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The role of mycorrhizas in plant community structure and dynamics: lessons from grasslands

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Introduction

Research on the mycorrhizal associations over the past several decades has yielded increased understanding and appreciation of the important role of this symbiosis in the functioning and performance of plants in a wide array of terrestrial ecosystems. We now understand that the role of mycorrhizal fungi extends beyond the symbiotic acquisition of phosphorus for the host plant and reciprocal carbon provision from the host to fungus. Additional effects of mycorrhizal fungi on the functioning of their host plants including increased disease resistance, improved water relations, acquisition of other soil nutrients, and alterations in other soil physico-chemical properties have been documented. Other aspects of the ecology of mycorrhizas, including variation in the costs and benefits of carbon and nutrient exchange, the ecological significance of mycelial networks, the role of mycorrhizal symbiosis in multi-species interactions, and the extent and consequences of host-specificity in these associations have also recently been explored.

The effects of mycorrhizal fungi on the function and growth of individual plants have numerous consequences that extend to the plant population and community levels. The costs and benefits of colonization by mycorrhizal fungi for plant resource availability can strongly influence patterns of plant reproduction and demography, responses to competitors, herbivores, and other biotic interactions, and patterns of species composition, diversity, and succession. This ancient mutualistic symbiosis may be one of the most important but least understood biotic interactions regulating plant community structure and dynamics. Hopefully, an increased understanding of these patterns, their underlying mechanisms, and the costs and benefits of this symbiosis will lead in the future to the formulation of general predictive theory of mycorrhizal effects on plant communities.

In this paper, we examine the consequences of mycorrhizal symbiosis at the plant community level, with a primary focus on grasslands. Mycorrhizal fungi are ubiquitous and abundant in grasslands and savannas worldwide (e.g., Chiariello et al., 1982; Davidson and Christensen, 1977; Fitter, 1986; Koide et al., 1988; Miller, 1987; Newsham and Watkinson, 1998; O'Connor et al., 2001; Perez and Frangi, 2000; Smilauer and Smilaveraer, 2000; van Auken and Brown, 1998). Indeed, our sampling of >100 herbaceous species in North American tallgrass prairie and southern African low veld grasslands revealed that all species thus far examined are colonized by mycorrhizal fungi and that most dominant grasses in these systems are obligate mycotrophs. In addition, studies over the past decade have demonstrated that mycorrhizas have particularly large influences on several aspects of grassland community and ecosystem functioning, and experiments in grasslands have contributed much to the lessons learned and new questions raised about the ecological role of this symbiosis. Here we review evidence for the varied effects of mycorrhizas on the composition and diversity of plant communities, discuss the various hypothesized mechanisms by which mycorrhizal fungi influence plant community structure, and explore the role of this symbiosis in the broader context of the complex array of biotic interactions characteristic of grasslands and many other terrestrial ecosystems.

Mycorrhizas and plant community structure

The processes regulating the composition and diversity natural communities has been a central focus in ecology. The roles of species interactions, natural disturbances operating at different scales, and historical and biogeographic factors have all been explored (e.g., Brown, 1995; Huston, 1994; Pickett and White, 1985; Ricklefs and Schluter, 1993). Studies of the

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role of biotic interactions influencing plant community structure have focused largely on plant competition and plant-herbivore interactions (e.g., Frank et al., 1998; Grace and Tilman, 1990). The important role of mycorrhizal symbiosis in shaping plant community structure has recently become recognized and gained significant attention. This has been a result of both a general increase in research on mycorrhizas, and an increasing recognition that positive interactions (e.g., direct and indirect facilitation) are common in natural communities and may have large effects on plant community structure (Bengtsson et al., 1994; Callaway, 1995; Clay and Holah, 1999).

