
Mechanisms of Arbuscular Mycorrhizal Mediation of Plant–Plant Interactions

James D. Bever and Peggy A. Schultz

Department of Biology, Indiana University, Bloomington, Indiana, USA

22.1 INTRODUCTION

Ecologists have historically focused on interspecific competition as the major factor determining plant–plant interactions. While there is abundant evidence that interspecific competition between plants can be strong and important, competition alone does not provide a complete framework for understanding plant community structure (Tilman and Pacala, 1993). Over recent years, a series of studies has suggested that plant–plant interactions could be mediated by interactions with other organisms, including interactions with herbivores (Holt and Lawton, 1994) and pathogens (Van der Putten et al., 1993; Bever, 1994). Many authors have also suggested that plant–plant interactions could be influenced by their interactions with mycorrhizal fungi (see references within this chapter). Mechanisms through which interactions with mycorrhizal fungi could alter plant–plant interactions are the focus of this chapter.

Early work exploring the potential of mycorrhizal fungi to alter plant–plant interactions focused on the possibility that shared mycorrhizal networks could provide conduits for sharing of resources, thereby reducing or altering interspecific interactions (Francis and Read, 1984; Grime et al., 1987). To date, shared networks remain a frequently discussed hypothesis for understanding mycorrhizal mechanisms for the mediation of interactions among plants (see recent reviews by Robinson and Fitter, 1999; Simard et al., 2002). Alternative hypotheses for mycorrhizal mediation of plant interactions have also been suggested, including indirect effects through changes in mycorrhizal fungal density (Janos, 1980) or community composition (Bever, 1999, 2002b), and the possibility that

mycorrhizal fungi facilitate niche differentiation and thereby decrease interspecific competition (Bever et al., 2001; Van der Heijden, 2002; Reynolds et al., 2003).

In this chapter, we review and develop mechanisms for mycorrhizal mediation of plant–plant interactions. In particular, we identify two fundamentally different ways that arbuscular mycorrhizal (AM) fungi can alter plant–plant interactions: (1) through modifying interspecific competition (e.g., resource sharing and mediation of niche differentiation) and (2) through indirect effects mediated by changes in the AM fungal community. As the framework for indirect effects builds on a population ecology perspective of the plant–AM fungal interaction, we first develop this perspective by identifying the separate forces that influence plant and AM fungal population growth rates, and then explore the co-dependence of these factors in a discussion of the range of interactions in individual plant–fungal pairs. We then combine these pairwise modules to infer types of indirect interactions between plant species as mediated through changes in mycorrhizal fungal population densities or community composition.

22.2 BASIC POPULATION ECOLOGY OF THE INTERACTION OF PLANTS AND AM FUNGI

Most plants interact with arbuscular mycorrhizal fungi. This interaction is classically described as mutually beneficial. Plants can benefit from the association through improved uptake of soil nutrients, particularly relatively immobile nutrients such as phosphorus. AM fungi may also improve drought tolerance and resistance to soil pathogens. The fungus, in turn, appears to be solely dependent on the plant for energy. Consequently, the plant–AM fungal interaction is a textbook example of a nutritional mutualism. However, the interaction between plants and AM fungi can range from the fungus parasitizing the plant to the plant parasitizing the fungus. We begin our consideration of these possibilities by first discussing the separate influences on plant and AM fungal population growth rates.

22.2.1 Variation in Plant Response to Mycorrhizal Fungi

Plants are known to vary in their response to mycorrhizal fungi. While some plants and plant families do not associate with mycorrhizal fungi, most associate and depend on arbuscular mycorrhizal fungi, and still others associate and depend on other types of mycorrhizal fungi (e.g., ecto- or ericoid mycorrhizal fungi). There is also variation among plants that interact mutualistically with mycorrhizal fungi. In describing this variation, Janos (1988) has identified a useful distinction between responsiveness of a plant to mycorrhizal fungi (i.e., the net increase in growth with inoculation) and the dependence of a plant (i.e., how much phosphorus fertilizer would have to be added to allow an uncolonized plant to grow similarly to the same plant genotype grown with mycorrhizal fungi). While these two aspects of plant response are likely correlated in that they reflect overall benefit from the association, they are not exactly collinear. Responsiveness of a plant is also a function of many other aspects of plant life history, such as plant growth rate. For example, slow-growing plants may be very dependent on mycorrhizal fungi in that they might have little growth without inoculation. Yet, their growth response may be less than that of a fast-growing plant that is not as dependent on the fungus for its phosphorus acquisition, but able to rapidly translate the incremental increase in phosphorus availability into growth. This is an essential difficulty in measures of plant response and of experiments testing the role of mycorrhizal fungi in mediating plant–plant interactions, particularly when comparing plants of different life histories (e.g., comparison of fast-growing early successional species and slow-growing late successional species). In much

of the current chapter, we will be discussing plant response in the context of the effect of the mycorrhizal fungi on the growth rates of plant populations. In most experimental work, the population consequences are inferred from measures of relative growth rates of individual plants (i.e., measures of responsiveness *sensu* Janos). This is likely a valid approach if plants have similar life histories.

The association between plants and AM fungi is often noted for having low specificity because a given fungus is likely to be able to associate with a broad range of hosts. However, plant response can depend on the species of mycorrhizal fungi with which they are associated. While some fungi are generally more efficient at growth promotion than others, plant growth promotion also depends on the particular pairing of plant and fungus. It has been shown repeatedly that the fungal species that delivers the most benefit to one host may not be the most effective fungus for a second host (Adjoud et al., 1996; Van der Heijden et al., 1998b; Bever, 2002b; Helgason et al., 2002). Therefore, plants can have high specificity of response to AM fungi while having low specificity of association with AM fungi (Bever, 1999; Bever et al., 2002).

Plant response to mycorrhizal fungi also depends critically on the environment. As expected for a nutritional mutualism, plants benefit the most when the nutrient that is being provided is in short supply. As a result, when phosphorus is abundant relative to other plant resources, many plants do not show positive responses to mycorrhizal fungi, and plants may be negatively affected by fungal colonization (i.e., the fungi are parasitic). The environmental dependence of the interaction is interesting, but this will not be the focus of this paper. Rather, for much of the discussion, the abiotic environment is assumed to be constant as we focus on the population consequences of the plant-AM fungal interaction.

22.2.2 Variation in Fungal Response to Plants

All AM fungi are dependent on plants for their growth, with different plant species varying in their overall quality as hosts. In general, there is likely to be a correlation between the overall responsiveness of a plant to AM fungi and their quality as host plants. We found support for such a correlation in comparisons of plant species in an old field, where *Allium vineale* was the most overall responsive plant to AM fungi and was the best host, while *Anthoxanthum odoratum* was generally nonresponsive and was the worst host for AM fungi (Bever, 2002a). We also found that ecotypes of big bluestem from Kansas were more responsive to AM fungi, and also better hosts for AM fungi, than ecotypes from Illinois (Schultz et al., 2001). However, this association of responsiveness and quality of host does not always hold, as illustrated by the observation that mycoheterotrophic plants, plants that derive carbon from the fungus (Leake, 1994), respond positively to mycorrhizal fungi but likely have negative effects on fungal growth rates.

