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Penetration and Postinfection Development of *Meloidogyne incognita* on Cotton as Affected by *Glomus intraradices* and Phosphorus[1]

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Abstract: The influence of the vesicular-arbuscular mycorrhizal fungus *Glomus intraradices* (Gi) and superphosphate (P) on penetration, development, and reproduction of *Meloidogyne incognita* (Mi) was studied on the Mi-susceptible cotton cultivar Stoneville 213 in an environmental chamber at 28 C. Plants were inoculated with Mi eggs at planting or after 28 days and destructively sampled 7, 14, 21, and 28 days after nematode inoculation. Mi penetration after 7 days was similar in all treatments at either inoculation interval. At 28 days, however, nematode numbers were least in mycorrhizal root systems and greatest in root systems grown with supplemental P. The rate of development of second-stage juveniles to ovipositing females was unaffected by Gi or P when Mi was added at planting, but was delayed in mycorrhizal root systems when Mi was added 28 days after planting. Nematode reproduction was lower in mycorrhizal than in nonmycorrhizal root systems at both Mi inoculation intervals. Nematode reproduction was stimulated by P when Mi was added at planting, but was similar to reproduction in the low P nonmycorrhizal treatment when Mi was added 28 days after planting. Eggs per female were increased by P fertility when Mi was added at planting.

Key words: endomycorrhizae, *Gossypium hirsutum, Meloidogyne incognita,* root-knot nematode, phosphorus, cotton.

Plant-parasitic nematodes and vesicular-arbuscular mycorrhizal (VAM) fungi are indigenous to all soils where cotton is grown throughout the world (4,12). Several plant-parasitic nematodes are important root pathogens on cotton, with *Meloidogyne incognita* (Kofoid & White) Chitwood the major cause of yield losses (12). *M. incognita* (Mi) disrupts root function and nutrient absorption, reduces numbers of feeder roots, and suppresses plant growth and yield (7).

VAM fungi are obligately symbiotic fungi that colonize cortical cells of feeder roots and enhance, through an extensive network of extramatrical hyphae, phosphorus (P) and minor element absorption (4). VAM fungi and Mi colonize similar tissues in cotton roots, but each exerts an opposite effect on plant growth. With concomitant infections by Mi and VAM fungi, plant growth is usually enhanced and in some cases nematode reproduction is suppressed (6,11,13). In greenhouse experiments conducted with P-deficient soil, supplemental P mimicked the mycorrhizal effect on plant growth, but nematode reproduction was not affected (10). In field microplot studies with cotton, however, P fertility increased the severity of nematode damage (13).

Mycorrhizal and P effects on Mi parasitism and reproduction have not been adequately documented. Detailed studies of the development of Mi in root systems grown in soil infested with mycorrhizal fungi or varied levels of P should help to understand these interactions. Our objective was to determine the effect of the VAM fungus, *Glomus intraradices* Schenck & Smith, and P fertility on penetration, development, and reproduction of Mi on cotton.

MATERIALS AND METHODS

Two experiments were conducted in an environmental chamber adjusted to 28 C (±1 C), 330 microeinsteins m^{-2} sec^{-1}, and 14-hour light–10-hour dark diurnal day-length regimes. Degree-days required for *M. incognita* to develop to a certain life-stage were calculated by the equation $D = (T - T_1) \times$ hours to sample date, where

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the base developmental threshold (T_1) = 10 C (17). Mi-susceptible cotton (*Gossypium hirsutum* L. cv. Stoneville 213) was grown in a Marlboro loamy sand (Plinthic Paleudult series, 92% sand, 6% silt, 1.5% clay, and 0.5% organic matter) amended with 740 mg 10-10-10 (N = 10%, P = 4.3%, K = 8.2%), 920 mg $MgSO_4 \cdot 7H_2O$, and 185 mg NH_4NO_3 per kilogram of soil and fumigated with methyl bromide (Dowfume MC-2, 2.2 kg/200 kg soil).

