

Interactions of Vesicular-Arbuscular Mycorrhizal Fungi, *Meloidogyne incognita*, and Soil Fertility on Peach

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ABSTRACT

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Growth of cultivar Lovell peach trees infected with *Meloidogyne incognita* or free of the nematode was enhanced by *Gigaspora margarita* and *Glomus etunicatus* in some greenhouse tests, but not in others. Beneficial effects of the mycorrhizal fungi on growth were accompanied by improved foliar P, Cu, and Zn status and were greater on nematode-free plants grown in a soil with 500 μg than in one containing 1,000 μg 10-10-10 NPK per gram of soil. *G. margarita* suppressed reproduction of *M.*

incognita only in tests where the fungus improved plant growth; however, *G. etunicatus* had no effect on nematode reproduction in either case. Sporulation of the fungi was not significantly affected by the nematode. In split-root studies involving *G. margarita*, the fungus suppressed nematode reproduction, and the nematode was injurious to growth of mycorrhizal plants only if both microorganisms occupied the same half-root system.

Vesicular-arbuscular mycorrhizal (VAM) fungi colonize roots and stimulate growth of a wide range of plant species, primarily by improving host nutrition (4). Since peach (*Prunus persica* (L.) Batsch) rootstocks are either commonly grown in or sometimes transplanted into soils that have been fumigated, an opportunity to reintroduce VAM fungi exists, but the value of this practice has received little investigation. Gilmore (5) reported that several isolates of VAM fungi increased growth and uptake of phosphorus and zinc by peach seedlings grown in a zinc-deficient soil. Lambert et al (11) found that VAM fungi also increased copper uptake of peach seedlings grown in a fumigated nursery soil. In both cases, poor growth of nonmycorrhizal peach trees occurred.

Meloidogyne incognita (Kofoid and White) Chitwood is a part of a complex of interacting factors that reduces peach tree vigor and contributes to peach tree short life (12,14), a problem often associated with new plantings on sites recently cleared of old peach trees. In Georgia, peach tree short life has led to reduced yield and high mortality, sometimes before newly established trees reach bearing age (19).

VAM fungi reduce the damage caused by a wide variety of plant pathogens, including several *Meloidogyne* spp. (8,15,16,18) and sometimes retard nematode reproduction (7,8,18); however, the interaction of VAM fungi and *M. incognita* on peach has not been investigated. The recent ban on 1,2-dibromo-3-chloropropane (DBCP), the most widely used and effective postplant fumigant for peach orchards, makes the potential of VAM fungi in increasing peach tree vigor and serving as biological control agents from *M. incognita* worthy of investigation.

This paper reports the effects of soil fertility, two VAM fungi, and *M. incognita*, singly and in combination, on peach growth, and the influence of these variables on reproduction of two VAM fungi and *M. incognita*.

MATERIALS AND METHODS

Plant propagation. Lovell, a peach cultivar susceptible to *M. incognita*, was used in all studies. The cultivar was propagated by rooting semihardwood cuttings collected during early August as

described by Couvillon and Erez (3). Rooted cuttings were stored at 5 C for a minimum of 1,200 hr to satisfy the chilling requirement for bud break. They were then removed as needed, their roots washed free of vermiculite, and transplanted while still dormant or in early stages of budbreak. Buds of dormant plants usually opened within 7 days.

Plants for split-root experiments were propagated with several modifications of the rooting method (3). Cuttings 25 to 30 cm long with 4-5 mm stem diameter were stripped of the lower leaves, wounded on two sides of the scion base, and a median cut made between the wounds with a utility knife to form a split 0.5 to 1.0 cm long. After a dip in an indole-butyric acid solution (3), the split cutting was placed on the wedge-shaped union formed by two 250-ml tapered plastic tumblers taped together at the top and filled with vermiculite. The cutting was carefully forced downward over the wedge causing an even split approximately 7.5 cm long, then raised slightly so that only the 2-cm wounded portion of each half-stem was buried in the moist vermiculite. Following maintenance in a mist bed, only cuttings with two generally uniform, independent half-root systems were given the cold treatment and kept for further studies.

