

Mycorrhizal Fungal–Plant–Insect Interactions: The Importance of a Community Approach*

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ABSTRACT Mycorrhizal fungi and insects are important components of most ecosystems that are likely to interact with one another indirectly through a common host plant. In this paper, we review the literature examining the effects of insects on mycorrhizal fungi and the effects of mycorrhizal fungi on insects and show that both groups of organisms can indirectly and, occasionally directly, influence each other. We explore the mechanisms for these interactions and test a recently proposed model predicting mycorrhizal fungal community responses to herbivory. We emphasize the results of several recent studies that showed that experiments conducted in isolation are unlikely to predict the outcome of interactions between insects, plants, and mycorrhizal fungi, and we highlight the need for a community approach to the study of mycorrhizal fungal–plant–insect interactions.

KEY WORDS arbuscular mycorrhiza, ectomycorrhiza, insect herbivory, insect pollination

Mycorrhizas are symbiotic associations between fungi and the roots of numerous species of plants in which soil resources accessed by fungi are exchanged for photosynthetic carbon produced by plants (Smith and Read 2008). Associations with mycorrhizal fungi not only influence the performance of individual plants but also alter plant community structure, plant productivity, and nutrient cycling (Smith and Read 2008). Insects also associate with plants in most ecosystems, where they influence individual plants, plant communities, and ecosystems through their roles as herbivores, parasitoids, seed dispersers, and pollinators (Price 1997). Recent research showed that insects and mycorrhizal fungi interact with one another in complex ways likely to be important to fungi, insects, and host plants. Several reviews have been published synthesizing many of these findings and proposing conceptual models by which the enormous variation in interaction outcomes can be understood (Gehring and Whitham 1994, 2002; Gange and Bower 1997; Bennett et al. 2006; Gange 2007).

The purpose of this paper is two-fold. First, we will briefly review the research describing the indirect interactions between mycorrhizal fungi and insects and discuss potential mechanisms. Our goal is to describe the breadth of the results of these studies and to indicate some of their limitations. Second, we will highlight very recent research that emphasizes (1) the importance of examining the species composition of mycorrhizal fungi to improve our understanding of

mycorrhiza/insect interactions; (2) the need to place insects, mycorrhizal fungi, and their host plants into a broader community context that includes other interactions; and (3) the potential for mediation of interactions between insects and mycorrhizal fungi by the genotype of the fungus or host plant. These recent studies showed that consideration of functional variation at a variety of scales (genotype, species, community) is critical to understanding how plants and insects interact to influence the fitness of their host plants and each other.

Studies examining the interactions between mycorrhizal fungi and insects have focused on the two most widespread types of mycorrhizal fungal associations: the arbuscular mycorrhizas (AM) and the ectomycorrhizas (EM). Arbuscular mycorrhizas are formed by mosses, ferns, gymnosperms, and angiosperms in a variety of habitats including the temperate zone, the tropics, and many agricultural ecosystems. These fungi belong to the division Glomeromycota, an ancient lineage that contains only 140–160 described species (Johnson and Gehring 2007). Ectomycorrhizas occur in mostly woody gymnosperms and angiosperms and are dominant components of some temperate and most boreal forests. The fungi forming EM associations consist of ≈6,000 species, mostly from the divisions Ascomycota and Basidiomycota (Johnson and Gehring 2007). Significant functional variation among species has been shown for both AM and EM fungi in terms of reproduction and colonization strategies, resource utilization, and tolerance of environmental extremes (Taylor and Bruns 1999, Hart and Reader 2002). This variation in function affects plant performance (Klironomos 2003, Nara 2006), and we will highlight how it also influences the relationships between plants and insects.

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How Do Insects Influence Mycorrhizal Fungi?

Synthesis of Findings. Insects have been shown to influence mycorrhizal fungi by consuming fungal hyphae (mycophagy), by dispersing mycorrhizal fungal propagules, and by feeding on host plant tissues that directly or indirectly contribute to fungal performance (Friese and Allen 1993, Smith and Read 2008). Predators of herbivorous insects might also influence mycorrhizal fungi indirectly through a trophic cascade, but this possibility has not been studied. Likewise, insect pollinators may affect mycorrhizal fungi indirectly through altered energy investment or plant fitness, but this possibility has not been explored. In this paper, we will consider only the indirect effects of herbivory on mycorrhizal fungi because of the likely ubiquity of these interactions and their potential importance to insects, plants, and mycorrhizal fungi.

