Interaction Between Vesicular-Arbuscular Mycorrhizal Fungi and Plant Pathogens

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The benefit of endotrophic, vesicular-arbuscular (VA) mycorrhizae in the nutrition and development of host plants is well known (19,23,27,38). Many reports also indicate an interaction between VA mycorrhizal fungi and plant pathogenic organisms (31,32,35,38). The interpretation of these results, however, is not as easy as the interpretation of nutritional effects.

To evaluate the influence of VA mycorrhizal fungi on disease incidence and development, the variable factors, plant pathogen, symbiotic fungus, and environmental conditions, have to be considered. Mostly, the interactions between pathogen and symbiont are mediated by the host. The characterization of these interactions should, therefore, include information on the mechanisms involved.

This review is an attempt to evaluate and summarize most of the research results obtained during the last two decades. Generalization will be unavoidable and therefore the risk of oversimplification must be considered. For a better understanding of the possible influence of VA mycorrhizae on plant pathogens, disease incidence, and on the symbiosis under practical conditions, some recent results will be presented in more detail.

INFLUENCE OF VA MYCORRHIZAE ON PLANT DISEASES

Diseases caused by soilborne fungi. Because VA mycorrhizae are established in the roots of host plants, research on mycorrhizae-disease incidence interactions has been concentrated on diseases caused by soilborne pathogens. Although most of the experiments differ in approach and methods, a summary of the results is given in Table 1. Diseases caused by soilborne fungi can be influenced by the formation of VA mycorrhizae in the root system. In general, mycorrhizal plants suffer less damage and the incidence of disease is decreased or pathogen development is inhibited.

However, some reports indicate an increase in disease severity under the influence of VA mycorrhizal fungi. The improved nutrition (19,23,27,38) of mycorrhizal plants in nutrient-deficient soils may lead to an increase in disease incidence according to the rule: what is good for the plant will also be good for the pathogen. From this point of view the better-developed mycorrhizal plant should be more susceptible to pathogens than the poorly grown nonmycorrhizal one. The above statement may be confirmed by several reports (1,11,13,29) that describe increased susceptibility of mycorrhizal plants to disease. Several authors noted greater damage of mycorrhizal plants by soilborne fungi (11,13,29). Davis et al (12) showed that mycorrhizal cotton plants grew better, but suffered more from Verticillium wilt, compared to nonmycorrhizal plants. High phosphorus fertilization equally increased the vascular disease incidence on both mycorrhizal and nonmycorrhizal plants.

The nutritional requirements of the plant must be considered along with those of the VA fungus in studies of plant nutrition and disease. Theoretically, better plant growth may increase the specific potential of a plant to serve as a nutrient source for pathogenic organisms. On the other hand, improved plant nutrition may enhance plant development and, especially under field conditions, increased plant vigor may lead to disease escape or to higher tolerance towards soilborne pathogens. These effects seem to be more a question of altered nutrition and its influence on plant diseases than of interactions between mycorrhizal fungi and plant pathogens.

A specific influence of VA mycorrhizae on diseases can be recognized if mycorrhizal and nonmycorrhizal test plants are of similar size and developmental stage. It is apparent in the summary of interactions with soilborne fungal pathogens that most host-parasite relationships lead to less disease incidence on mycorrhizal plants (32,35,38). This influence can be seen within a broad range of host plants and rather different fungi. The effect proved to be dependent on the virulence of the pathogen. Detrimental pathogenic infections of the host roots or high inoculum levels of the parasite tend to decrease the positive influence of the symbiosis. This could be shown, for example, with the effect of VA mycorrhizal fungi on Fusarium wilt of tomato (16). Mycorrhizal plants had less mycelium inside the stem tissue as a result of vascular infection. Increased inocula of the pathogen altered this effect.

A similar influence could be seen if the decrease of pathogen reproduction (eg, the sporulation of *Thielaviopsis basicola* on tobacco roots) is considered. Increasing inoculum levels led to higher sporulation of the pathogen on the roots of the host plant and decreased the inhibitory influence of VA mycorrhizae on the pathogen (4). These observations indicate that the interactions between mycorrhizal fungi and plant pathogens are only relative and are based on a modification of disease development. This can be considered to be a general characteristic of induced resistance.

