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Mycorrhizal diversity: Cause and effect?

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Summary

Mycorrhizal fungi play a critical role in nutrient cycling and ecosystem function. They improve plant growth and survival through a mutualistic relationship in which photosynthates are exchanged for increased access to water and nutrients. Because the benefits realized are not equal among different plant–fungal species combinations, mycorrhizal fungi may help govern plant community structure and successional trajectories. In fact, both plant productivity and plant diversity have been shown to increase with increasing diversity of mycorrhizal fungi. The diversity and species composition of plant communities also exert a reciprocal influence on associated mycorrhizal communities, although edaphic factors may also play a role. Given this inherent bi-directionality of mycorrhizal relationships, the potential exists for positive feedback mechanisms which may promote and maintain both plant and mycorrhizal fungal diversity. This review considers recent literature on both arbuscular and ectomycorrhizal fungal–plant community relationships within a variety of environments, including artificially constructed systems and naturally occurring grasslands and forests.

Introduction

Mycorrhizal fungi are the main pathway through which most plants obtain mineral nutrients and, as such, are critical in terrestrial ecosystem functioning. In this mutualistic symbiosis, plants exchange photosynthates, not only for mineral nutrients, but also for increased resistance to disease, drought and extreme temperatures (Smith and Read, 1996). Some groups of mycorrhizal fungi may also mediate plant competition through the formation of mycelial linkages, through which carbon is shared among different plant species (Simard and Durall, 2004).

Six general types of mycorrhizal symbioses are currently recognized (Read, 1999), although the majority of terrestrial plant species belong to groups which form arbuscular mycorrhizae (AM) (Trappe, 1987). The fungi involved in AM symbioses have recently been recognized as comprising their own phylum, the Glomeromycota (Schüssler et al., 2001), which reproduce by soil-borne spores and have yet to be grown in pure culture.

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The ectomycorrhizal (EM) symbiosis is also common and well studied. In contrast to AM, however, the range of host plants is much narrower, and includes mainly woody species. The fungi involved in EM include a wide range of ascomycetes and basidiomycetes, many of which form macroscopic fruiting bodies and may be cultured separately from their host plants. Other groups of mycorrhizal symbioses involve specific plant groups, (e.g. orchid, ericoid and arbutoid mycorrhizae). However, as the vast majority of information on the ecological relationships between plant and fungal partners has been obtained from studies of either AM or EM symbioses, only these groups will be treated here.

Research into the influence of mycorrhizal colonization on plant growth and community structure has progressed further in the AM symbioses, because of the relative speed and ease with which artificial herbaceous plant communities can be manipulated. Research into EM ecology on the other hand, has progressed further with respect to the structure of the fungal community, due to the greater understanding of the biology and taxonomy of the fungal partner.

The importance of mycorrhizal fungi in the relationship between biodiversity and ecosystem functioning is now being recognized, particularly with respect to their potential to control plant diversity and productivity (van der Heijden et al., 1998a). There is also a growing understanding of the role of the plant community in determining the structure of mycorrhizal fungal communities (Burrows and Pfleger, 2002; Kernaghan et al., 2003). Results from these two lines of research suggest that reciprocal influence (feedback) between plant and mycorrhizal fungal communities may play a fundamental role in determining the species composition and diversity of both plant and fungal communities.

Consequences of mycorrhizal diversity

Influence of mycorrhizal diversity on individual host plants

Mycorrhizal colonization influences not only host plant survival and productivity, but also other traits, including foliar quality (Goverde et al., 2000), clonal morphology (Streitwolf-Engel et al., 1997) and fitness (Xiaohong and Koide, 1994). The benefit to host plants from increased root colonization by a single fungal species has proven inconsistent (Fitter, 1991; Fitter and Meryweather, 1992), and the outcome of different plant–fungal species combinations is highly variable (Klironomos, 2003). However, the diversity of fungal species involved in colonization has emerged as an important determinant of plant benefit from mycorrhizal colonization. Two recent experiments have demonstrated increased productivity in tree seedlings with increasing numbers of EM fungi. Jonsson et al. (2001) found increased growth after inoculation with mixtures of up to eight EM fungi, although the results were dependent on host species and substrate fertility. Baxter and Dighton (2001) saw a similar effect using *Betula* seedlings, although the positive response was restricted to root growth and nutrient uptake.

