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INTERACTIONS AMONG MYCORRHIZAL FUNGI, RHIZOSPHERE ORGANISMS, AND PLANTS

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1 INTRODUCTION

In this chapter we discuss interactions of mycorrhizal fungi with rhizosphere organisms and the consequences of those interactions to belowground and aboveground organisms. Colonization of roots by mycorrhizal fungi results in changes in (1) the types and amounts of exudates produced by roots; (2) the manner in which plant carbon is allocated among leaves, shoots, and roots of plants; (3) the nutrient status of plants (most notably in concentrations of phosphorus, nitrogen, micronutrients, and heavy metals), and perhaps, (4) in drought tolerance or resistance of the plants. These changes affect more than the symbiotic relationship of the plant and fungus but also influence other organisms which comprise the belowground food web (Hunt et al., 1987). As a result, a broad group of processes, such as nitrogen fixation, litter decomposition, nutrient cycling, disease or pathogen incidence, soil aggregation, plant competition, and succession, may be directly or indirectly affected.

In this chapter we concentrate on interactions occurring after colonization occurs, not on factors which influence the mycorrhizal colonization processes. Related topics are thoroughly addressed in other literature: phylogenetic relationships, taxonomy, and classification of mycorrhizal fungi (Trappe and Molina, 1986); biotic and abiotic factors influencing mycorrhizal fungi before root colonization [Bowen, 1987; Rabatin and Stinner, this volume (Chapter 5)]; and cytological processes during colonization (Harley and Smith, 1983).

The differences between nonmycorrhizal and mycorrhizal plants are based on the physiological effects of colonization (or infection) by either vesicular-arbuscular mycorrhizal (VAM) or ectomycorrhizal (EM) fungi on the plant host. In the first part of this chapter we summarize data on the influence of mycorrhizal colonization on plant processes, such as root exudation, carbon allocation, and nutrient uptake. In the remainder of the chapter we discuss the effects of mycorrhizal colonization on (1) the belowground food web (including bacteria, saprophytic fungi, protozoa, nematodes, and microarthropods); (2) pathogen attack of plants; (3) litter decomposition rates; (4) aboveground grazing by herbivores; (5) plant growth hormones; (6) soil aggregation; and (7) plant competition, community structure, and succession.

2 PLANT PROCESSES INFLUENCED BY MYCORRHIZAL COLONIZATION

2.1 Root Exudation

That mycorrhizae modify root exudation seems clear. However, less is known about the exudate that diffuses into the rhizosphere before colonization, the amount that is shunted to the fungus, the amount released into the rhizosphere, and whether these amounts vary under different conditions. Changes in exudation patterns not only affect further colonization by mycorrhizal fungi but markedly change substrate quality, and thus the growth of pathogens and beneficial organisms in the rhizosphere [see Benedict et al., this volume (Chapter 6)].

Both VAM and EM colonization have been reported to reduce and change the quality of root exudates. Ratnayke et al. (1978) and Graham et al. (1981) suggested that increased root exudation by phosphorus (P)-deficient plants stimulates VAM colonization. Rambelli (1973) showed that following VAM colonization, root exudation decreased, causing a qualitative change in rhizosphere biota. As colonization occurs, root concentrations of P increase, leakage of exudates through the plant plasmalemma decrease, and mycorrhizal colonization diminishes proportionately (Harris and Paul, 1987). Mycorrhizal colonization probably changes root exudation from easily utilizable sugars to more complex amino acids (Katznelson et al., 1962). Laheurte and Berthelin (1986a) found that total monosaccharide release was reduced with VAM colonization, but the relative amounts of glucose, mannose, and amino acids (mainly arginine) were higher. At low colonization rates, the growth of maize was promoted by vesicular-arbuscular mycorrhizae (VAM), and total root exudation was decreased; at high colonization rates plant growth was not improved, but root exudation increased (Laheurte and Berthelin, 1986a). Although root exudation may trigger mycorrhizal colonization, the amount of plant exudate produced is not sufficient to support continuous mycorrhizal development (Schwab et al., 1983).

Pathogens and mycorrhizal fungi compete for plant exudates, and the "winner" often changes plant exudation, presumably to suppress the competitor or improve its own colonization. Graham and Menge (1982) found that the decrease in wheat take-all disease, caused by *Gaeumannomyces graminis*, resulted partly from improved plant P levels following VAM colonization, but mostly from decreased root exudation prior to pathogen attack. Increased P concentration in the plants decreased net exudation from roots and reduced pathogen activity. Malajczuk (1979) found that the microflora around ectomycorrhizae of pine suppressed *P. cinnamomi*, probably as the result of a change in root exudation. Alternatively, an increase in arginine exudation following VAM colonization reduced chlamydospore production by *Thielaviopsis basicola* (Baltruschat and Schonbeck, 1975).

In other cases, pathogens can outcompete mycorrhizal fungi for root exudates. In *Verticillium* attack of tomatoes (Baath and Hayman, 1983), *Ver-*

ticillium was a better competitor for root exudates than were VAM fungi, and once infection was established, *Verticillium* reduced root exudation and VAM colonization.

2.2 Plant Carbon Allocation

The carbon-sink theory states that in plants limited by P (e.g., nonmycorrhizal plants), the conversion of sucrose to sucrose-6–P is limited. Basal plant respiration is altered by mycorrhizal colonization (reviewed by Harley and Smith, 1983). Starch, the sucrose precursor, accumulates in the leaves, producing a feedback signal that slows photosynthesis. Low concentrations of inorganic P in the chloroplast also reduces the ratio of ADP to ATP, slowing the fixation of CO_2. When plant roots are colonized by mycorrhizal fungi, the demand for plant C increases, mobilizing starch reserves from the leaves and removing the starch-sink inhibition of photosynthesis. Increased P reduces the ADP/ATP limitation of photosynthesis, allowing increased photosynthesis. Thus, increased photosynthesis in colonized plants is not indicative of increased demand by the symbiont but rather, release of an inhibition (Harris and Paul, 1987).

