Interaction of Vesicular-arbuscular Mycorrhizal Fungi and Phosphorus with *Meloidogyne incognita* on Tomato[1]

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Abstract: The influence of two vesicular-arbuscular mycorrhizal fungi and phosphorus (P) nutrition on penetration, development, and reproduction by *Meloidogyne incognita* on Walter tomato was studied in the greenhouse. Inoculation with either *Gigaspora margarita* or *Glomus mosseae* 2 wk prior to nematode inoculation did not alter infection by *M. incognita* compared with nonmycorrhizal plants, regardless of soil P level (either 3 μg [low P] or 30 μg [high P] available P/g soil). At a given soil P level, nematode penetration and reproduction did not differ in mycorrhizal and nonmycorrhizal plants. However, plants grown in high P soil had greater root weights, increased nematode penetration and egg production per plant, and decreased colonization by mycorrhizal fungi, compared with plants grown in low P soil. The number of eggs per female nematode on mycorrhizal and nonmycorrhizal plants was not influenced by P treatment. Tomato plants with split root systems grown in double-compartment containers which had either low P soil in both sides or high P in one side and low P in the other, were inoculated at transplanting with *G. margarita* and 2 wk later one-half of the split root system of each plant was inoculated with *M. incognita* larvae. Although the mycoorhizal fungus increased the inorganic P content of the root to a level comparable to that in plants grown in high P soil, nematode penetration and reproduction were not altered. In a third series of experiments, the rate of nematode development was not influenced by either the presence of *G. margarita* or high soil P, compared with control plants grown in low P soil. These data indicate that supplemental P (30 μ/g soil) alters root-knot nematode infection of tomato more than *G. mosseae* and *G. margarita*. *Key words: Glomus mosseae, Gigaspora margarita,* root-knot nematode.

Journal of Nematology 15(3):410-417. 1983.

Interest in interactions between vesicular-arbuscular mycorrhizal fungi (VAMF) and plant pathogens developed soon after ectomycorrhizae plants were observed to be less susceptible to infection by root pathogens (24). Although the literature suggests (20) that VAMF generally suppress the severity of root diseases and enhance shoot diseases, the actual situation is more complex, especially for root diseases. The interaction of VAMF with plant pathogens may increase (6,18), decrease (17,19), or not effect (4) the severity of root diseases. Apparently the specific combination of host, pathogen, and VAMF often determines the type of interaction that will occur (4,19).

Since plant-parasitic nematodes and VAMF are often intimately associated in young roots, an interaction between these two groups of organisms seems likely. Several investigations showed that VAMF can markedly alter plant responses to plant-parasitic nematodes (12). The beneficial effect of VA mycorrhizae on a nematode-susceptible cotton cultivar offset damage caused by *Meloidogyne incognita* (17). Soybeans inoculated with *Glomus macrocarpum* and *M. incognita* had fewer galls per gram of root, increased root weights, and increased yields, compared with plants inoculated with the nematode alone (15). When tomato plants were pre-inoculated with a VAMF, fewer *M. incognita* second-stage larvae penetrated and developed to maturity in roots of mycorrhizal tomato, compared with nonmycorrhizal controls (21). Tomato roots colonized by *G. fasciculatum* and infected by *M. incognita* or *M. hapla* had fewer and smaller galls than did nematode-infected nonmycorrhizal plants (3). Small giant cells with few nuclei and retarded nematode development were also observed in mycorrhizal tomato roots infected with *M. incognita* (21). In addition to the effects on nematode penetration and development, there are indications that nematode reproduction may also be suppressed on mycorrhizal plants (11,21). Such studies suggest VAMF have potential for reducing plant diseases caused by certain plant-parasitic nematodes. However, other reports suggest that the beneficial effects of VAMF are negated by *Meloidogyne* sp. (1) and that the reproduction of *M. incognita* increased on mycorrhizal soybeans (19).

Received for publication 26 August 1982,

[1]This research was supported by the Science and Education Administration of the U.S. Department of Agriculture under Grant 7800244 from the Competitive Research Grants Office and by State and Hatch Act funds allocated to the Georgia Agricultural Experiment Stations.

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Our research was initiated to determine if two species of VAMF influence *M. incognita* penetration, development, and reproduction in tomato. Since the primary role of mycorrhizae is the enhancement of phosphorus uptake by the host, the influence of phosphorus on the nematode-mycorrhizal interaction was also investigated.

