Plant coexistence mediated by arbuscular mycorrhizal fungi

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Recent research has indicated the importance of arbuscular mycorrhizal fungi (AMF) in mediating plant coexistence. Coarse-scale studies compare the effects of the presence versus absence of AMF on plant coexistence, a phenomenon that is most relevant in early successional ecosystems where AMF are patchily distributed. By contrast, fine-scale studies investigate interactions that might occur once AMF have developed more fully within ecosystems, and most plants come into contact with AMF. Whereas coarse-scale effects are well understood, our understanding of fine-scale factors is just developing, as a result of investigations into AMF–plant specificity, AMF species richness, shared mycelial networks, and plant–AMF feedback effects. Further research into these areas will provide a better understanding of factors that mediate plant species co-existence and, ultimately, the maintenance of biodiversity within plant communities.

The term ‘coexistence’ has been used by ecologists to describe a balanced mixture of species in a biotic community. Such coexistence is a biological riddle, because the tendency towards competitive exclusion should favour a monoculture. Theories attempting to explain plant coexistence have focused on either interactions among species, such as competitive balance [1–3], or the avoidance of interaction among species [4,5]. Non-interaction theories have traditionally examined the role of spatial segregation and disturbance in promoting or suppressing plant coexistence.

Agent-mediated coexistence is a non-interaction theory proposed as a mechanism for maintaining multi-species assemblages in plant communities [6,7]. When the ‘agent’ is a pathogen or a predator, it can reduce the ability of a plant to compete for resources if the tissues affected are involved in resource gathering (root or leaf). Often, the effects of pathogens and predators can be density dependent, in that the most abundant host plant species loses more tissue than do less abundant plant species. As a result, less abundant plant species experience reduced competition, lessening their chance of competitive exclusion, and thus promoting species coexistence within plant communities.

It has been suggested that arbuscular mycorrhizal fungi (AMF), a common group of symbiotic fungi in the order Glomales (Division Zygomycota), might also be important agents promoting plant coexistence [8–11]. These fungi infect the roots of most plant species and provide their hosts with greater access to mineral resources. If an otherwise less competitive plant species is infected by more AMF than is a highly competitive plant species, then AMF should promote coexistence by increasing the ability of less competitive species to access nutrients [12,13]. Alternatively, if a highly competitive plant species is also more infected by AMF, then AMF would simply reinforce competitive dominance by that species [14].

There is significant evidence in the literature to support the hypothesis that the presence and abundance of AMF can mediate plant species coexistence. Recent research has identified several other mechanisms involving interactions among AMF, plants and the soil environment that can further influence plant species coexistence and the maintenance of biodiversity within plant communities. Our objective here is to summarize these recent findings and to recommend areas of research that will advance our understanding of AMF as agents of plant coexistence and, ultimately, of their role in plant community structure and ecosystem dynamics.

Coarse-scale and fine-scale effects of AMF on plant coexistence

Traditionally, researchers have investigated the influence of AMF on plant coexistence by comparing the outcome of plant competition with AMF presence versus absence, an approach that enables the study of coarse-scale effects (i.e. the impact of presence or absence of AMF biomass) (Table 1). Such effects would be relevant to the outcome of plant interactions mainly in early successional ecosystems, where plants and soil have been severely disturbed and AMF are either absent or are in low abundance and patchily distributed.

More recent studies have considered the effects of AMF on plant coexistence at a fine scale, where all experimental treatments contain AMF (Table 1). The experimental manipulations can involve the composition and diversity of AMF, and the ways in which they interact with plants and their soil environment. Such experiments are more relevant to later-successional situations, in which AMF are more abundant and less patchy, and the roots of most plants come into contact with them. At this scale, factors such as host specificity, AMF multifunctionality, shared mycelial networks, and plant–fungus feedback interactions might be important determinants of plant coexistence.