The population growth rates of AM fungi also depend on particular combinations of plants and fungi (again a specificity of response). Evidence for this comes from measures of sporulation on different host plants (Sanders and Fitter, 1992; Bever et al., 1996; Eom et al., 2000). While the importance of spores in fungal life histories may vary among species, host-specific differences in sporulation have been found to represent host-specific differences in fungal population growth rates (Bever, 2002a, 2002b). We observed, for example, that *Scutellospora calospora* had the highest rate of population growth in association with *Plantago lanceolata*, while *Archeospora trappei* had the highest rate of population growth with a second plant species, *Panicum sphaerocarpon*. This observation of specificity of fungal response to plants could reflect preferential association between plant and fungi, as observed by Helgason et al. (2002). Alternatively, the association could be nonspecific and differences in fungal population growth rates could result from differences in benefit the fungus derives per active infection. In the former case, the effect could

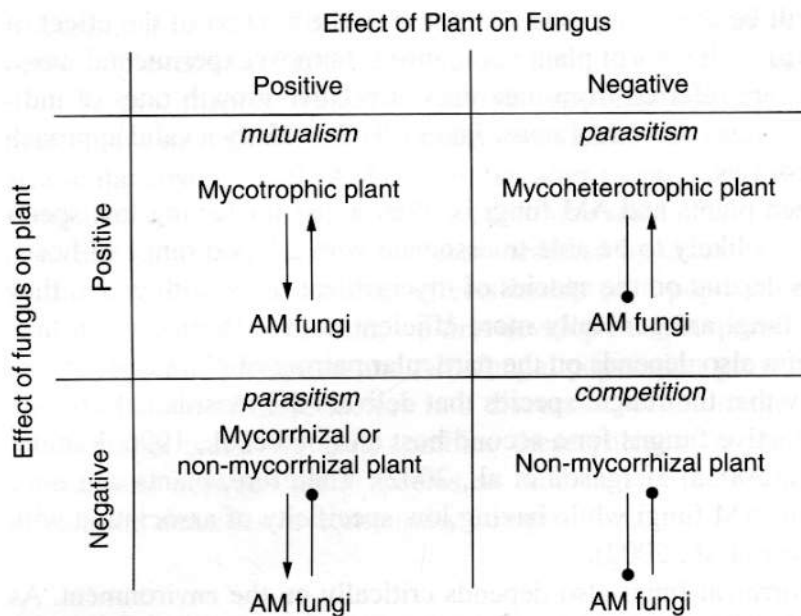


Figure 22.1 Varieties of interactions between plants and AM fungi. The interactions between plants and AM fungi range from mutually beneficial to different forms of antagonism. Under some environmental conditions, facultative mycotrophic plants are negatively affected by AM fungi. Alternatively, mycoheterotrophic plants specialize in parasitizing AM fungi. The interaction between nonmycotrophic and nonmycorrhizal plants and AM fungi could range from pathogenic to potentially competitive.

be mediated by competition between the fungi for infection sites, while in the latter case the effect could be mediated by allocation patterns of the host. Both competition and preferential plant allocation could generate context dependence in the specificity of fungal response to plants, in that the relative growth rates of particular fungi would depend on what other fungi are in the root system. We found evidence of such context dependence when the removal of the dominant fungus, *Acaulospora colossica*, from the root system of *Allium vineale* apparently permitted *Scutellospora calospora*, a previously subordinate fungus, to thrive (Bever, 2002a).

Growth rates of AM fungal populations also depend on the environment. The environmental dependence of AM fungal population growth rates can be due to direct effects of the physical environment on the fungus (e.g., heavy metal toxicity). Alternatively, the environmental influence could be mediated through changes in the physiology of the host plant (e.g., in the case of elevated atmospheric CO₂). Fertilization by phosphorus could cause both direct and indirect effects on fungal population growth rates.

22.2.3 Pairwise Interactions between Plants and AM Fungi

While determinants of population growth of plants and AM fungi need to be considered independently, the discussion above also identifies that plant and AM fungal population growth rates are interdependent, because they are linked by dependencies on each other's densities. These interdependencies can result in a full range of ecological interactions. We briefly consider each of four possible dynamic modules as presented in Figure 22.1.

22.2.3.1 Plant-AM Fungal Mutualism

Many, perhaps most, plant species interact mutualistically with mycorrhizal fungi; i.e., both plant and fungal populations have higher growth rates in the presence of each other.

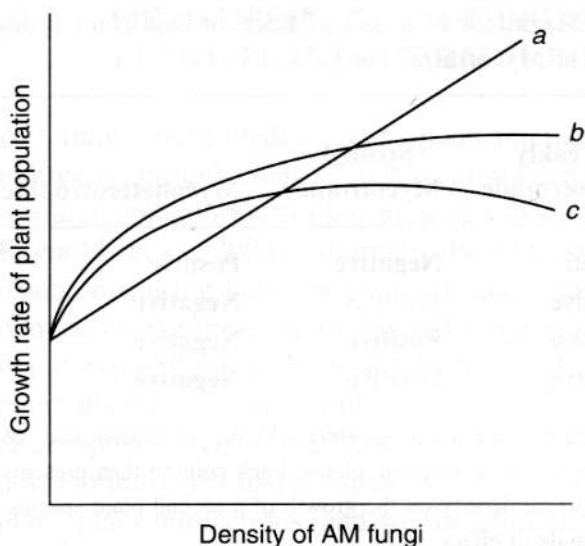


Figure 22.2 Dependence of plant population growth rates on AM fungal density. The dependence of population growth rate on the density of AM fungi could range from linear (line a) to saturating (line b) to having an intermediate maximum (line c).

The benefit that plants receive from the fungus is density dependent, with plants deriving more benefit from the presence of AM fungi at low plant densities than at high plant densities (Koide and Dickie, 2002). Theoretical studies have shown that such density dependence in delivery of benefit can stabilize the dynamics of mutualists (Dean, 1983). It is also likely that the benefit that plants receive from AM fungi depends nonlinearly on the density of AM fungi (Gange and Ayres, 1999). By AM fungal density, we mean measures of AM fungal density in the environment rather than in particular root systems, though colonization in roots is certainly a major component of overall fungal density. While volumes of experimental work have established plant growth promotion due to the presence of AM fungi, less work has investigated the incremental change in plant growth with incremental increases in density of AM fungi. The benefit that plants receive from AM fungi likely saturates at higher AM fungal densities, and it may decrease as the density of AM fungi gets too high (Gange and Ayres, 1999). We represent three potential forms of this relationship in Figure 22.2. This relationship between plant growth and AM fungal density can be a critical issue in consideration of AM fungal mediation of plant–plant interactions through changes of AM fungal density, as discussed below. To date, no one has fit general models of population growth incorporating such density dependencies to the dynamics of particular plant–AM fungal mutualisms.

