

# Interactions between aboveground herbivores and the mycorrhizal mutualists of plants

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**M**ycorrhizal fungi colonize the roots of most higher plants, where they improve growth and survival of the plant by enhancing nutrient uptake and providing protection from pathogens. These mutualists are thought to be especially important in nutrient-poor environments where plant survival may not otherwise be possible<sup>1</sup>. Mycorrhizae do not come without costs, however; an estimated 10–60% of a plant's photosynthate goes to support mycorrhizae<sup>2</sup>. In contrast to mycorrhizae, herbivores often negatively affect plant growth, survival, fecundity and fitness. Antiherbivore defense can be costly, reducing investment in plant growth and reproduction by 30–50% (Ref. 3).

Herbivores and mycorrhizal fungi both require energy from

plants, albeit in different forms, and therefore are likely to interact. When plants lose photosynthetic tissue to herbivores, they may also lose their ability to support their normal complement of mycorrhizae. Where herbivore outbreaks are positively associated with environmental stress such as in conifers<sup>4</sup>, the impacts of herbivory may be most severe in the very environments in which mycorrhizal mutualists are thought to be most important.

Herbivore-induced changes in mycorrhizae also have the potential to affect community structure in diverse ways. If herbivory reduces mycorrhizal colonization in one plant species, it may become a poorer competitor and decrease in abundance relative to species not so affected. Mycorrhizae may also provide their host plants with protection from herbivores as they do from some pathogens<sup>5</sup>. Variable levels of mycorrhizal colonization may provide a mechanism of resistance to herbivory that could help explain patterns of resistance and susceptibility in plant populations.

In this article, we review recent research on the relationships between aboveground herbivores and two types of mycorrhizas, the vesicular–arbuscular mycorrhizas (VAM) and the ectomycorrhizas (EM). We then explore how these interactions could be important at the community level. It is important to emphasize that the interactions between mycorrhizal fungi and herbivores are mediated through changes in the condition of the host plant. The mechanisms by which mycorrhizae enhance nutrient uptake and the major differences between VAM and EM are discussed in Box 1.

**Plant growth, reproduction and survival can be affected both by mycorrhizal fungi and aboveground herbivores, but few studies have examined the interactive effects of these factors on plants. Most of the available data suggest that severe herbivory reduces root colonization by vesicular–arbuscular and ectomycorrhizal fungi. However, the reverse interaction has also been documented – mycorrhizal fungi deter herbivores and interact with fungal endophytes to influence herbivory.**

**Although consistent patterns and mechanistic explanations are yet to emerge, it is likely that aboveground herbivore–mycorrhiza interactions have important implications for plant populations and communities.**

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## Aboveground herbivore impacts on mycorrhizae

The effects of aboveground herbivores on mycorrhizae have been studied in 37 plant species, most of which were colonized by VAM fungi and subjected to manual defoliation or grazing by ungulates (Table 1). Of the species examined, mycorrhizal colonization (1) declined following herbivory in 23 species, (2) was unaffected by herbivory in ten species, (3) was positively associated with herbivory in two species, and (4) showed variable responses in two species (*Agropyron desertorum* and *Bouteloua gracilis*) (Table 1). The negative association between mycorrhizae and herbivory was observed in a variety of plants including VAM-colonized grasses and EM-colonized conifers. For example, levels of VAM coloniz-

ation declined in 14 of 17 grass species exposed to heavy livestock grazing (continuous grazing or grazing during the growing season) at sites in Nevada, North Dakota and Arizona, USA<sup>6</sup>. Levels of VAM colonization were on average 47% lower in heavily grazed plants than in ungrazed plants.

Similarly, levels of ectomycorrhizal colonization in pinyon pine (*Pinus edulis*) were approximately 30% lower in trees susceptible to herbivory by either a stem- and cone-boring moth (*Dioryctria albovitella*) or a sap-feeding scale insect (*Matsucoccus acalyptus*) than in trees resistant to these insects<sup>7,8</sup>. Insect-removal experiments were performed to determine whether susceptible trees had inherently lower levels of ectomycorrhizal colonization or if their lower ectomycorrhizal levels were herbivore-induced. Removal of the insects from susceptible trees resulted in a rebound of EM colonization, demonstrating that herbivory was responsible for the declines in EM colonization and that the resistance traits of plants can determine the abundance of both herbivores and mycorrhizae (Fig. 1).