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Table 1. Coarse- and fine-scale effects of AMF on plant coexistence[a]

Type of AMF effect	Habitat type	Refs
Coarse scale		
The presence/absence of AMF affects competitive balance among plants	Tallgrass prairie	[9,11,21,22]
	Grassland	[12–14,23,24]
	Meadow	[20]
	Semi-arid herbland	[25]
Fine scale		
Different AMF confer different advantages to different plants		
Host specificity	Tallgrass prairie	[33]
	Grassland	[31,35]
	Meadow	[36–38]
	Agroecosystem	[32]
	Tropical Forest	[34,43]
	Temperate Forest	[44]
Multifunctionality	Grassland	[39]
	Meadow	[37]
Feedback among plants and AMF	[b]	
AMF species richness affects plant diversity	Grassland	[49]
	Meadow	[49]
AMF can link different plant species via common mycelial network	Tallgrass prairie	[53]
	Grassland	[52]
	Meadow	[20,54,55]

[a] Abbreviation: AMF, arbuscular mycorrhizal fungi.

[b] See Box 1.

Coarse-scale AMF effects on plant coexistence

The presence of AMF is known to have a strong effect on the direction of succession [8,10,15,16]. Early in succession, AMF levels are likely to be both low and restricted to physically separated patches, because of recent soil disturbance [17,18]. The immigration and subsequent presence of AMF could thus affect plant coexistence by enabling a mycorrhizal-dependent plant (one whose growth responds significantly to AMF infection) to become more competitive because of its increased uptake of limiting soil nutrients [10]. When two competing plants differ in mycorrhizal dependency, the coexistence of those plants will be promoted in the presence of AMF when the inferior competitor is more mycorrhizal dependent, but coexistence will be inhibited if the superior competitor is more mycorrhizal dependent.

Results of experimental studies involving the addition or removal (using fungicide) of AMF provide strong evidence that AMF control plant coexistence [19]. In a mesocosm study in which seeds of many species were sown and plant communities developed in the presence versus absence of AMF, adding AMF promoted plant coexistence by increasing the biomass of competitively subordinate species relative to that of the dominants [20]. Conversely, removing AMF from tall grass prairie soil promoted plant coexistence because the dominant grasses were more mycorrhizal dependent than were subdominant species [21,22]. Similarly, experimental removal of AMF promoted coexistence by reducing the ability of mycorrhizal-dependent *Centaurea maculosa* to invade native grasslands of western North America [23,24], and of *Medicago minima* to invade an Australian grassland [25].

Additional studies of coarse-scale effects of AMF are needed to determine the relative importance of AMF concentration and soil nutrient availability. At a high concentration of AMF inoculum, infection by AMF might become detrimental rather than beneficial because heavily infected plants might experience a large carbon removal that outweighs any benefit. Gange and Ayres' model [26] suggests that the benefits accrued to the plant from an AMF infection is greatest at an intermediate level of infection or AMF inoculum density. Further experimental studies should therefore include more than just two levels of AMF (presence versus absence) to explore AMF concentration-dependent effects on plant coexistence.

Regardless of AMF concentration, soil phosphorous (P) availability could determine whether AMF will affect the outcome of competition among neighbouring plants. When soil P availability is low, competition for it should be strong and AMF should mediate plant coexistence by influencing the pattern of nutrient uptake by neighbouring plants. In soils with high P availability, the benefit of increased P uptake owing to AMF is probably negligible. In fact, the cost of an AMF association might exceed any benefit [27,28], reducing the ability of a mycorrhizal plant to coexist with its non-mycorrhizal neighbours. Janos [8] predicted that, in highly fertile soils, mycorrhizal-dependent plants would be selected against, whereas infertile soils would support a highly mycorrhizal-dependent plant community. Fertilization of soil reduces the abundance and diversity of AMF [29] and could select for AMF that are less beneficial [30]. However, it is not known whether changes in soil nutrient availability alter the ability of AMF to mediate plant coexistence.