22.2.3.2 *AM Fungal Parasitism of Plants*

AM fungi can have negative impacts on mycorrhizal plants, particularly in conditions of high nutrient availability (Johnson et al., 1997; Smith and Read, 1997). While population growth rates of AM fungi may decline with increasing soil resource levels, AM fungi still benefit from association with plants under these conditions. Therefore, the interaction is characterized by fungal parasitism of the plant (Table 22.1). AM fungi can also have negative effects on the growth of weakly mycorrhizal and nonmycorrhizal plants under a broader range of environments. These interactions could also fall into parasitism if the fungi derive some benefit from the plants (see competition discussion below). In parasitic situations, the negative impact of AM fungi likely increases with increasing fungal density, but this has not been tested to our knowledge.

Table 22.1 Expected Direction and Relative Magnitude of Indirect Effects of One Plant Type on a Second Plant through Changes in Density of Mycorrhizal Fungi

	Non-Mycorrhizal	Weakly Mycotrophic	Strongly Mycotrophic	Mycoheterotrophic
Non-Mycorrhizal	Positive	Negative	Negative	Positive
Weakly Mycotrophic	Negative	Positive	Positive	Negative
Strongly Mycotrophic	Negative	Positive	Positive	Negative
Mycoheterotrophic	Negative	Positive	Positive	Negative

Note: The presence of mycotrophic plants can increase fungal density, while AM fungal density may be decreased due to the presence of nonmycorrhizal and mycoheterotrophic plants. Each column then presents the expected consequences of these changes in AM fungal density on the growth of a second plant species. The bold words indicate greater than expected magnitude of effect.

22.2.3.3 Plant Parasitism of AM Fungi

A specialized group of plants, called mycoheterotrophs, have evolved the ability to derive energy from fungi. These plants can be completely achlorophytic or partially so and have been found to be associated with a range of fungi, including ectomycorrhizal fungi and AM fungi (Leake, 1994; Bidartondo et al., 2002). The growth rates of AM fungi would presumably decrease with increasing density of these plants, and the growth rates of the plants would be expected to increase with increasing densities of AM fungi (Table 22.1), though these effects remain to be demonstrated. The expected pairwise dynamic would be one similar to other antagonistic interactions in which there is negative feedback between abundance of mycoheterotrophs and abundance of AM fungi.

22.2.3.4 Competition between Plants and Mycorrhizal Fungi

Interactions in which both populations have reduced growth rates in the presence of the other are classified as competitive. Competitive interactions can result from depletion of a common resource. Because plants are autotrophs, they are not likely to compete with fungi for carbohydrates (though the existence of mycoheterotrophs causes one to pause). Plant roots and mycorrhizal fungi are likely to compete for access to soil minerals. The competition for mineral resources would cause the net sign of the effect of fungi on plants to depend on the environment. Mineral resource competition, however, is unlikely to cause the sign of the net effect of plants on fungi to become negative because mycorrhizal fungi are still dependent on plants for their carbohydrates. Therefore, resource competition between plants and AM fungi is unlikely to generate a mutually antagonistic interaction. Such mutually antagonistic interactions may result, however, from interference competition, particularly in the interaction between mycorrhizal fungi and some nonmycorrhizal plant species. Plants in the Brassicaceae, which are typically nonmycorrhizal, have been shown to have negative responses to mycorrhizal fungi, and these plants have also been shown to produce allelochemicals that inhibit mycorrhizal fungal hyphal extension and spore germination (Allen et al., 1989; Johnson, 1998; Roberts and Anderson, 2001). As a result, this interaction may fit the classic definition of competition. It remains to be demonstrated that the density of mycorrhizal fungi declines more quickly in the presence of these antagonistic hosts than in the absence of any host plant.

22.3 MECHANISMS OF AM FUNGAL MEDIATION OF PLANT–PLANT INTERACTIONS

AM fungi could mediate plant–plant interactions by modifying resource competition or indirectly through changes in AM fungal density or composition. AM fungi would modify resource competition if their presence modifies the plant's niche (Van der Heijden, 2002; Reynolds et al., 2003). Alternatively, AM fungi could modify competition by facilitating resource sharing between plants (Francis and Read, 1984; Grime et al., 1987). In these two views, the presence of the AM fungi is required, but the modification of competition is not explicitly a function of AM fungal density. Separate from modifying competition, plant–plant interactions could be indirectly affected through changes in AM fungal density or composition (Bever, 2002b; Bever et al., 2002). While these potential mechanisms are not mutually exclusive, they develop different views of mycorrhizal mediation of plant–plant interactions, and we therefore discuss them separately.

22.3.1 Modification of Resource Competition by AM Fungi

Mycorrhizal fungi could modify competitive interactions among plant species by influencing the realization of a plant's abiotic niche. Given the role of mycorrhizal fungi in resource acquisition, it is likely that the presence of mycorrhizal fungi could alter plant nutritional niches (Van der Heijden, 2002; Reynolds et al., 2003). It is also possible that particular fungi can be important for expression of other niche dimensions, including seasonality (Bever et al., 2001). To alter competitive interactions, mycorrhizal fungi would have to differentially affect the niche of competing species. Van der Heijden (2002) identified that the presence of mycorrhizal fungi could alter the resource niche of mycorrhizal plants relative to nonmycorrhizal plants. He imagined a scenario in which the presence of mycorrhizal fungi shifts the resource uptake of mycorrhizal plants in a manner that could lead to dominance of the mycorrhizal plants or to their coexistence with nonmycorrhizal plants.

Mycorrhizal fungi could also differentially shift niches of mycotrophic plant species. In particular, it is possible that different fungal species are necessary for partitioning of belowground resources. AM fungal species have been shown to forage for resources differently (Smith et al., 2000), and different fungal species may provide differential access to soil nutrients. For example, some may be better at foraging for organic phosphorus, while others are better at foraging for mineral phosphorus. In this case, the presence of particular fungi may be required for plant species to occupy different soil nutritional niches (Reynolds et al., 2003). As a result, the interspecific competitive interactions could be modified by AM fungal community composition, with plant species coexistence dependent upon individual plants having their appropriate mycorrhizal fungal symbionts. At present there is little evidence for this scenario, though the observation that overall resource use increased with increasing diversity of AM fungi (Van der Heijden et al., 1998b) is consistent with this mechanism.

Plants can also partition resources across seasons (Fowler and Antonovics, 1981), and it is possible that different species of AM fungi are necessary for the success of cool-season plants vs. the warm-season guild. Indeed, AM fungal species have also been found to differ in their seasonality (Merryweather and Fitter, 1998; Pringle and Bever, 2002). Moreover, within one community, the fungus with the most markedly cool-season phenology grew best with, and was spatially associated with, the plant that shared a markedly cool-season phenology (Bever et al., 1996; Schultz, 1996; Pringle and Bever, 2002).