In contrast to the above studies, a neutral or positive relationship between mycorrhizal colonization and herbivory has been documented in some grasses and herbs (Table 1). VAM colonization was positively correlated with grazing intensity in a Serengeti grassland<sup>9</sup>. However, no consistent relationship between VAM colonization and herbivory was found in either a grazing-tolerant grass (*Agropyron desertorum*) or a grazing-sensitive grass (*Agropyron spicatum*) exposed to four years of clipping designed to mimic cattle grazing<sup>10</sup>.

**Box 1. Mycorrhizal associations**

Mycorrhizae improve plant growth and survival, in part by enhancing the uptake of nutrients such as phosphate and some forms of nitrogen that are poorly soluble and occur in low concentrations in the soil<sup>1,28</sup>. This enhanced uptake results from hyphae that extend from plant roots into the soil and thereby increase the total surface area for absorption<sup>1,28</sup>. Mycorrhizal symbioses are not usually species-specific and fungal species can differ substantially in the benefits they provide to plants<sup>1</sup>.

The VAM and EM associations discussed in this review differ morphologically and in the types of fungi and plants involved in the symbiosis. Although both VAM and EM produce hyphae that extend into the soil, EM also produce a mantle of fungal hyphae that covers the absorbing roots<sup>1,28</sup>. EM fungal hyphae extend inward between the cortical cells of the plant root, forming a structure termed the Hartig net, where the plant and fungus exchange materials<sup>1,28</sup>. In contrast, VAM do not form a fungal mantle, and VAM hyphae penetrate the cell walls of root cortical cells forming two characteristic structures; vesicles that serve as fungal storage units, and arbuscules that function as an exchange surface between plant and fungus<sup>1</sup>. The EM association is found only in woody perennials such as conifers, but involves fungi belonging to a large number of genera in the ascomycetes or basidiomycetes<sup>28</sup>. VAM associations are found in a great variety of herbaceous and woody plants, but generally belong to a single family (Endogonaceae) of zygomycetous fungi<sup>28</sup>.

In the studies reviewed here, degree of mycorrhiza formation was generally determined by measuring the intensity of root system colonization as indicated by the presence of the characteristic fungal structures described above. The percentage of the root length colonized by VAM fungi was usually measured in VAM associations, while the percentage of living root tips colonized by EM fungi was usually measured in EM associations.

In spite of the latter examples, most studies suggest that mycorrhizal colonization usually declines in response to herbivory. This raises three questions: (1) What mechanism(s) can account for the decline in mycorrhizae in response to herbivory? (2) What are the potential consequences of herbivore-induced mycorrhizal reduction for plants? (3) Why are the responses so variable both within and between plant species?

The negative effects of aboveground herbivory on VAM colonization have been attributed to photosynthate limitation<sup>9,11-13</sup>. Herbivore-induced reductions in aboveground biomass reduce the carbon-source capacity of plants to such a degree that there is insufficient carbon to meet the demands of mycorrhizal fungi, leading to reductions in mycorrhizal colonization. For example, carbohydrate pools (percent of total non-structural carbohydrates × biomass) of winter wheat (*Triticum aestivum*) were so reduced by grazing that VAM colonization declined by 38% and the yield by 16% (Ref. 13).

Herbivore-caused mycorrhizal reductions could have serious consequences for plants, such as reduced nutrient uptake, increased susceptibility to pathogens, and even sex-biased impacts. For example, a parasitic mistletoe (*Phoradendron juniperinum*) which has effects similar to those of herbivores (loss of photosynthetic tissue and removal of carbon via the xylem sap) occurred at three-fold higher densities on female junipers (*Juniperus monosperma*) than male junipers<sup>14</sup>. Although VAM colonization was negatively associated with mistletoe density in both sexes, the negative effect was greater on female trees. As a consequence of the distributional pattern of the mistletoe, female trees were more likely to experience mycorrhizal reductions than male trees. This could explain the male-biased sex ratio observed in this study and contribute to the pattern of male plants being more common in stressful environments.