The cuttings, after the vermiculite was washed from the roots, were weighed and set into holes prepared in the soil, into which either inoculum of the VAM fungi or nematode, spore filtrate, or both was placed. The roots were separated and soil was added to bring the soil line above the roots. Stem caliper at the soil line was measured approximately at the time of budbreak. All experiments were conducted in a greenhouse.

Soil preparation. All tests were conducted in a nutrient-poor Dothan loamy sand having no recent history of use in agricultural production. The soil was analyzed by the University of Georgia Soil and Plant Testing Laboratory, Cooperative Extension Service, Athens. Results of tests on the raw soil were: pH 5.4; $\text{NO}_3\text{-N}$ 9, P 3.5; K 50, Ca 599, Mg 119, Zn 2, Mn 97, and B 0.2 $\mu\text{g/g}$; 2.5% organic matter; and 10×10^{-5} mhos soluble salts. The soil was screened to remove large debris and blended with #2 vermiculite and washed river sand (4:1:1, v/v) in a soil mixer. During this operation, the mix was amended to adjust the pH to 6.0-6.3 and to establish various fertility levels. In one experiment (designated complete fertilizer experiment), reagent grade chemicals were used: a blend of $\text{Ca}(\text{OH})_2$ and MgO was used to adjust the pH and NH_4NO_3 , $\text{Ca}(\text{H}_2\text{PO}_4)_2 \cdot \text{H}_2\text{O}$ and KCl were added at rates equivalent to 500 or 1,000 μg 10-10-10 NPK fertilizer (N = 10%, P =

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4.3%, and K = 8.2%) / g soil. In other experiments (phosphorus and split-root experiments), pH was adjusted with a commercial hydrated horticultural lime derived from dolomitic sources, and three phosphorus fertility levels were established by initially adding 500 µg fine ground commercial 10-10-10 fertilizer per gram of soil and varying the concentration of additional Ca(H₂PO₄)₂ · H₂O to attain the following actual rates of added P: P₀ = no additional P, P₁ = 50 µg/g and P₂ = 150 µg/g. Due to trace element deficiencies observed in the complete fertilizer experiment, a fritted trace element mixture (Peter's FTE #555, W. R. Grace and Co., Allentown, PA 18105) was added at the manufacturer's recommended rate to all soil mixes used in the phosphorus and split-root experiments. The soil was fumigated with methyl bromide (Dowfume MC-2, Dow Chemical Co., Midland, MI 48640) at a minimum rate of 1.4 kg/800 L of mix for 48 hr under polyethylene and vented for approximately 5 days prior to transplanting. In most studies, soil was placed in 4-L plastic pots and maintained on a greenhouse bench. For split-root experiments, P₀ or P₂ soil was placed in units consisting of two 1.8-L plastic freezer containers bolted together.

Inocula increase and inoculation. Chlamydozoospores of *Glomus etunicatus* Becker and Gerd. were increased on *Sorghum bicolor* (L.) Moench. 'Shallu' in pot culture. Azygospores of *Gigaspora margarita* Becker and Hall were increased on *S. bicolor* and *Coleus pumilus* cv. Blanco 'Trailing Red Queen' in pot culture. Spores were extracted from the soil using a modified centrifugal-flotation procedure (9). The inoculum concentration was adjusted to deliver approximately 250 spores per pot in 25 ml of water, which were poured into the hole (10 cm deep) into which trees were transplanted. To standardize the microflora in all nonmycorrhizal treatments, a 25-ml aliquot of spore suspension filtrate collected after a passage through Whatman #1 filter paper was added to each pot.

M. incognita was propagated on greenhouse-grown tomato (*Lycopersicon esculentum* Mill. 'Rutgers'), and eggs for use as inoculum were collected with 0.5% NaOCl as described by Hussey and Barker (6). Inoculations were made at transplanting by pouring approximately 15,000 eggs per plant into the planting hole, with the exception of split-root studies, in which 7,500 eggs per half-root system were used.