A likely explanation for the observed increase in plant productivity with diversity of mycorrhizal fungi lies in the physiological variation (functional diversity) among species of mycorrhizal fungi. Dighton et al. (1990) found variation in phosphate uptake by different EM fungal symbionts of *Betula* and Jakobson et al. (1992) and Smith et al. (2000) demonstrated differences in mycelial growth and phosphorus foraging strategies among species of AM fungi. Variation in resource acquisition patterns should mean that an increased diversity of mycorrhizal fungi will more efficiently extract resources from the soil and therefore elicit a greater host plant response. An extreme example of a functionally diverse mycorrhizal symbiosis involves the concurrent colonization of the same host plant (and even the same root tip) by both AM and EM fungi (Lodge, 2000). Given that AM and EM fungi have been shown to access different soil nutrient pools (Michelsen et al., 1998), nutrient scavenging in these tripartite relationships should be much greater than with AM or EM fungi alone.

Mycorrhizal diversity may also influence host plants indirectly via fungal productivity. Diversity and productivity are thought to be strongly linked in plant communities (Tilman et al., 1996) and evidence suggests that this is may be a property of communities in general (Naeem et al., 1994). If this relationship also holds true for mycorrhizal fungi, a more diverse mycorrhizal community should be more productive in terms of spores and mycelium, which should translate into increased inoculum potential, root colonization rates, and plant growth response.

Effects of mycorrhizal diversity on plant populations and communities

The repercussions of a diverse community of mycorrhizal fungi inhabiting the soil are not limited to the physiological responses of individual plant species. In fact, the influence of the mycorrhizal community appears to extend to the level of plant populations and communities (Miller and Kling, 2000). With respect to plant populations, either naturally occurring or as cropped monocultures, the increased vigor and fitness afforded by mycorrhizal colonization should benefit the population as a whole (Koide and Dickie, 2002). Colonization by AM fungi may also increase intraspecific plant competition by magnifying differences among individuals (Facelli et al., 1999; Marler et al., 1999) or, in the case of EM fungi, reduce intraspecific competition by transferring carbon among plants along a source sink gradient through a shared mycorrhizal network (Newman, 1988; Perry et al., 1989a; Simard et al., 1997).

With respect to plant communities, Grime et al. (1987) found that AM colonization influenced the structure of artificially constructed assemblages of annual plants by promoting the growth of subordinates and thereby increasing plant diversity. Mycorrhizal fungal control of plant community structure was also demonstrated by van der Heijden et al. (1998a), who found that increasing the number of introduced AM fungal species in artificial mesocosms led to increases in both plant productivity and diversity. The proposed mechanism for this effect was based on previous experiments (van der Heijden et al., 1998b), which demonstrated variable plant growth responses to different AM plant–fungal species combinations. The relationship between fungal richness and plant diversity is therefore thought to be due to a greater probability of "functionally compatible" plant–fungus combinations (Read, 1998). It is now generally accepted that variation in host response to individual mycorrhizal fungal species is an important determinant of plant community species composition and diversity (Hart and Klironomos, 2002; van der Heijden, 2002).

Although several authors have reported a positive relationship between plant diversity and AM fungal colonization (Grime et al., 1987; Gange et al., 1993; van der Heijden et al.,1998a), others report that artificially decreasing mycorrhizal colonization has lead to increasing plant diversity (Wilson and Hartnett, 1997; Hartnett and Wilson, 1999). These seemingly contradictory results are likely due to variation in the dependence on mycorrhizal colonization among plant species. Urcelay and Diaz (2003) propose a model in which a positive relationship between mycorrhizal colonization and plant diversity should occur in plant communities in which all species, or at least the subordinate species, exhibit a strong growth response to mycorrhizal colonization (high mycorrhizal dependence). On the other hand, plant diversity could decrease if the dominant plant species are strongly dependent on mycorrhizal colonization and subordinate species are not. In the latter situation an increase in the diversity of mycorrhizal fungi would not necessarily promote increased plant diversity. Clearly, more research into individual plant and fungal species interactions is needed in order to understand relationships at the community scale.

