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Interaction of Endomycorrhizal Fungi, Superphosphate, and *Meloidogyne incognita* on Cotton in Microplot and Field Studies[1]

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Abstract: Microplot and field experiments were conducted to determine the effects of two vesicular-arbuscular mycorrhizal (VAM) fungi, *Glomus intraradices* (Gi) and *Gigaspora margarita* (Gm), and dicalcium phosphate (P) on *Meloidogyne incognita* (Mi) reproduction and seed cotton yield of the Mi-susceptible cotton cultivar, Stoneville 213. In 1983 population densities of Mi juveniles were significantly lower 60 and 90 days after planting in microplots receiving Gi. Mycorrhizal fungi reduced the severity of yield losses to Mi, whereas P fertilization increased yield losses to Mi. In 1984 microplot yields were reduced linearly as nematode inoculum densities increased in treatments of Mi alone, Gm, or P, but the response was curvilinear with Gi. Yield suppressions in the 1984 field experiment occurred only in plots infested with Mi alone. In the 1984 microplots, numbers of Mi juveniles penetrating seedling roots increased linearly with increasing nematode inoculum densities and was favored when mycorrhizal fungi or superphosphate were added. Juvenile penetration of roots was negatively correlated with yields in all treatments ($r = -0.54$ to -0.81) except Gm and with number of bolls in Mi alone ($r = -0.85$) and P ($r = -0.81$) treatments. Mycorrhizal fungi can increase host tolerance to *M. incognita* in field conditions and may function as important biological control agents in soils infested with high population densities of efficient VAM species.

Key words: biocontrol, endomycorrhizae, interaction, *Meloidogyne incognita*, root-knot nematode, microplots.

Vesicular-arbuscular mycorrhizal (VAM) fungi and plant-parasitic nematodes are indigenous to all cotton producing areas worldwide, with *Meloidogyne incognita* (Kofoid and White) Chitwood (Mi) primarily responsible for yield losses on cotton (17). In contrast, the obligately symbiotic VAM fungi can stimulate plant growth primarily through improved uptake of phosphorus (5). These two groups of microorganisms are commonly found inhabiting the same soil and colonizing roots of host plants, with each exerting a characteristic, but opposite, effect on plant growth (8,21,22).

VAM fungi may act as biocontrol agents of plant-parasitic nematodes when both organisms co-inhabit the roots of host plants. Field surveys of soybean and cotton have reported negative correlations between population densities of endomycorrhizal fungi and plant-parasitic nematodes (14,19). Interactions between Mi and VAM fungi have been primarily evaluated on tomato (1,23,27), soybean (10,11,20), cotton (8,15,24), and peach (26) in greenhouse studies. Usually, root colonization by VAM fungi increases plant tolerance to nematode parasitism (8,18) or adversely affects nematode reproduction (1,8,10,11,23,24). However, VAM fungi may promote nematode reproduction (15,20) by stimulating root growth through improved phosphorus (P) nutrition or may have no effect on nematode activities (27). Specific host–symbiont–nematode responses or P nutrition interactions may explain these various results.

The role of P in mycorrhizae–nematode interactions remains incompletely understood and requires additional research. A study of the influence of P on nematode–host relationships might help clarify the interaction of VAM fungi with plant-parasitic nematodes. If mycorrhizal fungi merely increase host tolerance to nematode parasitism by improving P nutrition of the host and stimulating root growth, then research on effective nematode management might include varying applications of P fertilizers to increase yields in nematode infested soils. If, however, mycorrhizal colonization of host roots adversely affects nematode parasitism and reproduction, then investigations should be of management practices designed to improve the mycorrhizal status

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of soils while maintaining adequate fertility for plant growth. Our objectives were to determine 1) the effect of mycorrhizal fungi and P fertilization on seed cotton yields and Mi reproduction in fumigated microplots and nonfumigated field soils and 2) the effect of high P fertility on mycorrhizal development in the field.