Low P and high P levels were established by adding 138 mg or 430 mg $CaHPO_4$ per kilogram of soil. Preliminary research demonstrated that the low P level was sufficient for normal cotton growth and VAM fungal root colonization and the high P level stimulated seedling growth and inhibited VAM fungal root colonization. Soil analysis results were as follows. Experiment 1: (low P) pH = 5.8, P = 61, K = 76, Ca = 332, Mg = 121, N-NO_3 = 48; (high P) pH = 5.8, P = 135, K = 73, Ca = 463, Mg = 130, N-NO_3 = 48 mg/kg. Experiment 2: (low P) pH = 6.2, P = 58, K = 86, Ca = 500, Mg = 119, N-NO_3 = 35; (high P) pH = 6.2, P = 92, K = 72, Ca = 453, Mg = 99, N-NO_3 = 23 mg/kg.

Treatments in both studies consisted of Mi alone and Mi + Gi at low P level and Mi at high P level. In both experiments cotton plants were inoculated with 250 Mi eggs per 100 cm^3 soil either at planting or 28 days after planting. Inoculation with Mi 28 days after planting allowed the mycorrhizal fungus to colonize roots extensively and provided a method to simulate mycorrhizal effects on the development of secondary or subsequent nematode generations. Plants were destructively sampled 7, 14, 21, and 28 days after seedling emergence when Mi was added at planting or after Mi inoculation when Mi was added 28 days after planting. Treatments were replicated five times for Mi inoculation at planting and three times for delayed Mi inoculation for each sample date and arranged in a randomized complete block design. Data presented are from experiment 1 unless indicated otherwise. Plants sampled 7 or 14 days after seedling emergence were grown in 12.5-cm-d (800 cm^3) pots, whereas other plants were grown in 15-cm-d (1,600 cm^3) pots. The smaller pot size used with Mi inoculation at planting was sufficient for unrestricted root growth of cotton up to 14 days, whereas the larger pots allowed unrestricted root growth for up to 60 days. Total eggs used for inoculum differed with pot size to maintain uniform egg inoculum densities per unit volume of soil.

Mi was propagated on greenhouse-grown tomato (*Lycopersicon esculentum* Mill. cv. Rutgers), and eggs were collected with 0.5% NaOCl (5). When added at planting, a 10-ml aliquant (30 ml total) of eggs was added 2, 4, and 6 cm below the soil surface in 12.5-cm-d pots and 3, 6, and 9 cm below the soil surface in 15-cm-d pots. When added 28 days after planting, the inoculum was applied in a 3-ml aliquant placed into each of 10 holes (five holes at 5 cm deep and five holes at 10 cm deep) positioned around the plant. The soil was infested with approximately 2,500 chlamydospores of *G. intraradices* by mixing 25 g of pot culture soil and root inoculum per pot throughout the soil.

Plant growth was measured by weighing fresh shoots and by measuring total root length on plants inoculated with Mi at planting or weighing fresh roots for the delayed Mi inoculation. At each harvest date, whole root systems were carefully washed to ensure retrieval of all roots. Since Mi second-stage juveniles (J2) preferentially penetrate near the root tip and are not uniformly distributed in the root system, recovery of the entire root system was necessary to accurately assess total nematode population density in a root system. Thus, this technique precluded assaying soil samples for J2 population densities. Washed root systems were immersed in 0.01% phloxine B to stain egg sacs for counting. In the delayed Mi inoculation, 0.5-g root samples were removed from plants and cleared and stained to assay for VAM fungal colonization using a modified technique of Phillips and Hayman (9). After counting egg masses, roots were cleared in 1.0% NaOCl and eggs were collected on a 25-μm-pore sieve. Roots were stained for nematodes as described by Byrd et al. (2). Total nematodes per root system were determined, and individual nematodes were assigned to one of five classes according to their developmental stage: 1) vermiform J2; 2) vermiform J2 that had established a feeding site; 3) swollen J2, J3, or J4 with tail; 4) saccate adult female without eggs;

TABLE 1. Effect of *Glomus intraradices* (Gi) and superphosphate (P) on shoot growth of cotton inoculated with *Meloidogyne incognita* (Mi) at planting or 28 days later.