Although VAM colonization declined following herbivory in 62% of the plant species that have been studied, no association, a positive relationship or a variable relationship was observed in the other 38%. Three hypoth-

eses may explain this variability. First, species of VAM fungi may vary in their tolerance to any reductions in carbon supply caused by herbivory. In a Nevada rangeland, VAM species diversity was lower in grazed plots than in ungrazed controls, suggesting that certain VAM species were tolerant of grazing while others were not<sup>12</sup>. Similarly, Johnson<sup>15</sup> found that different species of VAM fungi predominated in fertilized soils compared to non-fertilized soils, and hypothesized that these differences were due to variation in the root-exudate carbohydrate content of fertilized and non-fertilized plants. Results of a bioassay indicated that the VAM fungi from fertilized soils were also inferior mutualists<sup>15</sup>. Given that herbivory is also likely to influence root-carbon content, it is important to examine fungal species diversity and efficacy when comparing grazed and ungrazed plants. Although overall mycorrhizal colonization may not differ, there may be differences in the effectiveness of the species that are present.

Second, differences in the intensity of the herbivory experienced by plants also may explain the variation in mycorrhizal responses to herbivory. Plants in the studies reviewed here were exposed to a wide range of herbivory, from annual clipping to intense cattle grazing. Unfortunately, few studies have compared mycorrhizal responses over a range of herbivore damage, and comparison across studies was difficult because herbivory was not quantified in the same way. In one of the few studies that compared the same plant species exposed to a range of herbivore damage, mycorrhizal colonization declined substantially both in corn (*Zea mays*) and tomatoes (*Lycopersicon esculentum*) exposed to severe defoliation (foliage reduced by 60% relative to non-defoliated controls), but declined substantially only in corn when defoliation was more moderate (foliage reduced by 40% relative to controls)<sup>11</sup>. In this example, both the level of herbivory and the plant species involved had an important influence on the mycorrhiza-herbivore interaction.

Finally, differences between plants, both in their investment in antiherbivore defenses and their ability to tolerate herbivory, may influence the mycorrhizal response to herbivory. This is illustrated by the resource-availability hypothesis, which predicts that plants growing in resource-poor environments tend to grow slowly, to have low photosynthetic rates, and to invest heavily in antiherbivore defenses<sup>16</sup>. Such plants may be less likely to experience severe herbivory, but, because of their low photosynthetic rates, they may be more likely to lose mycorrhizae following herbivory than plants growing where resources are abundant. In contrast, the mycorrhizal symbionts of plants that compensate or overcompensate for herbivory may also remain unaffected or even benefit from herbivory. Some of the mechanisms by which plants compensate for herbivory (e.g. increased photosynthesis of remaining leaves and removal of carbon from storage tissues)<sup>17</sup> could also allow plants to maintain their mycorrhizal mutualists following herbivory. Because mycorrhizae significantly stimulate photosynthesis in some plants<sup>18</sup>, they may facilitate compensation. For example, in a C<sub>4</sub> grass (*Panicum coloratum*) grown in a low nitrogen environment, severe clipping (to 5 cm height every six days) inhibited photosynthesis in non-mycorrhizal plants but not in mycorrhizal plants<sup>9</sup>.

Although herbivores and mycorrhizae are important in most environments, the studies examining the effects of herbivores on mycorrhizae are limited in number and scope. Only a few types of herbivory have been examined (ungulate grazing, clipping and two cases of insect

herbivory) on a small number of plants (mostly grasses, some crops and one conifer species) in a limited range of environments (mostly semi-arid). Future research should broaden the scope of these studies and address such questions as: (1) Are herbivores more likely to have negative effects on the mycorrhizae of plants growing in resource-poor environments such as nutrient-deficient soils or the tropical forest understorey where carbon is likely to be limited? (2) How important is the type and level of herbivory in affecting mycorrhizal colonization? (3) Does mycorrhizal species-composition differ between grazed and ungrazed plants, and how does this affect the efficiency of the symbiosis?