MATERIALS AND METHODS

Host plant propagation and soil preparation: Tomato seed (*Lycopersicon esculentum* L. cv. Walter), susceptible to *Meloidogyne* species, were planted in vermiculite and seedlings were transplanted after 7–10 days into 250-ml paper cups containing a fumigated sandy loam soil. Plants were grown for 2 wk in the greenhouse, roots washed free of soil, and transplanted into the soils used in the experiments.

Plants with split-root systems were used in certain studies. When seedling tap roots were about 3 mm in diameter (generally 2–3 wk after transplanting into paper cups), the tip of the tap root was excised and the remaining portion of the tap root was split in half up to the stem. Plants with equal lateral distribution of roots were selected and each half-root was planted in separate sides of a double-compartment plastic container (750 cm^3 per side).

A low phosphorus (P) Dothan loamy sand mixed with washed river sand (4:1 v/v) was used in the experiments. Analysis of the raw soil gave the following results: pH 4.9, P 3, K 35, Ca 257, Mg 54, Zn 2, Mn 64, B 0.25, NO_3-N 3.5 μg/g; 1.7% organic matter; 74% sand, 14% silt, and 12% clay (analysis by the University of Georgia Soil and Plant Testing Laboratory, Cooperative Extension Service, Athens, Georgia). Commercial hydrated horticultural lime was used to adjust the pH to 6.0–6.5. Two P fertility levels were used in these studies: low P = no P added to the soil mix; and high P = 50 μg P/g of soil added as $Ca(H_2PO_4)_2$. The available P levels, determined by double acid extraction, were approximately 3 and 30 μg P/g of soil for low P and high P, respectively. The soil was fumigated with methyl bromide (Dowfume MC-2, 1.36 kg/800 L, Dow Chemical Co., Midland, Michigan). Hoagland's solution (9) minus P was added as needed.

Preparation of inocula and inoculation: Glomus mosseae (Nicol. & Gerd.) Gerd. & Trappe and *Gigaspora margarita* Becker & Hall were maintained on *Sorghum bicolor* (L.) Moench. 'Shallu' in pot culture, and spores for use as inoculum were extracted from soil by centrifugal-flotation (13). Individual plants were inoculated with either 250 chlamydospores of *G. mosseae* or 1,000 azygospores of *G. margarita*. The inoculum was added to a 2-cm deep trench around the stem base and was covered with soil after inoculation. Spore suspensions were filtered through Whatman #1 filter paper and the filtrate collected was applied to all non-mycorrhizal plants to standardize microflora in all experiments.

Meloidogyne incognita (Kofoid & White) Chitwood was propagated on greenhouse-grown 'Rutgers' tomato. Nematode inoculum consisted of either eggs extracted from galled roots with 0.5% NaOCl (10) or freshly hatched second-stage larvae collected in a mist chamber. Nematode inoculum was added to a 2-cm deep trench around the stem base and was covered with soil after inoculation.

Collection of data: Plant growth was measured by weighing fresh shoots and roots. Phosphorus content of roots in split-root experiments was determined by taking a 0.1-g sample from each half-root system in a treatment. Roots collected from replications within a treatment were combined to give a 1.0-g sample representing each half root. Roots were dried at 80 C for 24 hr and weighed and ashed at 500 C for 12 hr prior to determining the total inorganic P content per half-root system (14).

Mycorrhizae assays were made by cutting roots into 2.5-cm sections and randomly selecting 0.5-g samples. Samples were autoclaved for 5 min in 100 ml of 10% KOH, rinsed several times in tap water, and soaked in tap water for a minimum of 4 hr (2). Roots were stained in 0.1% trypan blue in lactoglycerol (lactic acid:glycerol:water; 1:2:1 v/v/v) for 12 hr and were transferred to lactoglycerol for storage. The percentage of root colonization by VAMF was measured by the Newmann grid line technique (7). Reproduction of VAMF was determined by extracting (13) and counting spores from soil samples.

Root-knot nematodes in the remaining root tissue that had been stained with acid fuchsin (16) were examined using a stereoscopic microscope. The number of nematodes in the entire root system was counted. Nematode reproduction was measured by extracting and counting eggs (10). In certain experiments the eggs in 10 egg masses from individual plants were counted to ascertain the number of eggs per egg mass.