22.3.2 Carbon Transfer in Common Mycorrhizal Networks

Because of low specificity of association, shared AM fungi could alter plant–plant interactions by providing conduits for sharing resources, such as carbon (Francis and Read, 1984; Grime et al., 1987). This hypothesis has been supported by the observation that labeled carbon fixed by one plant has subsequently been found in greater abundance in a second plant with which it shares mycorrhizal fungi than plants that do not share mycorrhizal fungi. To date, studies of carbon transfer suggest that it is more substantial and common in ectomycorrhizal fungi (Robinson and Fitter, 1999; Simard et al., 2002), but there is also a recent report of transfer to the leaves through AM fungi (Lerat et al., 2002).

It is possible that the carbon transfer between plants via mycorrhizal networks could alter plant–plant interactions. One hypothesis for predicting the direction of these effects is the *source–sink hypothesis*. This hypothesis builds on the physical process of resource flow from plant physiology and views mycorrhizal hyphae as passive conduits (Robinson and Fitter, 1999). Under this hypothesis, carbon is expected to flow from the strongest source to the strongest sink, thereby potentially alleviating interspecific competition through facilitation of the weakest competitor. This prediction was supported by a mesocosm study in which inoculation with mycorrhizal fungi in a mixed community of plants greatly decreased the dominance of the best competitor (Grime et al., 1987).

Several studies specifically designed to test the source–sink hypothesis have given little support for its predictions. For example, while the source–sink hypothesis predicts that the smaller plant will be the net recipient of nutrient transfer, Kytöviita et al. (2003) found that seedlings of four subarctic meadow plant species connected by a common mycorrhizal network to a larger plant were significantly smaller than mycorrhizal seedlings unconnected to a larger plant. This suggests that the common mycorrhizal network facilitated the competitive superiority of the larger plant, thus contradicting the source–sink hypothesis. In separate studies, shading of plants, which would be predicted to increase sink strength, actually decreased transfer of labeled carbon (Hirrel and Gerdemann, 1979). Similarly, clipped plants, which were predicted to be sinks, actually acted as sources of carbon (Waters and Borowicz, 1994).

There is no disputing that there is a net movement of carbon between photosynthetic plants and mycoheterotrophs via mycorrhizal hyphae. Nevertheless, the ecological importance of carbon transfer among photosynthetic plants remains in doubt (Robinson and Fitter, 1999). In the work on the plant–AM fungal interaction in particular, the amount of carbon transferred was very small (Robinson and Fitter, 1999). Even in the ectomycorrhizal system, it remains to be demonstrated that a photosynthetic recipient of carbon receives more carbon from the fungus than it gives that fungus. This is a critical point, as an alternative explanation is that the carbon movement from fungus to plant is incidental to symbiosis establishment or transfer of soil minerals (Smith and Read, 1997). Organic signaling molecules may be transferred from fungus to plant as part of the initiation of the symbiosis, or soil minerals may be transferred to the plant in organic form. In either case, some carbon would move from fungus to plant even while that plant rewards the fungus with a greater amount of energy. As a result, labeled carbon from one plant would show up in a second plant as a consequence of fungal growth from the root of one plant to the root of another (Fitter et al., 1998). In this view, carbon exchange between plants may not reflect a meaningful energetic subsidy of the second plant. It does reflect interactions with the same AM fungi, which can have consequences on plant–plant interactions mediated by changes in fungal density, a perspective developed below. It is interesting to speculate that mycoheterotrophic plants could have evolved by capitalizing on such normal transfers of carbon between mycorrhizal fungi and their hosts.

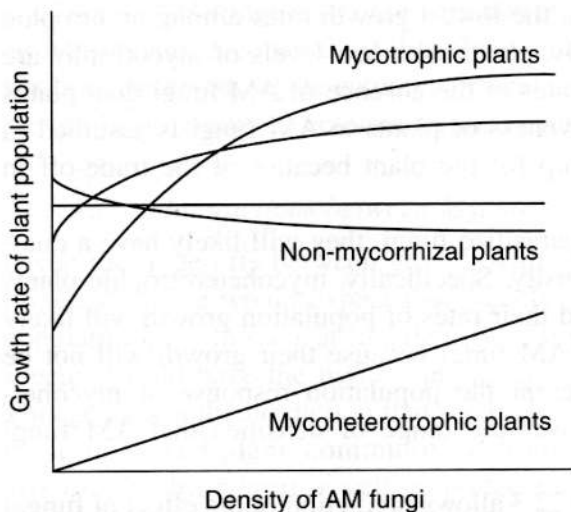


Figure 22.3 The expected relationships between plant population growth rates and density of AM fungi for different types of plants assuming a saturating response and a trade-off in the ability to grow with AM fungi and the ability to grow without AM fungi. The population growth rate of the mycoheterotrophic plant is assumed to increase approximately linearly over the range of densities of AM fungi commonly observed.

22.3.3 Indirect Effects between Plants Mediated by Changes in AM Fungal Density

Interactions between plants may be mediated by changes in the density of shared AM fungi (Figure 22.3). That is, the presence of a given plant type can cause changes in the density of AM fungi, which can then alter the growth of that plant type compared with a competing plant species. Such indirect effects are likely given the low specificity of association where plants will often be interacting with the same fungal population, both positively and negatively. Indeed, the level of infection of plants in the field has been shown to depend on the identity of their neighbor (Jastrow and Miller, 1993). The dynamics resulting from such feedback through changes in fungal density have been explored previously using a general model (Bever et al., 1997; Bever, 2003). Here, we develop specific expectations for interactions between four types of plants identified in Table 22.1. We do this by building up from the modules of pairwise interactions (Table 22.1) in a way that has proven successful in understanding antagonistic interactions (Holt and Lawton, 1994).

The role of AM fungal density in mediating plant-plant interactions depends on the relationship between plant population growth rates and density of AM fungi (Figure 22.2). In light of these relationships, we build on an assumption of a trade-off in growth with and without AM fungi; i.e., plants that grow best with AM fungi grow worst without AM fungi. The existence of this trade-off is well supported, both by empirical observations of plant growth rates (Fitter, 1977; Allen and Allen, 1984) and by the mechanistic observation that plants that are not responsive to AM fungi generally invest greater resources in fine roots and root hairs that allow them to directly acquire soil resources (St. John, 1980; Hetrick et al., 1992; Schultz et al., 2001). Conversely, plants that are more responsive to AM fungi generally have coarser roots and therefore perform poorly in the absence of AM fungi.

The trade-off in plant growth with and without AM fungi translates into different intercepts and maxima in the response of plant population growth rates to AM fungal density, as illustrated for a saturating relationship between plant growth and AM fungal density (Figure 22.3). Nonmycorrhizal plants are assumed to have the highest population

growth rates in the absence of AM fungi, but the lowest growth rates among autotrophic plants in the presence of AM fungi. Similarly, plants with low levels of mycotrophy are expected to have higher population growth rates in the absence of AM fungi than plants with high mycotrophy. That is, the responsiveness of plants to AM fungi is assumed to correlate with the obligacy of the relationship for the plant because of the trade-off in nutrient acquisition.