Factors controlling mycorrhizal diversity

Direct effects of host plant community

Numerous biotic and abiotic factors interact to govern the structure of mycorrhizal fungal communities. The most obvious of these is the structure of the above ground plant community, through specificity or preference exhibited by either partner in the mycorrhizal symbiosis. Plant roots exude not only carbohydrates, to be used as the energy source for mycorrhizal fungi, but also a wide variety of other organic compounds including amino acids, nucleotides, phenols aldehydes, keytones, esters, and terpenoids (Koske and Gemma, 1992). Some of these accumulate in the rhizosphere and are used by rhizosphere microorganisms living in close proximity to the root. However, many low molecular weight compounds may diffuse through the soil and influence microbes living at a distance from the host (Curl and Truelove, 1986). Root exudates from compatible host plants have been shown to influence both spore germination and hyphal growth in some species of AM (Gianinazzi-Pearson et al., 1989) and EM (Fries, 1983) fungi. Although the exact mechanisms controlling host specificity or preference are still unknown, it seems clear that it involves host–symbiont communication via secondary compounds (Anderson, 1988; Horan and Chilvers, 1990). These may include plant flavanoids (Vierheilig and Piché, 2002) and fungal auxins (Podila, 2002), both of which have been implicated in signaling between mycorrhizal fungi and host roots during the initiation of mycorrhizal formation.

Host specificity is well known in the EM symbioses and often acts at the generic level (e.g. host genus–symbiont genus) (Newton and Haigh, 1998; Massicotte et al., 1999), although many examples of genus–species and species–species specificity exist (Molina et al., 1992). Although some studies have demonstrated low levels of host specificity between pairs of coniferous species (Horton and Bruns, 1998; Cullings et al., 2000), it is likely that the importance of host specificity will increase with decreasing relatedness among host plants. For example, Kernaghan et al. (2003) found large variations in EM communities colonizing the roots of different host trees (including coniferous and deciduous species), intertwined in the same soil sample (Fig. 1).

Several studies have demonstrated strong relationships between plant and EM fungal community structures on the basis of fruiting body surveys (Billis et al., 1986; Nantel and Neumann, 1992; Såstad, 1995; Ferris et al., 2000). Fruiting body production, however is influenced by several environmental factors and may not be a reliable indicator of the mycorrhizal fungi actually colonizing host roots (Gardes and Bruns, 1996). Although fewer in number, studies which have assessed the relationship between plant diversity and EM diversity directly from roots, lead us to a similar conclusion. Jones et al. (1997) found that the EM communities associated with *Betula* and *Pseudotsuga* were more even in mixed stands than in single species plantations and Kernaghan et al. (2003) found that host specificity was related to a positive correlation between tree diversity and EM diversity in a range of boreal mixed-wood forest types.

EM diversity may also be related to stand age, as fungal species composition tends to change predictably over time (Last et al., 1987) and older conifer forests often support a greater number of fungal species than younger stands (Visser, 1995; Rao et al., 1997; Smith et al., 2002). However, the observed changes in EM fungal communities over time may have as much to do with developmental stage of the soil, as with host age per se (Blasius and Oberwinkler, 1989).

In contrast to EM, AM fungi have gained a reputation as broad generalists (Leake et al., 2004). However, it is clear that AM fungal communities are also influenced by the structure of their associated plant communities. Using artificially constructed plant assemblages, Burrows and Pfleger (2002) found that richer plant communities supported greater spore production and spore richness. Johnson et al. (2003) assessed AM fungal DNA and found that the composition of artificial plant assemblages had a significant impact on AM genetic diversity. Recently, host specificity and the influence of plant species composition have also been demonstrated in natural ecosystems, using both spore production (Eom et al., 2000) and AM fungal DNA (Husband, 2002; Vandenkoornhuyse et al., 2002).