Nematode penetration and reproduction studies: Two-week-old tomato plants were transplanted into 7.5-cm-d pots containing either low P or high P soil and were fertilized with 10 ml/pot of a 0.01 M KNO_3:0.01 M $Ca(NO_3)_2$ solution (1:1 v/v) at 2 and 5 wk after transplanting. Plants at each P level received either spore filtrate (control) or spores of either *G. margarita* or *G. mosseae* at transplanting. Individual plants to be inoculated with *M. incognita* received 5,000 eggs at 3 or 5 wk after transplanting. Treatments with plants that were inoculated with the nematode had 15 replications; all others had 10 replications. Treatments were arranged in a completely random design on a greenhouse bench. Ten plants from each treatment were harvested 7 wk after transplanting to measure plant growth, the number of nematode penetrations, and VAMF development. The remaining plants were transplanted into 15-cm-d pots and harvested 4 wk later to determine the number of eggs per egg mass. The experiment was repeated using only the high P soil and the following modifications: Hoagland's solution (9) minus P was added twice weekly to overcome fertility deficiencies, and nematode inoculations were made 2 and 4 wk after transplanting. In this experiment fungal and nematode reproduction were also determined.

Split-root studies: Split-root tomato seedlings were transplanted into double-compartment containers which had either low P soil in each side or high P soil in one side and low P soil in the opposite side. During transplanting into the double-compartment containers, one half-root of each plant was either inoculated with *G. margarita* spores or received a spore filtrate (control). Two weeks after transplanting, the tomatoes were inoculated with 900 nematode eggs per half-root; various combinations of nematode, *G. margarita,* and P fertility were used with 20 replications for each treatment (Table 3). Ten plants from each treatment were harvested 4 wk after transplanting so that plant growth, nematode penetrations, and percentage VA mycorrhizal fungal colonization of roots could be measured. Seven weeks after transplanting, the remaining 10 plants in each treatment were harvested to assay for mycorrhizae and nematode reproduction. These treatments were repeated in two additional studies.

Nematode development: Two-week-old seedlings were transplanted into 1-liter cups containing either low P soil, low P soil plus *G. margarita* spores, or high P soil. Each plant was inoculated with 2,000 second-stage larvae of *M. incognita* 3 wk after transplanting. To follow temporal changes in plant growth and mycorrhizal and nematode development, three plants from each treatment were harvested at 0, 7, 21, and 35 days after nematode inoculation. Nematode development within the root was scored using the following index: (1) vermiform second-stage larvae that had not established a feeding site, (2) swollen larvae, (3) adult females without eggs, (4) females with eggs. The experiment was repeated and combined data presented.

RESULTS

Nematode penetration and reproduction: Meloidogyne incognita infection and VAMF colonization of tomato roots were influenced by the concentration of phosphorus in the soil. Plants grown in a high P soil had 44% fewer nematodes per gram of root and 38% less root length colonized by mycorrhizal fungi than did plants grown in a low P soil (Table 1). However, the total number of nematodes in the roots increased by 91% when plants were grown in high P soil, probably reflecting the threefold increase in root weight over plants in the low P soil. Numbers of eggs per egg mass were not significantly different among treatments, but the total number of nematode eggs produced on roots of plants grown in high P soil was 81% higher than for plants grown in low P soil because of the increase in number of egg masses.

The two VAMF had no effect on root-

Table 1. The effect of soil phosphorus level on penetration of tomato roots by second-stage larvae of *Meloidogyne incognita* and subsequent nematode reproduction and mycorrhizae development.

Treatment*	Root wt† (g)	Nematodes/ plant†	Nematodes/ g root†	Eggs/ plant≠	Eggs/ egg mass≠	Mycorrhizae†§ %
Low P	2.4	402	168	30,863	545	36.3
High P	8.1	768	95	55,970	346	22.5
$FLSD_{0.05}$//	0.51	122	50	24,760	NS	8.4

*Low P = 3 μg available P/g soil; high P — 3 μg availagle P/g soil.

†Plants harvested 7 wk after transplanting and inoculation with *Gigaspora margarita* and *Glomus mosseae*. Plants were inoculated with *M. incognita* either 3 or 5 wk after transplanting and data were combined for this analysis.

≠Inoculated same as "†" but harvested 11 wk after transplanting.

§Percentage of root length with structures of mycorrhizal fungi.