Materials and Methods

Site preparation: Microplot experiments were conducted for 3 years (1982–84) and a field experiment was conducted in 1984 at a site with Pacolet sandy loam soil (Typic Halpludult, clayey, kaolinitic, thermic, 90% sand, 6% clay, 3% silt, 1% OM). Two phosphorus levels were established in all experiments. Fiberglass microplots (82 cm d) were fumigated 3 weeks before planting with methyl bromide (Dowfume MC2, 1.02 kg/30 m^2). Field plots (82 cm long × 64 cm wide) were not fumigated. The experimental site was fertilized with 27.5 kg/ha of 0-0-60 fertilizer (50% K) each year before planting and in 1984 with 4.5 kg/ha of elemental magnesium as $MgSO_4 \cdot 7H_2O$. In 1982, each microplot was fertilized with 23 g 10-10-10 (N = 10%, P = 4.3%, and K = 8.2%), and each microplot designated as a high P treatment received an additional 28 g $CaHPO_4$ as finely pulverized dicalcium phosphate (18% P). In 1983 and 1984 each microplot and field plot designated as a low P treatment were fertilized with 23 g 10-10-10 plus 28 g $CaHPO_4$, and those plots designated as high P treatments were fertilized with 23 g 10-10-10 plus 63 g $CaHPO_4$. The superphosphate was mixed with approximately 1 liter of soil, spread evenly throughout the microplot or field plot, and incorporated 23 cm deep before the soil was infested with nematodes or mycorrhizal fungi. Soil samples collected at planting each year were analyzed by the University of Georgia Soil and Plant Testing Laboratory, Cooperative Extension Service (Table 1). Sixty days after planting all plots and border rows received 9.2 kg N/ha as ammonium nitrate except in 1982 when no additional N was applied.

Border rows of cotton (*Gossypium hirsutum* L. cv. Stoneville 213) were planted between microplot and field plot rows and between microplots and field plots within each row. Twenty pregerminated cotton seed were planted in a row in each plot and thinned to 10 plants 1 week after seedling emergence. Plots were irrigated at planting with 2.5 cm water and thereafter on a periodic basis whenever a 2-week period elapsed without measureable precipitation. In 1983 and 1984, trifluralin (*a,a,a*-trifluoro-2,6-dinitro-*N,N*-dipropyl-*p*-toluidine, Treflan, 0.56 kg a.i./ha) was applied for weed control, and acephate (*O,S*-dimethyl acetylphosphoramidothioate, Orthene) was applied 2 weeks after emergence for thrip control. Recommended insecticidal sprays were applied on a 5–7-day schedule.

TABLE 1. Soil analysis results (mg/kg soil) at planting in cotton microplots and field plots by year.

Experiment	pH	P*	K	Ca	Mg	Zn
Microplots						
1982 Low P	6.7	43	55	362	34	1
High P	6.7	82	57	414	31	1
1983 Low P	6.0	82	99	438	36	1
High P	5.9	142	151	502	35	1
1984 Low P	6.2	70	75	473	51	1
High P	6.0	139	85	698	60	1
Field plots						
1984 Low P	6.2	103	82	675	44	1
High P	6.1	175	92	597	49	1

* Phosphorus values determined by Bray II double acid extraction.

Preparation of inocula and inoculation: *Glomus intraradices* Smith & Schenck and *Gigaspora margarita* Becker & Hall were propagated on bahiagrass (*Paspalum notatum* Flugge) in pot culture for 1 year in the greenhouse. Soil and root inoculum was prepared by chopping soil and roots and stored at 5 C. Each inoculum source was assayed for spore density, and minimum values were estimated at 100 chlamydospores per gram of soil for Gi and 20 azygospores per gram of soil for Gm. Four hundred grams of soil and root inoculum were incorporated in a 15-cm-wide band 15–20 cm deep before planting. To standardize the microflora, 400 ml pot culture filtrate was applied to plots not receiving mycorrhizal inoculum. Culture filtrate was obtained by decanting and wet-sieving 400 g pot culture soil through a 25-μm-pore sieve. Gi was used in all experiments, whereas Gm was used only in the 1984 microplot experiment.