As sugars, organic acids, and amino acids diffuse into the interface between plant and fungus, the fungus generates a gradient by converting these compounds into ones not utilized by the plant host. These altered compounds are thus not susceptible to diffusion back across the fungal membrane (Paul et al., 1985). Lewis and Harley (1965) suggested that ectomycorrhizae convert plant substrates into carbohydrates, such as trehalose and mannitol, not normally metabolized by the host. The strategy of VA mycorrhizae appears to be the conversion of plant substrates, especially sucrose, into lipids (Cooper and Losel, 1978; Cox et al., 1975). Fungal-produced hormones may encourage passive diffusion of carbohydrates into the interface of plant and fungus, whereupon either carbohydrates or converted substrates are actively transported into the endophyte, a process involving ATPase activity (Woolhouse, 1975). As a result, polyphosphate is hydrolyzed in the arbuscule and inorganic P diffuses across the fungal cell membrane. Phosphorus is then actively transported across the plant plasmalemma, utilizing ATPase. However, direct measurements of both C and P fluxes across the host–fungus interface have not been performed, and direct evidence of where and how this occurs is needed before the carbon-sink theory can be validated (Harris and Paul, 1987).

The carbon-sink theory has been supported by several studies with VA mycorrhizae. Snellgrove et al. (1982) reported that leek plants with mycorrhizae had less dry matter, greater specific leaf area, and photosynthetic rates 13% greater on a dry weight basis than those of P-compensated, nonmycorrhizal plants. Mycorrhizal colonization increased specific leaf area by increasing leaf hydration, increased P concentrations, and reduced starch in leaves by 50%, but did not change leaf weight or water content (Harris and Paul,

1987). Increased translocation and respiration of photosynthate in VAM-colonized roots can range from 8 to 21% higher than in fertilized, nonmycorrhizal plants. Such increases have been observed in mycorrhizal onion plants (Losel and Cooper, 1979); *Bouteloua gracilis* (Allen et al. 1981); *Vicia faba*, *Glycine max*, sorghum, and *Allium porrum* (Harris and Paul, 1987; Kucey and Paul, 1982); and leek plants (Snellgrove et al., 1982). Decreased photosynthetic rates have been observed following VAM colonization, although control plants did not emulate the growth of the colonized plants (Paul et al., 1985). Maintaining nonmycorrhizal controls at the same nutrient levels as mycorrhizal plants, to differentiate the nutritional effects of improved P, nitrogen (N), or micronutrients (see below) from the C cost of the fungus, is one of the most difficult experimental issues in mycorrhizal research.

The cost of EM colonization may be as high as 40–50% of total plant photosynthate, although these estimates were based on high values for specific fungal maintenance rates and on the assumption that all hyphae in roots are active (Fogel and Hunt, 1979; Harris and Paul, 1987). Paul et al. (1985) suggested that 4–14% of total plant photosynthate is redirected to VAM colonized roots, concomitant with an increase of 8–21% in net photosynthesis as compared to nonmycorrhizal control plants supplied with P.

A variety of researchers have found that some mycorrhizal fungi reduce plant carbon (C) levels and growth by significant amounts, especially during early stages of colonization (Bethlenfalvay et al., 1982; Buwalda and Goh, 1982; Janos, 1985; Mosse et al., 1981; Sparling and Tinker, 1978; Stribley et al., 1980). Jones and Hendrix (1987) reported a case where *Glomus macrocarpum* appears to be the causative agent of tobacco stunt disease. Inoculation of tobacco seedlings with disinfected spores reduced root length and weight and, at times, reduced shoot weight. Application of benomyl reduced stunt disease concomitant with reduction in *G. macrocarpum* root colonization. In field studies, Modjo et al. (1987) found that fumigation of soil with methyl bromide and chloropicrin improved tobacco growth, reduced VAM colonization by a factor of 10, and decreased the number of spores of *G. macrocarpum*.

Paul et al. (1985) compared rates of carbon utilization by fungal biomass (3.6 mg plant C/day as determined by microscopic estimation) with labeled CO_2 incorporation in soybeans (3.7 mg plant C/day), suggesting that VAM fungi use a significant portion of the photosynthate produced by a plant. Respiration rates for VAM and EM fungi were similar, between 11.0 and 11.7 mg of CO_2 per gram of hyphae per hour (Harris and Paul, 1987). This C cost must be met by the plant, and if fungal demand is greater than that available to the plant, the symbiosis becomes negative for the plant.

The cost of EM colonization to the plant may be offset by non-plant-derived C. Recent studies have shown that the external hyphae of ectomycorrhizae produce enzymes which degrade lignin, cellulose, and complex organic material (Dighton et al., 1986; Griffiths et al., 1989; Mosse et al., 1981; Read, 1987; Trojanowski et al., 1984; see Section 3.3). Demonstrations of enzymes

capable of breaking down complex substrates have been limited for VAM fungi (Read, 1987; St. John et al., 1983).

2.3 Nutrient Uptake

Ectomycorrhizal fungi distribute fixed C obtained from the plant through an often widely distributed external fungal mycelium (Bowen, 1987; Cox et al., 1975). External hyphae allow plants to obtain nutrients from a larger volume of soil without the expense of root production by the plant (St. John and Coleman, 1983). Through this expanded root system, and when particular nutrients (especially P) are limited, mycorrhizal fungi improve the substrate quality of leaves, stems, and roots (Stribley, 1987). Moore (1988) found that once VAM colonization reached 12%, benefit from VAM colonization would not greatly increase. This suggests that colonization does not have to be extensive to realize maximum benefit, at least in semiarid grasslands.

Nitrogen can be translocated by VAM fungi (Ames et al., 1983) and its uptake improved by both VA and ectomycorrhizae (Bowen and Smith, 1981; France and Reid, 1983; Read, 1987; Smith et al., 1986). VA mycorrhizae enhance, under certain conditions, the uptake of micronutrients by plants, including Cu, Co, Mg, Ni, Ca, S, and Cl (Killham, 1985), Zn and Cu (Lambert et al., 1979), Br and Cl (Buwalda et al., 1983), and K (Powell, 1975). Alternatively, Gildon and Tinker (1983) found reduced VAM colonization when heavy metals were present. The proportion of the total level of P, Zn, Cu, and Fe taken up by mycorrhizal beans increased as the levels of these nutrients in soil were decreased (Kucey and Janzen, 1987). Wheat did not show the same relationship. Kucey and Janzen (1987) suggested that because wheat has a more fibrous root system than beans, the root–soil contact was similar between nonmycorrhizal wheat and mycorrhizal beans, allowing both plants to come in contact with the same amount of nutrient, even as nutrient levels decreased.

