relationship of AM symbiosis with established P levels and *L. esculentum* was documented.

The comparison of inoculated and non-inoculated plants of *L. esculentum* at different P levels revealed that plant responses to AM inoculation was related to the particular level of available soil P. *L. esculentum* responded positively to AM fungus inoculation except at the two highest levels of soil P. However, the magnitude of response differed widely among soil P levels. Shoot dry matter, stem diameter and P concentration of *L. esculentum* increased significantly in response to inoculation at the lowest three levels of soil P (Figs. 1, 2 and 3). The best responses to AM fungi inoculation were observed at the first two soil P levels.

The beneficial effect of AM fungi colonization on plant growth has been

most often attributed to enhanced phosphorus nutrition (Mosse, 1973). The observation of the present investigation support this finding since the mean shoot dry matter and P content were generally higher in the inoculated plants than in their non-inoculated counterparts (Declerck *et al*., 1995). The lack of significant improvement in dry matter yield and stem diameter above a soil P level of 0.32 ppm clearly demonstrates that the external P requirement for the production of maximum biomass was met at these soil P levels (Manjunath and Mitiku Habte, 1992).

The reduction in dry matter yield, stem diameter and shoot P concentration in inoculated plants at soil P level greater than 0.12 ppm may be due to the suppression of AM fungi activity at higher P levels. It is known that high soil P suppresses AM fungus activity mainly indirectly through the internal P of the plant species (Menge *et al*., 1978). Soil P in excess than needed for the establishment of mycorrhizae generally inhibits AM fungi colonization (Mitiku Habte and Manjunath, 1987). Similarly Plenchette *et al*. (1983) indicated that increasing P fertilizer levels depressed the root endomycorrhizal colonization index but mycorrhizae were not totally eliminated by the highest levels of P fertilization. Percent MHC and AC by AM fungi were the highest (93.2% and 32.8%, respectively) at soil P level of 0.02 ppm (Fig. 4).

Apparently, the native level of soil P was appropriate to allow for development of optimum symbiosis between AM fungi and the host plant (*L. esculentum*). Soil P levels of 0.02, 0.04 and 0.12 ppm appear to be optimum for beneficial symbiosis in this case (Fig. 4).

Above 0.12 ppm, there existed a low colonization with AM fungi but the symbiosis was not found to be beneficial based on shoot dry matter yield or P concentration in shoots (Figs. 1, 2 and 3). Miyasaka *et al*. (1993) observed that if the host plant was not able to produce sufficient carbohydrates to allow the AM fungal hyphae to fully exploit the soil volume for available P, then the benefits of this symbiotic association would be restricted. Linderman and Hendrix (1982) observed that mycorrhizal dependent species typically did not respond appreciably to P unless optimum levels of nutrient were present in the soil.

On the basis of MD values observed in the present study, it can be concluded that the dependence of *L. esculentum* upon AM fungi is dependent on P level. Mycorrhizal dependency is linked to a given level of P fertility, and so the available P content of the soil should be expressed in terms of MD values (Plenchette and Morel, 1996). Mycorrhizal dependency

ranged from less than zero to 33.8% (Fig. 5).

The dependency values decreased with soil P above 0.04 ppm (Fig. 5). Mitiku Habte and Manjunath (1987) also found similar pattern on *Leucaena leucocephala*. They observed that the effects of mycorrhizal inoculations diminished progressively as the soil P level was increased beyond a certain critical value. The ability of a plant to absorb P from low P soils is often thought to be the major contributing factor to the differences observed in MD (Mosse, 1973). Mycorrhizal dependency values clearly indicated that *L. esculentum* was more dependent on AM fungi for growth at soil P level of 0.04 ppm (Fig. 5). These organisms are very helpful in most Ethiopian soils, dominated by vertisol and oxisol, where the available phosphorus contents are within the very low range (< 5 ppm) as compared to that of the references given by London (1984): less than 5 ppm very low, 6-13 ppm low, 14-19 ppm medium and 20-28 ppm high.

The negative dependency values observed at the highest level (0.32 and 0.92 ppm) of soil P suggested that the relationship prevailing between the plant and the endophyte used was parasitic. Mitiku Habte and Turk (1991) observed that AM fungi might behave as parasites at both very low and very high level of soil P. Growth increase in AM fungi-inoculated plants under limiting P availability has been reported as the most common effects of AMF (Melloni and Cardoso, 1999; Graham, 2000; Melloni *et al*., 2000) but less common is the plant growth depression under high P supply (Graham, 2000; Jifon *et al*., 2002). Under high P availability, AM fungi infection may become a carbon sink (Graham *et al*., 1997), which carries the host to a growth depression in relation to non-inoculated plants.

The results of this experiment show the importance of AM fungi in agriculture in general and horticultural practices in particular in Ethiopia when the high cost of inorganic fertilizers is considered. As tomato has been found to be very much dependent on indigenous AM fungi, it can be used as a trapping host to produce these fungi as massive inocula for different purposes. For instance, it is important in plant nursery establishment both for horticultural practices and aforestation programs.

Moreover, these fungi are found to be very important in the production of food crops in low input agriculture. In general, it was indicated by several authors that mycorrhizal fungal diversity determined plant biodiversity, ecosystem variability and productivity. In the future it is worth working on mycorrhizal dependency of tomato in the field using isotopically labelled phosphorus fertilizer to investigate the possibility of phosphorus uptake

from different depths or distances of phosphorus pool due to mycorrhizal colonization.

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