In general, studies on the effects of insect herbivory on mycorrhizal fungi have focused on aboveground herbivores (but see Currie et al. 2006) and their effects on mycorrhizal colonization, an estimate of the proportion of the root system occupied by mycorrhizal fungi. Insect herbivory has generally negatively influenced colonization by EM fungi (Gehring and Whitham 1991, Del Vecchio et al. 1993, Gehring et al. 1997, Kolb et al. 1999, Mueller et al. 2005), with evidence that high levels of herbivory have a larger effect on EM colonization than low levels of herbivory (Kolb et al. 1999). However, studies that mimic herbivory by clipping frequently show no effect on overall EM colonization (Saikkonen et al. 1999, Cullings et al. 2001, Markkola et al. 2004, Saravesi et al. 2008), although changes in fungal biomass or sporocarp production have been documented in some of these studies (Last et al. 1979, Kuikka et al. 2003, Markkola et al. 2004). Insect herbivory has had variable effects on root colonization by AM fungi with both negative (Gange et al. 2002a, Wamberg et al. 2003) and positive responses (Wamberg et al. 2003, Currie et al. 2006, Kula et al. 2005, Mueller et al. 2005). Wearn and Gange (2007) did not observe changes in overall colonization by AM but saw changes in the proportion of arbuscules, the site of resource exchange between fungus and host plant, after insect herbivory during some times of the year. The variation in response of AM fungi to insect herbivory has been attributed to the age of the plant (Wamberg et al. 2003), the degree of defoliation (Gange et al. 2002a), and the timing of AM colonization relative to herbivory (Currie et al. 2006). Given that less than a dozen studies have examined the effects of insect herbivory on mycorrhizas and that studies of defoliation have taken place in widely varying study systems under different clipping regimens, it is not surprising that a consistent view of the impact of insect herbivory on mycorrhizal fungi has yet to emerge.

Potential Mechanisms. Changes in mycorrhizal colonization after insect herbivory are thought to result from changes in the amount of carbon plants allocate below ground (Gehring and Whitham 1994). Similar mechanisms have been proposed for changes in my-

corrhizal colonization or fungal biomass in response to manual defoliation and vertebrate grazing (Eom et al. 2001, Markkola et al. 2004). The increases in mycorrhizal colonization observed in the early stages of insect herbivory (Wamberg et al. 2003) or after low to moderate levels of insect herbivory (Kula et al. 2005) may result from increased root exudation by plants, potentially leading to increased nutrient acquisition for regrowth after defoliation (Wamberg et al. 2003, Gange 2007). For example, the increased AM colonization observed in prairie microcosms after grasshopper herbivory was associated with plant regrowth resulting in overcompensation by plant species highly responsive to the mycorrhizal symbiosis (Kula et al. 2005). In contrast, higher levels or longer durations of insect defoliation may result in reduced carbon allocation belowground and reduced mycorrhizal colonization relative to control plants, particularly under stressful environmental conditions that limit aboveground regrowth (Kolb et al. 1999, Gehring and Whitham 2002, Gange 2007). In support of this hypothesis, AM colonization was higher in pea plants that experienced 10 d of beetle herbivory than in noneaten plants, but the result was reversed after 16 d of herbivory (Wamberg et al. 2003). Similarly, Gange et al. (2002a) showed that insect herbivory on *Plantago lanceolata* caused reductions in AM colonization only when a threshold of herbivore damage was reached.

Importance of a Community Perspective. The growing acknowledgment that species of mycorrhizal fungi vary in a number of attributes including nutrient acquisition strategies and carbon cost to host plants (Smith and Read 2008) has resulted in research determining if this functional variation extends to responses to insect herbivory and other forms of defoliation. In several studies, manual defoliation of forest trees resulted in changes in EM morphotype communities, favoring fungi that invested less in fungal structures (low biomass morphotypes) and presumably had lower carbon costs (Saikkonen et al. 1999, Markkola et al. 2004, Saravesi et al. 2008). Similarly, manual defoliation resulted in altered EM fungal community composition measured at a finer scale of resolution using molecular analysis of EM root tips (Cullings et al. 2001). Only two studies have assessed EM community responses to insect herbivory directly (Gehring and Whitham 2002, Kosola et al. 2004). One study observed no change in the EM fungal community (Kosola et al. 2004), whereas the other observed significant differences in the EM fungal species composition of insect resistant and insect susceptible trees (Gehring and Whitham 2002). Duration of herbivory varied markedly between the two studies and may explain the variable responses. The effect of insect herbivory on AM fungal communities has not been assessed directly, but clipping and grazing studies suggest that spore (Eom et al. 2001, Frank et al. 2003) and root-associated (Saito et al. 2004) AM communities respond to defoliation. Furthermore, Klironomos et al. (2004) found differences in the colonization of three AM fungal species growing on the same host plant

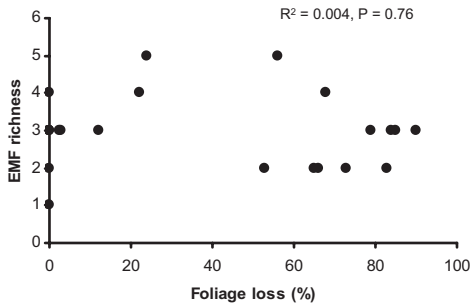


Fig. 1. The relationship between EM fungal (EMF) communities and percentage foliage loss caused by scale insect herbivory in pinyon pine does not follow the pattern predicted by Gange (2007). Instead, percentage foliage loss caused by scale herbivory is not significantly correlated with EM fungal species richness.

species in response to clipping. These findings suggest that species of AM fungi vary in their tolerance of aboveground herbivory, providing a potential mechanism for changes in mycorrhizal fungal species composition with insect herbivory.