Diseases caused by soilborne nematodes. Since mycorrhizae affect a broad range of soilborne fungal pathogens, it may be concluded that the beneficial influence is (to a certain extent) independent of the pathogen. The parasitization of plants by nematodes (mainly endoparasitic) can be influenced by the establishment of a VA mycorrhiza (Table 1). The penetration rate of parasitic nematodes can be decreased, their development inside the root may be retarded, or the degree of damage caused by the nematode may be lowered. In general, these biotrophic parasites are not as aggressive as some of the fungal root pathogens.

Even though the symbiotic plant may grow better than the nonmycorrhizal plant and, therefore, the absolute reproduction rate of the nematode may be higher and the damage to mycorrhizal plants can be lower than to control plants as shown by Roncadori and Hussey (28). The growth reduction of cotton plants due to the root knot nematode was about 30% in nonmycorrhizal plants, but only 10% in the better-growing mycorrhizal plants. In this case, the tolerance of plants to disease was higher under the influence of the symbiosis, even though nematode development was improved.

Other reports demonstrated a specific effect of mycorrhiza formation on the development of plant parasitic nematodes (15,21,25,41–43). If the environmental conditions are not only favorable for the parasite, but also for the mycorrhizal fungi, there can be a permanent influence on the development of the pathogen. Kellam and Schenck (21) found more root-knot galls on nonmycorrhizal soybeans. On mycorrhizal root systems the nematode population stayed nearly unchanged. This influence on gall formation is strictly limited to roots colonized by the mycorrhizal fungus (15,25). Even in the root system of heavily infected mycorrhizal plants, parts of the roots can be free of

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mycorrhizal colonization. At these sites the development of sedentary nematodes is nearly the same as at root sites of nonmycorrhizal plants (15,21).

In addition to a reduced penetration rate of the nematode into the roots of mycorrhizal host plants and reduced development inside these roots, Priestel (25) found a specific decrease in the reproduction rate of the parasite. The development of larvae of *Meloidogyne* into females and egg production in females was strongly retarded. This observation may be of importance for the epidemiology of sedentary nematodes in the field and may explain the findings of other authors (42,43) that the population dynamics of nematodes can be reduced in mycorrhizal root systems.

The question remains, what kind of interaction might be responsible for this effect? Sedentary nematodes like *Meloidogyne* species induce the formation of hypertrophic tissue, the formation of galls. Inside this more or less meristematic gall the host reacts to

TABLE 1. Influence of VA/mycorrhizae on soilborne plant pathogenic fungi and nematodes