Experimental design, plant maintenance, and collection of data. Complete fertilizer experiment (1979). Rooted cuttings were inoculated individually with either *G. etunicatus*, *G. margarita*, or *M. incognita*, or coinoculated with a fungus and the nematode. Plants receiving only a fungal spore filtrate served as controls. The effects of fertility level (500 or 1,000 µg 10-10-10 NPK fertilizer equivalent per gram of soil) were evaluated for each of the above combinations. A minimum of 10 replications were arranged in a randomized complete block design and the study was terminated after 117 days. A duplicate study with eight replications was

terminated after 97 days. A routine foliar spray program of alternate applications of dienochlor (*bis* [pentachloro-2,4 cyclopentadiene-1-yl] Pentac 50% WP, Hooker Chemicals and Plastics Corp., Niagara Falls, NY 14302) and Cyhexatin (tricyclohexyl hydroxystannane, Plictran 50% WP, Chevron Chemical Co., Richmond, CA 94808) at recommended rates was used to minimize mite damage in all tests.

Phosphorus experiment (1980). Three soil mixes (described above) with varying P rates were used. Treatments consisted of individual inoculations with either *G. etunicatus*, *G. margarita*, or *M. incognita*, joint inoculations, and appropriate controls. All fungal inoculations, singly or in combination with the nematode, were made on plants grown only in P₀ soil, whereas plants grown in soil with the three P levels were inoculated with nematode eggs. A minimum of 10 replications were arranged in a randomized complete block design and the study was conducted for 108 days. A duplicate study with a minimum of 10 replications was conducted for 97 days.

Split-root experiment (1980). Cuttings with split-root systems were transplanted so that each half-root system was placed in one half of a double-compartment container filled with either P₀ (basal rate of 500 µg 10-10-10 NPK fertilizer per gram of soil) or P₂ (basal fertility rate + 150 µg P/g soil) soil in various combinations. Treatments included inoculations with *M. incognita* and either *G. margarita* or high phosphorus soil (P₂) on the same or opposing half-root system. A minimum of six replications were arranged in a randomized complete block design and the test was terminated 81 days after transplanting. A duplicate study contained a minimum of five replications and was conducted for 94 days.

Collection of data. Initial plant weight and stem diameter (near soil line) were recorded at the beginning of each experiment. Shoot and root fresh weights, stem diameter, and number of branches were determined at harvest. Roots from individual nematode-free plants were assayed for mycorrhizae by clearing and staining (2). Spore population densities in the soil, determined by a centrifugal-flotation procedure (9), were considered to be an additional indication of mycorrhiza development. Nematode reproduction was measured by collecting and counting eggs (7). Egg counts were log transformed for analysis. Data of duplicate studies were pooled and subjected to a general linear models procedure. Treatment means were compared, when appropriate, by using Fisher's least significant difference test ($P = 0.05$).

RESULTS

Complete fertilizer experiment. Both VAM fungi stimulated peach growth particularly at the low fertility level, increasing shoot weight, and stem diameter when compared with nonmycorrhizal nematode-free plants (Table I and Fig. 1). At the high fertility level *G. etunicatus* increased shoot growth, but *G. margarita* caused a

TABLE I. Effect of *Glomus etunicatus*, *Gigaspora margarita*, and *Meloidogyne incognita* on growth of peach trees at two fertility levels