Building on the ideas of Saikkonen et al. (1999) and Gehring and Whitham (2002), Gange (2007) proposed a model of mycorrhizal responses to herbivory that included this community perspective. Briefly, Gange (2007) hypothesized that, with no herbivory or very low levels of herbivory, mycorrhizal species composition was limited by competition for carbon, leading to low mycorrhizal fungal species richness. As herbivory increased, stimulation of photosynthesis and increased carbon allocation belowground would lead to greater mycorrhizal fungal species richness. However, with further increases in herbivory, carbon allocation belowground would be reduced, leading to the survival of only a few species of mycorrhizal fungi and reduced species richness.

We tested the hypothesis of Gange (2007) using data on the EM fungal communities associated with juvenile pinyon pines attacked by a needle-feeding scale insect, *Matsucoccus acalyptus*, in the field. This herbivore is widespread in the southwestern United States where its feeding results in premature leaf abscission that can leave chronically attacked trees with only a single cohort of needles (Gehring et al. 1997). We analyzed the EM fungal communities of 21 trees that experienced 0–85% foliage loss as a result of scale herbivory using restriction fragment length polymorphism analysis of >100 EM root tips/per tree as described by Mueller and Gehring (2006). We did not find a peak in mycorrhizal species richness with moderate defoliation as predicted by Gange (2007). Instead, there was no significant correlation between EM fungal species richness and foliage loss (Fig. 1; $R^2 = 0.004$, $F = 0.094$, $P = 0.76$). Species richness did not decline precipitously as predicted by Gange (2007), even when trees had lost most of their needles. However, EM fungal species composition was linearly associated with scale herbivory, with foliage loss explaining nearly 60% of the variation in EM species

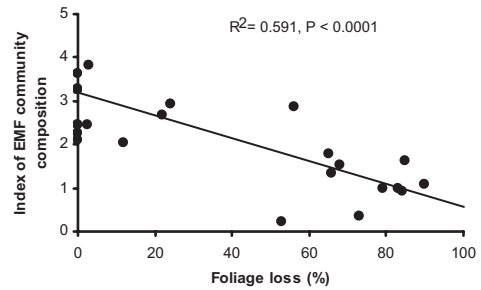


Fig. 2. EM fungal (EMF) species composition is significantly correlated with percentage foliage loss caused by scale insect herbivory in pinyon pine. EMF species composition is represented by a single axis ordination score as described in the text.

composition (Fig. 2; $R^2 = 0.591$, $F = 30.39$, $P < 0.0001$). For the latter analysis, we used a nonmetric multidimensional scaling (NMDS) ordination to obtain a single axis score (Shuster et al. 2006) representative of the EM fungal community of each tree and regressed that score against foliage loss caused by scale herbivory. The results of these two analyses suggest that fungal species composition may be more responsive to herbivory than species richness and that more species of fungi may be capable of persisting in severely carbon-limited situations than predicted by Gange (2007). Alternatively, severe defoliation may not impose the strong carbon limitation belowground that Gange (2007) and others (Gehring and Whitham 2002) have predicted. Further tests of the model of Gange (2007) are needed, particularly in more species-rich systems. It is also important to determine the potential feedback effect of shifts in mycorrhizal fungal communities with herbivory to both host plants and subsequent herbivores.

The above studies clearly showed the importance of including mycorrhizal species composition into studies of insect herbivore–mycorrhiza interactions, yet a broader community perspective is also needed. In addition to one another, plants, insect herbivores, and mycorrhizal fungi all interact with myriad other organisms, both above- and belowground. Mycorrhizal fungi provide food for animals, compete with other fungi, connect tree neighbors belowground, and form mutually beneficial relationships with bacteria (Johnson and Gehring 2007). These interactions and others may influence the responses of mycorrhizal fungi to herbivory. For example, competition among species of AM fungi and herbivory interacted to influence AM colonization of *Plantago lanceolata* (Bennett and Bever 2008). When three species of AM fungi were inoculated onto plants individually (no competition), herbivory by the native butterfly, *Junonia coenia*, caused AM colonization to decrease. However, no reduction in colonization was observed when the three species of AM fungi were co-inoculated and allowed to compete with one another. In fact, colonization by *Archaeospora trappei* increased after herbivory when it was in competition with the other