Mycorrhizal plants are more tolerant of drought (Allen and Allen, 1986; Allen et al., 1981; Nelsen, 1987), but possibly as a result of the increased soil volume exploited by mycorrhizal plants and not as a result of increased transfer of water to the plant by mycorrhizae (Nelsen, 1987; Safir, 1987; see Section 3.6). Drought reduces nutrient diffusion in the soil, and only those plants exploiting a wide volume of soil, and thus nutrients and water, can survive. Reduced stomatal transpiration has not been shown in mycorrhizal plants, although increased water use efficiency has been suggested (Allen et al., 1982). However, Parke et al. (1983) showed that mycorrhizal colonization, not expanded exploitation of the soil, was involved in recovery of photosynthesis in Douglas-fir colonized by the ectomycorrhizal fungus *Rhizopogon vinicolor* after water stress.

3 MYCORRHIZOSPHERE INTERACTIONS

Mycorrhizal colonization results in changes in root exudation, nutrient uptake, and plant C allocation. As a result, mycorrhizal colonization (1) modifies the

belowground food web and selects for certain populations of rhizosphere bacteria, saprophytic fungi, protozoa, nematodes, and microarthropods; (2) protects the host plant against root pathogen attack; (3) influences litter decomposition and nutrient cycling rates; (4) influences aboveground herbivore grazing; (5) changes plant growth hormones; (6) influences soil aggregation; and (7) affects plant competition, community structure, and succession [also see Jones, this volume (Chapter 3); Moore et al., this volume (Chapter 4); Rabatin and Stinner, this volume (Chapter 5)].

3.1 Belowground Food Web

Energy in the belowground or soil detrital food web moves through decomposers, grazers, predators, and generalists (see Hunt et al., 1987, and Ingham et al., 1986, for detailed discussions). Organic inputs to the detrital food web are provided by plants (leaf litter, root cells, and exudates), by animals (urine and fecal material), and by all dead organisms (necromass), including aboveground herbivores and predators, and by organisms comprising the detrital food web. Organic inputs correspond to the producer or first trophic level in aboveground food chains. Decomposers (i.e., bacteria and fungi) comprise the second trophic level and utilize dead organic material, producing microbial biomass, secondary metabolites, and carbon dioxide. Certain bacteria, such as *Rhizobium*, *Frankia*, and *Azospirillum*, convert atmospheric nitrogen to organic nitrogen, and other bacteria have been shown to solubilize inorganic phosphorus to phosphate. Plant-feeding nematodes and microarthropods should also be included in the second trophic level, as they "short-circuit" the decomposers and feed directly on living plant roots. Bacteria are grazed (alternative terms are *eaten* or *preyed upon*) by protozoa and bacterial-feeding nematodes, whereas fungi are grazed by fungal-feeding amoebae, nematodes, and microarthropods.

The first-level predators, such as protozoa, microbial-feeding nematodes, and fungal-feeding microarthropods, are preyed upon by higher-level predators and omnivores. The precise trophic status of higher-level predators is indistinct, partly because feeding studies have not been performed for many nematodes and microarthropods, and partly because many are omnivorous, capable of feeding on more than one level of the trophic chain (see Hunt et al., 1987). Thus, nematodes observed feeding on fungi could also feed on plant roots and other nematodes. Microarthropods which consume fungal-feeding nematodes may prey on plant roots or nematode-feeding nematodes. An example of a known omnivore is the earthworm, which ingests soil in order to digest the bacteria, fungi, protozoa, nematodes, and microarthropods contained within pore spaces. All belowground organisms undoubtedly interact with mycorrhizal hyphae which surround plant roots or grow through the soil [see Rabatin and Stinner, this volume (Chapter 5)]. The following sections summarize what is known about these interactions.

3.1.1 Interactions with Nitrogen Fixers Inoculations of two different species of beneficial organisms often result in a synergistic effect on plant growth.

For example, increased N fixation and nodulation by *Rhizobium* and actinomycetes occur with VAM colonization (Cluett and Boucher, 1983). Mycorrhizae provide the high levels of P required by N-fixing bacteria (Bowen, 1987; Miller, 1987). Nitrogen fixers, in turn, improve C supply to mycorrhizae, by supplying nitrogen to the plant. Miller (1987) summarizes the studies demonstrating improved N-fixation rates by *Rhizobium*, increased VAM colonization, and enhanced growth of the host legume, when all three symbionts occur together. In addition, N-fixing bacteria select for the presence of P-solubilizing bacteria in the rhizosphere (Azcon et al., 1976).

Fewer studies have examined the synergism between asymbiotic N-fixers and mycorrhizae. Asymbiotic N-fixation in the rhizosphere is not stimulated by EM colonization in oak or pine (Jain and Vlassak, 1975), although some ectomycorrhizae secrete mannitol, which is utilized by N-fixing rhizosphere bacteria (Hassouma and Wareing, 1964). Bagyaraj and Menge (1978) reported that *Azotobacter chroococcum* populations in the tomato rhizosphere were maintained for longer periods of time if the plants were colonized by VAM fungi. Li and Hung (1987) attributed enhanced nitrogenase activity of surface-sterilized ectomycorrhizae of Douglas-fir to increased numbers of *Clostridium* and *Azospirillum*. Li and Castellano (1987) isolated *Azospirillum* from sporocarps of three EM fungi and postulated that these N-fixing bacteria improved N availability during fungal fruiting, which requires high levels of N.

Labeled N, fixed by *Rhizobium* nodules on the roots of a soybean (a legume), was transferred through VAM hyphae to a maize plant which was also colonized by the fungus (Van Kessel et al., 1985). The legume was grown with half its roots in a soil containing the bacterium and the other half in separate soil containing VAM fungi and the maize plant. The rates and conditions under which these transfers occur in field situations, whether nitrogen transfers from N-fixing bacteria through VAM influence plant survival, succession, or community structure, and what management techniques encourage or eliminate transfers of nitrogen through symbiotic organisms, have yet to be determined.

3.1.2 Bacteria The bacterial community that develops following mycorrhizal colonization is often composed of a greater number of beneficial, as opposed to pathogenic organisms (Linderman, 1988), possibly because pathogens tend to utilize simple soluble substrates and mycorrhizal colonization selects for more complex root exudates (see also Section 3.2.2). Mycorrhizal colonization may change the bacterial community in the rhizosphere from one requiring simple mineral nutrients to one requiring more complex amino acids, and reduce the percentage of phosphate-solubilizing bacteria (Katznelson et al., 1962). Numbers of bacteria, especially fluorescent pseudomonads and actinomycetes, were greater around EM roots of birch (Katznelson et al., 1962) and onions (Ames et al., 1984) than around nonmycorrhizal plants. Fewer fluorescent pseudomonads and more facultative anaerobes were

found in the mycorrhizosphere, but higher total numbers of bacteria and fluorescent pseudomonads occurred on the surface of the roots (Meyer and Linderman, 1986). Foster and Marks (1967) found that increased bacterial populations were closely associated with the EM mantle and suggested that because of their proximity to fungal exudates, these bacteria could exclude other rhizosphere organisms.