As mycoheterotrophic plants directly parasitize fungi, they will likely have a qualitatively different response to AM fungal density. Specifically, mycoheterotrophic plants cannot grow in the absence of AM fungi, and their rates of population growth will likely not saturate until a much higher density of AM fungi because their growth will not be limited by light or soil minerals. We represent the population response of mycoheterotrophic plants as approximately linear over the range of densities that AM fungi typically vary (Figure 22.3).

Examination of Figure 22.1 and Figure 22.3 allows prediction of the effect of fungal population dynamics in mediating plant–plant interactions. We address these issues by considering pairwise plant–plant interactions. Specifically, we consider the effect that each plant type has on the density of AM fungi, and then consider whether this change in fungal density will have positive or negative effects on a second plant species (Figure 22.3). The direction and an estimate of the relative strengths of these effects are tabulated in Table 22.1. We infer the long-term dynamics by contrasting the effect of each category of plant on plants in the same category with the effect on plants in other categories as derived in Bever et al. (1997).

22.3.3.1 *Interactions with Nonmycorrhizal Plants*

The category of nonmycorrhizal plants likely includes species that interact antagonistically with AM fungi and those that have no effect on AM fungi. For nonmycorrhizal species that inhibit the growth of AM fungi, we would expect the decreased density of AM fungi to have indirect positive effects on the growth of other nonmycorrhizal plants. To the extent that nonmycorrhizal plants reduce the density of AM fungi, such plants would also have indirect negative effects on the growth of mycotrophic plants. This indirect inhibition would be small for plants with low mycotrophy, but could be substantial for plants with high levels of mycotrophy (Figure 22.3). This indirect effect could generate a positive feedback dynamic that could reinforce an initial dominance of nonmycorrhizal species and inhibit the establishment of highly mycotrophic species. Alternatively, once mycotrophic plants are established, the density of AM fungi may increase, thereby inhibiting the growth of nonmycorrhizal plant species. These expectations are supported by empirical work in which nonmycorrhizal plants are competitively superior to mycotrophic plants in the absence of mycorrhizal inoculum, but competitively inferior in the presence of mycorrhizal inoculum (Allen and Allen, 1984). Also, positive feedback was observed between nonmycorrhizal introduced plant species and mycotrophic native species by Klironomos (2002), which may have been mediated by changes in AM fungal density.

22.3.3.2 *Interactions between Ecto- and Arbuscular Mycorrhizal Plants*

A similar positive feedback dynamic might be expected between plants that are dependent on AM fungi and plants dependent on ectomycorrhizal fungi. Dominance by ectomycorrhizal plants could reduce the density of AM fungi, thereby reducing the success of plants that are dependent on AM fungi. An experimental test of this possibility found no reduction in AM fungal inoculum density under an ectomycorrhizal canopy (Lovelock and Miller,

2002). The AM fungi under the oak, however, was less effective at promoting growth of an AM mycotrophic seedling (Lovelock and Miller, 2002). The flip side of this dynamic has been observed, where ectomycorrhizal seedlings enjoy inoculum potential and greater growth in proximity to ectomycorrhizal canopy trees (Dickie et al., 2002).

22.3.3.3 *Interactions between Mycotrophic Plants*

Given the trade-offs between growth with and without mycorrhizal fungi represented in Figure 22.3, we would expect that weakly mycotrophic species would have the highest population growth rates at low density of mycorrhizal fungi, while strongly mycotrophic species would have the highest population growth rates at high densities of AM fungi. This generates the prediction that the highly mycotrophic plant species would benefit the most in mixed-plant communities from the presence of mycorrhizal fungi. This *mycotrophic hypothesis* is well supported empirically and offers a very credible alternative explanation to attempts to explain the effect of AM fungi on plant–plant interactions through carbon transfer (Bergelson and Crawley, 1988). Several studies have found that the most mycotrophic plant species benefited the most in mixture from mycorrhizal inoculation (Grime et al., 1987; Van der Heijden et al., 1998b; Hartnett and Wilson, 1999).

All mycotrophic plants are expected to serve as capable hosts of AM fungi, with the highly mycotrophic species likely the better hosts (as argued above). As a result, all mycotrophic plants have the potential to increase the density of AM fungi and thereby facilitate each other's growth (Table 22.1). The most mycotrophic plants are expected to benefit the most from this feedback through change in density, potentially making the most mycotrophic plant species the net beneficiaries of AM fungal density dynamics, as has been hypothesized in discussions of the role of mycorrhizal dynamics in succession (Janos, 1980; Reynolds et al., 2003). In a test of feedback through changes in AM fungal community, the density of AM fungi did reach highest densities in association with the most mycotrophic plant species, *Allium vineale*. However, *Allium* did not grow best with its own fungal community as predicted (Bever, 2002a), perhaps because of confounding changes in the composition of the AM fungal community, as discussed below.

22.3.3.4 *Interactions with Mycoheterotrophic Plants*

By supporting growth of AM fungi, mycotrophic plants indirectly facilitate the growth of mycoheterotrophic plants. Conversely, by reducing the population growth rates of AM fungi, mycoheterotrophic plants indirectly inhibit the growth of mycotrophic plant species. This effect may be small; however, if the relationship between mycotrophic plant growth and AM fungal density is best described as a plateaued function (Figure 22.2 and Figure 22.3), then the net interaction is one in which mycoheterotrophic plants indirectly parasitize mycotrophic plants through their effects on densities of AM fungal populations (Leake, 1994). Mycoheterotrophic plants are expected to exert negative density dependence on their own rates of population growth through their negative effects on the density of their AM fungal resource. This negative density dependence could regulate the population size of mycoheterotrophic plants.

To the extent that mycoheterotrophic plants decrease AM fungal population density, they will indirectly facilitate the growth of nonmycorrhizal plant species. The success of mycoheterotrophic plant species could then create ecological opportunities for nonmycorrhizal plant species in areas otherwise dominated by mycotrophic plants. Conversely, to the extent that nonmycorrhizal plant species decrease AM fungal densities, they indirectly inhibit the growth of mycoheterotrophic plant species.

22.3.4 Indirect Effects between Plants Mediated by Changes in AM Fungal Composition

In much of the discussion of the impact of the presence and change in density of mycorrhizal fungi above, the AM fungal community is simplified into a homogeneous population. However, there is accumulating evidence that AM fungal communities are diverse and that individual fungal species are ecologically distinct. For example, we have found 37 species of AM fungi coexisting within a single old field (Bever et al., 2001), and molecular characterization of communities suggest that this level of diversity is not unusual (Helgason et al., 2002; Husband et al., 2002). Because these AM fungal species also differ in ecologically important ways, including their response to environmental gradients, average growth promotion, and specificity of growth promotion, the composition and dynamics of communities of AM fungi can also mediate plant–plant interactions (Fitter, 2000; Bever et al., 2001). In the next section, we develop different ways in which this mediation can happen, focusing exclusively on mycotrophic plant species.

