

Vesicular-Arbuscular Mycorrhizae May Limit Nematode Activity and Improve Plant Growth

The activities of root- or rhizosphere-inhabiting microorganisms have a significant influence on plant health. Plant-parasitic nematodes and vesicular-arbuscular (VA) mycorrhizal fungi commonly occur together in the roots or rhizosphere of the same plant, each having a characteristic but opposite effect on plant vigor. The obligately symbiotic VA mycorrhizal fungi may stimulate plant growth, whereas the obligate plant-parasitic nematodes usually suppress plant growth. Recent research indicates that VA mycorrhizal fungi have potential as biocontrol agents when both groups of microorganisms occur simultaneously in the roots or rhizosphere of the same plant.

Plant-Parasitic Nematodes

Plant-parasitic nematodes, a cosmopolitan and important menace to the production of agricultural crops, are often placed into three groups based on the manner in which they feed on roots. These feeding habits may influence how these pathogens interact with VA mycorrhizal fungi. Species feeding as *sedentary endoparasites* penetrate roots as vermiform juveniles; after feeding commences, the body swells, the somatic musculature system degenerates, and the nematode becomes immobile. Further development and reproduction by the nematode depends on the plant cells adjacent to its head providing nourishment. These cells are usually modified by the nematode into elaborate feeding cells that become the permanent feeding site for the parasite. *Migratory endo-*

parasites remain vermiform throughout their life cycle. They bodily penetrate roots and migrate throughout the root tissue, feeding on different cells without establishing a localized or permanent feeding site. Considerable destruction of root tissue usually occurs with this type of feeding. *Ectoparasites* remain outside the root, using their stylet to feed on internal cells. With the exception of a few species that feed at root tips, nematodes with this type of feeding habit generally cause the least amount of tissue damage.

The reaction of host plants both in their ability to support nematode reproduction and in their response to nematode attack may be modified by VA mycorrhizal fungi colonizing the same root tissues infected by nematodes. The following terms and meanings, defined by Cook (1), will be used in this article to characterize nematode-host relationships: *Resistance* (low nematode reproduction) and *susceptibility* (high nematode reproduction) characterize host efficiency, whereas *tolerance* (little suppression of growth or yield) and *intolerance* (high suppression of growth or yield) delineate host sensitivity. The influence of VA mycorrhizae on the outcome of these relationships may be dramatic.

Vesicular-Arbuscular Mycorrhizae

Vesicular-arbuscular mycorrhizal fungi are associated with a greater variety of plant species and are more widely spread geographically than other types of mycorrhizal fungi. These endophytes have a wide host range and thus are common to most cultivated crops as well as to natural plant communities (2). Despite this universality, VA mycorrhizae had not been investigated extensively until the last decade. This oversight came primarily because they have little effect on root morphology and the fungal endophytes cannot be grown in pure culture. However, improved research

techniques and proof of the role of VA mycorrhizae in plant nutrition have stimulated great interest in this symbiotic association.

The fungi forming VA mycorrhizae are members of the Zygomycetes and assigned to the family Endogonaceae. In the soil these fungi produce such structures as azygospores, chlamyospores, sporocarps, vesicles, and mycelia. Mycorrhizal plants are characterized by an extensive network of hyphae projecting from the feeder roots into the surrounding soil, thus increasing the absorptive area of the root system for nutrient and water uptake. The relationship aids primarily in the absorption and translocation of phosphorus, an ion of low solubility and immobile in the soil. Other elements, such as sulfur, copper, and zinc, are sometimes involved. Thus, by increasing the supply of phosphorus and nutrients to the plant the VA mycorrhizal fungi stimulate growth and in return receive organic nutrients from the host.

Because the VA mycorrhizal portion of the root system is morphologically similar to the nonmycorrhizal portions, roots must be cleared and stained to show fungal development in the epidermis and cortex. The diagnostic feature of VA mycorrhiza is the presence of arbuscules (Fig. 1) and, for certain species, vesicles in the cortex (Fig. 2). Vesicles, spherical swellings at the tips of intercellular or intracellular hyphae, probably serve a storage function. Arbuscules, developed from repeated dichotomous branching of intracellular hyphae, are considered to be the major site for nutrient exchange.

