Interactions between aboveground herbivores and the mycorrhizal mutualists of plants

Catherine A. Gehring and Thomas G. Whitham

Mycorrhizal 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. Mycorrhizae do not come without costs, however; an estimated 10–60% of a plant’s photosynthate goes to support mycorrhizae. 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, 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. 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 observed 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–mycorrhizal interactions have important implications for plant populations and communities.

Catherine Gehring and Thomas Whitham are at the Dept of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA.

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 colonization 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. 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 (Utatruma bettia) or a sap-feeding scale insect (Matsucoccus acalyptus) than in trees resistant to these insects. 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. 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.

REVIEWS

TREE vol. 9, no. 7 July 1994 © 1994, Elsevier Science Ltd 251
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 solubilized in soils. This enhanced uptake results from hyphae that extend from plant roots into the soil and thereby increase the total surface area for absorption\textsuperscript{1,2}. Mycorrhizal symbioses are not usually species-specific and fungal species can differ substantially in the benefits they provide to plants.\textsuperscript{2,25}

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\textsuperscript{1,2,21,22}. In contrast, VAM do not form a fungal mantle, and VAM hyphae penetrate the cell walls of root cortical cells forming arbuscules that function as an exchange surface between plant and fungus\textsuperscript{1}. The EM association is found only in woody perennials such as conifers, but VAM associations are found in a variety of herbaceous and woody plants, but generally belong to a single family (Endogonaceae) of basidiomycetes\textsuperscript{9,13,26,27}. VAM associations are found in a great variety of herbageous and woody plants, but generally belong to a single family (Endogonaceae) of basidiomycetes\textsuperscript{9,13,26,27}. Mycorrhizal symbioses are not usually species-specific and fungal species can differ substantially in the benefits they provide to plants. 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\textsuperscript{1,2,21,22}. In contrast, VAM do not form a fungal mantle, and VAM hyphae penetrate the cell walls of root cortical cells forming arbuscules that function as an exchange surface between plant and fungus\textsuperscript{1}. The EM association is found only in woody perennials such as conifers, but VAM associations are found in a great variety of herbaceous and woody plants, but generally belong to a single family (Endogonaceae) of basidiomycetes\textsuperscript{9,13,26,27}. VAM associations are found in a great variety of herbaceous and woody plants, but generally belong to a single family (Endogonaceae) of basidiomycetes\textsuperscript{9,13,26,27}.

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 solubilized in soils. This enhanced uptake results from hyphae that extend from plant roots into the soil and thereby increase the total surface area for absorption\textsuperscript{1,2}. Mycorrhizal symbioses are not usually species-specific and fungal species can differ substantially in the benefits they provide to plants. 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\textsuperscript{1,2,21,22}. In contrast, VAM do not form a fungal mantle, and VAM hyphae penetrate the cell walls of root cortical cells forming arbuscules that function as an exchange surface between plant and fungus\textsuperscript{1}. The EM association is found only in woody perennials such as conifers, but VAM associations are found in a great variety of herbaceous and woody plants, but generally belong to a single family (Endogonaceae) of basidiomycetes\textsuperscript{9,13,26,27}. VAM associations are found in a great variety of herbaceous and woody plants, but generally belong to a single family (Endogonaceae) of basidiomycetes\textsuperscript{9,13,26,27}.
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 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) 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. If these compounds can be transported aboveground they may provide a second mechanism by which mycorrhizae could deter aboveground herbivores.

Rabin and Pacovsky demonstrated that mycorrhizae negatively affected two insect herbivores; they examined 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 (Table 2). When all cultivars and insects were combined, percentage VAM colonization was positively correlated with days to pupation.

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

<table>
<thead>
<tr>
<th>VAM Plants</th>
<th>Neutral</th>
<th>Negative</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glycine max</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Serengeti grassland</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sorghum bicolor</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Asinaria smithii</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. spicatum</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Andropogon gerardii</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bouteloua curtipendula</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B. filifolia</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B. gracilis</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crepis linears</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dicranurus alpigenanthus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eragrostis lehmanniana</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Panicum virgatum</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. setaceum</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Schizachyrium scoparium</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>EM Plants</th>
<th>Positive</th>
<th>Neutral</th>
<th>Negative</th>
</tr>
</thead>
<tbody>
<tr>
<td>Betula spp</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pinus edulis</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

---

* These two species showed both neutral and negative responses depending upon the study and are therefore listed in both columns.  
  1 The authors observed no difference between four other species of forbs when growing in grazed versus ungrazed sites, but referred to Crepis linears as ‘the palatable forb’ so we excluded the others because we could not be sure they had actually been grazed.  
  2 Last et al. 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.
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\textsuperscript{21} compared the levels of herbivory on \textit{Plantago lanceolata} in fungicide-treated (low VAM) and 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 (\textit{Arcta 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 (\textit{Myzus persicae}) achieved greater adult weights and contained more embryos when reared on high-VAM plants\textsuperscript{21}. Thus, leaf-feeding herbivores performed 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 aboveground 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\textsuperscript{1}. Likewise, herbivore-induced changes in plant species diversity and even subsequent changes in animal communities have been documented\textsuperscript{22}. 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\textsuperscript{22}. For example, the yield of a grass, \textit{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\textsuperscript{22}. Mycorrhizal fungi may also interact with other mutualists to influence herbivore feeding and reproduction.
Barker 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 conaboring moth herbivory had 47% less annual trunk growth, 57% fewer cones and 33% lower ectomycorrhizal colonization than genetically susceptible to stem- and conaboring moth herbivory. Because of their reduced cone crops, susceptible trees were more infected with the endophyte, 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. By dispersing mycorrhizal inoculum, gophers enhanced the survival of colonizing plants.

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, and mycorrhizal fungi can act as mutualists or parasites depending upon the environment. 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.

Acknowledgements
We thank N. Cobb, T. Del Vecchio, S. Denton, L. Dickson, A. Martin, G. Martinsen, T. Theimer, B. Wade and three anonymous reviewers for helpful comments on the manuscript. Our research is supported by USDA grants 91-37302-6224 and 92-37302-7854 and NSF grant BSR-9107042.

References
33 Reeve, P.E. and Bondlum, C.D. (1975) J. Range Manage. 31, 149-151

TREE vol. 9, no. 7 July 1994

255