22.3.4.1 *Change in Overall Effectiveness of AM Fungal Community*

Variation in the average effectiveness of growth promotion of the AM fungal community could alter plant–plant interactions in a similar fashion as changes in overall AM fungal density. An increase in the average effectiveness of the AM fungal community would benefit all mycotrophic plant species at the expense of nonmycorrhizal plants, and it would also benefit highly mycotrophic plants more than less mycotrophic plants. If the most mycotrophic species also promotes the growth of the most effective AM fungal isolates, then this could generate a positive feedback, reinforcing the abundance of the most mycotrophic plant species and the most effective AM fungal species.

22.3.4.2 *Host Specificity in AM Fungal Growth Promotion*

The fact that individual species of AM fungi vary in their host specificity of plant growth promotion has several important consequences for plant–plant interactions. At the most basic level, the success of a given plant species may depend on the abundance of a particular fungal species, while the success of a second plant species may depend on the abundance of a second plant species. Evidence for this level of specificity has been found in several systems (Adjoud et al., 1996; Van der Heijden et al., 1998a, 1998b; Bever, 2002b; Helgason et al., 2002). Therefore, the composition of the AM fungal community could alter plant–plant interactions.

In this scenario, the long-term dynamics of the plant community would depend on the dynamics of the AM fungal community. If the composition of the AM fungal community is spatially heterogeneous, then the composition of the AM fungal community would remain an important source of environmental heterogeneity for plants and a potential determinant of plant–plant interactions. Fine-scale spatial heterogeneity in the AM fungal community composition is well documented and is correlated with both plant and environmental parameters (Bever et al., 1996; Schultz, 1996; Helgason et al., 2002; Lovelock et al., 2003). If the distribution of individual species of AM fungi is stochastic or is determined by environmental factors, then AM fungal community composition could alter the outcome of plant–plant interactions, with the spatial variation possibly contributing to the maintenance of diversity in the plant community.

However, if the distribution and abundance of AM fungal species respond to local plant species composition, as noted above and as expected from the evidence that the relative population growth rates of AM fungi are host species specific, then the role of

AM fungi in plant–plant interaction will be determined by feedback through changes in the AM fungal community composition (Bever, 1999; Bever et al., 2002). AM fungal community feedbacks can be positive or negative, and these feedbacks will generate frequency dependence in the outcome of plant–plant interactions.

Positive feedback results from symmetry in fitness relationships in which the fungus that promotes the growth of a given plant is also the fungus that has the highest growth rate on that plant host. As a result, an initially high frequency of one plant type will result in an increase in abundance of its preferred fungus, which thereby increases the plant's growth rate relative to that of other plants (Bever, 1999; Bever et al., 2002). This positive feedback generates positive frequency dependence between plant species, in which the most common plant species inhibits the growth of the less common plant through changes in the AM fungal community. The ultimate outcome of this dynamic is the exclusion of the less common species, at least on a local scale. This dynamic was suggested by the results of Klironomos (2002), though it is also possible that the positive feedbacks observed in this study were mediated by changes in AM fungal density (as discussed above) rather than composition. Other evidence for positive feedback comes from work on frequency dependence between genotypes of *Allium vineale*. Ronsheim (1996) found that *Allium* genotypes grew better when planted near neighbors of the same genotype. The positive frequency dependence could result from AM fungal community dynamics, as supported by the observation of positive soil community feedback between *Allium* genotypes (Bever et al., 1997) and from factorial manipulations of the soil community and neighbors (Ronsheim and Anderson, 2001).

Alternatively, the dynamics between plants and fungi may be characterized by negative feedback. In this case, the presence of one plant can facilitate the growth of a second plant species through changes in the composition of the AM fungal community (Bever, 1999; Bever et al., 2002). This dynamic results from highly asymmetric fitness relations in which the fungus that promotes the growth of a given plant has the highest growth rate on a second plant species. As a result, the AM fungal community dynamic will generate negative frequency dependence in plant–plant interactions and, thereby, will contribute directly to coexistence of competing species. Testing such feedbacks is made difficult by the potentially confounding effects of accumulation of host-specific pathogens (Bever, 2002a; Bever et al., 2002). In a study that eliminated pathogens, we found evidence of negative feedback mediated by changes in the AM fungal community composition between two co-occurring plant species. Specifically, we found that the AM fungus *Scutellospora calospora* accumulated in association with the plant *Plantago lanceolata*. However, *Plantago* grew best with two other species of fungi, *Archaeospora trappei* and *Ac. morrowiae* (Figure 22.2), and these fungi accumulated under *Panicum* (Bever, 2002b). As a result, the presence of *Panicum* caused a change in the composition of the AM fungal community that facilitates growth of *Plantago*. Evidence of a similar dynamic was also found between co-occurring plant species in native grasslands in the eastern U.S. (Castelli and Casper, 2003). How common this dynamic is and what prevents this dynamic from degrading the mycorrhizal mutualism remain to be investigated.

22.4 COMPARING AND CONTRASTING THE MECHANISMS

Mechanisms identified above differ in their long-term predictions for the effect of AM fungi on plant community dynamics. Several mechanisms could facilitate the coexistence of competing plant species, including differential effects on resource utilization, the sharing

of resources, and negative feedback through changes in AM fungal density or composition. Alternatively, positive feedback through changes in the AM fungal density or composition could decrease the likelihood of coexistence of competing plant species. In fact, mycorrhizal fungi have been found to have both positive (Grime et al., 1987; Gange et al., 1990; Van der Heijden et al., 1998b) and negative (Hartnett and Wilson, 1999; O'Connor et al., 2002) effects on plant diversity. Measures of plant diversity have also been found to respond positively to manipulation of the number of AM fungi (Van der Heijden et al., 1998b). This result could be generated by several of the mechanisms through which mycorrhizal fungi may mediate plant–plant interactions, including AM fungal enabling of resource partitioning and negative feedback through changes in AM fungal community composition.

Mechanisms through which AM fungi mediate plant–plant interactions are not mutually exclusive. Rather, we might expect them to act simultaneously. For example, if the presence of AM fungi modifies the interspecific competitive ability of plants through changing the resource utilization of plant species, then it is likely that there are also important effects mediated by changes in mycorrhizal fungal density or composition. The joint effects of interspecific competition and soil community feedbacks have been explored theoretically (Bever, 2003), identifying conditions in which the ultimate dynamics can be determined by either force. In this analysis, the nature of competition was not changing with changing density or composition in the fungal community. Simultaneous effects of AM fungi in modifying resource competition and indirectly affecting plant growth through changes in density have not been investigated. One can imagine that competing best-matching plant and fungal pairs, which would otherwise lead to exclusion, could be stabilized and coexist if the AM fungi contributed to the partitioning of resources between the plant species (Bever et al., 2001).