Roots colonized by VA mycorrhizae select for phosphate-solubilizing bacteria (Azcon et al., 1976), and certain strains of both EM fungi and rhizobacteria solubilize mineral phosphates such as tricalcium phosphate, ferric phosphate, and silicate mineral with 1% P (Leyval and Berthelin, 1986). Dual inoculation of P-solubilizing bacteria and mycorrhizal fungi can be synergistic, but there are examples of competition between these beneficial organisms. For example, Katznelson et al. (1962) found phosphate-solubilizing bacterial populations reduced by VAM colonization. Laheurte and Berthelin (1986b) reported that powdered rock phosphate could be solubilized by *Enterobacter agglomerans* in pure culture, but when grown with plants with or without VA mycorrhizae, the bacterium did not solubilize rock phosphate, instead competing with roots for P. Krishna et al. (1982) found that a *Streptomyces* species improved the growth and P nutrition of finger millet but reduced mycorrhizal colonization and spore production when inoculated simultaneously with *Glomus fasciculatus*. Conversely, the presence of the VAM fungus reduced bacterial numbers. Contrary to both these cases, Bagyaraj and Menge (1978) found that VAM colonization increased the number of actinomycetes in the rhizosphere. Thus, at present, the nature of the interaction between species of mycorrhizal fungi, plants, and rhizosphere bacteria cannot be predicted. Case-by-case studies will be necessary until a unifying hypothesis can be developed.

3.1.3 Saprophytic Fungi Interactions between mycorrhizal fungi, saprophytic fungi, and plants have been studied on a case-by-case basis, and even fewer cases have been studied than for bacterial interactions. The only example of a positive interaction between saprophytic fungi and mycorrhizal plants was given by Kucey (1987), in which a P-solubilizing strain of *Penicillium bilaji* increased plant dry matter production and P uptake by VAM-colonized beans and wheat. Examples of negative interactions include a *Pythium*-like fungus growing in both internal and external hyphae of *Glomus macrocarpus*, a species of *Phlyctochytrium* growing in the spores of *G. macrocarpus* but not in *G. gigantea* (Ross and Ruttencutter, 1977), *Humicola fuscoatra* and *Anguillospora pseudolongissima* parasitizing VAM fungi (Daniels and Menge, 1980), and several other fungal species parasitizing VAM fungal spores (Daniels and Trappe, 1980), thus reducing inoculum potential for new plants. Antibiotic production protects *Leucopaxillus cerealis* var. *piceina* against *Penicillium cinnamomi* (Marx, 1973). Attack of mycorrhizal hyphae and spores by saprophytic (pathogenic) fungi could seriously reduce mycorrhizal inoculum potential, relative colonization success, and ability to exploit the soil volume.

Parke and Linderman (1980) reported synergistic interactions between VAM fungi and moss. Fixation of N by moss increased the exudate level released to the mycorrhizal fungus, and the fungus, in turn, improved plant levels of P. Many fungal studies concentrate on the effect of mycorrhizae in reducing fungal pathogen attack (Schenk and Kellam, 1978) and these are discussed in a following section.

3.1.4 Protozoa Protozoan–mycorrhizal interactions have not been investigated to any extent. Fungal-feeding protozoa and mycorrhizal fungi may, like most predators and their prey, interact in accord with the grazing optimization theory (Hilbert et al., 1981). When predator densities are low, growth of prey may be stimulated. When predator densities are high, prey numbers may be reduced to suboptimal levels. Interactions which support only the overgrazing portion of the theory have been reported for protozoa. Colonization of tree roots by the EM fungus *Rhizopogon* was depressed by mycophagous amoebae feeding on the external hyphae (Chakraborty et al., 1985). VAM fungal spores were attacked by amoebae (Old and Chakraborty, 1986), which reduced colonization of new roots.

3.1.5 Nematodes Mycorrhizal colonization can have no effect, can reduce or enhance the effect of plant parasitic nematodes (Schenk and Kellam, 1978). A review of mycorrhizal–plant parasitic nematode interactions concluded that, in general, endoparasitic nematodes and VAM fungi are mutually inhibitory; although the response depends on plant cultivar, nematode and fungal species, soil nutrient status, and timing of inoculation and harvest (Ingham, 1988). Mycorrhizal fungi do not colonize regions of roots already infected by nematodes, and nematodes only rarely infect regions previously colonized by VAM fungi. Generally, VA mycorrhizae inhibit nematode penetration and development and increase plant resistance to nematodes. The mechanisms by which VAM fungi bring about these changes may be either larger root systems or increased nutrient availability for the plant. In some associations, nematodes reduce the growth stimulation provided by VA mycorrhizae; in other instances, VAM colonization diminishes the growth reduction resulting from nematode parasitism.

Nematodes have been observed feeding on roots colonized by EM fungi, but only Barham et al. (1974) studied the interaction between ectomycorrhizae, nematodes, and pathogenic fungi under controlled conditions. *Phytophthora cinnamomi* did not infect EM roots when nematodes were absent and infected nearly all roots without ectomycorrhizae, but invaded 27% of *Thelephora terrestris* EM roots and 36% of *Pinus taeda* roots when nematodes were present. In another case, root feeding by *Pratylenchus penetrans* decreased the ability of EM fungi to colonize Douglas-fir seedlings, resulting in greater pathogenic fungal attack of roots (McElroy, 1989). Thus, ectomycorrhizae appear to protect roots against pathogenic fungi unless nematodes are present, possibly because nematodes wound roots and augment pathogen penetration.

Investigators have observed fungal-feeding nematodes grazing directly on external mycelia of VA mycorrhizae (Ingham, 1988; Linderman, 1988). Both Riffle (1971) and Sutherland and Fortin (1968) showed that *Aphelenchus avenae* and *Aphelenchoides cibolensis* could feed on and reduce the growth of a wide variety of EM fungi, although *Rhizopogon roseolus* appeared to produce a toxin that prevented nematode feeding and growth. Two species of *Aphelenchoides*, feeding on *Suillus granulatus* associated with *Pinus ponderosa*, suppressed EM formation in several ways: by feeding on hyphae before they could reach the roots; by reducing mantle width; or by removing external hyphae, all of which would reduce the available surface area for nutrient absorption. Fungal-feeding nematodes, such as *Aphelenchoides*, *Deleadenus*, and *Aphelenchus*, feed on VA mycorrhizae (summarized in Ingham, 1988), reduce mycorrhizal colonization, and decrease host plant establishment. In another case, fungal-feeding nematodes destroyed sufficient VAM hyphae that phosphorus uptake was inadequate for successful nodulation by nitrogen-fixers (Salawu and Estey, 1979). Additionally, when fungal-feeding nematode densities were reduced in a short-grass prairie, active arbuscular colonization was increased by a factor of 6 to 10, and plant nitrogen levels were increased by a factor of 2 to 5 (Ingham et al., 1986). This suggests that nematodes reduce the ability of VAM fungi to colonize roots, but whether by eating spores, grazing on hyphae, or modifying the root has not been determined.