Fertility ^a	Mycorrhizal fungus	Shoot weight (g)		Root weight (g)		Increase in whole plant weight (g)		Increase in stem diameter (mm)		Branch count
		<i>M. incognita</i> -	<i>M. incognita</i> +	<i>M. incognita</i> -	<i>M. incognita</i> +	<i>M. incognita</i> -	<i>M. incognita</i> +	<i>M. incognita</i> -		
Low	None	13.0	6.9 ^b	25.3	15.4	30.7	14.6	1.5	0.5	0.2
Low	<i>G. etunicatus</i>	34.5	12.3	51.7	19.9	77.8	26.0	3.7	1.5	2.4
Low	<i>G. margarita</i>	34.2	17.5	41.4	23.9	65.8	33.5	3.3	1.9	1.5
	FLSD ($P = 0.05$) ^c	6.4	4.6	NS ^d	NS	NS	9.3	0.7	0.7	NS
High	None	29.0	12.1	43.5	27.6	64.7	31.7	2.8	1.4	0.3
High	<i>G. etunicatus</i>	48.8	20.9	47.2	33.0	89.2	45.6	4.3	2.3	2.6
High	<i>G. margarita</i>	31.1	21.0	33.6	29.1	57.3	42.0	2.9	1.6	0.6
	FLSD ($P = 0.05$)	10.7	NS	9.2	NS	17.6	NS	0.7	0.7	NS

^a Fertility: low = 500; high = 1,000 µg 10-10-10 NPK per gram of soil.

^b Data from nonmycorrhizal plants underscored by the same line in rows are significantly different ($P = 0.05$).

^c FLSD = Fisher's least significant difference.

^d NS = not significant.

23% reduction in root weight. Both mycorrhizal fungi affected foliar nutrient status at low and high fertility, increasing concentrations of P, Fe, Cu, and Zn (Table 2) and alleviating the stunting and leaf chlorosis observed on nonmycorrhizal plants.

Increasing the rate of NPK fertilization significantly increased shoot weight (123%), whole plant weight (110%), and stem diameter (87%) (Table 1). This did not result in improved foliar Fe, Cu, and Zn status at midstudy (Table 2), or alleviate the leaf chlorosis.

M. incognita suppressed shoot and root growth of nonmycorrhizal peach by approximately 50% at both fertility levels (Table 1). The poor growth of nematode-infected plants was accompanied by low foliar concentrations of Fe at low fertility and P at low and high fertility (Table 2), and the most severe nutrient deficiency symptoms in the study.

Foliar analyses for other elements did not reveal any high degree of association with specific treatments. All plants contained inadequate Ca, whereas concentrations of Al, B, Mg, and Mn were within their sufficiency ranges (13).

TABLE 2. Effect of individual and joint inoculations of either *Glomus etunicatus* or *Gigaspora margarita* and *Meloidogyne incognita* on midstudy foliar nutrient status of peach plants grown at two fertility rates^a

Treatment		Nutrient					
Fertility ^b	Inoculum ^c	N (%)	P (%)	K (%)	Fe (μg/g)	Cu (μg/g)	Zn (μg/g)
Low	None	4.20	0.11	1.34	39	2.1	15
Low	Ge	2.59	0.22	2.63	56	5.3	25
Low	Gm	3.35	0.26	2.86	54	5.7	35
Low	Mi	3.10	0.09	2.13	28	2.2	13
Low	Mi+Ge	2.36	0.26	2.75	32	5.2	28
Low	Mi+Gm	3.97	0.23	2.62	38	4.7	41
High	None	3.99	0.18	2.96	39	1.6	16
High	Ge	3.56	0.26	3.15	59	5.0	25
High	Gm	3.48	0.31	3.98	50	5.2	43
High	Mi	3.34	0.12	2.70	38	1.8	46
High	Mi+Ge	2.84	0.22	2.77	40	4.6	27
High	Mi+Gm	3.21	0.21	2.64	45	3.8	38
Sufficiency range ^d		2.45 to 3.00	0.12 to 0.50	1.25 to 2.50	60 to 400	5 to 20	15 to 50

^aData of first trial of experiment I; foliar samples consisted of mature leaves from current terminal growth.

^bFertility: low = 500; high = 1,000 μg 10-10-10 NPK per gram of soil.

^cInoculum: Ge = *Glomus etunicatus*; Gm = *Gigaspora margarita*; and Mi = *Meloidogyne incognita*.

^dSufficiency ranges (13).