Data do not currently exist to allow identification of the relative importance of the mechanisms that may mediate plant–plant interactions. The modification of a plant's fundamental niche seems to be a particularly likely mechanism through which AM fungi could modify interspecific competition. A definitive test that this mechanism mediates plant–plant interactions remains to be done. While experimental measures support carbon transfer between plants via mycorrhizal fungi, available data do not suggest that carbon transfer modifies plant–plant interactions. In contrast, there is relatively strong support for the hypothesis of modification of plant–plant interactions through changes in AM fungal density, particularly in successional contexts (Janos, 1980; Medve, 1984; Gange et al., 1990). Negative feedbacks through changes in AM fungal composition have also been demonstrated (Bever, 2002b; Castelli and Casper, 2003), though their relative importance in determining plant–plant interactions remains to be demonstrated. It is our hope that the development and delineation of the potential mechanisms of AM fungal mediation of plant–plant interactions in this chapter will encourage further experimentation that will allow differentiation and substantiation of these processes.

ACKNOWLEDGMENTS

We are grateful to members of our lab for engaging discussions of these issues and particularly to Scott Mangan and Elizabeth Porter for their suggestions for the manuscript. This work was supported by grants from the NSF, Nature Conservancy, Mellon Foundation, and California Department of Transportation.

REFERENCES

- Adjoud, D., Plenchette, C., Halli-Hargas, R., Lapeyrie, F. 1996. Response of 11 eucalyptus species to inoculation with three arbuscular mycorrhizal fungi. *Mycorrhiza* 6:129-135.
- Allen, E.B., Allen, M.F. 1984. Competition between plants of different successional stages: mycorrhizae as regulators. *Can. J. Bot.* 62:2625-2629.
- Allen, M.F., Allen, E.B., Friese, C.F. 1989. Responses of the non-mycotrophic plant *Salsola kali* to invasion by vesicular arbuscular mycorrhizal fungi. *New Phytol.* 111:45-49.
- Bergelson, J.M., Crawley, J.M. 1988. Mycorrhizal infection and plant species diversity. *Nature* 334:202.
- Bever, J.D. 1994. Feedback between plants and their soil communities in an old field community. *Ecology* 75:1965-1977.
- Bever, J.D. 1999. Dynamics within mutualism and the maintenance of diversity: inference from a model of interguild frequency dependence. *Ecol. Lett.* 2:52-61.
- Bever, J.D. 2002a. Host-specificity of AM fungal population growth rates can generate feedback on plant growth. *Plant Soil* 244:281-290.
- Bever, J.D. 2002b. Negative feedback within a mutualism: host-specific growth of mycorrhizal fungi reduces plant benefit. *Proc. R. Soc. Lond. B* 269:2595-2601.
- Bever, J.D. 2003. Soil community dynamics and the coexistence of competitors: conceptual frameworks and empirical tests. *New Phytol.* 157:465-473.
- Bever, J.D., Morton, J.B., Antonovics, J., Schultz, P.A. 1996. Host-dependent sporulation and species diversity of arbuscular mycorrhizal fungi in a mown grassland. *J. Ecol.* 84:71-82.
- Bever, J.D., Pringle, A., Schultz, P.A. 2002. Dynamics within the plant-AM fungal mutualism: testing the nature of community feedback. In *Mycorrhizal Ecology*, Van der Heijden, M.G.A., Sanders, I.R., Eds. Berlin, Springer-Verlag, pp. 276-294.
- Bever, J.D., Schultz, P.A., Pringle, A., Morton, J.B. 2001. Arbuscular mycorrhizal fungi: more diverse than meets the eye, and the ecological tale of why. *Bioscience* 51:923-931.
- Bever, J.D., Westover, K.M., Antonovics, J. 1997. Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *J. Ecol.* 85:561-573.
- Bidartondo, M.I., Redecker, D., Hijri, I., Wiemken, A., Bruns, T.D., Dominguez, L., Sersic, A., Leake, J.R., Read, D.J. 2002. Epiparasitic plants specialized on arbuscular mycorrhizal fungi. *Nature* 419:389-392.
- Castelli, J.P., Casper, B.B. 2003. Intraspecific AM fungal variation contributes to plant-fungal feedback in a serpentine grassland. *Ecology* 84:323-336.
- Dean, A. 1983. A simple model of mutualism. *Am. Nat.* 121:409-417.
- Dickie, I.A., Koide, R.T., Steiner, K.C. 2002. Influences of established trees on mycorrhizas, nutrition, and growth of *Quercus rubra* seedlings. *Ecol. Monogr.* 72:505-521.
- Eom, A.H., Hartnett, D.C., Wilson, G.W.T. 2000. Host plant species effects on arbuscular mycorrhizal fungal communities in tallgrass prairie. *Oecologia* 122:435-444.
- Fitter, A. 1977. Influence of mycorrhizal infection on competition for phosphorus and potassium by two grasses. *New Phytol.* 79:119-125.
- Fitter, A., Graves, J.D., Watkins, N.K., Robinson, D., Scrimgeour, C. 1998. Carbon transfers between plants and its control in networks of arbuscular mycorrhizas. *Funct. Ecol.* 12:406-412.
- Fitter, A.H. 2000. Specificity, links and networks in the control of diversity in plant and microbial communities. In *Ecology: Achievement and Challenge*, Huntly, N.J., Levin, S., Eds. Oxford, Blackwell Science M.C. Press, pp. 95-114.
- Fowler, N., Antonovics, J. 1981. Competition and coexistence in a North Carolina grassland. *J. Ecol.* 69:825-841.
- Francis, R., Read, D.J. 1984. Direct transfer of carbon between plants connected by vesicular-arbuscular mycorrhizal mycelium. *Nature* 307:53-56.
- Gange, A.C., Ayres, R.Y. 1999. On the relation between arbuscular mycorrhizal colonization and plant "benefit." *Oikos* 87:615-621.
- Gange, A.C., Brown, V.K., Farmer, L.M. 1990. A test of mycorrhizal benefit in an early successional plant community. *New Phytol.* 115:85-91.