Colonization by the endophyte and development of VA mycorrhizae, as well as subsequent plant benefits, are conditioned by numerous factors, including soil fertility and pH, soil moisture, light intensity, pesticides, and plant susceptibility. Most experiments showing growth stimulation in VA mycorrhizal plants have been conducted with soils of

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Table 1. Possible effects of interactions between plant-parasitic nematodes and VA mycorrhizae

Type of interaction	Component	Effect on component
Neutral	Fungus Host	Root infection or sporulation not altered Mycorrhizal stimulation of vegetative growth or yield not altered; nematode suppression of vegetative growth or yield not offset
	Nematode	Attraction to roots, penetration, or subsequent development and reproduction not altered
Positive	Fungus Host	Root infection or sporulation increased Nematode suppression of vegetative growth or yield offset
	Nematode	Attraction to roots, penetration, or subsequent development and reproduction suppressed
Negative	Fungus Host	Root infection or sporulation suppressed Vegetative growth or yield response to mycorrhizae suppressed
	Nematode	Attraction to roots, penetration, or subsequent development and reproduction increased

low fertility that have been heat-treated, irradiated, or fumigated to remove the indigenous mycorrhizal fungi. Such responses in untreated field soils or in heavily fertilized soils, however, are less common.

Interactions Between Nematodes and VA Mycorrhizal Fungi

Since plant-parasitic nematodes and VA mycorrhizal fungi are intimately associated in feeder roots, it is logical to consider an interaction between these two groups of organisms in terms of their combined effect on plant growth. Interactions can be quantified by measuring the effect on fungal colonization of roots or sporulation and nematode attraction to roots, penetration, or subsequent development and reproduction. Plant responses to concomitant infection can be assessed by determining the influence of the interaction on plant growth or yield, by either stimulation from mycorrhizal development or suppression from nematode infection; the latter effect is emphasized in this article.

The possible effects of interactions between plant-parasitic nematodes and VA mycorrhizae on each component are summarized in Table 1. Where no changes are evident, the interaction is categorized as neutral. An interaction is rated positive if VA mycorrhizae offset nematode damage to plants; since the response of a plant to the endophyte is rarely enhanced in the presence of plant-parasitic nematodes, we will not discuss this interaction. VA mycorrhizae, however, could have an antagonistic effect on plant-parasitic nematodes, and such an effect could have either a physiological or a physical basis. VA mycorrhizal fungi may 1) improve plant vigor and growth to offset yield loss normally caused by nematodes, 2)

physiologically alter or reduce root exudates responsible for chemotactic attraction of nematodes, or 3) directly retard nematode development or reproduction within the root tissue. An interaction could have a physical basis if the endophytes and endoparasitic nematodes in the root compete for the same site, rendering it unfavorable for nematode activities. A negative interaction occurs when plant growth or yield of dually infected plants is less than that of unchallenged mycorrhizal plants or if root colonization or sporulation by the mycorrhizal fungus is suppressed. Although the presence of the endophyte in the cortex is not expected to enhance nematode damage, the symbionts could increase nematode reproduction.

The effects of VA mycorrhizae on nematode-host relationships deserves special attention. Mycorrhizal fungi that render nematode-susceptible plants tolerant to plant-parasitic nematodes or affect nematode development may prove to be very valuable in limiting crop losses to these pathogens. Figure 3 shows the effects of VA mycorrhizae on host efficiency (nematode reproduction) and host sensitivity (growth suppression or yield loss) of nematode-infected plants normally susceptible and intolerant to nematodes in the absence of endophytes. Nematode reproduction (bar C) and plant growth or yield (bar C') for a dually infected plant may both vary over a wide range (dashed line) and will not necessarily fall at the same position. Although plant response (bar C') may vary between bar A (nematode only) and bar D (mycorrhizae only), it usually falls somewhere in the range between bar B (uninfected plant) and bar D. Nematode reproduction (bar C), however, may fall anywhere along the dashed line either above or below the red line.

