Plant-mediated ‘apparent effects’ between mycorrhiza and insect herbivores

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**Abstract**

Plants mediate indirect ‘apparent’ effects between above-ground herbivores and below-ground mutualistic mycorrhizal fungi. The herbivore-plant-mycorrhiza continuum is further complicated because signals produced by plants in response to herbivores can be transmitted to other plants via shared fungal networks below ground. Insect herbivores, such as aphids, are likely to affect the functioning of mycorrhizal fungi by changing the supply of recent photosynthate from plants to mycorrhizas, whereas there is evidence that mycorrhizas affect aphid fitness by changing plant signalling pathways, rather than only through improved nutrition. New knowledge of the transfer of signals through fungal networks between plant species means we now need a better understanding of how this process occurs in relation to the feeding preferences of herbivores to shape plant community composition and herbivore behaviour in nature.

**Keywords**

Common mycorrhizal networks; aphids; signalling; carbon cost; evolution; ecosystems; above-below ground interactions

**Introduction**

Above and below ground interactions with plants have tended to be considered separately. However, plants are physical conduits of mineral nutrients and water from soil, and energy from the atmosphere that mediate indirect interactions between above and below ground organisms [1]. In many terrestrial systems, such above-ground-below-ground interactions linked via plants involve a plethora of mycorrhizal fungi that colonise roots, numerous insect herbivores (such as aphids and caterpillars) which interact with plant leaves and the herbivores’ enemies (such as parasitoid wasps). Mycorrhizal fungi form symbiotic relationships with plants, whereby the fungi provide mineral nutrients to the plants [2] while the plants provide carbohydrates to the fungi [3]. The mycorrhizal fungus-plant-herbivore-enemy continuum (Fig. 1) has resulted in the evolution of a repertoire of elaborate signalling mechanisms that either up- or down-regulate plant defences [4, 5]. Importantly, mycorrhizal hyphae form underground networks that interconnect individual plants [6]. Recent research has demonstrated that, astonishingly, these fungal networks can transfer signals between plants in response to herbivore [7] and pathogen infestation of leaves [8], thereby warning neighbouring plants of nearby enemies (Fig. 1). This plant-plant signalling is likely to have fundamental consequences at the community level for mycorrhiza-plant-herbivore interactions, and add selective pressure on insect herbivores to evolve counter-mechanisms. Previous work has reviewed interactions between mycorrhizal fungi and herbivores mediated via plant responses [9, 10] but these were before the discovery of plant-plant below-ground anti-herbivore signalling. Recent reviews have discussed the implications of below-ground plant-plant signals for the fitness benefits to the fungi and potential applications in crop pest control [11], as well as speculating on the potential mechanisms of signal transfer and the ecological scenarios that may have given rise to the evolution of these signals [12]. However, our understanding of the impact of these underground signals on the continuum of interactions is in its infancy and, therefore, here we address the following questions: 1. What are the costs to plants of mediating mycorrhiza-insect herbivore indirect ‘apparent’ effects? 2. How will below-ground mycorrhizal-based signalling between plants impact on these apparent effects at the community level in the short-term and through evolutionary timescales?

**1. What are the costs to plants of mediating apparent effects between mycorrhizal fungi and insect herbivores?**

The costs and benefits to plants of mycorrhizal fungi and of insect herbivores separately are relatively well characterised. Many mycorrhizal fungi form extensive extra-radical mycelial networks that greatly increase the volume of soil available to the plant and, although there is increasing evidence that neutral and negative effects can occur, the response of plants to colonisation by mycorrhizal fungi is generally positive (Fig. 2) [9,10]. Mycorrhizal fungi generally increase plant mineral nutrient acquisition [2,5,13] and are especially important for increasing access to phosphorus (P), often resulting in increased plant biomass [13], and they can also increase plant tolerance to root and shoot pathogens and nematodes [14]. In return, mycorrhizal fungi obtain carbon from the plant for use in mycelial growth, which can be 10-20% of plant photosynthate [2]. Mycorrhizal fungal colonisation also induces changes to plant defences through the jasmonic and salicylic acid signalling pathways [4, 15], enabling them to achieve compatibility with the plant [16], and the cocktail of volatile organic compounds (VOCs) released from the leaves is also altered [5, 13, 17, 18].

In contrast to the general beneficial effect on plants of arbuscular mycorrhizal (AM) fungi, infestation by insect herbivores has detrimental effects on the plant (Fig. 2), for example aphids drain the plant of nutrients (including C) [19], can infect the plant with pathogens [20] and can reduce plant fitness and biomass [5, 13, 21]. Insect herbivore attack also induces costly chemical responses in the plant by affecting jasmonic and salicylic acid signalling pathways [23] (these responses can be plant-species specific [24]). These also affect the composition of the VOCs emitted from leaves [5, 10, 25] that render the infested plant less attractive or even repellent to subsequent herbivores, and attractive to natural enemies of these herbivores, such as parasitoids [26].