3.1.6 Arthropods Microarthropods, such as Collembola or mites, can consume large quantities of external mycorrhizal hyphae and negatively affect the benefit the fungus gives to plants, without reducing colonization levels (Moore and Walter, 1988; Shaw, 1985). Proturans feed on oak ectomycorrhizae and Collembola have been observed preferentially grazing on EM hyphae in pine plantations. Other studies, however, have indicated that Collembola do not graze common VAM or EM fungal species (Moore and Walter, 1988). Conversely, VAM fungal spores adhere to microarthropods and earthworms as they move along the surfaces of roots (Coleman, 1985), dispersing spores to new colonization sites, and thereby increasing colonization of roots. Additionally, VAM fungi utilize dead arthropods as sites for spore formation [Rabatin and Rhoades, 1982; Rabatin and Stinner, this volume (Chapter 5)].

The factors involved in determining whether arthropod feeding will be detrimental, neutral, or beneficial in field situations have not been explored. As applied to soil interactions, the optimum grazing theory states that low densities of grazers stimulate external hyphae to further exploit the soil, and high densities of grazers remove external hyphal biomass at a rate greater than it could be replaced, reducing nutrient flow to the plant. Overgrazing means that grazed hyphae must be continuously replaced, placing an increased carbon demand on the plant, and possibly reducing plant growth. Alternatively, the plant's carbon sink could be further released by increased mycorrhizal demand, increasing photosynthetic rates, and not affecting plant growth

significantly. At some point, of course, there is a negative impact, but at what density of protozoa, nematodes, or arthropods is not known.

*3.1.7 **Mammals*** Hypogeous fungi depend on mammals, such as marsupials in Australia and rodents in North America, and on invertebrate feeders to disperse their spores (Fogel and Trappe, 1978; Malajczuk et al., 1987). Mycorrhizal fungus mycophagy by small mammals is a more direct transfer of plant energy than that through the detrital food web (Hunt et al., 1987). Only one step is required in small mammal mycophagy, from dead organic carbon, through fungi, to a small mammal while in the detrital food web the transfer must start with decomposer fungi, and go through nematodes, microarthropods, and invertebrate feeders (e.g., centipedes, insect larvae, or beetles) to small mammals.

Small mammals facilitate the spread of both N-fixing bacteria and spores of hypogeous fungi. For example, Fogel and Trappe (1978) observed that small mammals fed on sporocarps. High levels of N-fixing bacteria occur in sporocarps of several fungal species (Li and Castellano, 1987) and N-fixing bacteria survive and grow in the feces of small rodents (Li et al., 1986), suggesting an important mutualism between the feeding strategy of rodents, the spread of EM fungi, and N-fixing bacteria.

Interactions of mycorrhizae with other food web organisms are recognized as important and potentially useful in the control of plant pests, especially as pesticide use becomes less acceptable. Major difficulties in the use of biotic interactions to manage crop systems is our lack of knowledge about the conditions which produce any given result. For example, interaction of plant parasitic nematodes with VA mycorrhizae depends to a large degree on the plant species, the specific nematode, and the abiotic conditions involved (Ingham, 1988; Schenk and Kellam, 1978). Specific interactions may occur only at precise temperatures and moistures or with specific soil rhizosphere communities. Mycorrhizal colonization, hyphal growth through the soil, and translocation of nutrients are influenced by the health of the plant, the availability of soil nutrients, and the feeding rate of grazers. How do interactions change as plant, fungal, or other food web species change? Are interactions observed in temperate climates likely to be the same in tropical systems? Unless mechanisms for interactions are elucidated, it will continue to be difficult to apply any of these results to other systems.

3.2 Protection of Plants against Root Pathogen Attack

Protection from pathogens is measured as less damage to the plant, decreased incidence of disease, or inhibition of pathogen development (Dehne, 1982). Five mechanisms appear important in mycorrhizal protection of roots from fungal and nematode pathogens. No information was found for bacterial pathogens. The mechanisms include (1) external hyphae as a physical barrier; (2) production of antagonistic chemicals; (3) competition between mycorrhizal

fungi or mycorrhizosphere associates and pathogens (discussed in the first part of the chapter); (4) improved plant nutrition, increasing host resistance to pathogen attack or tolerance to pathogens; and (5) modification of root exudation. These five mechanisms are similar to those discussed by Zak (1964), Marx (1973), and Bowen (1978). All, one, or several mechanisms may be involved in protection by mycorrhizae, although prior colonization by the fungus is usually necessary for protection to occur.

Toxic substance production may be a common mechanism in protection by ectomycorrhizae (Chakravarty and Unestam, 1986), whereas a common mode of protection for VA mycorrhizae has not been found. In general, VA mycorrhizae protect tomatoes, cotton, poinsettia, soybean, citrus, and wheat from *Fusarium*, *Gaeumannomyces*, *Pythium*, and *Rhizoctonia*, sometimes from *Phytophthora*, but not from *Verticillium*-caused diseases (Baath and Hayman, 1983; Schenck and Kellam, 1978). More research is needed to determine the mechanism(s) in specific situations.

3.2.1 Physical Protection Physical protection of roots has been invoked as a possible explanation of reduced disease incidence or severity in mycorrhizal plants. Ectomycorrhizal fungi produce massive external hyphae in the form of interwoven mats and rhizomorph structures that could limit pathogen advance. Although VAM fungi can produce an abundant external mycelium, mats and rhizomorphs are not formed, and thus physical protection is not as likely as with EM fungi. Nematodes, microarthropods, and larval insects are more likely to be physically excluded than are bacteria or saprophytic fungi.