Meloidogyne incognita was propagated on greenhouse grown tomato (*Lycopersicon esculentum* Mill. cv. Rutgers). Nematode inoculum consisted of eggs extracted from galled roots with 0.5% NaOCl (7). Nematode inoculum levels of 0 and 250 eggs/100 cm^3 soil were applied in the 1982 and 1983 microplot experiments and in the 1984 field experiment. In the 1984 microplot experiment, inoculum levels were 0, 83, 250, and 750 eggs/100 cm^3 soil. Eggs were suspended in 1,600 ml water, which was evenly distributed over each plot, and incorporated 23 cm deep.

Experimental design and collection of data: Experimental design for the 1982 and 1983 microplot experiments was a 2^3 factorial with eight treatments replicated six times in a randomized complete block design. Main effects consisted of Mi, Gi, and P treatments. The experimental design for the 1984 microplot experiment was a 4 × 4 factorial with 16 treatments replicated four times in a randomized complete block design. Main effects consisted of Mi alone, Gi, Gm, and P treatments at four Mi inoculum levels. The experimental design for the 1984 field experiment consisted of a multiple treatment comparison without interaction with five treatments replicated four times in a randomized complete block design. Individual treatments consisted of Gi, P, Mi, Gi + Mi, and Mi + P.

Nematode population density data were transformed to $(\log_{10} + 1)$ for statistical analysis. Population densities of second-stage juveniles extracted at three sampling dates from the 1984 microplot experiment were converted to a percentage based on the maximum population extracted and each population value was transformed using the logistic correction factor of $\log_e(Y/1 - Y)$. The transformed data (a measure of the rate of population density increase) and time were plotted and linear regression analysis employed to determine the best fitting lines. Slopes and intercepts of time–nematode population lines were tested for homogeneity (25). Data were also analyzed using analysis of variance, LSD, Duncan's multiple-range test, Waller-Duncan k-ratio *t*-test, regression analysis, and Pearson and Lee's correlation coefficient where appropriate.

Plant height measurements were recorded 60 and 90 days after planting, and soil samples were collected 60, 90, 120, and 150 days after planting. Soil samples were collected by removing the top 5 cm of soil with a hand spade and retrieving a core 5–20 cm deep. Four cores per microplot were collected each sample date. Nematode populations were assayed by elutriation (3) and sucrose centrifugation (9) of 500 cm^3 soil samples. Roots collected during elutriation were cleared and stained for VAM fungi by a modified technique of Phillips and Hayman (12). Percentage of mycorrhizal root colonization and root length per sample were measured using the gridline intersect method of Giovannetti and Mosse (6). Penetration of cotton roots by second-stage juveniles was recorded in the 1984 microplot experiment by destructive sampling 18 days after emergence of cotton seedlings planted adjacent to experimental plants. Roots were cleared in 1.0% NaOCl and stained as described by Byrd et al. (4). Number of juveniles penetrating roots was standardized by measuring root length per sample and expressing the data as juveniles per 100 cm root. Seed cotton was collected 150 days after planting and air dried in the laboratory for 48 hours. In the 1984 microplot experiment, mature open bolls were counted and weighed to determine the mean seed cotton weight per boll for each microplot.

Results

1982 and 1983 microplots: Meloidogyne incognita caused significant yield reductions in mycorrhizal infested and noninfested plots (Tables 2, 3). Plant tolerance to Mi was increased by Gi, whereas high P fertility increased the severity of nematode damage. Yields were suppressed 60% (1982) and 45% (1983) in plots infested with Mi at the high P rate compared with the low P rate. However, main effect treatments comparing low and high P fertility were nonsignificant in both years. The data were thus averaged over P rate to analyze main effect treatment comparisons between plots receiving and not receiving Gi and between plots receiving Gi + Mi and Mi alone (Table 3). Compared with noninfested plots, yields were increased 72% (1982) and 21% (1983) in Gi and 150% (1982) and 75% (1983) in Mi-infested plots.