Fine-scale AMF effects on plant coexistence

As succession proceeds, the distribution and abundance of AMF increase such that any effect of AMF on plant coexistence will reflect fine- rather than coarse-scale processes. Most plants are infected by AMF and, at this scale, host specificity, shared mycelial networks, AMF species richness and plant–fungal feedbacks might be important determinants of plant coexistence.

Host specificity

Traditionally, AMF have been considered to be generalists with regard to the hosts that they infect. They have also been considered to be functionally equivalent in their effects on a host. These beliefs are based largely on the fact that most AMF can successfully infect a wide range of plant species when grown experimentally in monocultures. However, when different plants and fungi are grown together, AMF growth and species composition is host specific [31–34]. Consequently, some AMF species are more beneficial to a host plant than are others, because of genetic and/or physiological incompatibilities between an AMF and its host [35–38]. In addition, AMF species differ in the services that they provide for host plants (e.g. nutrient uptake, protection against pathogens, and water uptake) [37,39]. The consequence of AMF–host plant specificity for plant coexistence is now being explored, both theoretically and experimentally. Bever [36] hypothesized that AMF might have differential feedback effects on plants (Box 1). Experimental tests of his model confirm that both negative and positive feedback occur between plant and AMF communities, and that this feedback could potentially contribute to plant coexistence (Box 1).

Although the roles of host specificity and feedback are important for host plant coexistence, evidence for both of these mechanisms remains indirect. Future research must determine the extent to which AMF and their hosts form specific associations, especially in natural communities. Researchers must first develop appropriate molecular tools to separate AMF species and to quantify their abundance, both within root systems and in the soil. Recent studies have uncovered a high taxonomic diversity of fungi associated with individual plants [40,41], especially in more natural systems compared with managed farmland [42]. More importantly, they are beginning to uncover significant associations among plant and AMF taxa under field conditions [43,44].

AMF species richness

As succession proceeds, AMF species richness increases because of immigration via wind dispersal and animal vectors [17]. This increases the probability that a compatible plant host and AMF will come into contact and that the AMF will affect plant growth. Increased AMF species richness is argued to be beneficial both in terms of host compatibility [31,33,35,37,45–48] and in terms of multifunctionality of AMF [37,39]. However, few studies have examined the link between AMF richness and plant coexistence. Using macrocosms, van der Heijden *et al.* [49] demonstrated superior host growth for a larger number of host species in experimental units containing a high diversity of AMF species compared with those containing few AMF taxa. The authors argued that the mechanism behind the observed results was host specificity and that an increase in hyphal lengths and nutrient exploitation occurred with increasing AMF richness. However, the mechanisms were not explicitly tested. Therefore, even though it is acknowledged that AMF diversity can be important for plant coexistence, theoretical and empirical studies are still needed [50]. One probable underlying mechanism is that there is tight association between plant and fungal taxa, and that plants differ in mycorrhizal dependency with different AMF taxa [50]. If this is the case, then higher AMF diversity could lead to higher plant coexistence simply by increasing the probability of individual plant species associating with a compatible and effective AMF partner. Future research addressing host specificity should also provide insight into this possible mechanism.

Other possible mechanisms might involve complex interactions, such as interference and exploitation competition, among coexisting AMF in the soil that is further modified by other soil factors, such as nutrient heterogeneity and predation pressure by invertebrates. Such interactions in decomposer fungi have been shown to influence greatly the productivity and composition of

Box 1. Feedback between plants and arbuscular mycorrhizal fungi

A feedback response occurs between interacting organisms (here, referred to as a ‘complex’) when one organism (A) affects the growth of another (B), which, in turn, has a positive (or negative) effect on the performance of the other organism (A) (Fig. Ia). Within such co-adapted complexes, organism A could be self promoting (positive feedback) or self limiting (negative feedback) by affecting the growth of organism B.