		Decrease (−) or increase (+) at mycorrhizal plants			
Pathogen	Host plant	Damage	Infection	Reproduction	Author
Fungi					
Olpidium brassicae	tobacco	···	−	···	Schoenbeck and Dehne (37)
	lettuce	···	−	···	Schoenbeck and Dehne (38)
Pythium ultimum	soybean	···	···	···	Chou and Schmitthenner (8)
	poinsettia	−	···	···	Stewart and Pfleger (44)
Phytophthora cinnamomi	'Lawson' pine	−	···	···	Baertschi et al (2)
	avocado	+	+	···	Davis et al (13)
P. megasperma	soybean	+	···	···	Ross (29)
	alfalfa	+	+	···	Davis et al (13)
	soybean	−	···	···	Chou and Schmitthenner (8)
P. palmivora	papaya	···	···	···	Ramirez (26)
P. parasitica	citrus	−	···	···	Schenck et al (34)
	citrus	+	+	···	Davis et al (13)
	citrus	−	−	+	Davis and Menge (11)
Fusarium oxysporum cepa	onion	−	−	···	Cole and Mokhtar (*personal communication*)
F. oxysporum cucumerinum	cucumber	−	−	···	Dehne (14)
F. oxysporum lycopersici	tomato	−	−	···	Dehne and Schoenbeck (16)
	tomato	+	···	···	McGraw and Schenck (22)
F. avenaceum	clover	−	···	···	Cole and Lim (*personal communication*)
F. solani	soybean	···	···	···	Zambolin and Schenck (45)
Verticillium dahliae	cotton	+	+	···	Davis et al (12)
Rhizoctonia solani	poinsettia	−	···	···	Stewart and Pfleger (44)
	soybean	···	···	···	Zambolim and Schenck (45)
Macrophomina phaseolina	soybean	···	···	···	Stewart and Pfleger (44)
Cylindrocladium scoparium	yellow poplar	−	−	···	Barnard (6)
Phoma terrestris	onion	−	−	···	Becker (7)
Pyrenochaeta terrestris	onion	−	−	···	Safir (30)
	onion	···	−	···	Cole and Mokhtar (*personal communication*)
Thielaviopsis basicola	tobacco	−	···	−	Baltruschat and Schoenbeck (5)
	alfalfa	−	···	−	Baltruschat and Schoenbeck (5)
	cotton	−	···	···	Schoenbeck and Dehne (36)
	citrus	···	···	···	Davis (10)
	onion	−	···	···	Cole and Lim (*personal communication*)
Nematodes					
Heterodera solanacearum	tobacco	···	···	−	Fox and Spasoff (18)
Meloidogyne arenaria	grape	+	···	+	Atilano et al (1)
M. hapla	carrot	···	···	−	Sikora and Schoenbeck (41)
M. incognita	tobacco	···	···	−	Sikora and Schoenbeck (41)
	tomato	···	···	−	Sikora and Schoenbeck (41)
	oat	−	···	−	Sikora and Schoenbeck (41)
	soybean	−	···	+	Schenck et al (33)
	soybean	−	−	···	Kellam and Schenck (21)
	cucumber	−	−	−	Priestel (25)
	cotton	−	···	+	Roncadori and Hussey (28)
	tomato	···	−	···	Bagyaraj et al (3)
Radopholus similis	citrus	−	···	···	O'Bannon and Nemec (24)
Rotylenchulus reniformis	bean	−	−	···	Sitaramaiah and Sikora (42)
	cucumber	−	−	···	Sitaramaiah and Sikora (42)
	cotton	−	−	···	Sitaramaiah and Sikora (42)
	tomato	−	−	···	Sitaramaiah and Sikora (42)
Pratylenchus brachyurus	cotton	−	···	···	Hussey and Roncadori (20)
P. penetrans	cucumber	···	···	−	Priestel (25)
Viruses					
Tobacco mosaic virus	tobacco	···	···	+	Schoenbeck and Schinzer (39)
	tomato	···	···	+	Daft and Okusanya (9)
	tomato	···	···	+	Schoenbeck and Spengler (40)
Potato virus X	tomato	···	···	+	Daft and Okusanya (9)
Arabis mosaic virus	petunia	···	···	+	Daft and Okusanya (9)
	strawberry	···	···	+	Daft and Okusanya (9)

nematode establishment with the formation of giant cells, which seem to function as transfer cells for the nutrient flow towards the parasite. Pathogenic fungi, which may influence nematodes, often parasitize these cells, destroy them, and thus inhibit nematode development.

Direct parasitization of galls by mycorrhizal fungi is not apparent. Mycorrhizal fungi are unable to infect meristematic tissue and the center of the nematode-induced gall has to be regarded as meristematic. So mycorrhizal fungi are only found near galls, not inside them. Usually the endophyte can be found on the unaltered, opposite site of the root (15,21,25).

The mycorrhizal fungi are competitors of sedentary nematodes: the parasite is committed to remain in the gall and be associated with a specific giant cell system, but the endophyte is not so limited and can continuously infect new appropriate root sites.

Diseases caused by viral plant pathogens. Considering the possibility of frequent colonization of root systems by the endophyte, any interaction between mycorrhizal fungi and plant pathogens should be expected to occur in roots. In contrast to the restriction of soilborne pathogens to the site of symbiosis between plant and endophyte, virus diseases are less restricted because they can spread systemically throughout the whole plant (Table 1). In every case, whether the infection by different viruses was systemic or local, mycorrhizal host plants always exhibited increased disease intensity. Virus multiplication and even the sensitivity to viral contamination was enhanced.