Examples of prevention of pathogen contact by physical exclusion are rare. In their studies, Sinclair et al. (1982), Dehne and Dehne (1986), and Chakravarty and Unestam (1986) found no evidence of physical protection of roots by mycorrhizae. However, Perrin and Garbaye (1983) observed that the fungal mantle of *Hebeloma crustuliniforme*, an EM fungus, provided a barrier against the entry of *Pythium ultimum* into short feeder roots of beech seedlings. Similarly, more callosities develop in VAM than nonmycorrhizal onion plants and delay the spread of *Pyrenochaeta terrestris* (see Schenk and Kellam, 1978). Physical exclusion of pathogens were also suggested when *Phytophthora cinnamomi* was excluded by VA mycorrhizae, although antibiotics were produced as well (Marx, 1973), and a VAM fungus induced tissue incompatibility between plant root cells and pathogens (Dehne and Dehne, 1986).

3.2.2 Production of Antagonistic Compounds Mycorrhizal hyphae can produce antibiotics, and toxins, such as phenols, terpenoids, tannins, glyceollin, isoflavenoids (Bowen, 1978; Marx, 1973), phytoallexin, and allelopathic substances (Bowen, 1978; Gianinazzi-Pearson and Gianinazzi, 1986). Some ectomycorrhizal fungi produce high levels of laminarinase, an enzyme that hydrolyzes β-1,3 glucan linkages which are important in secondary wall structures of pathogenic fungi, thus possibly suppressing pathogenic fungi (Griffiths et

al., 1989). The tannin layer produced in conjunction with some ectomycorrhizae is postulated to be highly toxic, providing a chemical barrier which most pathogens cannot penetrate (Foster and Marks, 1967). Metabolites of *Laccaria laccata* can induce deposition of phenolic compounds in radicles before mycorrhiza formation occurs, probably protecting seedlings with a chemical barrier (Sinclair et al., 1982). Oxalic acid, produced by mat-forming EM hyphae (Cromack et al., 1979), releases high levels of exchangeable Al and Fe within the mats, and precipitates calcium crystals in large quantities around the roots and hyphae (Malajczuk and Cromack, 1982). These elements may be toxic to other soil organisms and perhaps form a barrier against the entrance of other organisms. High peroxidase activity found in EM mats may interact with halides and phenolics to produce products toxic to root pathogens (Griffiths et al., 1989). Kaye et al. (1984) suggested that hyphal accumulation of Mn by *Glomus fasciculatum* protected poinsettia against *Pythium ultimum*.

Ectomycorrhizal fungi produce chelators of various kinds, such as hydroxamate siderophores (Szaniszlo et al., 1981). Chelators scavenge and reduce the availability of metal ions essential as enzyme cofactors, such as Fe^{3+}, inhibiting the growth and survival of other soil organisms, including pathogens (Szaniszlo et al., 1981).

Although antagonistic compounds of various types appear to mediate all or a part of mycorrhizal reduction of pathogen attack, Koch's postulates have not been satisfied. More quantitative work is needed to identify the antagonistic compounds responsible for mycorrhizal protection of plants from pathogens.

3.2.3 Improved Plant Nutrition When plants are not stressed by nutrient deficiency, roots usually are able to resist or tolerate disease-causing organisms. Citrus tolerates increased levels of *Phytophthora parasitica* root rot because of VA mycorrhizae improved plant P nutrition (Davis and Menge, 1980). Plant resistance to root and collar rots, wilt diseases, and nematodes was increased by VAM colonization (Schenk and Kellam, 1978), yet plant susceptibility to leaf pathogens and viruses may be increased because the quality of leaf material is higher. Dehne (1982) noted three reports of greater damage when plants were mycorrhizal: Two cases involved *Phytophthora* root rot and the other involved tobacco mosaic virus. In viral shoot and leaf diseases, increased susceptibility of aboveground portions of plants results from better nutrition for pathogen development rather than from increased frequency of infection. However, plants that are genetically resistant are not susceptible, even when nutrition improves following mycorrhizal colonization (Dehne, 1982).

3.2.4 Modification of Root Exudation As discussed earlier, mycorrhizal colonization changes root exudate production; both amounts and types of compounds produced. Obviously, pathogens dependent on root substrates, especially labile compounds, will be disadvantaged as mycorrhizae change root exudates to more complex substrates (see Section 2.1).

Starch is mobilized, reducing levels in leaves and roots, when photosynthesis is stimulated by mycorrhizal colonization (Harris and Paul, 1987). Pathogens utilizing starch will be less able to infect a mycorrhizal plant, whereas pathogens that utilize the C substrates produced by mycorrhizal colonization may be selected by mycorrhizal colonization. Dehne (1982) suggested that VAM-colonized roots (1) contain more lignin, which restricts parasite invasion; (2) increase chitinolytic activity of root cells during degradation of arbuscules, increasing the degradation of other fungal pathogens entering this area; and (3) produce and accumulate metabolites inhibitory to pathogens compared to non-VAM-colonized roots (Baltruschat and Schonbeck, 1975). These suggestions, however, have not been validated.

3.3 Litter Decomposition Rates and Nutrient Cycling

Gadgil and Gadgil (1975) directed attention to the effects that mycorrhizal colonization of roots have on decomposition processes. They found that EM colonization of roots reduced the rate of litter decomposition. In contrast, Trojanowski et al. (1984) showed that many species of EM fungi directly decompose wood and leaf material. Dighton et al. (1986) found that the presence of roots, with or without ectomycorrhizae, enhanced decomposition of several substrates. Roots colonized by *Suillus luteus* enhanced decomposition more than those colonized by *Hebeloma* sp. or nonmycorrhizal roots. Increased decomposer activity by *Suillus* was suppressed by a saprotrophic fungus, whereas phosphate-solubilizing bacteria increase the decomposer activity of *Pisolithus* (Chakly and Berthelin, 1982). Conversely, Harmer and Alexander (1985) found that digging trenches to remove active roots, and mycorrhizal hyphae connected to roots, had no apparent effect on decomposition rates. Dighton et al. (1986) suggested reasons why all of these types of observations could be true. Certain species of mycorrhizal fungi, rhizosphere organisms, and plants may interact such that there is a net immobilization of nutrients which slows decomposition. Other combinations of organisms may not affect the equilibrium of either nutrient cycling or decomposition, or may interact to increase nutrient quality of litter and thereby decomposition rates.