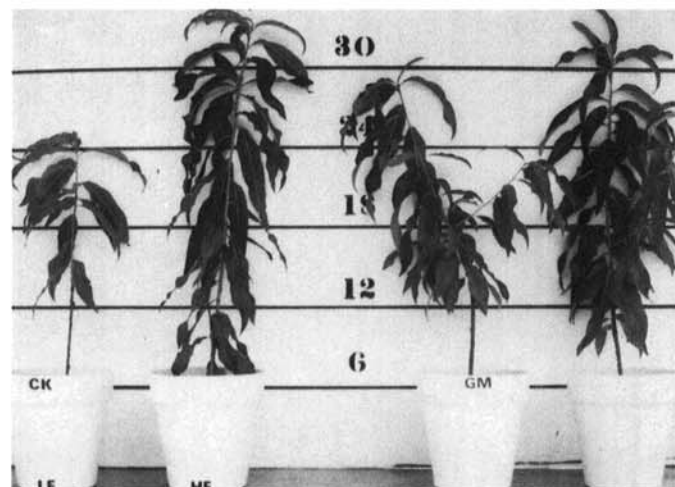


Fig. 1. Growth response of Lovell peach to *Gigaspora margarita* at two soil fertility levels. From left to right: controls (ck); 500 and 1,000 μg 10-10-10 NPK per gram of soil, and mycorrhizal plants (GM); 500 and 1,000 μg 10-10-10 NPK per gram of soil.

Mycorrhizal fungi improved growth of nematode-infected peach. At low fertility, both mycorrhizal fungi induced a twofold or more increase in shoot weight, whole plant weight, and stem diameter (Table 1). Growth increases of nematode-infected plants due to mycorrhizal fungi at high fertility were less marked (Fig. 2).

G. margarita decreased reproduction of *M. incognita*, but *G. etunicatus* or differences in soil fertility had no effect on nematode reproduction. The presence of *G. margarita* suppressed production of eggs per gram of root by 40% only at low fertility (1,500 compared to 2,500 for control plants). Sporulation of the VAM fungi was not affected by *M. incognita* or the soil fertility level. Cleared and stained root sections of nematode-free plants inoculated with the VAM fungi in all studies showed extensive development of arbuscules and intracellular and intercellular hyphae. Plants not inoculated with the VAM fungi remained free of mycorrhizae.

Phosphorus experiment. Growth and foliar levels of P, Fe, Cu, and Zn were greater in the nonmycorrhizal plants grown in the P₀ (micronutrient amended) soil than in comparable plants of the complete fertilizer experiment. The mycorrhizal growth response was also much less pronounced, although improved P, Cu, and Zn status did result from inoculation with the mycorrhizal fungi.

Additions of 50 and 150 μg P/g soil increased shoot growth, whole plant weight, stem diameter, and number of branches (Table 3). P fertilization also resulted in higher foliar concentrations of P and Zn, and lower concentrations of Cu relative to nonmycorrhizal controls grown in the P₀ soil.

Symptoms of imbalanced plant nutrition characterized by shot-hole appearance of foliage and shoot dieback with gumming were observed. Severe symptoms were accompanied by excessive Mn and B, inadequate Ca and Cu, and elevated P concentrations in foliage. Degree of symptom expression followed the order of P₂ > P₁ = mycorrhizae > P₀, and symptoms were intensified by *M. incognita*.

Inoculation of plants grown in the P₀ soil with *M. incognita* resulted in a reduction of shoot and root weights 55 and 21%, respectively (Table 3). Growth of nematode-infected peach was improved by both rates of added P, with the higher rate most effective (Table 3). In contrast with the complete fertilizer experiment, mycorrhizae had little effect on the growth of nematode-infected plants.

Reproduction of *M. incognita* was affected little by phosphorus fertilization and not by mycorrhizal development. Although this addition of P at a rate of 150 μg/g soil promoted a 100% increase in total eggs per root system it had no effect on eggs per gram of root. *M. incognita* had no influence on fungal sporulation.