//Fisher's least significant difference.

knot nematode penetration of roots or subsequent reproduction. When roots were examined for fungal colonization, tomato was found to be a better host for *G. margarita* than for *G. mosseae;* the percentage root colonization was 37.3% and 21.4%, respectively (Table 2). Since *G. mosseae* did not colonize as well or reproduce as well on tomato as did *G. margarita* and its presence suppressed root growth below that of other treatments, it was deleted in later experiments.

The size of the nematode population per plant and per gram of root did not differ for mycorrhizal and nonmycorrhizal plants; neither was there a difference in total egg production per plant nor in the number of eggs produced in an egg mass. In the repeat experiment when only high P soil was used, there was no difference in egg production on mycorrhizal and nonmycorrhizal plants. At the high soil P, *G. mosseae* produced 2 lspores/100 cm^3 of soil, compared with 792 *G. margarita* spores/100 cm^3 soil.

Split-root studies: In the split-root studies, the P concentration in each half-root system 2 wk after nematode inoculation was higher for plants grown in high P soil or colonized with mycorrhizal fungi than for control plants (Table 3). The presence of mycorrhizae or high P soil in one compartment raised the P concentration in both half-root systems to comparable levels. At the time root samples were taken for P analysis, *G. margarita* had colonized 20%

Table 2. The effect of vesicular-arbuscular mycorrhizal fungi on penetration of tomato roots by second-stage larvae of *Meloidogyne incognita* and subsequent nematode reproduction.

		Penetration		Reproduction		
Mycorrhizal fungus*	Root wt† (g)	Nematodes/ plant†	Nematodes/ g root†	Eggs/ plant≠	Eggs/egg mass≠	Mycorrhizae†§ %
None	6.0	558	93	49,769	493	—
Gigaspora margarita	5.9	642	109	43,585	444	37.3
Glomus mosseae	4.2	552	131	37,383	384	21.4
$FLSD_{0.05}$//	0.6	NS	NS	NS	NS	8.4

*Means of low (3 μg available P/g soil) and high (30 μg available P/g soil) P fertility.

†Plants harvested 7 wk after transplanting and inoculation with *Gigaspora margarita* and *Glomus mosseae*. Plants were inoculated with *M. incognita* either 3 or 5 wk after transplanting and data were combined for this analysis.

≠Inoculated same as "†" but harvested 11 wk after transplanting.

§Percentage of root length with structures of mycorrhizal fungi.

//Fisher's least significant difference.

Table 3. The influence of *Gigaspora margarita* and phosphorus on *Meloidogyne incognita* penetration and reproduction in a tomato split-root system and on the total inorganic phosphorus content of each half-root.

Treatment* (left half-root/right half-root)	μg Phosphorus/g dry root†		Penetration†		Reproduction‡	
	Left half-root	Right half-root	Nematodes/plant	Nematodes/g root	Eggs/plant (× 10^3)	Eggs/g root (× 10^3)
O/MI	626	909	430§	88§	30.3§	4.6§
GM/MI	1222	998	362	80	37.8	6.7
O/MI+GM	1637	1462	291	71	30.2	5.6
O+High P/MI	1178	1212	465	79	41.9	5.4
O/MI+High P	1315	1974	437	89	41.9	6.2
$FLSD_{0.05}$//			89	NS	NS	NS

*O = no inoculation; MI = *Meloidogyne incognita* inoculated half-root; GM = *Gigaspora margarita* inoculated half-root; compartments contained 3 μg available P/g soil unless otherwise indicated by high P (30 μg available P/g soil).

†Harvested 4 wk after transplanting; i.e., 2 wk after nematode inoculation and 4 wk after inoculation with *Gigaspora margarita*.

‡Harvested 7 wk after transplanting; i.e., 5 wk after nematode inoculation and 7 wk after inoculation with *Gigaspora margarita*.

§Values represent average from two trails.

//Fisher's least significant difference.

of the half-root systems of mycorrhizal plants.

While mycorrhizal plants had fewer nematodes per plant than did either control plants or those which had high P soil in one compartment, the difference was significant only when the fungus and nematode were present in the same half-root (Table 3). However, there were no differences among treatments in nematodes per gram of root. Nematode reproduction did not differ for any treatment, and the percentage of root colonized by *G. margarita* was comparable for both mycorrhizal treatments (GM/MI = 30.5% mycorrhizae; O/GM + MI = 34.4% mycorrhizae).