Recent studies have shown that mycorrhizal fungi can have large but quite variable effects on plant species diversity, composition, and successional dynamics (e.g., Allen and Allen 1984; Connell and Lowman, 1989; Grime et al., 1987; Hartnett and Wilson, 1999). There is also increasing evidence that the effects of mycorrhizal fungi on their host plant communities are context-dependent, varying with host species, plant life history stage, resource availability, and abiotic conditions (e.g., Bethlenfalvay et al., 1982; Fitter, 1986; Francis and Read, 1995; Hartnett et al., 1994; Johnson et al., 1997). In some herbaceous communities, mycorrhizas enhance plant species diversity by increasing the establishment and abundance of subordinate species relative to the community dominants (Gange et al., 1993; Grime et al., 1987; Newman and Reddle, 1988), and plant diversity may be positively correlated with the species diversity of mycorrhizal fungi (van der Heijden et al., 1998a). In other communities, evidence indicates that mycorrhizal fungi decrease plant species coexistence and diversity (e.g., Hartnett and Wilson, 1999; Newsham et al., 1995; O'Connor et al., 2001). Experiments in both North American tallgrass prairie (Figure 1) and European calcareous grasslands (Zobel and Moora, 1995) indicate that mycorrhizal symbiosis decreases plant species diversity by increasing the competitive success and abundance of the community dominants relative to subordinate species. Studies in other grasslands and grassland restorations indicate that mycorrhizal fungi may also alter species composition with no net effect on species richness (Smilauer and Smilauerova, 2000), or may alter rates of succession by hastening the displacement of ruderal species by native grasses (Smith et al., 1998).

Thus, it is clear that at the local community (alpha) scale, mycorrhizal fungi have the potential either to decrease or increase plant species diversity, alter plant species composition, and/or influence the rate and trajectories of community succession. The hypothesized underlying mechanisms causing these observed effects of mycorrhizas on plant communities are similarly varied and include: (1) direct and differential effects on plant species traits such as colonization, establishment, and competitive ability, (2) effects of mycorrhizal mycelial networks and interplant resource transfer through hyphal connections on plant growth and relative abundances, and (3) mycorrhizal mediation of other biotic interactions such as plant–herbivore or plant–pathogen interactions. In the following sections, we review the evidence and discuss various proposed mechanisms for mycorrhizal influence on plant communities.

Patterns of plant species diversity in nature are scale-dependent, and conservation of biodiversity at the regional or global scale should not be confused with maximization of species richness and diversity at the local community or patch scale (Poiani et al., 2000). Many natural grassland communities are and have historically been characterized by low diversity and high dominance at the local community (alpha) scale. In these systems, this low local patch diversity, coupled with significant heterogeneity at larger scales, results in a pattern of higher diversity at the landscape or regional scales. Furthermore, high alpha diversity at the local community scale is often associated with a larger number of invasive exotic or ruderal species, whereas stable, undisturbed communities are characterized by lower richness. Thus, high alpha diversity or species richness at the local scale is not necessarily a good indicator of the biotic integrity or stability of a community. The study of mycorrhizas or any other factors that influence patterns of diversity must consider spatial scale, and focusing solely on the maximization of local species richness as a conservation goal is an unwarranted oversimplification and generalization that ignores scale and overemphasizes species numbers relative to species composition and relative abundances. It is clear from the various studies reviewed above that mycorrhizas have large influences on plant community structure and are an important factor in the stability of plant species composition, as evidenced by the large magnitude of changes in plant communities reported in response to experimental alteration of mycorrhizal activity.