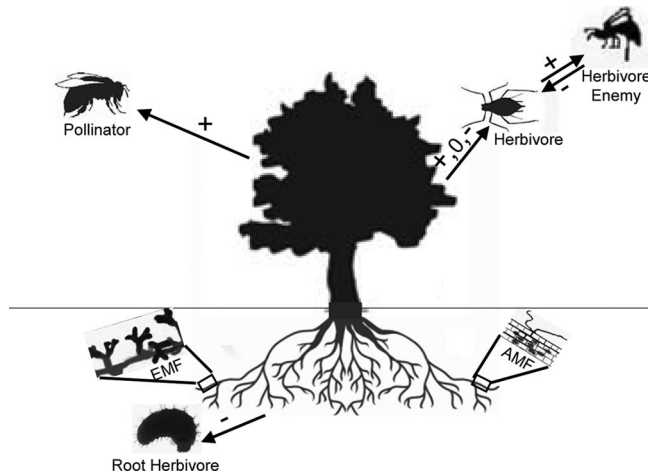


Fig. 3. A schematic depiction of the effect of mycorrhizal fungi on plant–insect interactions. Loosely based on the genus *Eucalyptus*, which associates with both AM and EM fungi and is subject to both insect herbivory (resulting from aphids and other insects) and pollination (from bees and other insects). Herbivores on these plants are also subject to enemies (such as parasitoid wasps), which are also influenced by plants associated with mycorrhizal fungi. Signs on arrows represent the effect (positive [+], neutral [0], or negative [–]) of a plant inoculated with either AM or EM fungi on the insect in question.

species of AM fungi (Bennett and Bever 2009). This study provides an example of the complexity we can expect when other interactions with mycorrhizal fungi are included into the study of herbivore impacts on mycorrhizal fungi. We predict an even more complex picture when interactions between insects and other biota also are included.

How Do Mycorrhizal Fungi Influence Insects?

Synthesis of Findings. The majority of mycorrhizal fungal–plant–insect studies have focused on insect herbivores and have observed many ways in which mycorrhizal fungi can influence the interaction between plants and their herbivores. Both EM and AM fungi have been shown to increase plant size and alter plant quality through changes in nutrient content (Smith and Read 1997), but given their effects on multiple plant traits, mycorrhizal fungi may also alter plant herbivore interactions through changes in constitutive and inducible defenses as well as tolerance to herbivory (Bennett et al. 2006). There are a growing number of studies focused on the indirect effects of EM and AM fungi on plant herbivores, and these studies primarily follow a similar protocol: plants are grown with a single mycorrhizal fungal species (for AM fungal studies, species are most commonly from the genus *Glomus*) and subjected to herbivory (often by a single herbivore species), and various traits (herbivore survival or growth, plant chemical content, or plant tolerance to herbivory) are measured and compared with control plants not inoculated with mycorrhizal fungi. However, this narrow glimpse into the role of mycorrhizal fungi in plant–herbivore interactions has largely ignored the variation in the ecology of mycorrhizal fungal species (Hart et al. 2001; Hart and Reader 2002, 2005; Klironomos 2003; Karst et al. 2008). Species of mycorrhizal fungi can vary greatly

(from parasitic to mutualistic) in the benefit they provide to hosts (Klironomos 2003, Karst et al. 2008), and, in AM fungi, variation in host growth benefit is thought to derive from variation in colonization or competitive ability in host roots (Hart et al. 2001, Hart and Reader 2002, Bennett and Bever 2008). Although only a small group of mycorrhizal fungal associates have been studied, experiments examining mycorrhizal fungal–plant–herbivore interactions have shown a wide array of results (Fig. 3).

The presence of mycorrhizal fungi in plant roots has been shown to both positively (45% of tested AM fungal–plant–herbivore combinations; 40% of tested EM fungal plant–herbivore combinations) and negatively (35% of AM fungal combinations; 20% of EM fungal combinations) influence aboveground herbivores, as well as have variable effects or no effect at all (21% of AM fungal combinations; 30% of EM fungal combinations; Table 1; Fig. 3). In contrast, mycorrhizal fungi have generally been shown to reduce attack by root herbivores (Gange 2007) (Fig. 3). The variation in response of herbivores to colonization by mycorrhizal fungi suggests that understanding the mechanisms through which mycorrhizal fungi alter plant–herbivore interactions would allow better predictions for the outcome of mycorrhizal fungal–plant–herbivore interactions.

Herbivores are not the only insects likely to be influenced by the mycorrhizal fungi. We predict that if mycorrhizal fungi influence the abundance of herbivores on host plants through changes in plant quantity, quality, defense, or tolerance, these changes in herbivore abundance are also likely to cascade up to herbivore enemies (Fig. 3). Gange et al. (2003) found that parasitism rates of leaf miners on plants associated with AM fungi in the field and greenhouse decreased and hypothesized that these differences were likely caused by increases in plant size, resulting in de-

Table 1. Summary of studies examining the effects of mycorrhizal fungi on insect herbivores