Nematode development: Neither P level nor *G. margarita* influenced the rate of development of *M. incognita* in tomato roots. Total number of nematodes in the root systems 1 wk after root-knot nematode inoculation were not significantly different regardless of treatment, but at 3 and 5 wk after inoculation there were more nematodes in roots of plants grown in high P soil compared with mycorrhizal and nonmycorrhizal plants grown in low P soil (Fig. 1). The proportion of nematodes at the stages designated in the development index did not differ significantly among treatments at each harvest.

The rate of VA mycorrhizal fungal colonization of roots was not affected by the presence of the nematode. The percentage of root systems colonized by *G. margarita* was 10.8%, 15.5%, and 37.1% at 1, 3, and 5 wk, respectively, which was the normal rate of colonization for *G. margarita* in nematode-free plants. In examination of the root systems for the presence of *G. margarita* in galls, the fungus was rarely found in cortical cells adjacent to a gall.

DISCUSSION

Although other investigators (20,21) have reported that certain VAMF protected plants from plant-parasitic nematodes, *G. margarita* did not reduce the infection (nematodes per gram of root) of tomato by *M. incognita* in our tests. For VAMF to be effective in reducing plant stress caused by nematodes, either plant tolerance (12) must be enhanced or the pre-infectional or post-infectional nematode-host relationship must be influenced. VAMF improve plant nutrition (5) and by doing so may aid the host in compensating for damage caused by parasitic nematodes, thereby increasing plant tolerance to these pathogens. The pre-infectional nematode-host interaction could be affected if the endophyte

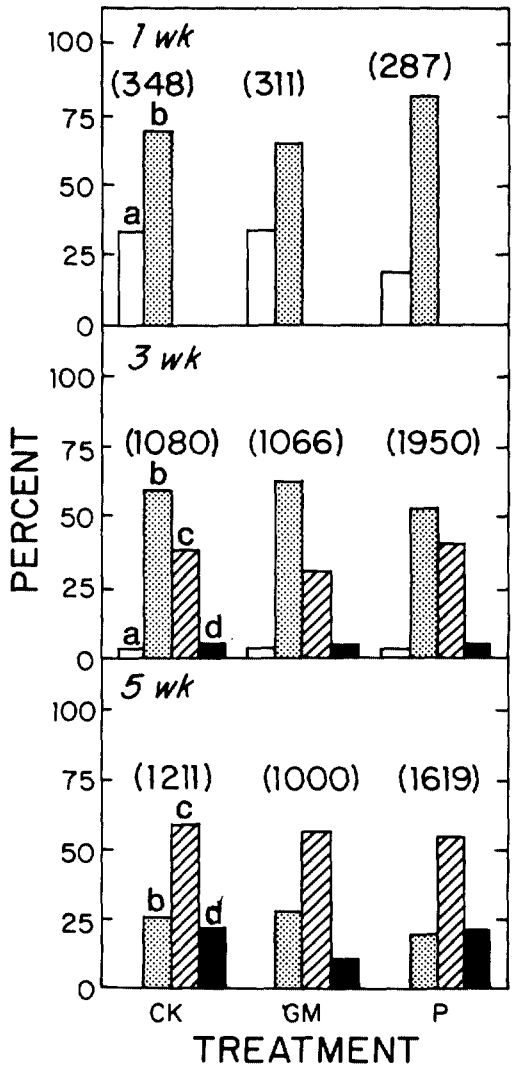

Figure. 1. Development of *Meloidogyne incognita* in tomato roots grown for 3 wk in either low P soil (CK), low P soil plus *Gigaspora margarita* azygospores (GM), or high P soil (P) prior to nematode inoculation. The total number of nematodes/plant, indicated in parentheses, and the percentage of the total at various stages of development designated in the development index were determined at 1 wk, 3 wk and 5 wk after nematode inoculation. a = vermiform second-stage larvae; b = swollen larvae; c = adult females without eggs; d = females with eggs.

were to cause an alteration in host attractiveness to nematodes. Fungal symbionts may affect the post-infectional nematode-host relationship by either competing with nematodes for their feeding sites or by having some systemic effect on the host that alters the nematode's ability to complete a normal life cycle.