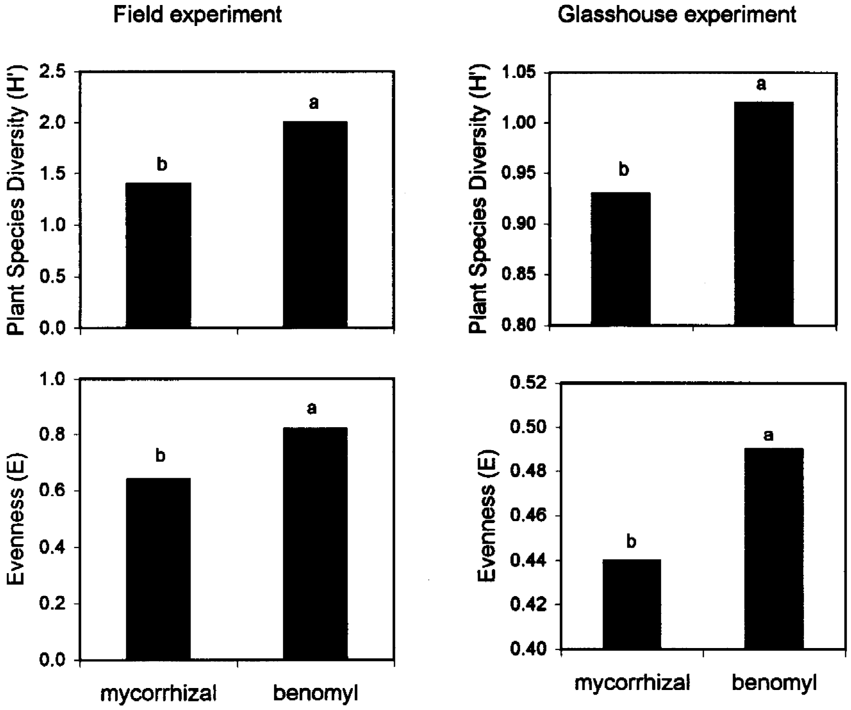

Figure 1. Field experiment: Plant species diversity and evenness of mycorrhizal (control) and mycorrhizal-suppressed (Benomyl application) plots in North American tallgrass prairie after five years of treatment application. Mycorrhizal and mycorrhizal-suppressed plots were not different prior to fungicide applications (year 1). Bars represent means of six transects (10 plots/transect). Different letters indicate that control plots are significantly different ($P \leq 0.05$) from mycorrhizal-suppressed plots. Data from Hartnett and Wilson (1999). Glasshouse experiment: plant species diversity and evenness of mycorrhizal (control) and mycorrhizal-suppressed (Benomyl application) tallgrass prairie microcosms maintained for 42 weeks under glasshouse conditions. Each microcosm contained warm- and cool-season grasses and native prairie forbs planted at approximate field densities (eight species total). Different letters indicate that control plots are significantly different ($P \leq 0.05$) from mycorrhizal-suppressed plots. Data from Wilson and Hartnett (1997).

The spatial heterogeneity hypothesis

Allen (1991) suggested that spatial heterogeneity of mycorrhizal fungal infectivity may increase plant species diversity, allowing nonmycotrophic and mycotrophic species to coexist in patches of low and high inoculum, respectively. This mechanism depends strongly on the existence of interspecific differences in responses to mycorrhizal colonization among co-occurring plant species. We extend Allen's hypothesis further and suggest that, in habitats with significant spatial heterogeneity in fungal infectivity, there will be a positive relationship between interspecific variability in host plant mycotrophy and plant species diversity.

Allen's hypothesis also assumes that fungal infectivity or inoculum potential is limiting to the growth of at least some plant species in the community. We know little about if, and under what conditions low mycorrhizal fungal populations and low root colonization levels may actually be limiting to their host plant populations. Variation in spore population densities or root colonization rates may have little effect on host plant populations if these factors are not limiting to the maintenance of functional mycorrhizal symbiosis in the field.

A related hypothesis is that spatial heterogeneity in infectivity, coupled with variation in host species dependency on mycorrhiza for colonization and establishment (e.g., regeneration niche differences) may enhance species diversity in plant communities. A field experiment in tallgrass prairie showed that plant species differed considerably in their requirement for mycorrhizal colonization for successful germination and establishment, and that some species which were highly dependent upon the symbiosis for establishment showed low dependency on mycorrhizas for adult plant growth, and *vice versa* (Hartnett et al., 1994). Effects of mycorrhizal colonization on plant growth may also differ from its effect on seed and vegetative reproduction within prairie species (Koide, 2000, and this volume; Wilson et al., 2001a). Thus, in these grasslands, mycorrhizal dependency is an important aspect of the regeneration niche of plants, and the dependency of the plant on the symbiosis may vary considerably among different plant life history stages. The mycorrhizal enhancement of germination and establishment of many tallgrass prairie plant species may not only promote species diversity, but may also increase the rate of succession by allowing highly mycotrophic species to more rapidly displace ruderal species (Smith et al., 1998).