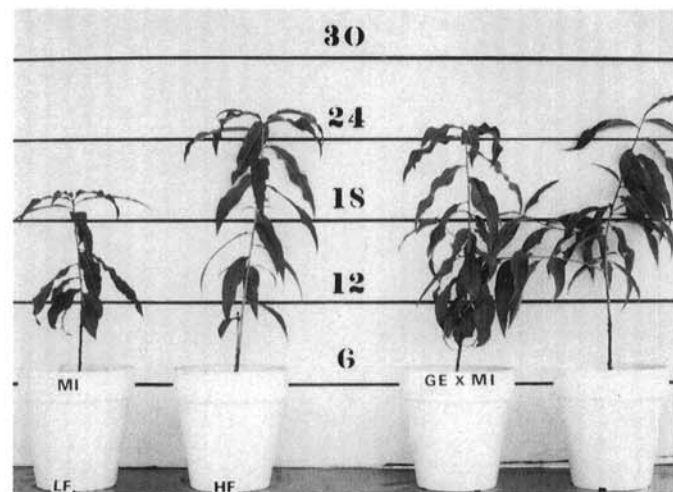


Fig. 2. Growth enhancement of *Meloidogyne incognita*-infected Lovell peach by mycorrhiza formed with *Gigaspora margarita*. From left to right: *M. incognita* (MI) alone; 500 and 1,000 μg 10-10-10 NPK per gram of soil, and concomitant inoculation with *M. incognita* and *G. margarita* (GM × MI); 500 and 1,000 μg 10-10-10 NPK per gram of soil.

Split-root experiment. To facilitate processing of samples, half-root systems inoculated with *M. incognita* were designated root A and the opposing nematode-free half-roots, root B. In the absence of nematode inoculum, half-roots treated with added P or *G. margarita* were designated root B (Table 4). Because of the nature of this split-root experiment it is useful to discuss treatment effects on roots A and B separately from those on other aspects of plant growth.

In the absence of the nematode, added P and *G. margarita* were equally effective in increasing the weight of root B as compared to that of controls grown in soil fertilized with the basal rate of NPK (Table 4). Both the fungus and added P increased the P concentration of the half-root to which they were added, but the effect due to added P was 176% greater. This high rate of P fertilization also promoted a 66% increase in the P content of the opposing (A) half-root system, whereas *G. margarita* did not. The translocated P was apparently insufficient to promote an increase in the weight of root A.

Inoculation of plants with *M. incognita* did not affect weights of A or B roots as compared with control plants (Table 4). When P was added to B roots, A roots inoculated with *M. incognita* were heavier than those not inoculated. This effect was not observed when *G. margarita* occupied B roots. The capacity of added P and the mycorrhiza to increase weight of the B roots to which they were added was not affected by the presence of *M. incognita* on the opposing (A) root system.

In the absence of the nematode, added P and *G. margarita* increased shoot growth of peach as compared with uninoculated plants grown in soil fertilized with only the basal rate of NPK (Table 4). Shoot weights of plants receiving added P were greater than those of mycorrhizal plants. Both additional P and the

mycorrhizae affected foliar P, Cu, and Zn status as in the phosphorus experiment. Symptoms of nutrient imbalances similar to those reported for the phosphorus experiment were observed in the order $0/P > 0/0 > 0/Gm$. *M. incognita* had little effect on growth of uninoculated controls receiving only the basal fertility rate. The nematode suppressed growth of mycorrhizal peach only if inoculated onto the same half-root system as the fungus (Fig. 3).

Added P increased growth of plants inoculated with *M. incognita* whether on the same or opposite half-root system from the nematode (Table 4). *G. margarita* most improved growth of nematode-infected plants when the fungus and nematode occupied separate half-root systems.

Reproduction of *M. incognita* was affected by *G. margarita* and added P. Eggs per root system and per gram of root were increased by the fungus and added P located either on the same or opposite half-root system from the nematode (Table 4). Total eggs per root system and per gram of root were greater when the nematode was added to P-treated roots than when coinoculated with the fungus. When separate from the nematode, no differences in reproduction between the P and fungus treatments were observed. Azygospore production by *G. margarita* was not affected by *M. incognita*.