Plant community productivity may also influence mycorrhizal diversity. Zak et al. (2003)

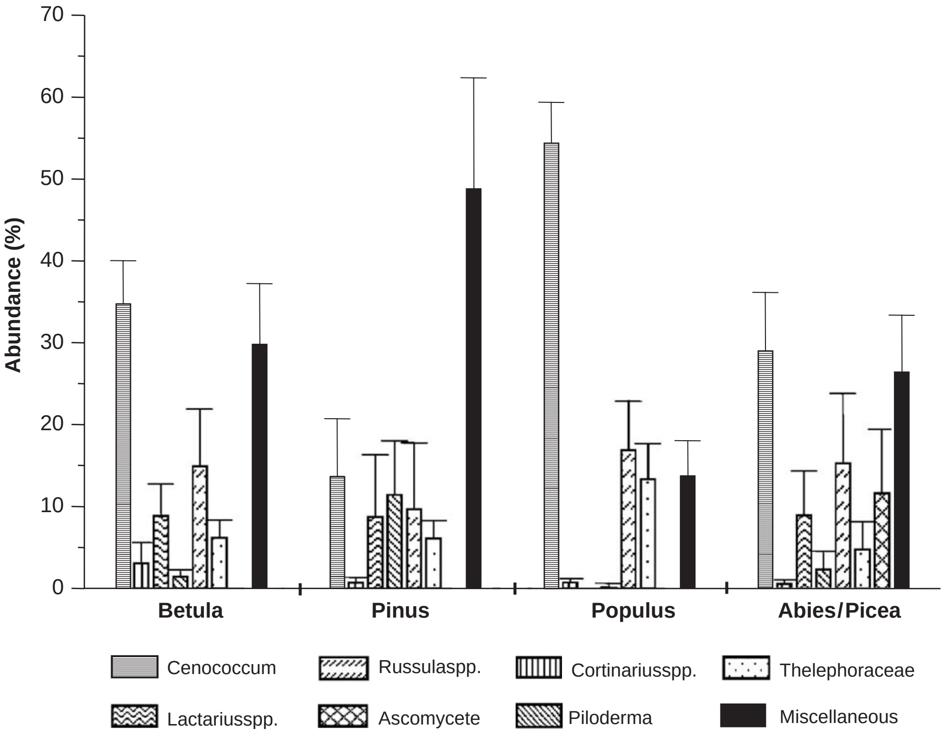

Figure 1. Variation in proportions of EM fungi colonizing co-occurring roots of different host tree species in southern boreal mixed woods. Values are averaged over 36 samples. Error bars represent the standard error of the mean. Based on data from Kernaghan et al. (2003).

demonstrated that several indicators of microbial activity, including fungal abundance, increased with plant productivity. However, as plant productivity is thought to be intimately linked to plant diversity (Tilman et al., 1996), discrimination between the effects of host plant diversity and host plant productivity on mycorrhizal fungi presents a significant challenge.

Effects of edaphic conditions

There is significant evidence pointing to the importance of soil conditions in the control of mycorrhizal fungal communities (Bruns, 1995; Erland and Taylor, 2002). Given that EM fungi are capable of utilizing organic forms of soil nutrients through the production extracellular enzymes (Read et al., 2004), and that some EM fungi possess limited saprotrophic ability (Colpaert and Van Tichelen, 1996), the quantity, quality and heterogeneity of soil organic matter is likely to have a significant influence on the structure EM fungal communities. Conn and Dighton (2000) demonstrated differences in EM fungi colonizing pine roots in artificially constructed mixtures of pine and oak leaf litter and suggest that the effect was due either to differences in nutrient availability or to the effect of leaf litter extracts on fungal growth (Baar et al., 1994). Rühling and Tyler (1990) identified soil base saturation and organic matter content as the most important factors governing the distribution of both mycorrhizal and non-mycorrhizal macrofungi in Swedish deciduous forests and Hansen (1988) suggested that EM fungal distribution in these forests, although obviously tied to host plant distributions, may be further influenced by edaphic factors. A similar trend was observed in the relationship between host plant diversity and EM diversity with increasing elevation across tree line in the Canadian Rockies (Kernaghan and Harper, 2001). Although plant diversity peaked at tree line, where the subalpine and alpine plant communities merge, EM diversity decreased with elevation (Fig. 2). In this case, the dramatic decrease in productivity and organic matter accumulation with increasing elevation appeared to override any effects of host plant diversity on mycorrhizal diversity.