**Mycorrhizal impacts on aboveground herbivores**

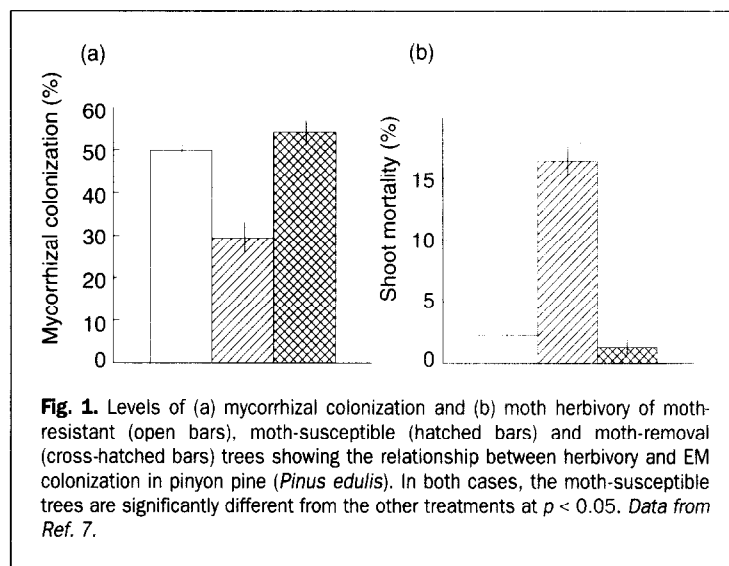
Although mycorrhizae can reduce a plant's susceptibility to some pathogens, few studies have examined the ability of mycorrhizae to reduce susceptibility to aboveground herbivores. Jones and Last<sup>5</sup> developed a model that combined the carbon-nutrient balance concept of the herbivore literature (the hypothesis that the relative, internal availability of carbon and nutrients in a plant is a major determinant of shoot growth rates and the types and quantities of antiherbivore defenses produced by plants)<sup>19</sup> with data on the role of ectomycorrhizae in plant physiological ecology. The model predicted the effects of ectomycorrhizal colonization on shoot growth and resistance to herbivory under a variety of conditions. For example, ectomycorrhizal plants were predicted to have greater shoot growth and herbivore resistance than non-ectomycorrhizal plants of the same species when soil nutrient-levels were low and light was not limiting. Ectomycorrhizal plants would perform better under these conditions because their more efficient nutrient uptake (increased nutrient uptake relative to carbon cost) would allow them to allocate more carbon to antiherbivore defenses and shoot growth. Although this model applied largely to fast-growing saplings growing in water-rich environments, it suggests that the costs and benefits of EM colonization can influence a plant's ability to produce chemical defenses against herbivores. Ectomycorrhizal fungi themselves synthesize carbon-based secondary metabolites that may protect plants from root pathogens, belowground grazers and nematodes<sup>5</sup>. If these compounds can be transported aboveground they may provide a second mechanism by which mycorrhizae could deter aboveground herbivores.

Rabin and Pacovsky<sup>20</sup> demonstrated that mycorrhizae negatively affected two insect herbivores; they examined