DISCUSSION

Inoculation of peach trees grown in a low fertility soil (complete fertilizer experiment) with either *G. margarita* or *G. etunicatus* was as effective as an additional 500 μg 10-10-10 NPK per gram of soil in stimulating growth, as was reported for cotton (15). A higher rate of NPK fertilization does not wholly substitute for mycorrhizae in peach, however, since the former did not improve foliar Fe, Cu, and Zn status to nearly the same degree as did the mycorrhizal fungi.

TABLE 3. Influence of phosphorus fertility on growth of peach plants infected by *Meloidogyne incognita*

Inoculum	Fertility ^a	Shoot weight (g)	Root weight (g)	Increase in whole plant weight (g)	Increase in stem caliper (mm)	Branch count
None	P ₀	26.3	33.0	51.7	1.9	0.6
None	P ₁	33.1	40.1	65.9	3.1	2.7
None	P ₂	36.8	45.2	74.6	3.1	4.4
	FLSD ($P = 0.05$) ^b	4.2	NS ^c	9.4	0.4	1.2
<i>M. incognita</i>	P ₀	11.9	24.4	28.3	1.1	0.0
<i>M. incognita</i>	P ₁	22.5	36.7	51.7	2.4	2.0
<i>M. incognita</i>	P ₂	29.9	49.6	71.4	2.9	3.4
	FLSD ($P = 0.05$)	9.5	6.0	9.3	0.4	1.0

^aFertility: P₀ = 0; P₁ = 50; P₂ = 150 μg P/g soil (as Ca [H₂PO₄]₂ · H₂O) + 500 μg 10-10-10 NPK per gram of soil.

^bFLSD = Fisher's least significant difference.

^cNS = not significant.

TABLE 4. Influence of *Meloidogyne incognita*, phosphorus fertility, and *Gigaspora margarita* split-root treatment combinations on growth of peach and reproduction of *Meloidogyne incognita*

Treatment (A/B) ^a	Root A weight (g)	Root B weight (g)	Shoot weight (g)	Increase in whole plant weight (g)	Increase in stem diameter (mm)	Eggs per root system ($\times 1,000$)	Eggs per gram of root ($\times 1,000$)
0/0	6.9	6.3	12.9	17.5	1.1
0/P	9.6	10.9	28.2	41.1	2.1
0/Gm	8.1	11.3	22.8	33.3	1.6
Mi/0	6.7	7.4	11.3	17.0	0.8	10.1 ^c	1.5 ^c
Mi/P	16.1	11.1	27.8	46.5	1.8	79.8	5.3
Mi/Gm	9.6	11.3	20.9	33.0	1.3	70.7	6.1
Mi + P/0	16.8	8.2	26.5	43.4	1.6	109.2	7.0
Mi + Gm/0	12.7	6.3	15.4	26.0	0.9	37.4 ^d	3.0 ^d
	FLSD ($P = 0.05$) ^b	6.1	2.9	3.9	11.3	0.7	...

^aTreatment: 0 = basal application of 500 μg 10-10-10 NPK per gram of soil; P = basal NPK + 150 μg P/g soil as Ca(H₂PO₄)₂ · H₂O; unless otherwise indicated with a P soils in all treatments are 0; Mi = *Meloidogyne incognita*; Gm = *Gigaspora margarita*; A/B: A = half-root inoculated with the nematode; and B = nematode-free half-root.

^bFLSD = Fisher's least significant difference.

^cSignificantly different from other column means ($P = 0.05$).

^dSignificantly different from Mi + P/0 ($P = 0.05$).