Mycorrhizal regulation of plant competition

A second hypothesis is that mycorrhizal fungi influence plant species coexistence, relative abundances, and diversity by altering the intensity and outcomes of interspecific plant competition. Given interspecific differences among plants in mycorrhizal effects on growth and competitive ability, any changes in mycorrhizal colonization or symbiotic function will alter plant species competitive effects and responses, resulting in shifts in species dominance, coexistence, and diversity. We predict that, in general, mycorrhizal symbiosis will strongly influence plant species diversity in any community in which the dominant competitors are significantly more strongly or more weakly mycotrophic than their neighbors.

In turfgrass microcosm experiments conducted by Grime et al., (1987), the dominant competitors (C_3 grasses) were more weakly mycotrophic than their neighbors. Thus, active mycorrhizal associations conferred greater benefit to subordinate competitors and increased species diversity. By contrast, in our tallgrass prairie experiment (Hartnett and Wilson, 1999), the dominant competitors (C_4 perennial grasses) were more strongly mycotrophic than their interspecific neighbors. Thus, AM fungal colonization further enhanced their dominance and reduced local species diversity in these grasslands. The abundance of C_4 grasses decreased with mycorrhizal suppression, with a concomitant increase in abundance of C_3 grasses, but with no effect on total aboveground plant production. This clearly indicates that the subordinate prairie species experience compensatory increases in growth and abundance as the competitive effects of the dominant grasses are greatly reduced in the absence of their mycorrhizal symbionts.

These conclusions from this 5-year field experiment are further supported by a series of pairwise competition experiments conducted in the glasshouse (Hartnett et al., 1993; Hetrick et al., 1989, 1994), and a neighbor removal experiment conducted in the field (Smith et al., 1999), which showed that mycorrhizas regulated the outcomes of intra- and interspecific competition among tallgrass prairie plant species. Connell and Lowman (1989) suggested that this mechanism of mycorrhizal alteration of plant competitive relationships may also explain low diversity and high dominance in some tropical forest communities.

Interspecific variability in plant response to mycorrhizal symbiosis

Both the ‘spatial heterogeneity hypothesis’ and the ‘mycorrhizal regulation of plant competition hypothesis’ depend strongly on a key assumption of significant variability among host plant species in their responses to mycorrhizal colonization, and indeed there is considerable evidence for such variability in grassland plant communities. For example, a study that assessed the growth responses to arbuscular mycorrhizal colonization of 95 species of tallgrass prairie grasses and forbs found high interspecific variation in host-plant benefit from the symbiosis. Species varied from large positive growth responses (e.g., non-mycorrhizal plant biomass $< 2\%$ of mycorrhizal plant biomass) to negative effects of AMF colonization on plant growth. The patterns of mycorrhizal dependence varied among plant life history and taxonomic groups (e.g., grass, forb, legume, annual, perennial) and phenological guilds (Wilson and Hartnett, 1998). In general, perennial warm-season C_4 grasses and forbs benefited significantly from the symbiosis, whereas growth of the perennial cool-season C_3 grasses and annual species were minimally affected. Mycorrhizal responsiveness of the prairie forbs was strongly related to root system architecture (lower colonization in species with highly branched, fine root structure) and, to a lesser extent, flowering phenology.

Variation among host plant species in mycorrhizal dependency may not always provide reliable predictions of mycorrhizal effects on community structure if host species responses are strongly influenced by the particular species of AM fungi present (van der Heijden et al., 1998a,b). While different AM fungal taxa have been shown to produce varying growth responses, it should also be noted that the dominant plant species in the C_3-dominated grasslands that have been studied thus far did not respond significantly to *any* AM fungi (e.g., van der Heijden et al., 1998a,b). Also, while plant growth benefits varied among fungal isolates, eight of 11 sub-dominant plant species failed to grow in the absence of the AM fungi. Therefore, suppression of the symbiosis necessarily reduces diversity due to the loss of obligately mycotrophic plant species from the system, with a concomitant increase in dominance of the non-responsive dominant grasses. In contrast, the dominant plant species of the C_4-dominated grasslands studied are obligately mycorrhizal, and although different AM fungi may differ in their benefit to host plants (e.g., Hetrick et al., 1986), these host species fail to grow at all in the absence of the symbiosis. Because many sub-dominant plant species of these grasslands are facultative mycotrophs (low responsiveness), elimination of mycorrhizal fungi differentially suppresses the dominant C_4 grasses and results in competitive release and increased abundance of the sub-dominants, thereby increasing plant species diversity. Therefore, while AM fungal community composition has the potential to differentially influence different plant species (van der Heijden et al., 1998b), the general patterns of mycorrhizal responsiveness of the dominant plant species appears to be the overriding factor influencing plant species diversity in these systems. In tallgrass prairie communities, both field and glasshouse microcosm studies comparing fungicide-treatments with non-sterile native prairie soil containing a natural AM fungal community produced the same effects on the plant communities as glasshouse experiments using steam-pasteurized soil and re-inoculation with one or several fungal taxa (Hartnett and Wilson, 1999; Wilson and Hartnett, 1997, 1998; Wilson et al., 2001b). This further suggests that the presence or absence of AM fungi, and general differences in mycorrhizal dependency among dominant and subordinate plant species is the primary mechanism accounting for mycorrhizal effects on plant species diversity in tallgrass prairie. Interspecific variation in mycorrhizal dependency is also a key factor influencing patterns of succession in many communities, as more weakly or non-mycotrophic species are replaced by obligate mycotrophs with time since disturbance (Miller, 1987).