Increased yields in 1983 were apparently due to improved nitrogen and phosphorus fertility regimes, more favorable growing conditions, and more effective insect control than in 1982.

Early season shoot growth and mycorrhizal root colonization were increased on plants growing in soil infested with Gi (Table 3). Sixty-day plant heights were increased in the presence of Gi and were highly correlated with yields in 1982 ($r = 0.84$, $P = 0.001$) and 1983 ($r = 0.87$, $P = 0.001$). Ninety-day plant heights were similar in both years in plots not infested with Mi because of high levels of root colonization by indigenous mycorrhizal fungi. However, plants were still significantly taller in Gi + Mi plots than in Mi plots. Ninety-day plant heights were also highly correlated with yields in 1982 ($r = 0.76$, $P = 0.001$) and 1983 ($r = 0.85$, $P = 0.001$). In both years Gi inoculation significantly increased VAM fungal colonization up to 90 days after planting. Although root colonization by VAM fungi was suppressed in Mi plots, the degree of suppression was slight. VAM root colonization percentages in 1983 were also lower at both sampling periods than in 1982.

The effect of Gi and P on nematode reproduction varied by year and sample date. Population densities of Mi were unaffected by Gi or P in 1982 (Table 4). In 1983 Gi inoculation resulted in significantly lower numbers of Mi juveniles 60 and 90 days after planting, but numbers of Mi juveniles at later sample dates were not affected. P also did not affect Mi juvenile numbers at any date in either year (thus the data are not presented).

1984 microplots: Yield reductions over increasing Mi inoculum densities were best described by fitting the data to a linear model for Mi, Gm, and P treatments and a quadratic model for Gi (Fig. 1). In Mi plots, 66% of the variation in yields was attributed to Mi, whereas only 48%, 49%, and 39% of the variation in yields were attributed to Mi in the Gi, Gm, and P plots, respectively. Cotton yields were greater in Gi and Gm and less in P compared with Mi alone in Mi-infested soil. Yields were similar with either mycorrhizal fungus except at the highest nematode inoculum density. Mycorrhizal plants yielded equivalent seed cotton at any Mi inoculum density compared with control plants growing in Mi-free soil.

TABLE 2. Seed cotton yields of Stoneville 213 grown in soil infested with (+) or without (−) *Meloidogyne incognita* (Mi) or *Glomus intraradices* (Gi) at two phosphorus (P) levels from 1982 and 1983 microplots and 1984 field plots.

Treatment			Seed cotton yield (g/plot)		
Mi*	Gi	P†	1982	1983	1984
−	−	low	44	161	nt‡
−	−	high	73	171	237 a
−	+	low	100	195	240 a
−	+	high	97	208	nt
+	−	low	20	89	142 b
+	−	high	8	49	190 ab
+	+	low	36	121	209 a
+	+	high	34	121	nt

Main effect treatment comparisons in 1982 and 1983 between controls (− −) and Mi (+ −) and between Gi (− +) and Mi + Gi (+ +) are significantly different ($P = 0.05$) when averaged over P levels. Means followed by the same letter are not significantly different ($P = 0.05$) according to Fisher's least significant difference.

* *M. incognita* inoculum level = 250 eggs/100 cm³ soil.

† Phosphorus levels (mg/kg) at planting were 1982 low = 43, high = 82; 1983 low = 82, high = 142; 1984 low = 103, high = 175.

‡ No treatment.

Plants growing in soil infested with mycorrhizal fungi or added P fertilizer had higher numbers of Mi juveniles penetrating seedling roots, but Mi juvenile densities from soil sampled 60–120 days after planting were similar in all plots. Numbers of second-stage juveniles penetrating roots after 18 days best fit a linear model over increasing Mi inoculum densities (Fig. 2). Highly significant R^2 values for all treatments were probably due to the uniform distribution of nematode inoculum, uniform seedling emergence, and similar environmental conditions at planting among microplots.