Virus diseases are often more prominent in vigorously growing plants. The increased sensitivity and higher reproduction of a virus in mycorrhizal plants may (to a certain degree) be due to the improved nutrient status of these plants. Experiments with split root systems showed that the increase in viral disease is not only due to better nutrition; mycorrhizal roots of the same plant had a higher TMV concentration than nonmycorrhizal roots (37). Immunofluorescent techniques indicated that the increased virus concentration in mycorrhizal host roots was mostly limited to the arbuscular stage of the endophyte (15,40). Electron microscopy revealed that TMV was restricted to the host cell cytoplasm, but was intensively concentrated in cells that contained arbuscular stages with rather fine branches (37). This indicates that the high metabolic activities in the host cytoplasm of those cells are favorable for the accumulation of virus particles. The increased exchange of substances from the fungus into the host cell and vice versa can be characterized by high phosphate metabolism and high concentrations of nucleic acids and proteins (23,35,38). Virus infections and virus multiplication may benefit from this high physiological potential in the root tissue. The increased synthesis of nucleic acids and proteins may promote virus multiplication and thus be responsible for a better spread over the whole plant.

The influence of VA mycorrhiza on viral plant diseases is affected by the increased nutrition of mycorrhizal plants. But this effect may be related less to quantitative nutrient changes in the whole plant, but more to a very specific alteration of the activity of mycorrhizal host cells. Virus particles can be regarded as chemical substances that benefit from the highly susceptible, mycorrhizal host-fungus association. The results obtained with virus diseases, therefore, cannot be compared to interactions between the endophyte and other plant pathogenic organisms.

Influence of VA mycorrhizae on shoot and leaf diseases. Growth responses due to VA mycorrhizal fungi may alter disease resistance in the shoot and leaf. When plants are grown under conditions that allow nonmycorrhizal plants to grow in the same way as mycorrhizal plants, mycorrhizal plants are still more susceptible to leaf pathogens (37). This indicates that the symbiosis can influence the whole plant (38).

A differentiation of the disease incidence on single leaves can explain the nature of this stimulatory influence of VA mycorrhizae in more detail. A different degree of infection by the powdery mildew fungus between comparable mycorrhizal and nonmycorrhizal cucumber plants, for example, occurred only in young leaves (38). The increase in susceptibility of the shoot was due rather to an enhanced development of the pathogen than to an increased frequency of infection. This influence seems also to be correlated with the nutritional aspect of mycorrhiza-disease interactions and higher physiological activities in the whole host plant. It should be noted that higher disease incidence in the symbiotic system, in general, does not affect genetically defined resistance to plant pathogens (38). Genetically resistant plants remain resistant, whereby susceptibility may be modified by the symbiosis.

INFLUENCE OF ROOT PATHOGENS ON VA MYCORRHIZAE

The competition between plant pathogens and VA mycorrhizal fungi for the same host can influence the development of both the pathogen and the mycorrhizal fungus. Priestel (25) found that under the influence of *Meloidogyne incognita* the colonization of cucumber roots by *Glomus mosseae* was adversely affected by the nematode. This happened although the nematode generally did not kill root cells. This negative influence on the mycorrhizal fungus was mediated by the host plant, as well as by the antagonism between endophyte and nematode.

Damage to the root from the outside (eg, by the action of toxins or by the development of root rotting fungi in the cortex) will destroy the food base for the mycorrhizal fungi in the living root tissue (13,29,32,45). Increased plant disease resistance as a consequence of interactions between mycorrhizal fungi and plant pathogens is dependent on the biological influence of the endophyte. High virulence of plant pathogens will be detrimental to host tissue and mycorrhizal associations.

THE INTERACTION OF PLANT PATHOGENS AND VA MYCORRHIZAE

Mechanisms of interaction. The interactions between VA fungi and plant pathogens can be described in two general statements about mechanisms of resistance: (i) Mycorrhizal fungi are able to retard pathogen development in the root system. This influence is restricted to the site of mycorrhiza establishment. (ii) Mycorrhizal fungi are able to increase disease incidence systemically, especially in nonmycorrhizal plant parts. So far as is presently known, the systemic influence can be attributed to better nutrition, enhanced plant growth, and physiological stimulations in mycorrhizal plants. With increased concentrations of assimilates those plants can serve as better nutrient sources for plant parasitic organisms (4,10,28).

On the other hand, there is a localized specific influence of VA mycorrhizal fungi on various alterations in host plant physiology. Mycorrhizal roots are more lignified than nonmycorrhizal ones, especially in the stelar tissue (14). This effect may be responsible for the restriction of the endophyte to the root cortex. The same mechanism of resistance may be effective against parasitic soilborne organisms invading the host root.