Within the last decade numerous

interactions between plant-parasitic nematodes and VA mycorrhizae have been studied. Evidence is accumulating to show that mycorrhizae can markedly influence plant health by altering plant reactions to nematodes. These interactions and their effects on each member of the nematode-symbiont-host system are summarized in Table 2. Cotton and soybean were the most frequently used hosts and the root-knot nematode (*Meloidogyne incognita* (K.&W.) Chitwood) was the predominant nematode tested in these studies. However, a wide variety of VA mycorrhizal fungi in the genera *Gigaspora* and *Glomus* have been combined with the nematodes in these interactions.

No attempt will be made to discuss each of the interactions listed in Table 2, but instead specific experiments will be selected to illustrate the different types of interactions (Table 1). The interactions are discussed according to the different types of nematode feeding habits. Most of these interaction studies involved sedentary endoparasitic nematodes, probably because they have worldwide importance as plant pathogens and are easily propagated. No interaction investigations involving ectoparasites have been reported for endomycorrhizal fungi.

Sedentary endoparasites. The interactions of *M. incognita* and several VA mycorrhizal fungi on cotton have been studied under greenhouse conditions. When nematode-resistant and nematode-susceptible cotton cultivars were inoculated jointly with *Gigaspora margarita* Becker & Hall and *M. incognita*, the beneficial effect of the endomycorrhizal development offset the nematode damage to the susceptible cultivar (Figs. 4 and 5) (6). This effect was attributed to increased host vigor rather than to any antagonistic physiological change induced by symbiosis. This conclusion was supported by the quantitative similarity in egg number per gram of root on both mycorrhizal and control plants. Therefore, mycorrhizal plants, because of larger root systems, supported a greater root-knot nematode population than did nonmycorrhizal plants. The growth stimulation by endomycorrhizal fungi of both susceptible and resistant cultivars was unaffected by the parasitic activities of the root-knot nematode. The nematode was not antagonistic to mycorrhizae synthesis or fungal sporulation. The overall effect of the endophyte was simply to increase the tolerance (Fig. 3) of the susceptible cultivar to the nematode pathogen.

In our current studies, *Glomus etunicatus* Becker & Gerd. and *Glomus mosseae* (Nicol. & Gerd.) Gerd. & Trappe influenced the reproduction of *M. incognita* on root-knot-susceptible cotton differently than did *G. margarita*. The total increase of *M. incognita* (total eggs per plant) was not altered on cotton

colonized by *G. etunicatus* or *G. mosseae* over control plants even though the root systems of the mycorrhizal plants were considerably larger than those of the nonmycorrhizal plants. Therefore, when rated as eggs per gram of root, reproduction was lower on mycorrhizal plants than on controls, indicating that these symbionts make cotton resistant (Fig. 3) to *M. incognita*. This nematode also failed to retard stimulation of plant growth by either symbiont on coinoculated plants.

The diversity of interactions between VA mycorrhizae and plant-parasitic nematodes was also illustrated by Schenck et al (7). In greenhouse studies involving soybean inoculations with *M. incognita* and three VA mycorrhizal fungi, they found that any given interaction was strongly influenced by nematode inoculum level, cultivar resistance to the nematode, and the specific fungal symbiont. The fungi used were: *Gigaspora heterogama* (Nicol. & Gerd.) Gerd. & Trappe, *Glomus macrocarpus* Tul. & Tul., and *Endogone calospora* Nicol. & Gerd. (= *G. margarita*). Although the endophytes tested usually stimulated plant growth and increased nematode densities, nematode reproduction was influenced differently by each symbiont. Among the mycorrhizal plants, nematode densities (expressed as juveniles per volume of soil) were highest on a nematode-susceptible soybean colonized by *E. calospora* and lowest on plants colonized by *G. macrocarpus*. All nematode densities, however, were higher on mycorrhizal than on nonmycorrhizal plants, indicating that the symbionts made soybean tolerant to the parasite.