Rates of population density increase from 60 to 120 days after planting were compared for the three initial Mi inoculum densities (Pi) by pooling treatments at each inoculum density (Fig. 3). Population densities had declined at 150 days, so this sample date was not used in the analysis. Slopes and intercepts of the low and medium Pi (83 and 250 eggs/100 cm³ soil) were similar but differed significantly from the high Pi (750 eggs/100 cm³ soil). Population densities in the low and medium Pi were

TABLE 3. Treatment comparisons of plant height, mycorrhizal (VAM) root colonization, and seed cotton yield between *Glomus intraradices* (Gi) inoculated (+) and noninoculated (−) Stoneville 213 that was grown in microplots infested with (+) or without (−) *Meloidogyne incognita* (Mi) in 1982 and 1983.

Treatment		60-day plant height (cm)		90-day plant height (cm)		60-day VAM (%)		90-day VAM (%)		Yield (g/plot)	
Gi	Mi	1982	1983	1982	1983	1982	1983	1982	1983	1982	1983
−	−	47	42	71	63	45	10	59	46	57	166
+	−	54	45	75	69	68	65	91	73	98	201
LSD (0.05)*		4	ns†	ns	ns	21	15	14	15	22	31
−	+	30	31	43	49	32	12	53	38	14	69
+	+	41	38	54	59	66	49	83	61	35	121
LSD (0.05)		6	4	10	5	13	16	8	11	16	30

* Fisher's least significant difference.
† Not significant.

significantly lower than the high Pi at 60 and 90 days, but by 120 days population density of the low Pi was significantly higher than the medium and high Pi.

Yields were positively correlated with number of bolls and 60-day plant heights in all treatments and negatively correlated with early root penetration by Mi and $\log_{10}$ of 90-day Mi juvenile population densities (Table 5). Correlations of 60-day plant heights with yields and number of bolls were lower in the Gi (r = 0.65 and 0.61) and Gm (r = 0.61 and 0.59) treatments than the Mi (r = 0.90 and 0.88) and P (r = 0.92 and 0.92) treatments. Evidence for an increased level of tolerance in mycorrhizal inoculated plants was supported by correlations between number of bolls and numbers of juveniles penetrating cotton roots after 18 days. Highly significant correlations occurred in Mi (r = −0.85) and P (r = −0.81) treatments, whereas none occurred in the Gi and Gm treatments.

Yield reductions in cotton by Mi were expressed as fewer bolls and lower seed cotton weights per boll. High correlations of yields with numbers of bolls indicated that the fewer bolls per plant caused by stunting of plants was the major contributing factor to suppressions of cotton yield by Mi (Table 5). However, lower seed cotton weights per boll over increasing Mi inoculum densities were 5.19, 5.10, 5.09, and 4.96 g at 0, 83, 250, and 750 eggs/100 cm^3 soil, respectively. Partitioning of the Mi inoculum density sum of squares into single degree of freedom components revealed that the quadratic and cubic components contributed significantly to the relationship. Mean seed cotton weights per boll were greater in Mi (5.19 g) and Gi (5.17 g), compared with Gm (4.99 g) and P (4.98 g).

1984 field experiment: Yields were suppressed less by Mi in cotton plants grown in nonfumigated soils than in plants grown in fumigated microplots, especially when plants received high P fertilization. Seed cotton yields were significantly reduced

TABLE 4. Numbers of second-stage juveniles of *Meloidogyne incognita* (Mi) recovered from 100-cm^3 soil samples at four sample dates from 1982 and 1983 microplots infested with Mi alone or Mi + *Glomus intraradices* (Gi).