Insect species	Mode of feeding	Host range	Plant species	AM/EM	Mycorrhizal fungal species	Effect on insect	Reference
<i>Myzus ascalonicus</i>	Phloem sap	Generalist	<i>Plantago lanceolata</i>	AM	<i>Glomus intraradices</i>	Positive	Gange et al. 1999
<i>Myzus persicae</i>	Phloem sap	Generalist	<i>Plantago lanceolata</i>	AM	<i>Glomus intraradices</i>	Positive	Gange et al. 1999
<i>Polymonatus tartus</i>	Leaf chewing	Specialist	<i>Lotus corniculata</i>	AM	3 unidentified <i>Glomus</i> spp.	Positive	Goverde et al. 2000
<i>Myzus persicae</i>	Phloem sap	Generalist	<i>Plantago lanceolata</i>	AM	Field	Positive	Gange and West 1994
<i>Chromatomyia syngenesiae</i>	Leaf miner	Generalist	<i>Leucanthemum vulgare</i>	AM	Field	Positive	Gange et al. 2005a
<i>Chromatomyia syngenesiae</i>	Leaf miner	Generalist	<i>Leucanthemum vulgare</i>	AM	<i>Glomus fasciculatum</i>	Positive	Gange et al. 2005a
<i>Tephritis neesii</i>	Seed		<i>Leucanthemum vulgare</i>	AM	<i>Glomus mosseae</i>	Positive	Gange et al. 2005a
<i>Ozarhincus leucanthemi</i>	Seed		<i>Leucanthemum vulgare</i>	AM	<i>Glomus mosseae</i>	Positive	Gange et al. 2005a
<i>Epilachna verticilis</i>	Leaf scraping	Specialist	<i>Glycine max</i>	AM	<i>Glomus calatium</i>	Positive	Borowicz 1987
<i>Scopella ornata</i>	Leaf chewing	Specialist	<i>Clinopodium vulgare</i>	AM	<i>Glomus fasciculatum</i>	Positive	Gange et al. 2002b
<i>Pyrusta aurata</i>	Leaf chewing	Specialist	<i>Organum vulgare</i>	AM	<i>Glomus fasciculatum</i>	Positive	Gange et al. 2002b
<i>Cryptomyzus ribis</i>	Phloem sap	Specialist	<i>Stachys sylvatica</i>	AM	<i>Glomus fasciculatum</i>	Positive	Gange et al. 2002b
<i>Myzus persicae</i>	Phloem sap	Generalist	<i>Stachys sylvatica</i>	AM	<i>Glomus fasciculatum</i>	Positive	Gange et al. 2002b
<i>Chaitophorus populiicola</i>	Phloem sap	Specialist	<i>Populus angustifolia</i> x <i>P. fremontii</i>	EM	<i>Pisolithus tinctorius</i>	Positive	Gehring and Whitham 2002
<i>Lagrus rugulipennis</i>	Meristem	Generalist	<i>Pinus sylvestris</i>	EM	field	Variable ^a	Manninen et al. 2000
<i>Lymntria dispar</i>	Leaf chewing	Generalist	<i>Castanea dentata</i>	EM	<i>Pisolithus tinctorius</i>	Positive ^b	Rieske et al. 2003
<i>Lymntria dispar</i>	Leaf chewing	Generalist	<i>Castanea dentata</i>	EM	<i>Pisolithus tinctorius</i>	Positive ^b	Rieske et al. 2003
<i>Lymntria dispar</i>	Leaf chewing	Generalist	<i>Castanea mollissima</i>	EM	<i>Pisolithus tinctorius</i>	Positive ^b	Rieske et al. 2003
<i>Schizaphis graminum</i>	Phloem sap	Generalist	<i>Sorghum</i> sp.	AM	<i>Glomus fasciculatum</i>	No effect	Pacovsky et al. 1985
<i>Anomala cupripes</i>	Leaf chewing	Generalist	<i>Eucalyptus urophylla</i>	AM	<i>Glomus calatium</i>	No effect	Gange et al. 2005b
<i>Strepsicrates</i> spp.	Leaf chewing	Specialist	<i>Eucalyptus urophylla</i>	AM	<i>Glomus calatium</i>	No effect	Gange et al. 2005b
<i>Zygogramma exclamationis</i>	Leaf chewing	Specialist	<i>Helianthus annuus</i>	AM	<i>Glomus aggregatum</i> , <i>G. clarum</i> , <i>G. deserticola</i> , <i>G. intraradices</i> , <i>G. monosporus</i> , <i>G. mosseae</i> , <i>Gigaspora margarita</i> , <i>Paraglomus bractianum</i>	No effect	Laird and Addicott 2008
<i>Lagrus rugulipennis</i>	Meristem	Generalist	<i>Pinus sylvestris</i>	EM	<i>Cenococcum geophilum</i>	No effect	Manninen et al. 1998
<i>Schizolachnus pineti</i>	Phloem sap	Specialist	<i>Pinus sylvestris</i>	EM	<i>Cenococcum geophilum</i>	No effect	Manninen et al. 1999
<i>Matsucoccus acaluptus</i>	Mesophyll	Specialist	<i>Pinus edulis</i>	EM	<i>Stullus variegatus</i>	No effect	Gehring et al. 1997
<i>Tephritis neesii</i>	Seed	Specialist	<i>Leucanthemum vulgare</i>	AM	field	No effect	Gange et al. 2005a
<i>Chromatomyia syngenesiae</i>	Leaf miner	Generalist	<i>Leucanthemum vulgare</i>	AM	<i>Glomus mosseae</i>	No effect	Gange et al. 2005a
<i>Ozarhincus leucanthemi</i>	Seed	Specialist	<i>Leucanthemum vulgare</i>	AM	<i>Glomus fasciculatum</i>	No effect	Gange et al. 2005a
<i>Tupiocoris notatus</i>	Mesophyll	Specialist	<i>Nicotiana rustica</i>	AM	<i>Glomus etunicatum</i>	Negative	Wooley and Paine 2007
<i>Chaitophorus populiicola</i>	Phloem sap	Specialist	<i>Populus angustifolia</i> x <i>P. fremontii</i>	AM	<i>Glomus</i> spp.	Negative	Gehring and Whitham 2002
<i>Idaea aversata</i>	Leaf chewing	Generalist	<i>Clinopodium vulgare</i>	AM	<i>Glomus etunicatum</i>	Negative	Gange et al. 2002b
<i>Udea prunalis</i>	Leaf chewing	Generalist	<i>Organum vulgare</i>	AM	<i>Glomus fasciculatum</i>	Negative	Gange et al. 2002b
<i>Phlogophora metulosa</i>	Leaf chewing	Generalist	<i>Lolium perenne</i>	AM	<i>Glomus mosseae</i>	Negative	Vicari et al. 2002
<i>Heliothis zea</i>	Leaf chewing	Generalist	<i>Glycine max</i>	AM	<i>Glomus fasciculatum</i>	Negative	Rabin and Pacovsky 1985
<i>Spodoptera frugiperda</i>	Leaf chewing	Generalist	<i>Glycine max</i>	AM	<i>Glomus fasciculatum</i>	Negative	Rabin and Pacovsky 1985
<i>Arctia caja</i>	Leaf chewing	Generalist	<i>Plantago lanceolata</i>	AM	field	Negative	Gange and West 1994
<i>Macrosiphum euphorbiae</i>	Phloem sap	Generalist	<i>Lycopersicon esculentum</i>	AM	<i>Glomus mosseae</i>	Negative	Guerreri et al. 2004
<i>Urophora cardui</i>	Callling	Specialist	<i>Cirsium arvense</i>	AM	field	Negative	Gange and Nice 1997
<i>Anomala cupripes</i>	Leaf chewing	Generalist	<i>Eucalyptus urophylla</i>	EM	<i>Laccaria laccata</i>	Negative	Gange et al. 2005b
<i>Strepsicrates</i> spp.	Leaf chewing	Specialist	<i>Eucalyptus urophylla</i>	EM	<i>Laccaria laccata</i>	Negative	Gange et al. 2005b