With respect to edaphic controls of AM fungal communities, Johnson et al. (1992) used different combinations of soil type and host species to demonstrate that the distribution of some AM fungal species was dependent on soil type, some on host species and some on specific plant–soil combinations. Although it has long been thought that AM fungi differ from EM fungi in their lack of ability to utilize organic forms of soil nutrients (Read, 1993), recent evidence suggests that some AM species can access organic phosphorus (Koide and Kabir, 2000) and organic nitrogen (Hawkins et al., 2000; Hodge et al., 2001). The characteristics of soil organic matter may therefore play a greater role in determining AM fungal species composition than previously thought.

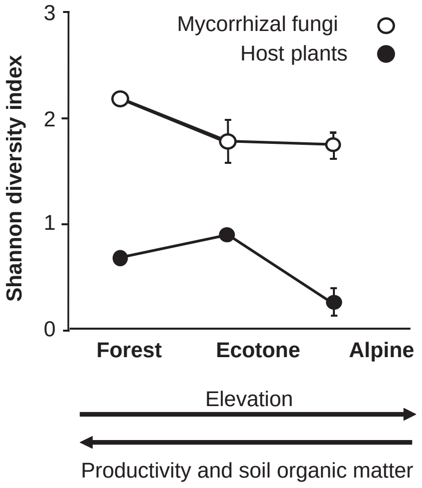

Figure 2. Shannon diversity indices for host plant genera (closed circles) and genera of ectomycorrhizal fungi (open circles) at three elevations across the alpine–subalpine ecotone of the Canadian Rockies. Based on data from Kernaghan and Harper (2001).

In these examples, however, many of the edaphic influences on the mycorrhizal fungi are, in fact, indirect effects of the plant community, via organic matter deposition. Differences in pH, nutrient status and phenolic content of the soil organic horizon (all of which may impact fungal growth) are mainly due to inputs from the plant community (Hobbie, 1992; Wardle, 2002).

Other factors influencing mycorrhizal diversity

Mycorrhizal fungal communities are also influenced by interactions with other soil organisms. Mycorrhizal helper bacteria (Garbaye, 1994) can improve root colonization by EM fungi, while competition with saprophytic fungi (Shaw et al., 1995), browsing of mycelia by soil fauna (Setala, 1995), and above-ground herbivory (Gehring and Whitham, 2002), may all decrease colonization.

Several anthropogenic influences are also known to decrease mycorrhizal diversity, or at least cause changes in species composition. These include forest harvest (Jones et al., 2003), wildfire (Dahlberg, 2002), atmospheric nitrogen deposition (Lilleskov et al., 2002), acid rain (Roth and Fahey, 1998), fertilization (Treseder, 2004) and tillage (Jansa et al., 2003). The effects of anthropogenic disturbances on EM fungi are reviewed by Erland and Taylor (2002). Microclimate and topography may also act on mycorrhizal fungi, but it is likely that much of this influence would be indirect, acting first on plant community structure.

Plant–fungal feedback and its role in succession

As mycorrhizal diversity promotes several plant community attributes which may, in turn, promote mycorrhizal diversity, we can envision a reciprocal influence or "feedback" between plants and mycorrhizal fungi (Castelli and Casper, 2003; Reynolds et al., 2003). At the level of the individual plant (or population), positive feedback is said to occur when the soil community promotes plant growth and vice versa. Conversely, negative feedback occurs when a host plant species performs poorly in its own native soil relative to others (Klironomos, 2002; Hart et al. 2003). In this model, positive feedback decreases diversity by increasing the abundance of certain plant species at the expense of others, while negative feedback has a homogenizing effect and promotes plant diversity (Bever et al., 1997; Bever, 2002). The influence on host plant diversity by this kind of feedback is dependent on mycorrhizal dependency and the dynamics of plant competition in the context of mycorrhizal colonization.