	Days after planting							
	60		90		120		150	
Treatment	1982	1983	1982	1983	1982	1983	1982	1983
Mi	nd*	310†	23	135	nd	483	112	423
Mi + Gi	nd	183	39	82	nd	527	153	462
LSD (0.05)‡	nd	113	ns§	50	nd	ns	ns	ns

* No data.
† Data averaged over two P levels (N = 12).
‡ For comparison of treatments within year and sampling date by Fisher's least significant difference.
§ Not significant.

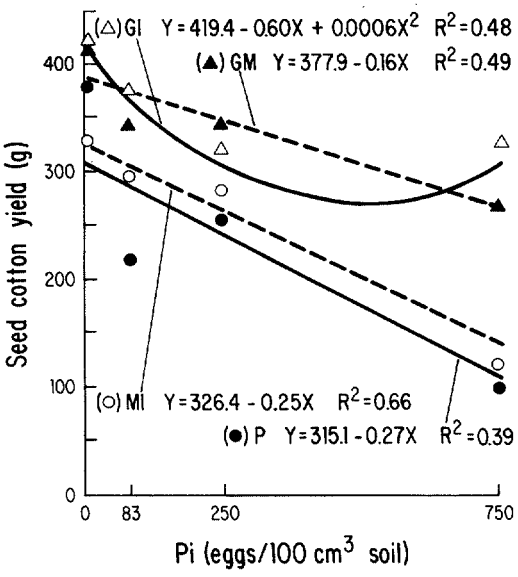

FIG. 1. Effect of initial *Meloidogyne incognita* egg inoculum densities (Pi) on seed cotton yields of Stoneville 213 from 1984 microplots infested with *M. incognita* only (Mi), *Glomus intraradices* (Gi), *Gigaspora margarita* (Gm), or fertilized with superphosphate (P). Each point represents the mean of four replicates.

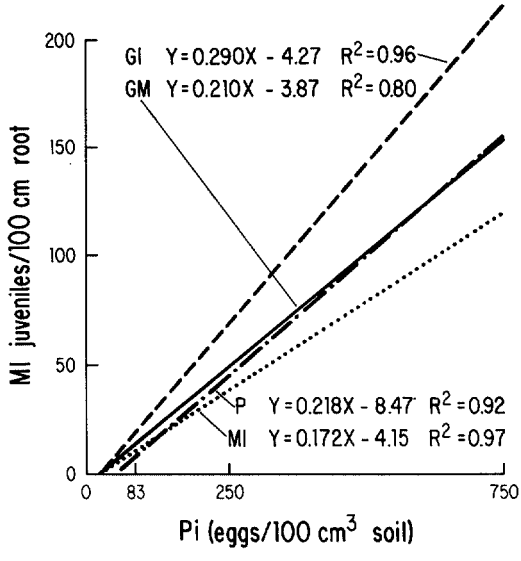

FIG. 2. Regression lines of number of *Meloidogyne incognita* (Mi) second-stage juveniles penetrating 100 cm Stoneville 213 cotton roots 18 days after emergence at different initial inoculum densities (Pi) of Mi eggs/100 cm³ soil from 1984 microplots. Treatment designations represent plots infested with *M. incognita* only (Mi), *Glomus intraradices* (Gi), *Gigaspora margarita* (Gm), or fertilized with superphosphate (P).

($P = 0.05$) only in plots infested with Mi alone (Table 2). Highest yields were obtained from plots infested with Gi or fertilized with P. Infesting the soil with Gi nullified yield suppressions by Mi. There were no differences in population densities of Mi juveniles at any sampling date. Percentage of VAM fungal root colonization was highest in plots infested with Gi (57%) and Gi + Mi (38%), compared with Mi (22%) and Mi + P (7%), 90 days after planting.