Nitrogen is released in the form of ammonium or organic nitrogen when microbes, including external hyphae of mycorrhizal fungi, are grazed (Coleman et al., 1983). While ammonium can be used by plants directly, organic nitrogen must be cycled again through the detrital food web. Some mycorrhizal fungi can "short-circuit" this cycle of nutrient immobilization-mineralization by directly decomposing organic material (Coleman et al., 1983; Hunt et al., 1987; Janos, 1985). Dighton et al. (1986) suggested that these fungi invest more energy in producing and maintaining a large and complex biomass with, presumably, an increase in saprophytic capabilities. Thus, organic N released from roots or due to grazing processes can be directly utilized by EM fungi to reduce the trophic steps and energetic investment needed to convert organic N into plant-available N. These saprophytic capabilities have

not been demonstrated for VAM fungi and it is unlikely that VAM fungi can short-circuit N cycling processes in this fashion. Those combinations of organisms which reduce or increase either litter decomposition or nutrient cycling, depending on what is desired in specific circumstances, could be determined and utilized in management practices to improve soil fertility.

3.4 Aboveground Herbivore Grazing

In field studies, heavily grazed crested-wheatgrass had up to 50% lower VAM colonization and lower VAM fungal biomass, and its rhizosphere soil had fewer spores than lightly grazed wheatgrass areas (Bethlenfalvay et al., 1985; Bethlenfalvay and Dakessian, 1984). This was interpreted to mean that reduced plant material results in less photosynthate available to the fungal symbiont. In other studies, grazing increased the density of mycorrhizal vesicles in *Bouteloua gracilis* roots (Reece and Bonham, 1978), and clipping increased the biomass of mycorrhizal hyphae in *Lolium perenne* roots, improving aggregate stability (Tisdall and Oades, 1979). Both tillering and a prostrate growth habit were promoted following VAM colonization, allowing a plant to tolerate increased grazing (Bethlenfalvay and Dakessian, 1984; Miller, 1987; Wallace et al., 1982). These disparate responses could be the result of different plants, grazers, fungal symbionts, rhizosphere food web populations, or abiotic conditions. A continuum of responses probably exists and could be related to mycorrhizal dependency (Janos, 1985, 1987). If a plant is a facultative associate or nonmycorrhizal, grazing may reduce the amount of photosynthate shunted into the roots and thus reduce mycorrhizal colonization. Alternatively, when obligately mycorrhizal plants are grazed, the proportion of photosynthate to roots may be increased, to increase nutrient uptake from the soil for growth of new shoot material.

Improved nutrition might cause preferential grazing of mycorrhizal plants by herbivores (Wallace et al., 1982). This may be offset by the fact that plants with a higher nutritive value are less utilized because grazer nutritional needs are met by less of the total plant population. Alternatively, the negative effects of grazing (clipping in lab trials) are probably reduced by mycorrhizal-mediated improvement of plant nutrition (Bethlanfalvay et al., 1985; Wallace et al., 1982). Another possible interaction is decreased grazer growth rates following grazing of mycorrhizal plants. For example, VAM colonization induced a decreased growth rate in defoliating lepidopteran but not phloem-feeding insects on soybean (Pacovsky et al., 1985). This might be the result of toxic substances or modifications of plant hormones which affect the insect grazers.

3.5 Plant Growth Hormones

Mycorrhizal fungi produce plant growth hormones (Allen et al., 1980, 1982; Barea, 1986; Slankis, 1973). Consistent with production of plant growth-

promoting hormones is the modification of bud-break, caused by EM colonization in young woody plants (Garbaye, 1986). Even at very low colonization rates, *Laccaria laccata* produced earlier bud-break, by as much as 6 days, compared to nonmycorrhizal plants. *Thelephora terrestris* was not effective in changing the date of bud-break.

Cell-free supernatants from rhizosphere bacterial cultures, as well as the bacteria themselves, contained plant growth regulators (Azcon et al., 1978). These growth regulators increased the rate of root growth, dry weights of plants, and VAM colonization. Strezelczyk et al. (1985) found that certain actinomycetes produced cytokinin-like substances that stimulated EM formation. Other researchers reported stimulation of EM formation by extracellular products of *Trichoderma*, *Azotobacter*, and fluorescent pseudomonads, whereas failures to form ectomycorrhizae were attributed to gliotoxin production by penicillia (in Strezelczyk et al., 1985).

Current knowledge of hormonal effects by mycorrhizae on plants can be summarized as follows (paraphrased from Read, 1987): Hormones are produced by VAM and EM fungi and hormonal changes occur in plants colonized by mycorrhizae. As yet, though, no unequivocal evidence shows that fungal hormones exert a direct effect in the plant.

3.6 Soil Aggregation

Tisdall and Oades (1982) found mycorrhizal hyphae to be important in the formation of water-stable soil aggregates, improving soil water-holding capacity by producing large (20–200 mm diameter) aggregates with large pore spaces. Such aggregates hold sufficient water to prevent moisture deficits around plant roots during dry periods but allow sufficient drainage to prevent waterlogging during wet periods (Miller, 1987). Increased aggregation of sand-dune soil and organic fractions occurred when external VAM hyphae were present (Sutton and Sheppard, 1976).

Soils high in clay and highly compacted soils can reduce by 80% EM hyphal growth into soil (Skinner and Bowen, 1974). Use of heavy machinery, continuous foot traffic, and high erosion rates can increase soil compaction and reduce the ability of mycorrhizal fungi to colonize plants. Alternatively, plowing of compacted soils ought to increase the ability of mycorrhizae to grow through the soil and improve plant nutrition.

3.7 Plant Competition, Community Structure, and Succession

Mycorrhizal hyphae encounter roots of the same and other plants and can colonize them, producing connections within, and between, plant root systems (Finlay and Read, 1986; Francis and Read, 1984; Read, 1987). Carbon and P can be transferred between plants via shared mycorrhizal hyphae (Chiariello et al., 1982; Heap and Newman, 1980; Whittingham and Read, 1982), and nutrients can be exchanged between two plants (Newman, 1985; Stribley,

1987). However, indirect transfer, in which root exudate from the labeled plant is taken up by external mycorrhizal hyphae from a second plant, has not been ruled out completely.

Mycorrhizal fungal connections and movement of nutrients between plants may play an important role in determining plant distribution and successional patterns. Since significant amounts of nutrients can be moved from a donor to a recipient, young seedlings connected to an existing root network by mycorrhizal fungi could be supplied with carbohydrates, P, N, micronutrients, and perhaps water, thereby improving its chance of establishment (Finlay and Read, 1986; Stribley, 1987). Plants limited in C, by shading for example, act as sinks, increasing C transfer to the C-limited plant (Read, 1987).