Time of Mi inoculation	Treatment	Fresh shoot weight (g)			
		Day 7	Day 14	Day 21	Day 28
At planting	Mi	1.1 a	1.8 a	3.1 a	4.2 a
	Mi + Gi	1.2 a	2.0 a	3.6 a	4.4 a
	Mi + P	1.1 a	2.3 a	3.6 a	5.3 b
28 days after planting	Mi	9.8 a	13.5 a	15.8 a	19.8 a
	Mi + Gi	10.1 a	15.6 ab	19.1 b	27.2 b
	Mi + P	13.0 a	19.2 b	22.0 b	27.0 b

Column means within Mi inoculation interval followed by the same letter not significantly different ($P = 0.05$) according to Waller-Duncan *K*-ratio *t*-test. Experiments 1 and 2 combined.

and 5) saccate adult female with eggs (16). Numbers of class 5 adults were determined by counting the number of egg sacs. Class 4 adults were determined by subtracting class 5 adults from the total adults counted after staining roots. Total nematodes per root system were adjusted in the delayed Mi inoculation to account for the 0.5-g sample removed from plants in the assay for mycorrhizae.

Analysis of variance, Waller-Duncan *K*-ratio *t*-test, and regression analysis were employed in data analysis. Nematode penetration and infection were determined by counting total numbers of nematodes in root systems at each sample date. Rate of population development over degree-days was determined by converting numbers of nematodes in each class to a percentage of the total number of nematodes in each root system. Vermiform J2 were deleted from the analysis at the 28-day sample to remove the influence of hatched progeny from the first-generation females on the rate of development. This percentage was multiplied by 100 and divided by a weighted value of 5 for class 1, 4 for class 2, 3 for class 3, 2 for class 4, and 1 for class 5. This method assigns increasing value based on nematode maturity stage, with an ovipositing female assessed five times the value of a vermiform J2. The maturity index at each sample date was calculated by summing the values from each class. The maturity index scale ranged from 20 to 100, where a value of 20 = 100% of the nematode population were vermiform J2 and a value of 100 = 100% of the nematode population were ovipositing females. The maturity index values were plotted over degree-days, and linear regression was employed to describe the best fitting line using least squares estimates (14). Slopes were tested for homogeneity to assess treatment differences in the rate of development of J2 to ovipositing females. Nematode reproduction was determined by counting the number of eggs recovered from root systems sampled 28 days after Mi inoculation. Total eggs, eggs per gram of root, eggs per female, and reproductive factor (Rf) were analyzed.

RESULTS

Plant growth: With Mi inoculation at planting, significant differences in fresh shoot weights among treatments occurred only after 28 days when growth was increased with P fertilization compared with the Mi and Gi treatments (Table 1). With Mi inoculation 28 days after planting, shoot growth was enhanced with P fertilization after 7 days compared with the Mi-only treatment. Mycorrhizal growth stimulation comparable to the high P treatment occurred by 14 days, and by 21 days both Gi and P enhanced shoot growth compared with Mi only.

Differences in total root length or fresh root weights occurred only among treatments after 28 days in either Mi inoculation time (Table 2). Total root length was increased by P when Mi was added at planting, and fresh root weight was greater with Gi when Mi was added 28 days after planting.

Penetration and infection: Total numbers of Mi penetrating and infecting cotton root systems were generally lower with Gi inoculation and higher with supplemental P fertility when compared with Mi only at the low P rate. At both Mi inoculation intervals, the total number of nematodes penetrating root systems did not differ

TABLE 2. Effect of *Glomus intraradices* (Gi) and superphosphate (P) on root growth of cotton inoculated with *Meloidogyne incognita* (Mi) at planting or 28 days later.