- Grime, J.P., Macky, J.M., Hillier, S.H., Read, D.J. 1987. Mechanisms of floristic diversity: evidence from microcosms. *Nature* 328:420–422.
- Hartnett, D.C., Wilson G.W.T. 1999. Mycorrhizae influence plant community structure in tallgrass prairie. *Ecology* 80:1187–1195.
- Helgason, T., Merryweather, J.W., Denison, J., Wilson, P., Young, J.P.W., Fitter, A.H. 2002. Selectivity and functional diversity in arbuscular mycorrhizas of co-occurring fungi and plants from a temperate deciduous woodland. *J. Ecol.* 90:371–384.
- Hetrick, B.A.D., Wilson, G.W.T., Todd, T.C. 1992. Relationships of mycorrhizal symbiosis, rooting strategy, and phenology among tallgrass prairie forbs. *Can. J. Bot.* 70:1521–1528.
- Hirrel, M.C., Gerdemann, J.W. 1979. Enhanced carbon transfer between onions infected with a vesicular arbuscular mycorrhizal fungus. *New Phytol.* 83:731–738.
- Holt, R.D., Lawton, J.H. 1994. The ecological consequences of shared natural enemies. *Ann. Rev. Ecol. Syst.* 25:495–520.
- Husband, R., Herre, E.A., Turner, S.L., Gallery, R., Young, J.P.W. 2002. Molecular diversity of arbuscular mycorrhizal fungi and patterns of host association over time and space in a tropical forest. *Mol. Ecol.* 11:2669–2678.
- Janos, D.P. 1980. Mycorrhizae influence tropical succession. *Biotropica* 12S:56–64.
- Janos, D.P. 1988. Mycorrhiza applications in tropical forestry: are temperate-zone approaches appropriate? In *Trees and Mycorrhiza*, F.S.P. Ng, Ed. Kuala Lumpur, Malaysia, Forest Research Institute, pp. 133–188.
- Jastrow, J.D., Miller, R.M. 1993. Neighbor influences on root morphology and mycorrhizal fungus colonization in tallgrass prairie plants. *Ecology* 74:561–569.
- Johnson, N.C. 1998. Responses of *Salsola kali* and *Panicum virgatum* to mycorrhizal fungi, phosphorus and soil organic matter: implications for reclamation. *J. Appl. Ecol.* 35:86–94.
- Johnson, N.C., Graham, J.H., Smith, F.A. 1997. Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytol.* 135:575–585.
- Klironomos, J.N. 2002. Feedback within soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417:67–70.
- Koide, R.T., Dickie, I.A. 2002. Effects of mycorrhizal fungi on plant populations. *Plant Soil* 244:307–317.
- Kytöviita, M.M., Vestberg, M., Tuomi, J. 2003. A test of mutual aid in common mycorrhizal networks: established vegetation negates benefit in seedlings. *Ecology* 84:898–906.
- Leake, J.R. 1994. The biology of myco-heterotrophic (“saprotrophic”) plants. *New Phytol.* 127:171–216.
- Lerat, S., Gauci, R., Catford, J.G., Veirhilig, H., Piché, Y., Lapointe, L. 2002. ¹⁴C transfer between the spring ephemeral *Erythronium americanum* and sugar maple saplings via arbuscular mycorrhizal fungi in natural stands. *Oecologia* 132:181–187.
- Lovelock, C.E., Miller, R. 2002. Heterogeneity in inoculum potential and effectiveness of arbuscular mycorrhizal fungi. *Ecology* 83:823–832.
- Lovelock, C.E., Andersen, K., Morton, J.B. 2003. Arbuscular mycorrhizal communities in tropical forests are affected by host tree species and environment. *Oecologia* 135:268–279.
- Medve, R.J. 1984. The mycorrhizae of pioneer species in disturbed ecosystems in western Pennsylvania. *Am. J. Bot.* 71:787–794.
- Merryweather, J.W., Fitter, A.H. 1998. The arbuscular mycorrhizal fungi of *Hyacinthoides non-scripta*. II. Seasonal and spatial patterns of fungal populations. *New Phytol.* 138:131–142.
- O'Connor, P.J., Smith, S.E., Smith, F.A. 2002. Arbuscular mycorrhizas influence plant diversity and community structure in a semiarid herbland. *New Phytol.* 154:209–218.
- Pringle, A., Bever, J.D. 2002. Divergent phenologies may facilitate the coexistence of arbuscular mycorrhizal fungi in a North Carolina grassland. *Am. J. Bot.* 89:1439–1446.
- Reynolds, H., Packer, A., Bever, J.D., Clay, K. 2003. Grassroots ecology: plant-microbe-soil interactions as drivers of plant community structure and dynamics. *Ecology* 84:2281–2291.
- Roberts, K.J., Anderson, R.C. 2001. Effect of garlic mustard *Alliaria petiolata* (Beib. Cavara & Grande) extracts on plants and arbuscular mycorrhizal (AM) fungi. *Am. Midland Nat.* 146:146–152.

- Robinson, D., Fitter, A. 1999. The magnitude and control of carbon transfer between plants linked by a common mycorrhizal network. *J. Exp. Bot.* 50:9-13.
- Ronsheim, M.L. 1996. Evidence against a frequency-dependent advantage for sexual reproduction in *Allium vineale*. *Am. Nat.* 147:718-734.
- Ronsheim, M.L., Anderson, S.E. 2001. Population-level specificity in the plant-mycorrhizae association alters intraspecific interactions among neighboring plants. *Oecologia* 128:77-84.
- Sanders, I.R., Fitter, A.H. 1992. Evidence for differential responses between host-fungus combinations of vesicular-arbuscular mycorrhizas from a grassland. *Mycol. Res.* 96:415-419.
- Schultz, P.A. 1996. Arbuscular Mycorrhizal Species Diversity and Distribution in an Old Field Community. Dissertation, Duke University, Durham, NC.
- Schultz, P.A., Miller, R.M., Jastrow, J.D., Rivetta, C.V., Bever, J.D. 2001. Evidence of a mycorrhizal mechanism for the adaptation of *Andropogon gerardii* to high- and low-nutrient prairies. *Am. J. Bot.* 88:1650-1656.
- Simard, S.W., Durall, D., Jones, M. 2002. Carbon and nutrient fluxes within and between mycorrhizal plants. In *Mycorrhizal Ecology*, Van Der Heijden, M.G.A., Sanders, I.R., Eds. Berlin, Springer, pp. 33-74.
- Smith, F.A., Jakobsen, I., Smith, S.E. 2000. Spatial differences in acquisition of soil phosphate between two arbuscular mycorrhizal fungi in symbiosis with *Medicago truncatula*. *New Phytol.* 147:357-366.
- Smith, S.E., Read, D.J. 1997. *Mycorrhizal Symbiosis*, 2nd ed. San Diego, Academic Press.
- St. John, T.V. 1980. Root size, root hairs and mycorrhizal infection: a reexamination of Baylis's hypothesis with tropical trees. *New Phytol.* 84:483-487.
- Tilman, D., Pacala, S. 1993. The maintenance of species richness in plant communities. In *Species Diversity in Ecological Communities: Historical and Geography Perspectives*, Ricklefs, R.E., Schluter, D., Eds. Chicago, University of Chicago Press, pp. 13-25.
- Van der Heijden, M.G.A. 2002. Arbuscular mycorrhizal fungi as a determinant of plant diversity: in search for underlying mechanisms and general principles. In *Mycorrhizal Ecology*, Van der Heijden, M.G.A., Sanders, I.R., Eds. Berlin, Springer-Verlag, pp. 243-266.
- Van der Heijden, M.G.A., Boller, T., Wiemken, A., Sanders, I.R. 1998a. Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. *Ecology* 79:2082-2091.
- Van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A., Sanders, I.R. 1998b. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 396:69-72.
- Van der Putten, W.H., Van Dijk, C., Peters, B.A.M. 1993. Plant-specific soil-borne diseases contribute to succession in foredune vegetation. *Nature* 362:53-56.
- Waters, J.R., Borowicz, V.A. 1994. Effect of clipping, benomyl and genet on ^{14}C transfer between mycorrhizal plants. *Oikos* 71:246-252.