creased parasitoid searching efficiency. This study did not measure volatile release, but Guerreri et al. (2004) has shown that, in the absence of herbivores, plants associated with AM fungi were significantly more attractive to parasitoids than plants not associated with AM fungi. In the case of protection mutualisms, the production of extrafloral nectaries, rewards produced by plants for protectors such as ants, decreased when *Vicia faba* was grown with eight AM fungal species versus none (Laird and Addicott 2007). Thus, research shows that mycorrhizal fungi can influence both herbivores and their enemies.

Potential Mechanisms. To date, few hypotheses for how mycorrhizal fungi might influence plant–herbivore interactions have been proposed (Bennett et al. 2006). Gange et al. (2002b) have suggested that specialist and sucking insects may respond positively to AM fungal colonization, whereas generalist and chewing herbivores are more likely to respond negatively to AM fungal colonization. They hypothesize that differences among these classes of insects in their feeding behavior make them more or less susceptible to changes in defensive compound concentrations that may change in the presence of AM fungi. For example, specialist herbivores lacking susceptibility to plant defenses or sucking herbivores may be unlikely to be influenced by any change in defenses as a result of colonization by mycorrhizal fungi (Gange and West 1994; Gange et al. 1999, 2002b). However, as discussed below, inoculation with AM fungi does not always lead to changes in plant defensive chemistry. Thus, although differences in feeding strategy likely explain some of the variation in herbivore response to host plant mycorrhizal inoculation, other mechanisms still need to be explored.

Bennett et al. (2006) has suggested that there are multiple mechanisms (through changes in plant quantity, quality, defensive strategies, and tolerance to herbivory) through which EM and AM fungi could influence plant herbivores. Changes in plant quantity and quality associated with mycorrhizal fungal colonization have been frequently shown (Smith and Read 1997) and suggested to influence plant–herbivore interactions (Gange and West 1994). Fewer studies have focused on changes in constitutive secondary (often defensive) compounds within plant tissues, and all studies of AM fungi have focused on the same plant species, *Plantago lanceolata*, and found conflicting results. Wurst et al. (2004) found that inoculation with AM fungi reduced catalpol levels, whereas Gange and West (1994) found that aucubin and catalpol production were reduced when AM fungal community was suppressed with fungicide, and Bennett et al. (2009) found that a suite of AM fungal species each influenced aucubin and catalpol production differently. The induction of jasmonic acid (Hause et al. 2002) and the presence of defense compounds in plant roots have been hypothesized to explain the reduction of root herbivory in the presence of mycorrhizal fungi (Gange 2007). Only one study to date has focused on the role of AM fungi in volatile release (Guerreri et al. 2004) and found that volatiles released by tomato