Time of Mi inoculation	Treatment	Sample day 7	14	21	28
		Total root length (cm)			
At planting	Mi	147 a	257 a	543 a	890 a
	Mi + Gi	151 a	224 a	524 a	853 a
	Mi + P	165 a	268 a	489 a	1,125 b
		Fresh root weight (g)			
28 days after planting	Mi	3.1 a	3.3 a	4.3 a	5.5 a
	Mi + Gi	2.5 a	4.0 a	4.3 a	7.5 b
	Mi + P	3.1 a	3.6 a	3.7 a	5.4 a

Column means within Mi inoculation interval followed by the same letter not significantly different ($P = 0.05$) according to Waller-Duncan K-ratio t-test. Experiments 1 and 2 combined.

among treatments at 7 days (Table 3). On plants inoculated with Mi at planting, total numbers of Mi at 28 days were significantly greater ($P = 0.05$) in root systems of plants receiving high P than in those receiving Gi; on root systems inoculated with Mi only, the numbers were not different from those receiving either P or Gi. When Mi inoculation was delayed, significantly fewer J2 had infected Gi root systems at 14 days. By 28 days total numbers of Mi were significantly higher in plus P root systems than in Mi only and significantly lower in mycorrhizal than in nonmycorrhizal root systems.

Development: The number of Mi developing into ovipositing females followed the same trends among treatments for both nematode inoculation intervals as total numbers of Mi (Table 4). When Mi was added at planting, the proportions of the total populations in roots developing to ovipositing females were 64%, 57%, and 66% in the Mi only, Gi, and high P treatments, respectively. When Mi inoculation was delayed 28 days, the percentages were 48%, 28%, and 42% in the Mi only, Gi, and high P treatments, respectively.

The rates of development of Mi populations in cotton root systems were best described by fitting the data to a linear model ($P = 0.0001$) when plotted over degree days (Figs. 1, 2). With Mi inoculation at planting, slopes within each treatment in experiments 1 and 2 were not homogeneous, so the data from experiment 1 are presented. There were no significant differences in slopes among treatments in either experiment (Fig. 1). With delayed Mi inoculation, similar slopes within each treatment from experiments 1 and 2 permitted combination of the data. The rate of J2 maturing to ovipositing females was reduced on the high P and Gi root systems, compared with root systems infected with Mi only (Fig. 2). The probabilities of a difference in slopes for the three treatment

TABLE 3. Effect of *Glomus intraradices* (Gi) and superphosphate (P) on infection of cotton roots by *Meloidogyne incognita* (Mi) added at planting or 28 days later.

Time of Mi inoculation	Treatment	Numbers of *M. incognita* Day 7	Day 14	Day 28
At planting	Mi	280 a	142 a	534 ab
	Mi + Gi	257 a	128 a	501 b
	Mi + P	300 a	159 a	604 a
28 days after planting	Mi	467 a	1,314 a	1,670 b
	Mi + Gi	578 a	839 b	1,394 c
	Mi + P	539 a	1,588 a	2,004 a

Column means within Mi inoculation interval followed by the same letter not significantly different ($P = 0.05$) according to Waller-Duncan K-ratio t-test.

TABLE 4. Effect of *Glomus intraradices* (Gi) and superphosphate (P) on the development of *Meloidogyne incognita* (Mi) ovipositing females on cotton root systems when Mi was added at planting or after 28 days.

Treatment	Ovipositing *M. incognita* females: Mi inoculation at planting	Mi inoculation 28 days after planting
Mi	341 ab	797 a
Mi + Gi	287 b	393 b
Mi + P	398 a	835 a

Column means followed by the same letter not significantly different ($P = 0.05$) according to Waller-Duncan K-ratio t-test.

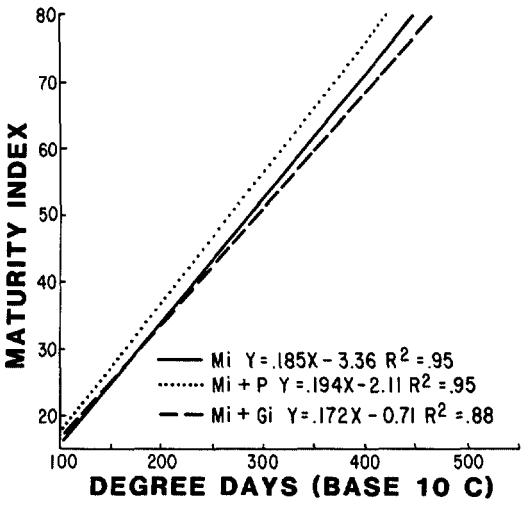

FIG. 1. Rate of development of *Meloidogyne incognita* (Mi) in root systems of cotton grown in soil infested at planting with 250 Mi eggs/100 cm³ soil (Mi), *Glomus intraradices* (Mi + Gi), and superphosphate (Mi + P). Each regression line based on 20 data points.