It is through these induced changes in plant health and defence responses that mycorrhizal fungi and insect herbivores interact with each other indirectly. For example, aphids can (at least in the short-term) increase or, more commonly, reduce AM fungal colonisation [9]. AM fungi can positively or negatively affect insect herbivores depending on whether they are generalists, specialists, chewers or suckers [8] and affect their enemies such as parasitoids [27]. New research provides evidence that a positive effect of AM fungi on aphids is mediated via changes in plant signalling pathways rather than only increased nutrition [13, 27]. Therefore, similarly to parasite-mediated apparent competition, where one host impacts on another host species through the action of the shared parasite (even though the two host species do not directly interact) [28], insect herbivores impact on AM fungi and *vice versa* through the induced changes in the shared plant.

When a plant is subject to both mycorrhiza and insect herbivores simultaneously, the net costs and benefits to the plant are much less clear. These three-way interactions raise several intriguing questions: (i) How does the timing of colonisation by mycorrhizal fungi and infestation by insect herbivores affect plant performance (Fig. 2)? (ii) Is there a predictable threshold of mycorrhizal colonisation combined with insect herbivore infestation that results in a net gain or loss of plant performance? And (iii) what are the consequences of any resource partitioning within a plant? Multi-factorial experiments of the three-way interactions are required to answer these questions. Babikova et al. [12] addressed the first question and found that total leaf P concentrations in bean plants depended on the timing of colonisation: P concentration was smallest in bean plants where pea aphids infested the plants before AM fungi colonised roots and greater in plants where AM fungi colonised before aphids (Fig. 2). The second question is a challenge to address; the threshold will likely depend on nutrient availability [13], the types of invertebrate herbivores, the community of mycorrhizal fungi and the plant species [9]. The final question of resource partitioning relates to plants having limited resources and the need to partition or allocate resources to where they are needed most at any one time. For example, if resources are used in defence responses against herbivores attacking leaves, are there fewer resources allocated to other parts of the plant, such as the roots? If so, could this be a mechanism explaining reductions in AM fungal colonisation often found in response to herbivore attack [5]? We could therefore predict that this would render roots more open to attack by below-ground herbivores and pathogens. However, plant defence responses and resource allocation is complex and difficult to predict. Several recent studies have found that some plants rapidly move sugars from leaves to roots in response to leaf herbivory [29, 30, 31], maybe in order to store resources below-ground for later re-growth [31] or to upregulate defence signals [29]. Some studies have reported positive (rather than the more common negative) effects on AM fungal colonisation in response to herbivory [32]; it would be intriguing to test whether the mechanism for this is associated with these recently found effects of herbivory inducing an increase in below-ground C allocation. Furthermore, it would be fascinating to explore whether the herbivore-induced shift in C allocation to roots is part of the mechanism for the recently discovered warning signals that aphid-infested plants send to their neighbours via AM fungal networks. Thus, a holistic analysis of the C economy of plants that are both in symbiosis with mycorrhizal fungi and infested with herbivores is required.

**2. How will signalling between plants via fungal networks impact on mycorrhiza-herbivore apparent effects at the community level?**

Few experiments have tested how the indirect apparent effects discussed above may work in a community context where multiple plant, mycorrhizal fungal and herbivore species coexist, with potentially different arrival orders [33]. One important process is interplant transfer of herbivore-induced signals, which can occur aerially [34], through root exudation [35] and, importantly, through the formation of ‘common mycorrhizal (or mycelial) networks’ (CMNs), that interconnect two of more plants of the same or different species [6]. These underground warning signals between plants have been shown to be transmitted through AM fungi between bean plants [7] and through ectomycorrhizal fungi between Douglas fir (*Pseudotsuga menziesii*)and ponderosa pines (*Pinus ponderosa*) [36]. Some of the evolutionary, functional and applied consequences of signal transfer have been speculated on [11, 37, 38] but evidence is needed to support these hypotheses. One major stumbling block currently limiting quantitative empirical studies is unravelling the nature of the signals themselves, which could involve transfer of molecules in solution though the hyphae or on liquid films on the surface of hyphae [38], or induction of ‘action potentials’ (electrical signals) [37, 39, 40].

Importantly, before inferring wider community implications of the CMN-based signals we need to know how species-specific the signals are, in relation to plants, mycorrhizal fungi and herbivores. We now know that signals in response to herbivory can be transferred between different plant species (Douglas fir and ponderosa pine) via ectomycorrhizal fungal networks [36], but further testing is needed for other plant groups, fungi and herbivores.