plants associated with AM fungi attracted the same number of parasitoids as plants associated with no AM fungi but infested with the potato aphid. However, they did not test the attractiveness of plants associated with AM fungi and potato aphids, so the question of how AM fungi influence volatile release in the presence of herbivores remains unanswered. Finally, Bennett et al. (2009) has shown that, on average, mycorrhizal fungi from three genera, singly and in combination, suppress inducible responses to herbivory in *P. lanceolata*. Thus, mycorrhizal fungi can influence plant defensive chemistry.

Given that mycorrhizal fungi influence plant growth, it seems likely that they might also play a role in plant regrowth, or tolerance, after herbivory. Few studies have explored the effects of mycorrhizal fungi on plant tolerance to herbivory, and all of those studies have been conducted with AM fungi. Kula et al. (2005) found that a community of mycorrhizal fungi increased the tolerance of a community of tallgrass prairie species after grasshopper herbivory. Using a single species of AM fungi, Borowicz (1997) showed no difference in the tolerance of soybean plants associated with *Glomus etunicatum* or sterile soil, and Bennett and Bever (2007) showed that three AM fungal species from three genera influenced tolerance positively, negatively, and neutrally and the outcome of all three fungal species in combination depended on the fungus with the dominant plant effect. As a result, AM fungi seem to be able to influence plant tolerance to herbivory in multiple ways, whereas the influence of EM fungi on tolerance still need to be explored.

If mycorrhizal fungi influence plant size, we might imagine that mycorrhizal fungi could influence the visibility of plants for pollinators, resulting in increased seed set and outcrossing rates. AM fungi have been shown to influence a variety of floral characteristics including changes in inflorescence size (Gange and Smith 2005, Wolfe et al. 2005, Cahill et al. 2008), flower number (Koide 2000, Poulton et al. 2002, Gange and Smith 2005), flower size (Gange et al. 2005a, Cahill et al. 2008), stem number (Cahill et al. 2008), nectar production (Gange and Smith 2005), and pollen production (Poulton et al. 2002), and these changes have often increased visitation by pollinators (Gange and Smith 2005, Wolfe et al. 2005) (Fig. 3). Increased pollinator visitation in many of these systems, but not all (Wolfe et al. 2005), has resulted in increased fruit mass (Poulton et al. 2002, Gange and Smith 2005) and seed number (Poulton et al. 2002, Gange and Smith 2005). Again the majority of these studies were conducted with a single species or multiple species of AM fungi from the genus *Glomus* (but see Wolfe et al. 2005), and no study to date has examined how EM fungi might influence plant pollinator interactions.

Importance of a Community Perspective. A large body of work has shown that not all mycorrhizal fungi are created equal, and, as discussed above, it is now well accepted that different fungal species produce different growth responses in hosts (Klironomos 2003, Karst et al. 2008). Thus, it seems likely that different EM and AM fungal species might also influence plant

herbivore interactions differently. In the simplest scenario, differences in growth promotion by different fungal species could increase attractiveness to herbivores (Gange 2007), and mycorrhizal fungal induced changes in plant quality (Borowicz 1997, Gange et al. 2003) should also benefit herbivores. As seen from the work above, different mycorrhizal fungal species can also influence defensive chemistry and herbivore tolerance differently. However, the majority of mycorrhizal fungal–plant–herbivore studies have focused on either a single fungal species or an entire community. For example, of the 13 studies examining AM fungal effects on aboveground herbivores, more than half (nine) (Pacovsky et al. 1985; Rabin and Pacovsky 1985; Borowicz 1997; Gange et al. 1999, 2002b, 2005b; Vicari et al. 2002; Guerrieri et al. 2004; Wooley and Paine 2007) used a single species from the genus *Glomus* (Table 1). Only three studies (Goverde et al. 2000, Gehring and Whitham 2002, Gange et al. 2005a) used more than one AM fungal species, and all but one of these studies (Gehring and Whitham 2002; three *Glomus* sp. and *Entrophospora colombiana*) used AM fungal species from the genus *Glomus* (Table 1). The remaining studies examined the effects of an unidentified natural community of fungi unmodified or suppressed with fungicide (Gange and West 1994, Gange and Nice 1997, Gange et al. 2005a). As a result, the majority of studies have focused on how *Glomus* species influence herbivores on AM fungal hosts. Although fewer in number, studies examining AM fungal effects on defensive compounds and plant tolerance are also heavily biased toward the fungal genus *Glomus* (Guerrieri et al. 2004, Wurst et al. 2004, Bennett and Bever 2007, Bennett et al. 2008) and whole soil communities (Gange and West 1994, Kula et al. 2005). In general, there are fewer studies (seven) examining EM fungal effects on herbivores, but these studies have included four different species from four different genera (*Pisolithus tinctorius*, Gehring and Whitham 2002, Rieske et al. 2003; *Cenococcum geophilum* Manninen et al. 1998, 1999; *Laccaria laccata*, Gange et al. 2005b; and *Suillus variegatus*, Manninen et al. 1999) representing both basidio- and ascomycetes as well as field communities (Gehring et al. 1997, Manninen et al. 2000) (Table 1). As a result, we have likely only captured a snapshot of the great diversity of mycorrhizal fungal effects on herbivores and plant responses to herbivores in previous studies, and, what is clear from that snapshot, is that even mycorrhizal fungi from a single genus can vary widely in their influence on plant–herbivore interactions.