Overall, evidence to date suggests that the presence or absence of mycorrhizal fungi, the growth responses or mycorrhizal dependency of host plant species, and/or differential plant species responses to the particular species of AM fungi present may all be potentially important factors influencing the performance and relative abundance of plant species within local herbaceous communities.

The resource sharing hypothesis

Grime et al. (1987) hypothesized that their observed increase in plant species diversity in turfgrass microcosms in response to the presence of mycorrhizas was due to extensive mycelial networks facilitating interplant resource transfer via hyphal connections. This, they argued, allowed small, suppressed plants to obtain carbohydrates from the larger, dominant species via shared mycorrhizal hyphae, ultimately increasing the equitability of species abundances. These workers suggested that the 'export of assimilate from 'source' (canopy dominants) to 'sink' (understory components) through a common mycelial network may be an important mechanism maintaining species-rich communities in infertile soils'. A fundamental distinction between this hypothesis and the mechanisms discussed above is that it suggests that a key role of mycorrhizal fungi is to *decrease* rather than *increase* interspecific differences in resource acquisition and competitive ability among co-occurring plant species. Secondly, this hypothesis invokes a network of interplant hyphal connections and interplant resource transfer as an important process operating in natural plant communities.

Observations that mycorrhizas can form hyphal connections between the roots of related or unrelated hosts (e.g., Chiariello et al., 1982; Heap and Newman, 1980; Newman et al., 1994) have stimulated debate and experimentation on the potential role of interplant nutrient transfer in natural and agricultural ecosystems (Eissenstat, 1990; Francis and Read, 1984; Francis et al., 1986; Frey and Schuepp, 1992; Hamel and Smith, 1992; Ritz and Newman, 1984; Whitingham and Read, 1982; Zobel et al., 1997) and on the evolution of functional mycelial networks (Wilkinson, 1998). If mycorrhizal fungi transfer significant amounts of nutrients among neighboring plants, they may potentially act as significant integrators of plant community dynamics, affecting seedling establishment near mature plants, nutrient cycling from dying roots, and the acquisition and allocation of plant resources. Ultimately, such resource movement may influence patterns of local neighborhood competition, succession, and species diversity (Allen and Allen, 1990; Eissenstat and Newman, 1990; Grime et al., 1987; Miller and Allen 1992; Newman, 1988; Read et al., 1985; Ritz and Newman, 1985).

The potential role and importance of interplant hyphal connections in grasslands and other plant communities remains a matter of debate and deserves much further study. It is unknown whether interplant transfer of resources occurs in sufficient quantities and over sufficient spatial scales to influence the relative performance and interactions of neighboring plants, and whether a net movement of resources occurs toward particular plant species. Furthermore, if a net movement of resources via hyphal connections does indeed occur, it remains unclear whether such resource movement results in a more or less equitable distribution of limiting resources among neighbors. Currently, there is little empirical support for the assumption that subordinate plant species will be stronger sinks and that the movement of resources through mycelial networks will necessarily result in an equitable sharing of resources and higher species diversity. Furthermore, processes such as hyphal grazing by soil invertebrates and high hyphal turnover rates may preclude the maintenance of interplant hyphal connections for a long enough period to influence the outcome of neighbor interactions in nature.