The presence of VAMF in plant roots may result in an alteration in root exudates that could affect the attractiveness of roots to plant-parasitic nematodes so that fewer nematodes would ultimately penetrate roots. In fact, Graham et al. (8) reported that root exudation of amino acids and reducing sugars are greater from non-mycorrhizal sudangrass grown in P-deficient soils than from mycorrhizal plants. Sikora and Schonbeck (22) reported a decrease in the number of *M. incognita* larvae that penetrated and developed to maturity in mycorrhizal plants, suggesting that some alteration in root attractiveness may have been involved initially. However, our results indicate that the presence of *G. mosseae* and *G. margarita* in tomato roots had no effect on the number of *M. incognita* penetrations per gram of root and high P fertilization did not affect nemtode infection.

Either a systemic or localized mycorrhizal effect on *M. incognita* should have been discerned in the split-root experiment. Chemical analysis of roots suggest that P nutrition was markedly improved by the VAMF, which is consistent with other reports (3,8). In addition, the high P soil increased the P concentration in the roots to a level comparable to that in roots of mycorrhizal plants. Any systemic effects due to *G. margarita* or P should have been observed in treatments where *G. margarita* spores or high P soil were opposite the nematode inoculated half-root system, and localized responses would have been revealed when those treatments were administered to the nematode inoculated half-root system. The reduced number of nematode penetrations of mycorrhizal plants reflected the smaller root size, since the number of nematodes per gram of root did not differ from any treatment. Neither P nor *G. margarita* had an effect on the pre-infectional nematode-host relationship in this experiment.

VAMF may cause changes in the post-infectional nematode-host interaction by altering nematode reproduction and/or development. Once second-stage larvae of *M. incognita* have entered a root, an alteration in the post-infectional relationship is evident if larval development is arrested or

if larvae either egress, die, or mature either as females that produced few eggs or as males. An earlier report (21) indicated that *M. incognita* development was impeded at 8 and 16 days after nematode inoculation of mycorrhizal tomato. In another study (22), 13% fewer *M. incognita* larvae developed into adults 30 days after inoculation of mycorrhizal tomato, compared to non-mycorrhizal tomato, although the difference was not statistically significant. In our studies no differences in the rate of *M. incognita* development were observed for any treatment. In absolute numbers, more fecund females developed when plants were grown in high P soil because there were more nematodes in the roots. However, the proportion of the total nematode population in roots consisting of fecund females was not affected by either soil P or *G. margarita*.

G. margarita had no effect on *M. incognita* reproduction on cotton (17), and the effect of mycorrhizae on egg production was inconsistent on peach (23). In fact, only a few VAMF have been associated with a suppression of nematode reproduction (12). In our study total egg production was not significantly different for mycorrhizal and non-mycorrhizal plants. Since high P soil and mycorrhizae had no effect on the number of eggs produced in an egg mass and the rate of nematode development was the same for all treatments, any differences in the total number of eggs produced on a plant resulted from varying numbers of fecund females present in the roots.

The presence of *M. incognita* in roots did not affect mycorrhizal development, but supplemental P retarded fungal root colonization and spore production. Maximum root colonization by *G. margarita* occurred by 4–5 wk after inoculation and did not exceed 40%, which corresponds well with previous reports (3,5). Therefore, competition for nematode feeding sites in the root apparently was not a major factor in this mycorrhizae-nematode interaction, as less than half of the cortical tissue usually is colonized by the fungus. Mycorrhizal fungi would have to induce a systemic response in plants that would be antagonistic to the development of the nematode to greatly reduce nematode infections, and our split-root experiments indicate that this does not occur with *G. mosseae* and *G. margarita* on tomato. For these two species of VAMF to be totally effective in reducing plant stress caused by nematodes, either the pre-infectional or post-infectional nematode-host relationship must be altered more than in the present experiments.

Enhancement of plant tolerance seems to be the most likely contribution of VAMF toward offsetting damage caused by plant parasitic nematodes, as has been demonstrated in cotton (17) and soybeans (19). Yield was not evaluated in our studies, so an accurate assessment of plant tolerance could not be made for tomato. Tolerance may be the principal type of protection mycorrhizae offer plants against parasitic nematodes, primarily by stimulating plant growth through improved nutrition (12). However, tomato often lacks a growth response to mycorrhizae (3,5).

In future work other species of VAMF should be screened for their ability to affect *Meloidogyne* development in plants. In addition, yield evaluations and field tests are needed for a realistic assessment of the significance of VAMF in altering plant stress caused by plant-parasitic nematodes. Further studies should determine whether VAMF can be of sufficient value to warrant the development of technology for using these organisms.

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