Variation in the ecology of different plant and insect species is also likely to add complexity to the outcomes of plant–herbivore–mycorrhizal interactions. Plants from a wide variety of plant families (eight) have been used in AM fungal studies, whereas EM fungal studies have focused on a narrower range of plant families (four), and the majority of studies have been conducted on pines (Table 1). However, as mentioned above, the majority of studies focused on AM fungal defensive responses have been conducted on *P. lanceolata*. Although a wide variety of insects have been

used for these studies, ranging from Lepidoptera to Diptera to Hemiptera (in particular Aphididae and scale insects) (Table 1), but, given the wide array of herbivorous insects, these studies have barely scratched the surface of the many herbivorous insects that are likely influenced by mycorrhizal fungi.

The majority of the studies examining mycorrhizal fungal–plant–insect interactions have been conducted with a single member of each trophic level in a pot, ignoring the wide variety of environmental factors that could influence the outcome of these interactions. The research described above has shown that mycorrhizal fungi can alter plant growth, quality, defensive traits, tolerance of herbivory, and floral morphology. However, community characteristics may be just as important as these changes in plant traits. To date, few studies have examined the relative importance of mycorrhizal fungi versus other soil organisms in determining multitrophic outcomes (but see Wurst et al. 2004). In addition, the mycorrhizal mutualism has rarely been placed in context aboveground, limiting our understanding of how surrounding plant and insect communities influence the outcome of mycorrhizal fungal–plant–insect interactions (but see Gange and West 1994; Gange et al. 2002a, 2003, 2005a; Cahill et al. 2008). For example, changes in floral morphology may not predict pollinator interactions in a community. Suppression of AM fungi using fungicide in a flowering plant community resulted in a change in plant evenness that led to changes in the type of pollinators and the number of pollinator visits per stem (Cahill et al. 2008). These changes were not caused by changes in flower morphology but were the result of changes in neighboring flowering plants, showing the need to place mycorrhizal fungal–plant–insect interactions in a broader community context.

How Important Is Intraspecific Variation?

Although much of the research described in this paper has focused on variation between species, recent evidence showed that variation within species can also have strong effects on mycorrhizal–plant–insect interactions and communities. Wooley and Paine (2007) found that, while the direction of the effects of *Glomus etunicatum* in tobacco roots on mirid herbivores was the same, the magnitude of those effects varied by isolate (or ecotype) of *G. etunicatum*. In addition, although the overall growth response of *P. lanceolata* to three different AM fungal species (*Glomus* sp., *Archaeospora trappei*, and *Scutellospora calospora*) was determined by the fungal species, the magnitude of the host response was determined by the plant genotype (Bennett and Bever 2009). In pinyon pine, genetically based resistance and susceptibility to a moth herbivore was linked with genetically based variation in EM fungal community composition and drought tolerance, suggesting the possibility of extremely complex interactions that result from variation in plant genotype (Stultz 2008). These results provide support for the importance of the emerging field of community genetics that shows that genetic

variation within foundation species predictably affects species distributions, community structure, and ecological interactions in a wide of range of ecosystems (Whitham et al. 2003, 2006).

Conclusion

Taken together, recent research on the relationships among insects, plants, and mycorrhizal fungi showed that a community perspective is important for at least two reasons. First, species of mycorrhizal fungi vary in both their responses to herbivory and their influence on herbivores, suggesting that measures beyond the abundance or presence/absence of mycorrhizal fungi are necessary to understand these three way interactions. Similar variation among plant and insect species and genotypes is likely to add further complexity to these interactions. Second, the few studies that have placed insect-mycorrhizal fungus-plant interactions into a broader community context have shown that interactions observed when insects, plants, and mycorrhizal fungi occur in isolation may not be representative of their interactions in a complex community of organisms, both above- and belowground. Although challenging because of the difficulty of experimentally manipulating mycorrhizal fungi and insects, we believe that one of the major goals of future studies of insect-plant-mycorrhizal fungal interactions should be further exploration of the importance of functional variation between and within species and increased attempts to include the dynamics of other interactions. In addition, further research on mechanisms could improve our ability to predict the outcome of insect-plant-mycorrhizal fungal interactions and allow us to place them in an evolutionary context.

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