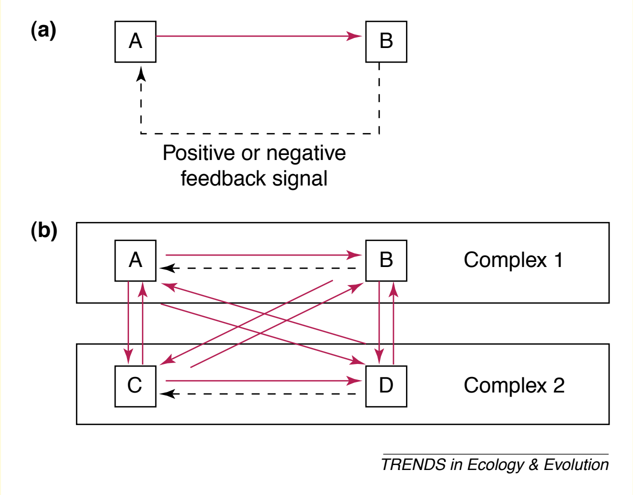

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Fig. I.

When considering multiple complexes, intra- and intercomplex interactions among members might become more complicated. For example, when considering two complexes, each containing two organisms, each organism can form a feedback relationship with each of the other organisms (Fig. Ib).

Arbuscular mycorrhizal fungi (AMF) and their plant hosts fit this feedback model very well. AMF are obligate biotrophs and are thus stimulated by their plant hosts. In return, AMF can either be beneficial, by stimulating plant growth via enhancing nutrient access, or they can be detrimental to plant growth by exerting a heavy carbon demand on the plant [27]. Furthermore, AMF can also positively or negatively influence the growth of neighbouring plant hosts. The traditional view is that host plants will receive the most benefit from their co-adapted AMF community (or complex). Thus, there is positive intracomplex feedback, and negative intercomplex feedback. Although there is some support for this view [58], it has not been widely tested.

Recent evidence suggests that the traditional view is too simplistic. Negative feedback can also occur within complexes and positive feedback can also occur between complexes. For example, in a study of two coexisting grassland plants, Bever *et al.* [59–61] showed that whereas an AMF species (*Scutellospora heterogama*) was most often associated with the host plant *Plantago lanceolata*, this plant received the most growth benefit when grown with the AMF associated with the neighbouring *Panicum* sp. (*Acaulospora* sp. and *Achaeospora* sp.)

According to the traditional view, positive feedback within complexes would promote plant coexistence only if all plants received equally strong positive feedback from their associated AMF. If there was differential positive feedback, then the plant with the strongest positive feedback should ultimately exclude other plants because of competitive dominance, thereby suppressing plant coexistence [36]. Negative feedback also has the potential to affect coexistence [62]. If all host plants receive some negative feedback from their associated AMF, then it should not be possible for any one plant to exclude another, because they would all be self limiting. Although there is initial evidence for negative feedback between AMF and their hosts, it remains to be demonstrated that this negative feedback mediates plant coexistence.

terrestrial ecosystems; however, this has not been done with AMF primarily because individuals within a community cannot be easily distinguished. To unravel these interactions, and their influence on plant coexistence, requires further development of molecular-based techniques to track individual AMF and to distinguish them from neighbouring AMF taxa. In addition, the spatial scale at which AMF diversity is important remains to be explored. Existing studies consider primarily scales of up to only 1 m^2. Larger scales must also be investigated, because mechanisms that determine species diversity vary with spatial scale [51]. Finally, future research should compare AMF effects in different habitats. AMF richness differs across a gradient of habitats and/or biomes, and this difference in diversity could have important functional implications.

Shared mycelial networks

As succession proceeds, the size of AMF patches increases, as does plant density, which creates an opportunity for a common mycelial network to be shared by neighbouring plants. This mycelial network might promote plant species coexistence by equalizing the distribution of soil resources among competitively dominant and subdominant host species. Soil nutrients and plant-derived carbon might flow through the network from dominant to subordinate host plants, because of a concentration gradient created initially when the dominant plant takes up more nutrients than does a subordinate plant.