We have recently conducted greenhouse studies with soybeans dually inoculated with *M. incognita* and either *G. margarita* or *G. etunicatus*. Both mycorrhizal fungi stimulated plant growth, but nematode reproduction (eggs per gram of root) was unaffected by *G. margarita* and suppressed by *G. etunicatus*, indicating the former makes the plant tolerant to the nematode and the latter increases plant resistance.

Nematode reproduction may be stimulated on certain hosts by mycorrhizal fungi. In a recent greenhouse study, we found peanut was a more suitable host for *M. arenaria* (Neal) Chitwood in the presence of either *G. etunicatus* or *G. margarita*. These symbionts caused an eightfold increase in number of eggs per gram of root and pods compared with reproduction on nonmycorrhizal plants. The endomycorrhizal stimulation of plant growth, however, was not affected by the nematode. Other tests using peanut plants with split-root systems revealed that nematode reproduction was significantly increased only when both organisms were present on the same side of the root system.

There are several possible reasons why these endophytes promoted an increase in root-knot nematode reproduction on peanut. Mycorrhizal roots may have directly attracted more second-stage infective juveniles than did nonmycorrhizal roots. Colonization of plant root systems by symbionts may have increased root development, resulting in more penetration sites for nematode infection. After juveniles entered the roots, the symbionts could have promoted their survival or enhanced their development. Adult females may have produced more eggs on plants made more vigorous by mycorrhizal fungi. Even though the mycorrhizal fungi increased the susceptibility of peanut plants to *M. arenaria*, the symbiont made the plants tolerant to infection by the parasitic nematode. In the field, this response may create a problem because peanut pods are produced underground and any increase in the soil population density of this

nematode could result in damage to the pods.

The sequence in which plants become colonized by mycorrhizal symbionts and infected by nematodes may affect the interaction between these organisms on certain plants. Preinoculation of tomato, tobacco, oats, and carrot with *G. mosseae* to allow this slow-growing symbiont to become established in the roots before introduction of *M. incognita* resulted in fewer juveniles penetrating and developing in roots of mycorrhizal plants than in roots of nonmycorrhizal controls (8). In tomato plants, nematode galls were more prevalent on roots poorly colonized with the symbiont and development of second-stage juveniles was retarded in well-colonized roots. The mycorrhiza caused tomato plants to become resistant to the root-knot nematode. Because growth data were lacking for this study, plant tolerance could not be assessed.

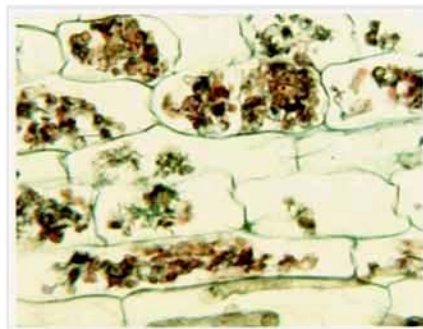


Fig. 1. Intracellular arbuscules and hyphae of a vesicular-arbuscular mycorrhizal fungus in cortical cells of a cotton root.

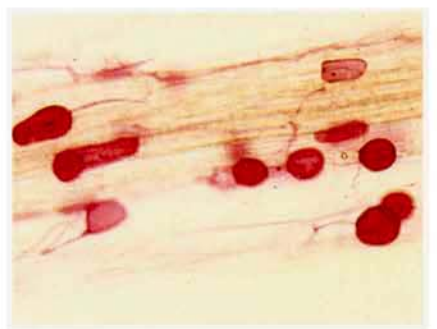


Fig. 2. Vesicles of a vesicular-arbuscular mycorrhizal fungus in the root cortex of a peach.