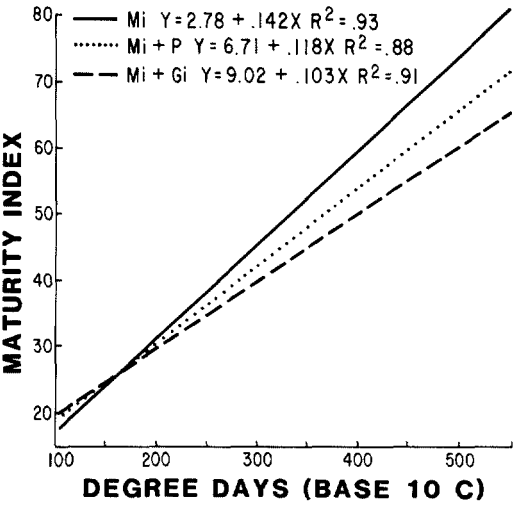

FIG. 2. Rate of development of *Meloidogyne incognita* (Mi) in root systems of cotton grown in soil infested 28 days after planting with 250 Mi eggs/100 cm³ soil (Mi), *Glomus intraradices* (Mi + Gi), and superphosphate (Mi + P). Each regression line based on 24 data points.

comparisions at this inoculation interval were $P = 0.04$ for Mi only vs. high P, $P = 0.005$ for Mi only vs. Gi, and $P = 0.07$ for Gi vs. high P.

Nematode reproduction: When Mi was added at planting, total eggs, eggs per female, and Rf were significantly ($P = 0.05$) increased by supplemental P (Table 5). Total eggs and Rf were increased 76% and 79%, respectively, by P fertilization. With delayed Mi inoculation, nematode reproduction was not affected by P rate. However, all nematode reproductive parameters in Gi root systems, except eggs per female, were significantly ($P = 0.05$) lower than the same parameters on the nonmycorrhizal root systems. Total eggs, eggs per gram of root, and Rf on Gi root systems were approximately 54%, 72%, and 54% lower, respectively, than on Mi only and high P root systems. Eggs per female did not differ among treatments.

In experiment 2 when Mi inoculation was delayed 28 days, nematode reproduction was highest in the nonmycorrhizal root systems, but reproduction in root systems receiving high P did not differ significantly from reproduction in mycorrhizal root systems.

DISCUSSION

Supplemental P fertility stimulated egg production per female and increased the number of ovipositing females when nematodes were added at planting but not when inoculation was delayed. Phosphorus is highly immobile and readily fixed in soil in forms that are unavailable to plants (3). In soil lacking VAM fungi, available P is rapidly depleted around the root zone and P effects on Mi development should be more pronounced in the early stages of plant growth. This would explain the results with Mi inoculation at planting where the number of ovipositing females and reproduction were stimulated with supplemental P fertility. The increase in eggs per female on root systems grown with supplemental P primarily accounts for the greater number of eggs per plant, as total nematodes and the proportion of total nematodes were not significantly different between the low and high P nonmycorrhizal root systems. Thomson Cason et al. (15) reported that supplemental P on tomato had no effect on eggs per egg mass, with increases in total eggs on high P root systems attributed to increased root growth. On more mature plants where Mi inoculation was delayed, Mi infection and reproduction were similar among the low and high P nonmycorrhizal root systems. Phosphorus fixation in the soil and absorption by the plant probably created soil and plants with

TABLE 5. Influence of *Glomus intraradices* (Gi) and superphosphate (P) on *Meloidogyne incognita* (Mi) reproduction on Stoneville 213 cotton when Mi was added at planting or 28 days later.

Time of Mi inoculation	Treatment	*M. incognita* reproduction			
		Total eggs (× 1,000)	Eggs/g root (× 1,000)	Eggs/female	Rf*
At planting	Mi	57.3 b	nd†	172 b	14 b
	Mi + Gi	56.8 b	nd	201 b	14 b
	Mi + P	100.4 a	nd	251 a	25 a
28 days after planting	Mi	211.0 a	36.4 a	265 a	53 a
	Mi + Gi	96.6 b	10.8 b	233 a	24 b
	Mi + P	207.9 a	41.8 a	248 a	52 a

Column means within Mi inoculation interval followed by the same letter not significantly different ($P = 0.05$) according to Waller-Duncan K-ratio t-test.