Previous reviews have speculated both on the ecological scenarios that might infer fitness benefits to the mycorrhizal fungi of sending the signals [11], and on the ecological circumstances (plant biodiversity and herbivore specificity) that might encourage the evolution of CMN-based inter-plant signals according to the benefits to the plants [37]. It is also interesting to hypothesise about the community level impacts of CMN-based inter-plant signals on insect herbivores, both in short-term and evolutionary timescales. It is useful to compare the concept of an ecosystem with plant-plant signals against one without signals. Since the signals are rapid (neighbouring plants respond within 24 h) [35, 37] and induce the plants to repel herbivores (and attract their enemies) even in uninfested neighbours [7, 8] and operate over at least 20cm [7], we can predict that, at least within localised patches, insect herbivores will fare worse and plants better if they are in the ecosystem with signals as compared to the ecosystem without signals. If the signals can operate over several CMNs and through several plants [11], and over longer distances (currently untested), the predicted positive effect on plants (and negative effect on insect herbivores) should occur over a wider area. In the long-term, what selective pressure might this exert on insect herbivores? If one incidence of herbivore attack on a plant renders whole patches (rather than an individual plant) less favourable for insect herbivores due to inter-plant signals, there may be greater selective pressure for insect herbivores to increase their motility and dispersal distances in order to reach favourable patches beyond the influence of the initial CMN-based signals (rather than merely moving to the adjacent plant). If signals are sent only between the same or similar plant species, wide dispersal would be unnecessary if the herbivore is a generalist, so an alternative evolutionary strategy to dispersal could be for specialists to become generalists. In contrast, if signals are sent between many plant species there is a greater need for wide dispersal, even for generalist insect herbivores, so becoming a generalist is predicted to be less advantageous in this situation.

Dispersal and migration are costly [41], and the delicate balance in the costs and benefits between staying on one plant or dispersing to a new plant is one of the many factors thought to contribute to the evolution of host specialisation and motility of insect herbivores [42]. Our new knowledge of inter-plant CMN-based signals implies that there may be fewer benefits of slow, short-range dispersal than previously thought. Given that fast, longer-range dispersal is costly (and often not even possible, e.g. for lepidopteran larvae) inter-plant CMN-based signals may therefore tip the balance, for some organisms and in some situations, in favour of remaining on the original plant and developing better resilience to the plant’s defences. This scenario may be more likely to result in the evolution of host specialisation. Thus, of the many factors influencing the evolution of insect herbivore specialisation and motility, inter-plant signals is yet another that needs to be considered.

**Conclusions**

The importance of aphid-plant-mycorrhiza interactions is gaining prominence from evolutionary, ecological and agricultural perspectives, but improving our understanding of these interactions requires integration of a range of different experimental approaches. Some are relatively straight-forward, such as quantifying the effect of insect herbivores on C allocation to mycorrhizal fungi. Others are more complex, however, and include gaining a better knowledge of the fundamental mechanisms by which plant communities interact with shared mycorrhizal fungal communities and *vice versa*. The role of signals in these interactions is crucial, but we need to identify what the signals are, their specificity, and whether their magnitude is related to functional responses. In particular, more experiments are required to better understand the role of signal transfer through common mycorrhizal networks in plant communities in nature, where plants support complex fungal communities and are attacked by both specialist and generalist insect herbivores.

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Figure legends

Fig. 1. Aphid-plant-mycorrhizal fungal interactions lead to changes in signalling pathways (1) that affect production of volatile organic compounds (VOCs), which are released aerially to induce defences in neighbouring plants or that serve as cues for insects. Aphids likely affect bi-directional transfer of mineral nutrients and carbon between mycorrhizal plants and fungi, and inter-plant signalling can also occur via common mycorrhizal networks (modified from [39]).

Fig. 2. a) Interactions among the mycorrhizal fungus, plant, aphid, parasitoid continuum. Red arrows indicate negative effects and green lines positive or neutral effects. Mycorrhizal fungi-plant interactions are generally positive (*1*) involving bi-directional transfer of nutrients. Plant VOCs are usually attractive to aphids (*2*), which use VOCs as cues to locate suitable leaves (*3*). Plants respond by producing VOCs that are repellent to aphids (*3*) but attractive to parasitoids (*4*), which predate aphids (*5*). Disruption of carbon physiology or signalling pathways of plants may feedback negatively to mycorrhizal fungi (*6*). Additional external biological drivers may affect the strength of interactions including inter-plant transfer of signals received aerially or via common mycorrhizal networks. b) The strength of interactions also depends on the arrival order of aphids relative to mycorrhizal fungi. Aphid infestation tends to have negative effects on mycorrhizal fungal colonisation of plant roots when the fungi are establishing, i.e. when aphids arrive on the plant before the fungi (dashed line, right hand axis) although the shape of the curve throughout the colonisation process is unknown. The attractiveness of the plant VOCs to aphids (solid line, left hand axis) is maximum for mycorrhizal plants without aphids, reduces when aphids infest already-mycorrhizal plants and plant become repellent to aphids if they are infested with aphids before mycorrhiza.

Fig 1



Fig 2