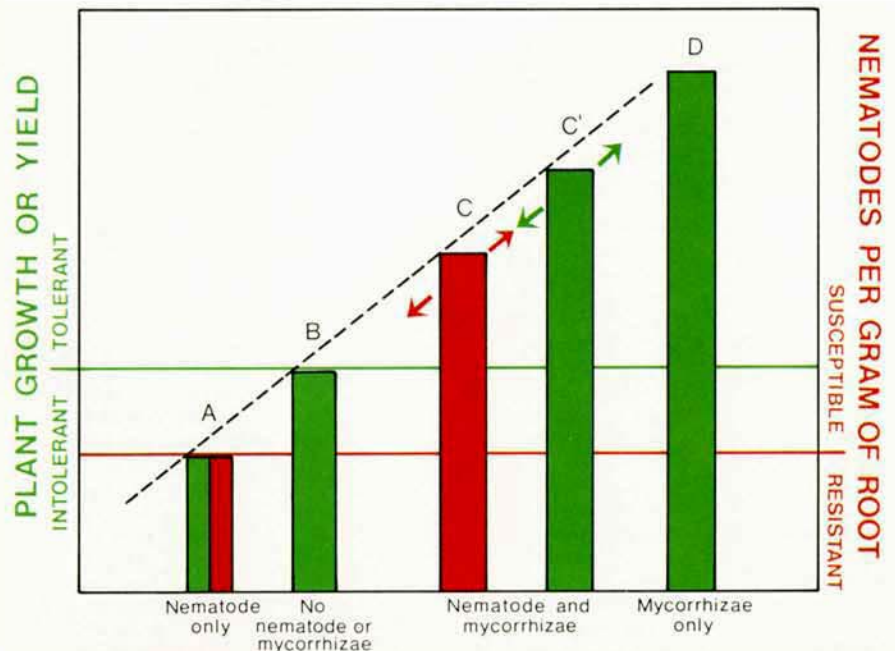


Fig. 3. Influence of vesicular-arbuscular mycorrhizae on the nematode-host relationship of a plant normally susceptible and intolerant to nematodes in the absence of the fungus. The solid green line indicates the level of plant response (equivalent to the growth or yield of an uninfected plant) that determines if a dually infected plant is tolerant (above the line) to feeding activities of nematodes. The solid red line indicates the relative density of nematodes (comparable to the population associated with a nonmycorrhizal plant) that determines whether a dually infected plant is susceptible (above the line) to nematodes.

The interaction of mycorrhizae and root-knot nematodes in recent studies in our greenhouse was quite different on peach seedlings. *G. margarita* or *G. etunicatus* alone stimulated growth of peach seedlings; when plants were simultaneously coinoculated with either fungus and *M. incognita*, however, this beneficial growth response was partially suppressed. When plants were pre-inoculated with the mycorrhizal fungus, the nematode had less effect on the beneficial mycorrhizal response than when plants were inoculated simultaneously. Apparently, certain VA mycorrhizal symbionts make peach seedlings more tolerant to root-knot nematodes when colonization of the root system by the symbionts precedes nematode infection. Nematode reproduction was affected little by *G. etunicatus* and inconsistently by *G. margarita* in either the preinoculated or coinoculated tests.

Another example of a nematode-symbiont interaction in which a mycorrhiza offsets a loss in plant growth caused by nematodes is seen in work reported by O'Bannon et al (4). *Tylenchulus semipenetrans* Cobb, a sedentary semi-endoparasite, was less severe on rough lemon in the presence of *G. mosseae*. Although dually infected seedlings grew less than seedlings inoculated only with *G. mosseae*, they had significantly more growth than seedlings inoculated only with *T. semipenetrans*, providing another example of mycorrhizal symbionts

increasing plant tolerance to nematodes.

Migratory endoparasites. Less is known about symbiont-nematode interactions involving plant-parasitic nematodes with a migratory feeding habit. In one of our recent studies (3), we found that cotton was a less suitable host for *Pratylenchus brachyurus* (Godfrey) Filip. & Schuur.-Stekh. when the roots were colonized by *G. margarita*. Nematode counts per gram of root were significantly less for mycorrhizal plants than for nonmycorrhizal plants. After staining samples of feeder roots, we found fewer nematodes in cortical tissue extensively colonized by the symbiont than in tissue lacking the endophyte. We concluded that lower nematode reproduction was caused either by the symbiont altering the cortex to make it an unfavorable food source for the nematode or by the symbiont competing with the nematode for space in the cortex. Enhanced growth occurred in mycorrhizal plants and was unaffected by *P. brachyurus*.