The symbiotic host-fungus-relationship is characterized by the formation of arbuscules. These specific, haustorialike structures of the endophyte are successively degraded. This process is interpreted as digestion of the fungus by the host (14,23,35). For this degradation to occur, the fungal cell wall of the endophyte has to be attacked by the host. Therefore, roots colonized by a mycorrhizal fungus exhibit high chitinolytic activities. These enzymes can be effective against other fungal pathogens as well (17).

The increased resistance of mycorrhizal roots to soilborne pathogens can be elicited by specific alterations in the physiology of the host plant due to the microbial metabolism of the endophyte. This particular influence can be demonstrated in the case of sporulation of *Thielaviopsis basicola* on mycorrhizal roots, which is inhibited by an accumulation of arginine (5,17).

Conditions for beneficial interactions. The induction of a higher resistance to root pathogens probably is limited to the biological interaction between host and endophyte. Increased resistance or (as it also may be called) decreased susceptibility requires optimum conditions for the development of the symbiosis, if possible before the attack of the pathogen.

Preinoculation of cotton with a mycorrhizal fungus reduced the development of the plant parasitic nematode *Rotylenchulus* *reniformis* to a greater degree than simultaneous inoculation with both organisms (42,43). This beneficial influence of VA mycorrhizae became evident, even though symbiont and parasite occupied the host root at the same time. However, heavy damage of the root will be inhibitory to mycorrhizal infestation and, therefore, diminish the positive influence of the symbiosis on disease incidence. The development of *Phytophthora parasitica*, which can be detrimental to the host root, could be decreased only by a high mycorrhizal infestation prior to the challenge with the pathogen (2). Simultaneous competition of both fungi for the root almost completely diminished the protection from disease offered by the symbiont.

Successful suppression of a pathogen, however, may not only depend on the mode of parasitism and the virulence of the pathogen, but also on the particular potential of the VA mycorrhizal fungus to induce resistance. The degree of decrease in nematode population, due to reduced penetration and retarded reproduction, can differ quantitatively with the endophyte species (33,42,43). This difference in effectiveness depends not only on the fungal species. Baertschi et al (2) found that an unidentified, mixed mycorrhizal population was considerably more effective in reducing pathogen development than a pure culture of *G. mosseae*. The single endophyte species caused only a delay of disease development, whereas the mixed population was able to reduce the damage of *Chamaecyparis* almost completely. These observations indicate that endophyte variability must be considered in studies of this type.

Importance of interactions. The influence of mycorrhizal fungi on plant diseases has not been demonstrated under field conditions, although there are some promising results that support the conclusions of the greenhouse studies. VA mycorrhizae have to be considered a part of the environment and of the plant itself, which is able to alter its disease resistance. From the present point of view it can be stated that VA mycorrhizal fungi stimulate nutrient uptake and thus increase growth and development of the host plant. This influence of mycorrhizal fungi on plant nutrition should be considered the most important effect of high practical value. In general, from the nutritional aspects of parasitism, those plants can be expected to be potentially better hosts for pathogens. However, under the direct influence of mycorrhizal fungi, root tissue becomes more resistant to pathogenic attack or has to be regarded as less suitable for parasitic organisms. This induced resistance is strictly limited to the site of the host-endophyte interaction and will only affect soilborne pathogens. The application of selected VA mycorrhizal fungi will not only benefit plant growth and development, but it offers the possibility of increasing resistance against soilborne pathogens as well. Under natural conditions this can be regarded as a positive side-effect of VA mycorrhizae, not, however, as a potential biological plant protection.

The comparison of biological characteristics of mycorrhizal and pathogenic fungi can provide information about similarities and differences in parasitism and symbiosis. The main sequences in the biology of biotrophic fungi are similar for pathogens and endophytes, but the consequences of infection are fundamentally different for the plant.

In direct competition with pathogens in a living host root cell, mycorrhizal fungi may be more successful due to a higher degree of plant susceptibility. Possible infection sites in those roots can be saturated by the symbiotic fungus, in effect inducing resistance to parasitic infection. Investigations into the interactions between mycorrhizal fungi and plant pathogens will provide more information on the phenomenon of induced resistance and susceptibility.

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