**Table 1. Summary of herbivore effects on mycorrhizal colonization**

Positive	Neutral	Negative
<b>VAM Plants</b>		
<i>Glycine max</i> <sup>29</sup> Serengeti grassland <sup>9</sup> (plant spp. not listed)	<i>Agropyron desertorum</i> <sup>10,a</sup> <i>A. spicatum</i> <sup>10</sup> <i>Andropogon gerardii</i> <sup>30</sup> <i>Bouteloua curtipendula</i> <sup>6</sup> <i>B. filiformis</i> <sup>6</sup> <i>B. gracilis</i> <sup>31-33,a</sup> <i>Crepis linearis</i> <sup>12,b</sup> <i>Dicanthelium oligosanthes</i> <sup>31</sup> <i>Eragrostis lehmanniana</i> <sup>6</sup> <i>Panicum virgatum</i> <sup>31</sup> <i>Paspalum setaceum</i> <sup>31</sup> <i>Schizachyrium scoparium</i> <sup>31,34</sup>	<i>Agropyron desertorum</i> <sup>12,35,a</sup> <i>A. smithii</i> <sup>6</sup> <i>Agrostis tenuis</i> <sup>11</sup> <i>Bouteloua gracilis</i> <sup>6,a</sup> <i>Bromus tectorum</i> <sup>12</sup> <i>Festuca rubra</i> <sup>11</sup> <i>Heteropogon contortus</i> <sup>6</sup> <i>Koeleria cristata</i> <sup>6</sup> <i>Lycopersicon esculentum</i> <sup>11</sup> <i>Medicago sativa</i> <sup>11</sup> <i>Nicotiana tabacum</i> <sup>36</sup> <i>Oryzopsis hymenoides</i> <sup>12</sup> <i>Panicum capillare</i> <sup>6</sup> <i>Poa compressa</i> <sup>6</sup> <i>P. pratensis</i> <sup>11</sup> <i>Sitanion hystrix</i> <sup>12</sup> <i>Stipa comata</i> <sup>6,12</sup> <i>S. thurberiana</i> <sup>12</sup> <i>S. viridula</i> <sup>6</sup> <i>Trifolium subterraneum</i> <sup>37</sup> <i>Ticachne californica</i> <sup>6</sup> <i>Triticum aestivum</i> <sup>13</sup> <i>Zea mays</i> <sup>11</sup>
<b>EM Plants</b>		
		<i>Betula</i> spp. <sup>38,c</sup> <i>Pinus edulis</i> <sup>7,8</sup>

<sup>a</sup> These two species showed both neutral and negative responses depending upon the study and are therefore listed in both columns.  
<sup>b</sup> The authors observed no difference between four other species of forbs when growing in grazed versus ungrazed sites, but referred to *Crepis linearis* as 'the palatable forb' so we excluded the others because we could not be sure they had actually been grazed.  
<sup>c</sup> Last *et al.*<sup>38</sup> did not determine EM colonization, but instead found that sporophore production by EM fungi stopped abruptly when birch trees were totally defoliated.



**Fig. 1.** Levels of (a) mycorrhizal colonization and (b) moth herbivory of moth-resistant (open bars), moth-susceptible (hatched bars) and moth-removal (cross-hatched bars) trees showing the relationship between herbivory and EM colonization in pinyon pine (*Pinus edulis*). In both cases, the moth-susceptible trees are significantly different from the other treatments at  $p < 0.05$ . Data from Ref. 7.

growth and survival in fall armyworm (*Spodoptera frugiperda*) and corn earworm (*Heliothis zea*) which had been fed leaves from VAM-inoculated and non-inoculated soybeans (*Glycine max*) of insect-resistant and insect-susceptible cultivars. Larval growth and pupal weight were lower, while time to pupation and larval mortality were higher in the VAM-inoculated plants than in the non-inoculated plants for both insects<sup>20</sup> (Table 2). When all cultivars and insects were combined, percentage VAM colonization was positively correlated with days to pupation

**Table 2. Larval growth and mortality of two insect species fed leaves from VAM inoculated (VAM) and P-fertilized nonmycorrhizal (control) soybeans<sup>a</sup>**

Insect species	Soybean cultivar	Larval weight		Mortality (%)	
		control	VAM	control	VAM
<i>Heliothis zea</i>	Resistant 1	80.8	44.4 <sup>b</sup>	17	42 <sup>b</sup>
	Resistant 2	52.6	36.7	17	25
	Susceptible 1	228.4	100.0 <sup>b</sup>	8	17
	Susceptible 2	452.5	166.6 <sup>b</sup>	0	17 <sup>b</sup>
<i>Spodoptera frugiperda</i>	Resistant 1	181.9	103.7 <sup>b</sup>	17	8
	Resistant 2	95.4	41.6 <sup>b</sup>	0	25 <sup>b</sup>
	Susceptible 1	270.4	190.5	0	0
	Susceptible 2	324.4	182.0 <sup>b</sup>	-	-

<sup>a</sup>Data from Ref. 20.