The only other report of a migratory endoparasite interacting with a mycorrhiza was a greenhouse study involving *Radopholus similis* (Cobb) Thorne and *G. etunicatus* on rough lemon (5). Reproduction of the nematode was similar on mycorrhizal and nonmycorrhizal seedlings. However, seedlings inoculated with the symbiont before nematode inoculation had nearly 28 times more dry weight at the end of the test than seedlings inoculated with

nematodes alone, indicating that VA mycorrhizae formed by *G. etunicatus* increase the tolerance of rough lemon to *R. similis*.

In the studies we have discussed, the effects of the nematode on sporulation by the VA mycorrhizal fungi were variable. In some studies fewer spores were formed in concomitant culture, but in others no differences were found. In most studies, however, nematodes had little influence on root colonization by the symbionts.

Histological work on cotton roots from interaction studies involving root-knot nematodes showed the symbiont rarely inside galled tissue but often in the tissue immediately adjacent to the gall (R. Hussey and R. Roncadori, *unpublished*). Also, mycorrhizal fungi have not been observed within the giant cells induced in plants by *Meloidogyne* species.

Only rarely has the role of phosphorus been considered in these interactions. Since VA mycorrhizal fungi aid plant growth primarily through the uptake and translocation of phosphorus, determining the influence of phosphorus on nematode-host relationships may furnish some insight into the nature of the interaction between nematodes and the endophytes. To determine whether an interaction between VA mycorrhizae and nematodes is influenced by the mycorrhizal fungus and not merely by improved plant nutrition, we need data showing that nematode parasitism on a mycorrhizal plant is different from that on a nonmycorrhizal plant at a comparable

Table 2. Interactions of plant-parasitic nematodes and VA mycorrhizae and the effect on each component of the system

Host	Mycorrhizal fungus	Plant-parasitic nematode	Interaction component ^a		
			Fungus	Host	Nematode
Cotton	<i>Gigaspora margarita</i>	<i>Meloidogyne incognita</i>	0 ^b	+	0
		<i>Pratylenchus brachyurus</i>	0	+	-
	<i>Glomus etunicatus</i>	<i>Meloidogyne incognita</i>	0	+	-
Soybean	<i>Glomus mosseae</i>	<i>Meloidogyne incognita</i>	0	+	-
	<i>Gigaspora margarita</i>	<i>Meloidogyne incognita</i>	+	+	0
		<i>Heterodera glycines</i>	0	+	+
Tomato	<i>Glomus etunicatus</i>	<i>Meloidogyne incognita</i>	-	+	-
		<i>Heterodera glycines</i>	0	+	+
	<i>Endogone calospora</i>	<i>Meloidogyne incognita</i>	0	+	+ ^c
	<i>Glomus macrocarpus</i>	<i>Meloidogyne incognita</i>	0	+	+ ^c
	<i>Gigaspora heterogama</i>	<i>Meloidogyne incognita</i>	0	+	+ ^c
	<i>Glomus mosseae</i>	<i>Meloidogyne incognita</i>	?	?	- ⁰
Tobacco	<i>Gigaspora margarita</i>	<i>Meloidogyne incognita</i>	-	0	0
	<i>Glomus mosseae</i>	<i>Meloidogyne incognita</i>	?	?	-
Oats	<i>Gigaspora gigantea</i>	<i>Heterodera solanacearum</i>	-	-	-
	<i>Glomus mosseae</i>	<i>Meloidogyne incognita</i>	?	?	-
Carrot	<i>Glomus mosseae</i>	<i>Meloidogyne hapla</i>	?	?	-
	<i>Gigaspora margarita</i>	<i>Meloidogyne incognita</i>	0	+	- ⁰ , +
Peach	<i>Glomus etunicatus</i>	<i>Meloidogyne incognita</i>	0	+	0
	<i>Gigaspora margarita</i>	<i>Meloidogyne arenaria</i>	0	+	+
Peanut	<i>Glomus etunicatus</i>	<i>Meloidogyne arenaria</i>	+	+	+
	<i>Glomus fasciculatus</i>	<i>Tylenchulus semipenetrans</i>	0	+	0, +
Citrus	<i>Glomus mosseae</i>	<i>Tylenchulus semipenetrans</i>	0	+	0
	<i>Glomus etunicatus</i>	<i>Radopholus similis</i>	-	+	0
Grape	<i>Glomus fasciculatus</i>	<i>Meloidogyne arenaria</i>	-	+ ⁰	+

^aComponent effect in interaction: Fungus = change in root colonization or sporulation of the symbiont when compared with unchallenged mycorrhizal plant. Host = change in plant growth when compared with nonmycorrhizal nematode-infected plant. Nematode = change in nematode reproduction (based on nematodes or eggs per gram of root) when compared with population on a nonmycorrhizal plant.