Janos (1985, 1987) and Reeves (1985) proposed a continuum in the dependence of plants on mycorrhizal fungi. Plant competition is influenced by the degree to which host plants depend on mycorrhizae (Allen and Allen, 1986; Janos, 1987). Mycorrhizal interactions influence the composition of plant communities by (1) the presence of fungal species that enables plants to grow on low-fertility sites, and (2) by the relative cost of the mycorrhizal symbiont to obligate versus facultative mycotrophs. Nonmycorrhizal plants never or rarely become infected because they (1) reject colonization, (2) produce substances that inhibit mycorrhizal formation, or (3) lack infective sites on their roots. To overcome P deficiency in soil, nonmycorrhizal species utilize a variety of strategies. Fine, highly branched root systems and root hairs search out P in low-P soil (Miller, 1987), much as mycorrhizal hyphae explore and utilize nutrients in the soil volume around roots. Nonmycorrhizal plants may secrete organic acid from their roots to solubilize occluded P, may increase root phosphatase production, may tolerate low mineral P levels, or may have slow growth rates in order to overcome low-P soil conditions. Facultative mycobionts (i.e., plant hosts) are colonized only when nutrient levels are low (Janos, 1987; Reeves, 1985). When growing in soil with adequate soil P, but not colonized by mycorrhizae, facultative plants produce the same dry mass as when growing in soil deficient in P, but are colonized. Obligate mycotrophs are mineral-limited and must have mycorrhizae to obtain P or other essential nutrients.

Janos hypothesized that more photosynthate is needed to maintain facultative mycorrhizae than obligate symbionts, and therefore the cost of mycorrhizal colonization is lower for obligate than for facultative mycotrophs. Thus, the less mycorrhizal dependent of two competing plant species will grow more slowly. As an example, plants with greater colonization were poorer competitors when two competing grass species were grown together (Allen and Allen, 1986). The poorer competitor sustained greater colonization when grown with an obligate mycorrhizal species than when grown with the mycorrhizal fungus alone. Seemingly, obligate species increase their competitive ability by "encouraging" colonization of the less dependent plants. If the less dependent plant could reject colonization, removing the cost of the symbiont, it would be a better competitor. In the case where mycorrhizal

dependence is similar between two species, sharing the mycorrhizal fungus between the two plants encourages coexistence (Janos, 1985).

The physiology of crop plants is different from many noncultivated plants (Chapin, 1980), and mycorrhizal interactions with cultivated plants could be noticeably different from interaction with noncrop plants. Miller (1987) pointed out that cultivated crops are bred to grow as rapidly as possible, directing most energy into fruit production. When nutrients are increased, crop plants grow faster. If nutrients are limited, the plant continues to grow but shows symptoms of nutrient deficiency. Plants adapted to poor soils do not exhibit these deficiencies. In nutrient-limiting situations, their growth rate is reduced. As nutrients increase, tissue concentrations of nutrients increase rather than growth rate. If nutrients are increased beyond the plant's ability to detoxify, symptoms of toxicity will result. Thus, work performed on mycorrhizal plants may not be completely applicable to all plants growing in natural ecosystems, especially those exhibiting different nutrient response strategies.

4 SUMMARY AND CONCLUSIONS

Many interactions occur between mycorrhizal fungi and rhizosphere organisms. Linderman (1988) suggested that mycorrhizal plant responses involve the entire mycorrhizosphere, not just the fungus alone. "Companion" fungi or bacteria, present in the mycorrhizosphere, promote plant growth through a variety of mechanisms. The microbial community may stimulate the development of EM hyphae and rhizomorphs or decrease the growth of pathogens (Linderman, 1988; Sutton and Sheppard, 1976). However, observations about some interactions are conflicting. For example, some observers have found that after mycorrhizal colonization, certain groups of bacteria were increased, whereas others showed that numbers of these same bacteria decreased. The explanation may be that interactions vary with plant and fungal species, with microbial and grazer populations in the mycorrhizosphere, with abiotic conditions, and with sampling time after inoculation or colonization. These factors need to be held constant when investigating the effects of mycorrhizal colonization.

Food web interactions can be indirect, and correlations between increasing mycorrhizal colonization and decreased plant growth do not necessarily mean that colonization is detrimental to plant health. For example, decreased *Glomus marcrocarpum* colonization and spore counts correlated with decreased tobacco stunt disease (Jones and Hendrix, 1987; Modjo et al., 1987), but alternative explanations are possible. Reduction in mycorrhizal fungi by benomyl application may force microarthropod grazers that normally feed on mycorrhizal fungi to switch and feed on pathogenic fungi, and as a result, increased plant growth might be observed after reduction in VAM colonization. Alternatively, as mycorrhizal colonization changes, root exudation is changed, and this may select for beneficial or plant pathogenic organisms. In

this particular instance, mycorrhizal colonization may have selected for pathogenic organisms.

Paul et al. (1985) suggested that mycorrhizal plants should be compared to plants fertilized to the same nutrient levels. Fertilization of nonmycorrhizal plants might be inadequate if the plant can only utilize ammonium and N is applied as ammonium nitrate. The improved growth of mycorrhizal plants would be incorrectly attributed to the mycorrhizae (F. B. Reeves, Department of Botany, Colorado State University; personal communication). A more realistic basis of assuring equal access to nutrients would be to measure the nutrient-absorbing surfaces of both plants (i.e., measure root, or root and hyphal, surface areas).

Several conclusions can be made about mycorrhizal interactions:

1. Plant health often improves, and beneficial rhizosphere populations are selected, following mycorrhizal colonization. These interactions increase the ability of the plant to withstand disease and change plant palatability to various herbivores, including microarthropods, insects, and nematodes. Alternatively, mycorrhizae can reduce plant growth, even apparently causing tobacco stunt disease in the case of *Glomus macrocarpum*. Janos (1985, 1987) has suggested a continuum of plant dependence on mycorrhizae which gives a framework for categorizing positive to negative interactions.
2. Fungal-feeding protozoa, nematodes, and arthropods can reduce both VAM and EM colonization and external hyphae, reducing nutrient concentrations in the plant. Studies have not investigated whether low densities of grazers stimulate mycorrhizal colonization, as suggested by the optimum grazing hypothesis.
3. Mycorrhizae protect plants from some pathogens, although the mechanisms of protection are not clear.
4. Mycorrhizosphere associates, or mycorrhizal fungi themselves, produce plant-growth-promoting substances. The relationship between production of these compounds and their influence on plant growth has not been established.
5. Plant-parasitic nematodes compete with mycorrhizal fungi for root exudates in the initial stages of colonization. After colonization of roots, plant parasites and mycorrhizae are mutually inhibitory.

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