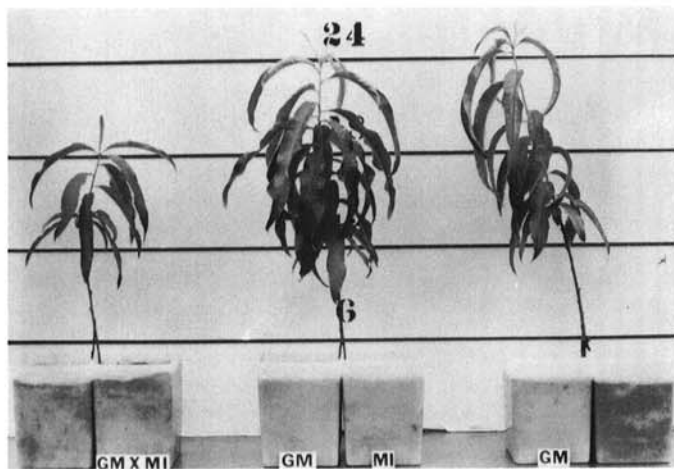


Fig. 3. Growth of split-root Lovell peach in treatments with *Gigaspora margarita* (GM) singly and in combination with *Meloidogyne incognita* (MI) at a NPK fertility rate of 500 µg 10-10-10 per gram of soil. From left to right: *G. margarita* and *M. incognita* coinoculated at planting on the same (GM × MI) or separate (GM and MI) root systems and *G. margarita* (GM) alone.

The highest rate of P fertilization (150 µg/g soil) promoted more rapid growth than did the mycorrhizal fungi, but also resulted in nutrient imbalances that were apparently detrimental to the quality of peach tree growth. The depressive effect of high P on plant Cu content has been reported for a number of crops (1,10,17,20).

The mycorrhizae formed by *G. etunicatus* and *G. margarita* stimulated plant growth in the complete fertilizer experiment, but were much less effective in the phosphorus experiment. The control plants had greater shoot weights in the phosphorus experiment which contained micronutrient-amended soil and had higher concentrations of foliar P, Fe, Cu, and Zn than in the other experiments, and therefore, mycorrhizal dependency may have been reduced. Furthermore, nutrient imbalances (excessive Mn and B and inadequate Ca) may have been detrimental to the mycorrhizal response in the phosphorus experiment. Increased mycorrhizal response under low fertility conditions as observed in our study is common on a wide range of plant species (4). The increases in foliar P, Cu, and Zn concentrations due to the VAM fungi that we observed are consistent with the observations of Gilmore (5) and Lambert et al (11).

The deleterious effects that *M. incognita* had on peach growth are not uncommon (14). Increased fertilization in all studies and mycorrhizae in the complete fertilizer and split-root experiments, however, conferred some degree of nematode tolerance in peach. Increasing tolerance is considered to be the principal effect VAM have on host reactions to plant-parasitic nematodes (8). The mycorrhizae were, in fact, as effective as doubling the NPK rate in complete fertilizer experiment, but were less effective than 150 µg P/g soil in increasing the quantity of growth of nematode-infected plants.

Although root colonization by *G. margarita* was extensive (>75% of root length colonized in nematode-free plants) in all studies, the effects of the mycorrhizae on nematode reproduction were inconsistent. The fungus exerted some suppressive influence on nematode reproduction (eggs per gram of root) in some experiments. In the split-root experiment, however, a suppressive effect, when compared with phosphorus, occurred only when the fungus and nematode were inoculated onto the same half-root system. *G. margarita* had no effect on the reproduction of *M. incognita* on cotton (15). Only a few mycorrhizal fungi are reported to suppress plant-parasitic nematode reproduction (8).

Because peach is a perennial plant that cannot be rotated with nonhosts of *M. incognita* on a short-term basis and highly effective

postplant nematicidal treatments for peach are not available, a mycorrhiza that would help maintain low densities of *M. incognita* and other nematode species pathogenic on peach, in addition to otherwise benefiting peach growth, would be desirable. In uncultivated orchards, peach trees normally make most of their root growth in cool soils during the spring. The soil temperature may be unfavorable to the activities of both mycorrhizal fungi and *M. incognita*. Phosphorus fertilization, however, at this time may stimulate root growth during the absence of nematode activity. The influence of soil temperature on activities and population dynamics of these organisms on peach, singly and in combination, with and without supplemental phosphorus, should be investigated in controlled environments.

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