^b0 = No change; + = increase; - = decrease; ? = undetermined.

^cBased on nematodes per volume of soil.

nutritional status. In our research, the effect of supplemental phosphorus on nematode-host relationships paralleled the influence of VA mycorrhizae. Increasing the phosphorus available to a nematode-infected plant under greenhouse conditions offset the nematode symptoms, making the plant tolerant to the parasite. Supplemental phosphorus resulted in fewer nematodes per gram of root in most studies but enhanced reproduction of the parasite in some studies. Sporulation of the VA mycorrhizal fungi, however, was almost invariably suppressed with increased phosphorus nutrition.

Prospects

The universal presence of VA mycorrhizal fungi in soil of major crop production areas and their beneficial effect on plant health present an interesting concept—one of symbionts altering biological stress caused by nematode pathogens. These fungi improve plant health directly through symbiosis and indirectly by offsetting damage due to pathogens. An understanding of specific beneficial as well as detrimental host-symbiont-pathogen relationships is essential. Such information may someday lead to the manipulation of fungi forming VA mycorrhizae by altering specific crop management systems for the purpose of minimizing crop losses. Learning to deal with VA mycorrhizae might permit some form of nematode control requiring less reliance on pesticides and might even allow a reduction in the high rates of phosphorus fertilizers currently used for certain crops.

The diversity of interactions between VA mycorrhizae and plant-parasitic nematodes currently being documented gives some indication that each nematode-mycorrhiza-fungus-plant combination may be unique and generalizations regarding such interactions will be difficult. Nonetheless, the single most common effect of VA mycorrhizal fungi on nematode-susceptible plants is promoting tolerance to nematodes. Thus, plants heavily colonized by mycorrhizal fungi are able to grow well in spite of the presence of damaging levels of plant-parasitic nematodes.

Most studies of interactions between plant-parasitic nematodes and VA mycorrhizal fungi have been conducted under greenhouse conditions. Although such controlled studies are important and necessary for characterizing the types of interactions that occur between these two groups of microorganisms, it is imperative that these systems, especially those known to be antagonistic to the nematode, be evaluated under field conditions. We must determine whether these fungi are important in altering plant stress caused by parasitic nematodes



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under natural conditions before we can assess their ultimate impact on crop yield.

The role of VA mycorrhizal fungi in altering plant stress caused by nematodes is not well understood. Recent work with phosphorus has suggested that improved nutrition through increased uptake of this element may be responsible for the increase in tolerance of mycorrhizal plants to parasitic nematodes. To have the greatest impact, the antagonistic effect of VA mycorrhizae on nematode-host relationships must be more than simply the result of an indirect effect that can be produced by improved phosphorus nutrition. Indeed, some tests have suggested that mycorrhizal fungi might affect the development of nematodes within roots (8). The possibility of the two organisms competing for space within a root may also be important in reducing certain nematode infections.

Recent proof that VA mycorrhizae also influence plant health by affecting the reaction toward nematodes should sharpen our awareness for a better understanding of this most common and universal type of symbiosis in our agroecosystem. Since field population dynamics of VA mycorrhizal fungi may be manipulated by certain cultural practices, such as soil fertility and choice of host crop, management schemes may

eventually be prescribed to promote desirable mycorrhizal relationships to offset nematode effects. For crops where seedlings are transplanted to the field (eg, tomato, peach, tobacco), a transplant tailored with the most effective mycorrhiza should be able to survive adverse conditions (root diseases and other