<sup>b</sup>Statistically significant at  $p < 0.05$ .

control (high VAM) plots in the field. Low-VAM plants had fewer leaves, higher levels of soluble sugars, starch and nitrogen, and suffered higher levels of damage by chewing and mining insects than high-VAM plants. Moth larvae (*Arctia caja*) reared on leaves from low-VAM plants consumed more leaf tissue and grew more rapidly than larvae reared on high-VAM plants, while aphids (*Myzus persicae*) achieved greater adult weights and contained more embryos when reared on high-VAM plants<sup>21</sup>. Thus, leaf-feeding herbivores per-

formed better or caused greater damage on low-VAM plants, while the reverse was true for the phloem-feeding aphid.

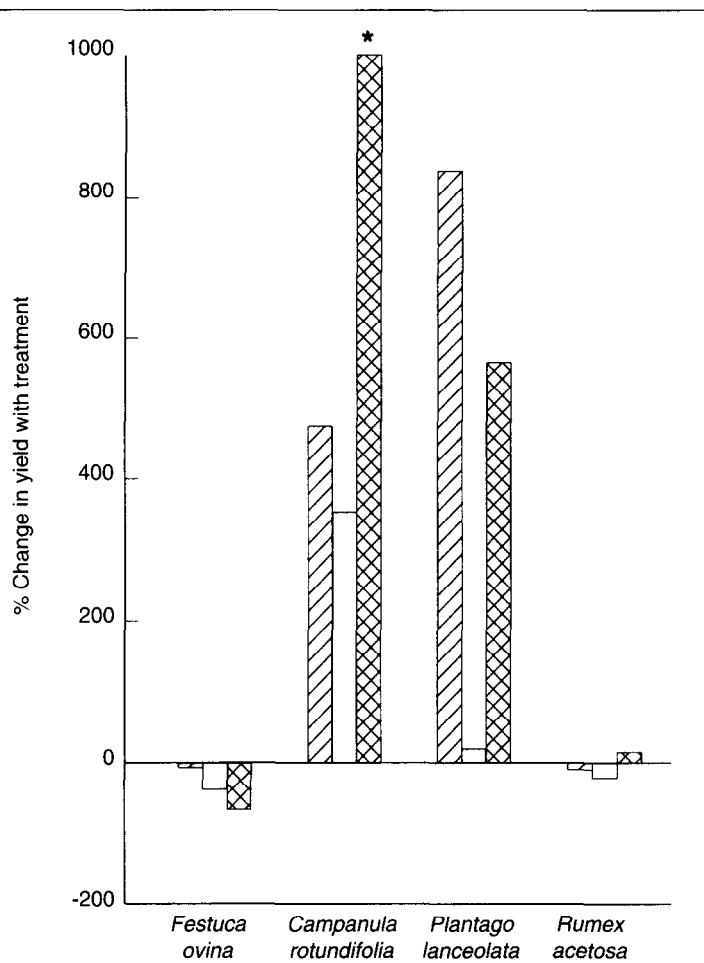
These two studies clearly demonstrate that above-ground insect herbivore growth, mortality and fecundity can be influenced by mycorrhizal colonization. However, reductions in herbivore vigor did not occur in all instances and were not consistently associated with plant nutrients or defensive compounds. In such instances, the higher plant tissue nutrient concentrations that can result from mycorrhizal colonization might make plants more attractive to herbivores. Detailed study of the mechanisms involved in mycorrhizally mediated herbivore deterrence or attraction would be a profitable area for future research.

**Effects of aboveground herbivore–mycorrhizae interactions on community structure**

Both mycorrhizae and herbivores have been shown to affect community structure. Changes in plant community composition, succession and tropical plant diversity have been attributed to mycorrhizae<sup>1</sup>. Likewise, herbivore-induced changes in plant species diversity and even subsequent changes in animal communities have been documented<sup>22</sup>. Because herbivores and mycorrhizae have important, independent impacts on plant and animal communities, we would expect interactions between the two to influence community structure as well.