However, feedback can also be thought of as acting at the community level, with positive interactions leading to ecosystem productivity and stability (Perry et al., 1989b). In this context, we can see how mechanisms such as host specificity and resource heterogeneity, which influence mycorrhizal diversity, and resource extraction patterns and functional compatibility, which influence plant diversity, could act reciprocally to promote or reduce plant and mycorrhizal diversities (Fig. 3).

Hart et al. (2001) propose that AM fungi may interact with their associated plant communities as either "drivers", controlling plant community composition, or as "passengers", with the plant community in control, over the course of succession. These models complement the concept of feedback in that the reciprocal influence between plant and mycorrhizal fungal communities is likely to be asymmetric, with either plant or fungal control dominating in different systems and under different conditions. For example, given the differences in specificity and organic matter utilization between AM and EM fungi, it is possible that EM fungal communities are controlled to a greater extent by their associated plant communities (i.e. more "passenger" like) than AM fungi (Fig. 3).

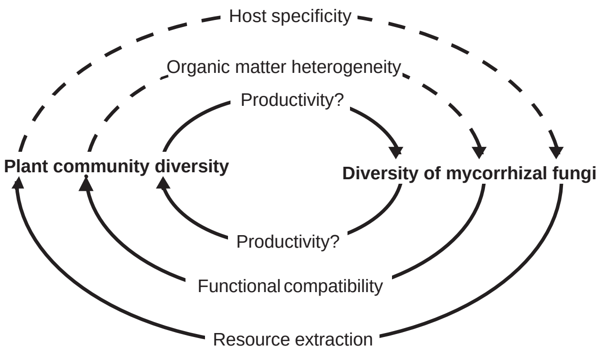

Figure 3. Model of reciprocal influence between plant community diversity and mycorrhizal fungal community diversity. Host specificity and heterogeneity of plant organic matter input act on mycorrhizal diversity, while host–symbiont functional compatibility and resource extraction efficiency act on plant diversity. Mechanisms represented by dashed lines are likely to be more important in EM than in AM systems. The influence of plant and fungal productivity have yet to be confirmed experimentally.

Given the interplay between the mycorrhizal fungal community and the plant community, it is easy to see how the structure of the mycorrhizal community may also influence plant successional trajectory (Janos, 1980; Terwilliger and Pastor, 1999; Gange and Brown, 2002). Mycorrhizal fungi also change in predictable successional patterns, along with plant species and soil nutrient status. The species occurring at a particular successional stage may therefore be those best able to acquire and transport nutrients under the current conditions (Gorham et al., 1979; Last et al., 1987; Read, 1993). These fungal species would therefore have the greatest influence on the recruitment of host plant species in the next seral stage. Again, we see the importance of feedback, with fungal species composition influencing plant successional trajectory, which may, in turn, govern fungal successional trajectory.

Feedback between plant and microbial diversities may also be involved in the overall increase in complexity which generally accompanies all but the later stages of succession (Reynolds et al., 2003). An example of this is seen in the succession from herbaceous (AM) plants, through woody shrubs such as *Alnus* and *Salix*, to conifers (EM) in boreal forests (Read, 1993). Because the woody shrubs are capable of forming both AM and EM symbioses simultaneously, they may facilitate the succession from AM dominated grassland to EM dominated forest by providing a temporary host for EM fungi, which are then available for EM dependent tree seedlings. In this scenario, plant species composition allows for a diversity of mycorrhizal types, which in turn allows for the recruitment of more plant species over the course of succession.

Conclusions

There is now strong evidence for the importance of mycorrhizal symbioses in determining plant community structure and trajectory. It is also clear that reciprocal influences between plants and their fungal symbionts can promote and maintain both above and below ground diversities. Our understanding of this system is still fragmentary, however, due to our lack of data on individual plant–fungal species interactions in complex systems. In the case of AM, this is mainly due to a complex fungal genetic structure, which makes species identification difficult, combined with our inability to grow the mycobionts in pure culture. With EM, progress is often restricted by the difficulties involved in the construction of experimental EM (woody) host plant communities. However, recent efforts in these and other areas hold promise for advancing our understanding of the role of mycorrhizal diversity in the functioning of natural ecosystems.

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