Transfer of inorganic nutrients through a common mycelial network was detected by Malcova *et al.* [52] under laboratory conditions and by Walter *et al.* [53] in a field experiment. Phosphorus was transferred differentially among co-occurring plant species. However, it is not known under what conditions, if any, such transfer is biologically important, because plant–plant transfer is minor relative to soil–AMF–plant transfer. A similar flow of carbon might occur from plant to plant across a source–sink gradient. In a mesocosm experiment, Grime *et al.* [20] used radioactive isotopes to show that carbon transfer occurred via hyphal links rather than through environmental leakage. However, is the amount of transferred carbon significant enough to have any biological significance? More recently, Graves *et al.* [54] and Robinson and Fitter [55] confirmed that plant carbon is transferred between plants through a shared AMF hyphal network, but that the transferred carbon remained within plant roots. Both set of authors argue that the carbon might remain in fungal tissues within the roots, rather than being transferred to other plant tissues. Overall, the possibility of nutrients and carbon flux from plant to plant via AMF is intriguing, but the ecological significance of this is unknown. Rather than simply determining the existence of common mycelial networks, future research should try to determine the effects of such links on the survival, growth and reproductive success of individual plants as well as species coexistence and the maintenance of plant diversity.

Prospects

AMF can affect plant coexistence on both a coarse and fine scale. However, whereas coarse-scale factors, such as AMF availability and distribution, are reasonably well understood, our understanding of fine-scale factors is just starting to develop. The combination of host specificity, AMF species richness and shared mycelial networks has the potential to influence plant coexistence, and hence plant community structure. To evaluate this potential, there is a need for field-based experimental research, in which complex AMF–plant interactions have already been established. The development of AMF populations and the interactions within AMF communities are difficult to study because of the cryptic nature of soil and our inability to distinguish among fungal individuals using morphological characteristics. However, work at this scale will be required to further our understanding of the influence of AMF on plant coexistence. The development and routine use of genetic markers that can be used to track the growth and spread of AMF within the soil will certainly help. With such techniques, it will also be possible to address whether different plant species prefer to associate with different AMF, or whether any AMF isolate is equally beneficial to plant growth and development. It will also be possible to determine whether individual AMF mycelia can colonize multiple plant species simultaneously and, ultimately, the functional dynamics associated with common mycelial networks.

Furthermore, major advances in our understanding of plant coexistence will require moving away from studying individual model plants under greenhouse conditions. Plant responses to AMF treatments will need to be assessed at the level of plant populations and communities. The effects of AMF on individual plants differ from those at the population and community level, because of density-dependent and species-dependent processes [56,57]. To achieve this move, we recommend two general approaches.

First, there must be a comparative approach of different ecosystem types, because the influence of AMF on plant coexistence is unlikely to be identical in all ecosystems. In particular, a comparison of mycorrhizal structure and dynamics in habitats containing species-rich versus species-poor plant communities will provide insights into the potential roles of AMF on maintaining plant diversity. Second, a manipulative approach will provide tests for any hypotheses that are developed from comparative studies. We recommend the use of macrocosms, in which plant and AMF communities can be established, because controlled manipulative experiments are too difficult to conduct directly in natural ecosystems owing to difficulties in experimentally eliminating all or a subset of the existing AMF from the soil.

We have come a long way since the classic coarse-scale experiments involving individual plants in pots, with or without the presence of AMF inoculum. AMF are not all functionally similar, thus coarse-scale approaches that ignore the composition of AMF assemblages provide limited power with which to determine mechanisms of action. Future progress will depend on the use of molecular techniques that will then enable the study of interactions within AMF communities. Future research also needs to be theory driven, as there is surprisingly little theoretical work about AMF symbioses; it should also be expanded to ecosystems other than grasslands as AMF occur in most terrestrial biomes.

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