Plant community changes are likely to result from the interactions between mycorrhizae and herbivores because plants vary both in their tolerance of herbivory and their dependence on mycorrhizae. In a study of 20 plant species grown in microcosms, VAM inoculation and clipping treatments (alone and in combination) significantly altered the yield (mg) of several plant species<sup>23</sup>. For example, the yield of a grass, *Festuca ovina*, declined 8% with VAM inoculation alone, 30% with clipping alone and 61% with both treatments. Although the negative effects of simulated herbivory were expected, the negative effects of VAM colonization suggest that VAM fungi were not mutualists in this case. The other plant species exhibited a range of responses to clipping and VAM colonization, including no significant change, increased yield in all treatments and increased yield with VAM colonization, but not clipping (Fig. 2). As a consequence of these varied responses, plant diversity was higher in all of the treatment groups than in the non-VAM, unclipped control<sup>23</sup>.

Mycorrhizal fungi may also interact with other mutualists to influence herbivore feeding and reproduction.



**Fig. 2.** Changes in yield of four of 20 plant species grown in microcosms and exposed to VAM inoculation (hatched bars), clipping (open bars) and both treatments (cross-hatched bars). Bars represent the percentage change in yield in the treatment groups relative to unclipped, non-inoculated controls. The asterisk denotes a yield increase greater than 1000%. Data from Ref. 23.

and insect mortality, and negatively correlated with larval weight. The mechanism of the mycorrhizal effect was not determined, but larval growth reductions were not significantly correlated with leaf nitrogen, amino acid, carbohydrate, micronutrient or phenolic contents, suggesting that these characteristics were not important in the mycorrhizal response.

Gange and West<sup>21</sup> compared the levels of herbivory on *Plantago lanceolata* in fungicide-treated (low VAM) and

Barker<sup>24</sup> examined the interactions among the Argentine stem weevil (*Listronotus bonariensis*), a foliar endophyte (*Acremonium loliae*; an aboveground fungal mutualist found in grass leaves), a vesicular-arbuscular mycorrhiza (*Glomus fasciculatum*) and perennial ryegrass (*Lolium perenne*). Infection of ryegrass by the foliar endophyte conferred resistance to the stem weevil by deterring feeding and oviposition and by increasing larval mortality. However, the ability of the endophyte to deter the weevil was reduced by the presence of the VAM fungus. In the absence of the endophyte, there was no interaction between VAM colonization and herbivory, suggesting that the two fungal mutualists negatively interacted with one another.

In pinyon pine, the ripple effects of plant/mycorrhizae/herbivore interactions extended to other diverse taxa including avian and mammalian seed consumers. Pinyons genetically susceptible to stem- and cone-boring moth herbivory had 47% less annual trunk growth, 57% fewer cones and 33% lower ectomycorrhizal colonization than pinyons genetically resistant to moth herbivory<sup>7,25,26</sup>. Because of their reduced cone crops, susceptible trees were less attractive to avian seed dispersers<sup>25</sup>. Instead, more of their seeds were consumed by mammals who may act as seed predators rather than seed dispersers. Thus, the genetic structure of the pinyon population affected the distribution of an important insect herbivore which then influenced the belowground ectomycorrhizal community and the aboveground, seed-consumer community.

Although our review has emphasized the effects of herbivores and mycorrhizae on one another as mediated through changes in the host plant, other types of interaction are also possible. For example, through their burrowing activities, herbivorous pocket gophers (*Thomomys* spp.) moved mycorrhizal inoculum to the newly deposited ash and cinders of Mount St Helens that lacked mycorrhizae<sup>1</sup>. By dispersing mycorrhizal inoculum, gophers enhanced the survival of colonizing plants<sup>1</sup>.

These studies suggest that the interactions among herbivores, mycorrhizae and host plants can have complex effects on community structure. The study of individual-plant responses in a natural field setting is key to understanding these interactions. Because different plant species and individual plants of the same species exhibit substantial variation in resistance to herbivory and in mycorrhizal associations, it is necessary to examine both in order to quantify the interaction effects. The responses of herbivores and mycorrhizae also vary with the environment; herbivore densities were associated with environmental stress in 75% of 450 studies<sup>4</sup>, and mycorrhizal fungi can act as mutualists or parasites depending upon the environment<sup>27</sup>. For this reason, the relationship between mycorrhizae and herbivores should be studied in diverse environments. Given the importance of mycorrhizae and herbivory in natural landscapes and agricultural crops, future studies of these interactions are likely to aid our understanding of community structure, as well as having considerable economic value.

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