DISCUSSION

Inoculation of fertile soils with mycorrhizal fungi increased yields and tolerance to Mi in a susceptible cotton cultivar. The mycorrhizal enhanced yield increases, which were greater in fumigated than in nonfumigated field soils, corroborate greenhouse studies (5,8,22). Investigations of the role of P in mycorrhizal–nematode interactions should employ soil P levels that are sufficient to avoid severely restricting plant growth in the absence of mycorrhizal fungi but not so high as to retard mycorrhizal development. These critical P levels vary with the crop and soil type and should be determined before interactions are tested. If mycorrhizal–nematode interactions are conducted in P-deficient soils, inoculations with mycorrhizal fungi will stimulate root and shoot growth which may support larger nematode populations compared with nonmycorrhizal plants whose root systems will be stunted by both the nematode and P deficiency. Inoculation with mycorrhizal fungi was reported to stimulate reproduction of Mi on cotton (15) and soybean (20) because of the larger root systems developed on mycorrhizal plants. Thus, mycorrhizal and P effects may be confounded and statistical interactions subject to errant conclusions.

Yields and nematode population densities from our 1982 microplots illustrate this point. Significant yield increases occurring in control plots not receiving Gi and fertilized with P suggest that yield reductions caused by Mi at the low P level were probably caused by a combination of nematode parasitism and nutritional deficiencies. Also, consistent nematode population density increases associated, albeit nonsignificantly, with Gi inoculation probably resulted from improved P nutrition. Thus,

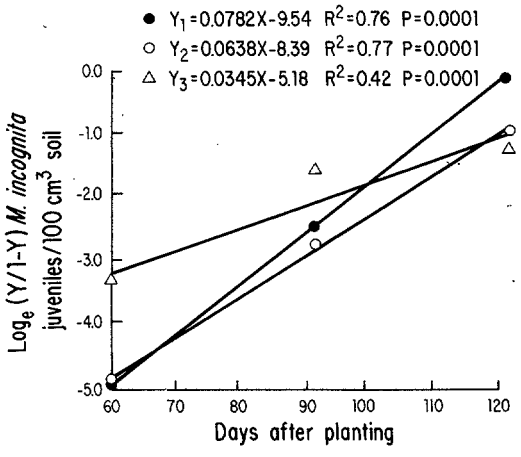

FIG. 3. Regression analysis of $\log_e(Y/1 - Y)$ of *Meloidogyne incognita* second-stage juvenile population densities sampled 60, 90, and 120 days after planting from 1984 cotton microplots infested with initial densities of 83 (Y_1—●), 250 (Y_2—○), and 750 (Y_3—△) eggs/100 cm^3 soil. Each point represents the mean of 16 samples.

soil P levels were doubled in 1983 and 1984 to avoid confounding mycorrhizal and phosphorus effects.

Lower VAM root colonization levels in 1983 microplots, compared with 1982 microplots, were probably caused by increased P fertilization, which may have inhibited mycorrhizal development, and improved fumigation efficiency, which reduced indigenous mycorrhizal population densities. Reductions in population densities of Mi at the 60-day and 90-day samples in plots infested with Gi suggests that increased tolerance to Mi in cotton mycorrhizal with Gi may result from antagonism between the fungus and nematode that is dependent on the density of VAM root colonization levels (16) or an alteration in host physiology (8,23).

In 1984 rates of population density increase reflected population dynamics involving plant-parasitic nematodes and other soil-borne organisms whose growth and reproductive potentials are limited by the availability of a food source (2). Population densities increased rapidly with the high Pi but quickly depleted available root infection sites and host resources to support later generations of Mi juveniles. Population densities had already begun to stabilize by 90 and 120 days, and this depletion of root infection sites and host resources was probably responsible for the lower R^2 value in the high Pi. The abundance of noninfected roots in the low and medium Pi plots at the earlier sample dates allowed the nematode to express its reproductive potential. This trend was most clearly demonstrated at 120 days where population densities in the low Pi had significantly exceeded the medium and high Pi.