* Reproductive factor = initial egg densities/final egg densities.

† No data.

similar P status so that effects on Mi were not different.

Mycorrhizal effects on Mi were more pronounced when the fungus was allowed to develop in roots for 28 days before Mi inoculation. Even though mycorrhizal fungi are relatively slow to colonize roots, more than 60% of the root system may be colonized during the first 60 days of cotton growth (13). Also, Harley and Smith (4) have estimated that mycorrhizal fungi utilize up to 15% of host photosynthates. If factors such as spacial and (or) host photosynthate competition occur between the fungus and the nematode to reduce Mi development and reproduction on mycorrhizal root systems, then a certain threshold of VAM fungal root colonization should be required for inhibition of Mi. In fact, Saleh and Sikora (11) reported that 55–60% mycorrhizal root colonization was required to suppress Mi reproduction on cotton. In our study, 20–30% of the roots were colonized by Gi when the plants were 35 days old. Prior to this plant age, Mi eggs per plant and the rate of development of Mi were not affected by Gi. However, Mi reproduction was reduced 54% on Gi root systems when the plants were 56 days old and more than 50% of the root system was mycorrhizal. Therefore, these root colonization percentages suggest that competition for host photosynthates or possibly the production of a nematistatic compound from the host-symbiont interaction may better explain nematode suppression than competition for space since more than half of the root system was not colonized by the fungus.

Our results support previous work on tomato (15) which indicated that neither VAM fungi nor P affect the pre-infectional Mi-host relationship, but they differ from work on onion (8) where 3-day J2 penetration was less on VAM plants. Also, both studies (8,15) indicated that neither VAM fungi nor P affected the rate of development, proportions of total nematode populations that were ovipositing females, or eggs per egg sac of Mi. However, the VAM fungus used in our studies did affect post-infectional development of Mi. Specific host–symbiont effects may explain these varying results.

On cotton inoculated with Mi 28 days after planting, the reduced numbers of Mi infecting mycorrhizal root systems by 14 days was the most obvious effect of VAM on post-infectional development of Mi. The reduction in infection suggests that Gi altered the nematode-host interaction, causing significant numbers of J2 either to migrate out of roots or die before they could establish feeding sites, or that the female : male ratio was reduced.

Precise determination of the stage of the life cycle of Mi most affected by VAM fungi remains difficult to pinpoint because the nematode parameters measured are interrelated. Inhibition of infection has a cumulative effect on the development of the population and its subsequent reproduction. Thus, the reduced rate of development of Mi cannot be attributed solely to any systemic effect of the VAM fungus on the host that alters the nematode's ability to complete its life cycle because it is confounded by the reduced or delayed in-

fection. Future research should employ methods that resolve these effects into quantifiable statistical parameters. Components analysis, an epidemiological tool used to identify the various stages of the infection process most affected by resistance genes, might prove useful if adapted to an appropriate experimental design (18). Also, factorial split-plot designs where mycorrhizae or phosphorus comprise the main plot effect and different initial nematode population densities comprise the subplot effects could be utilized (14). Such experimental designs might establish that certain thresholds of nematode densities, VAM fungal root colonization, or phosphorus content in root systems are required before nematode parasitism is stimulated by P or inhibited by VAM fungi.

Future research on VAM fungi–Mi interactions should use J2 instead of eggs for inoculum to minimize variations in age among eggs used for inoculum and in inoculum extraction procedures. In our experiments, Mi population densities in roots increased over sample dates except in experiment 2 with Mi inoculation at planting. Also, final population densities in roots in experiment 1 were approximately three times those in experiment 2. Since 12–18 days are required for development from the two-celled egg stage to eclosion (1), the number of J2 hatching from eggs may vary. Finally, the NaOCl used in inoculum preparation may have lowered J2 infection frequencies by predisposing eggs to premature mortality (5).

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