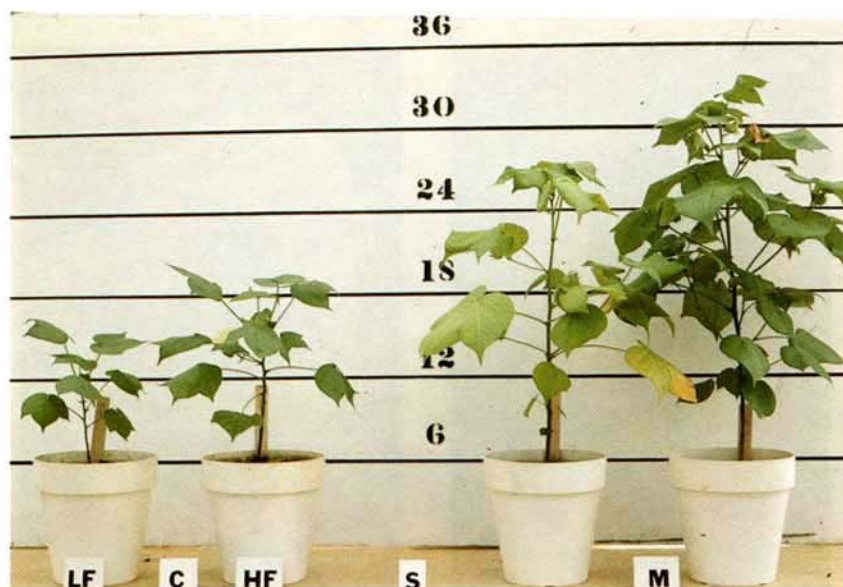


Fig. 4. Growth response of root-knot nematode susceptible (S) cotton symbiotic with *Gigaspora margarita* at low (LF) and high (HF) fertility levels: (left) control plants (C) and (right) mycorrhizal plants (M) at each fertility level.



Fig. 5. Effect of inoculation with *Gigaspora margarita* and *Meloidogyne incognita* on cotton growth at low (LF) and high (HF) fertility levels: (left) mycorrhizal only plants (M) and (right) mycorrhizal plants challenged with root-knot nematodes (M x Rk).

stresses) considerably better than a non-mycorrhizal seedling. Inoculating seedlings with a mycorrhizal fungus before transplanting would allow the slow-growing endophyte to become established in the roots in advance of being challenged by a plant-parasitic nematode. Some interaction studies have shown that the greatest antagonistic effect of mycorrhizae on nematodes occurs when the symbiont precedes the parasite in the root system (8).

VA mycorrhizal fungi are broadly distributed throughout a variety of geographical areas and crop species, indicating a considerable capacity to adapt and a promise for application or

manipulation in agroecosystems. With our current understanding, VA mycorrhizae may now be readily used in certain specialized crop management systems. However, any extensive exploitation of VA mycorrhizae, particularly on a large scale, is hampered by several factors. The primary limitation to employing the symbionts as biological fertilizers and biocontrol agents is the requirement to increase inoculum in pot culture, thus limiting the quantities produced and consuming excessive time. We also need a better understanding of VA mycorrhizal activities in untreated soils used for producing food and fiber crops as well as how to use the fungi at the intermediate

or higher fertility levels that already exist in many agricultural soils. Solving these problems could lead to widespread use of VA mycorrhizal fungi in routine crop management similar to the use of *Rhizobium* on certain legumes.

VA mycorrhizal fungi are and will continue to be common and natural components in our agroecosystem. We can no longer ignore them in the search for better crop management methods, particularly at a time when we are faced with simultaneous energy and environmental pollution problems. The fungi forming VA mycorrhizae may offer a viable alternative to the numerous cultural practices that have helped foster these crises. Interactions of plant-parasitic nematodes and endomycorrhizal fungi are often either antagonistic or stimulatory to the nematode. Since both groups of organisms are ubiquitous in the rhizosphere of most agronomic plants under field conditions, determining the type of interaction from their association is important in understanding the overall effect of each organism on plant vigor and also the effect of the interaction on the nematode population. The latter effect is important in understanding the population dynamics of nematodes.

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