Since inoculation with Gi and Gm stimulated yields and increased tolerance in cotton to Mi, a question remains as to whether the mycorrhizal effect is a species-specific phenomenon or simply increased inoculum potential brought about by inoculation. Even though fumigation reduced spore densities of indigenous VAM fungi, adequate spore numbers remained of the indigenous species, *Glomus macrocarpum* Tul. & Tul. and *Glomus mosseae* (Nicol. & Gerd.) Gerd. & Trappe, so that roots were heavily colonized 120 days after planting in all plots regardless of mycorrhizal inoculation or P fertilization. However, yields and root colonization were always enhanced by mycorrhizal inoculation, suggesting that increased yields and host tolerance to Mi may be species-specific phenomena. Other specific host–symbiont interactions have been reported on cotton and soybean (8,20). A species-specific increase in host tolerance to Mi is further supported by the yield data from the 1984 microplots where Gi-inoculated plants yielded significantly more seed cotton at the highest nematode inoculum density than did plants inoculated with Gm.

Increased yield suppressions in microplots receiving additional P contrasts with greenhouse studies reporting an increase in host tolerance to Mi at higher P rates (15,26). These unexpected results occurred consistently each year. Based on tissue and soil analysis, symptomatology, and soil pH, the lower yields in the high P plots infested with Mi were caused by a combination of zinc deficiency and Mi parasitism. Cotton leaf tissue analyzed from both high P and mycorrhizal plots infested with Mi, showed deficient levels of zinc (7 mg/kg) in tissue from the high P plots while zinc levels (12 mg/kg) were increased 70% in tissue from the mycorrhizal plots (13). This synergistic interaction between minor element nutrition and *M. incognita* were prob-

TABLE 5. Pearson and Lee's correlation coefficients (r) of listed dependent variables from 1984 microplots infested with *Meloidogyne incognita* only (Mi), *Glomus intraradices* (Gi), *Gigaspora margarita* (Gm), and superphosphate (P) at four Mi inoculum densities.

Correlations	Treatments			
	Mi	Gi	Gm	P
Seed cotton yield with:				
Number of bolls	0.99***	0.98***	0.98***	0.99***
60-day plant height	0.90***	0.65**	0.61**	0.92***
18-day root penetration by Mi	−0.81***	−0.54*	ns	−0.77***
Log_{10} 90-day Mi	−0.56*	−0.60**	−0.54*	−0.67**
Number of bolls with:				
60-day plant height	0.88***	0.61**	0.59**	0.92***
18-day root penetration by Mi	−0.85***	ns	ns	−0.81***
60-day plant height with:				
18-day root penetration by Mi	−0.55*	−0.65**	ns	−0.75***

$P > F$: *** = 0.001; ** = 0.01; * = 0.05.
ns = not significant.

ably caused by 1) soil fumigation which reduced indigenous mycorrhizal population densities, 2) high P fertilization, and 3) root growth stunted by Mi. These results offer insight into the biological interactions of the mycorrhizal symbiosis and the host's response to the soil environment. High levels of available P in the absence of mycorrhizal fungi stimulate root growth which results in high numbers of Mi second-stage juveniles invading seedling root systems. Root development is subsequently curtailed because of nematode parasitism which restricts uptake of phosphorus and zinc in the developing plant. The lack of mycorrhizal fungi in the root system exacerbates nutritional deficiencies resulting in stunted plants and greater yield losses in the high P than low P treatments.

Mycorrhizal fungi are essential for adequate P nutrition in cotton grown in soil that contains adequate levels of available P, and they increase cotton yields in Mi-infested soil. Increased fertilization with P does not mimic the essential role of these root symbionts in disease interactions with Mi. Mycorrhizal fungi may also affect resistance mechanisms that would reduce nematode reproduction in cotton. The current impracticability of producing sufficient quantities of these fungi for economical field inoculations precludes their use as biological control agents against plant-parasitic nematodes. However, their ubiquitous nature and ecological importance may play a vital role in preventing greater yield suppressions by plant-parasitic nematodes wherever cotton is grown.

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