A number of studies in grasslands have addressed some of these issues and suggest that interplant nutrient transfer via hyphae may be important in these communities. Glasshouse studies have shown that carbon and mineral nutrients can move from root to root directly via AM hyphal links (Fitter et al., 1998; Francis and Read, 1984; Read et al., 1985; Robinson and Fitter, 1999) or may be transferred among plants via leakage and subsequent uptake (Newman and Ritz, 1986). Several studies have also examined the patterns and controls of nutrient transfer between plants under glasshouse conditions (Frey and Schuepp, 1992; Haystead et al., 1988; Mader et al., 2000; Ritz and Newman, 1986; Rogers et al., 2001; Whittingham and Read, 1982).

Few studies have examined the patterns or controls of interplant nutrient transfer under natural field conditions. Chiariello et al., (1982) documented intra- and interspecific transfer of radio-labeled phosphorus between plants in a California annual grassland, but found no type of pattern that might be predicted based on a diffusion model, source-sink interactions, taxonomic specificity, or other factors. By contrast, in Kansas tallgrass prairie, significant interplant transfer of phosphorus occurs, but in a clearly non-random pattern. A field ^{32}P labeling experiment showed that transfer of phosphorus from the dominant grass *Andropogon gerardii* to its interspecific neighbors occurs over distances up to 50 cm, but with significantly different amounts of phosphorus transferred to different species within the local neighborhood, in patterns unrelated to relative plant size (Fisher-Walter et al., 1996). The results of this tallgrass prairie study suggest that hyphal interconnections and mycelial networks do not result in an equitable distribution of limiting nutrients among neighbors, as has been hypothesized for other grasslands. However, in this experiment, there was more phosphorus transferred from *A. gerardii* to the sub-dominant forbs and C_3 grasses than to other competitively dominant C_4 perennial grasses (Fisher-Walter et al., 1996). This pattern is consistent with the general hypothesis of Grime et al., (1987) that canopy dominants and subordinate species may function differentially as source and sink for resources moving through hyphal networks. Fisher-Walter et al., (1996) caution that their study did not demonstrate that mycorrhizal hyphal interconnections played a principal role in the interplant transfer process. Other mechanisms such as phosphorus leakage and uptake in the context of extensive and differential rhizosphere overlap among neighboring species were not ruled out.

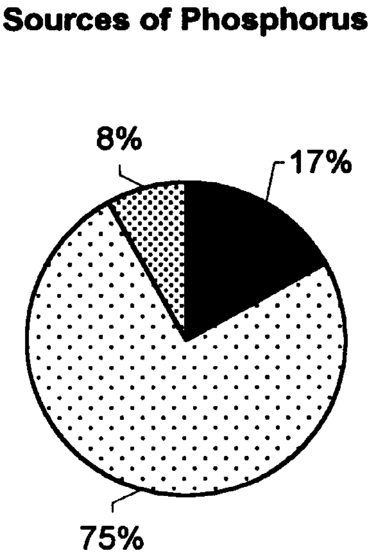

Figure 2. Differentiation of the sources of phosphorus taken up by *Andropogon gerardii*. (□) Mycorrhizal mediated uptake within the plant's own rhizosphere. (■) Mycorrhizal interplant transfer of phosphorus. (▨) Nonmycorrhizal uptake of phosphorus within the plant's own rhizosphere.

Although occurring over sufficient spatial scales, whether such transfer occurs in sufficient quantities to influence neighbor interactions in tallgrass prairie remains unknown. However, a glasshouse experiment examining phosphorus transfer between tallgrass prairie plant species via hyphal interconnections suggests that interplant transfer may make a significant contribution to the total phosphorus acquired by a plant. Using a dual-pot and dual-labeling (^{32}P and ^{33}P) experiment, we grew pairs of tallgrass prairie plant species together and variously manipulated the presence or absence of AM fungi and hyphal connections between plants. The use of two P isotopes enabled the differentiation of the sources of phosphorus taken up by a given plant. Through these experiments, and a series of simple difference equations, we were able to quantify the phosphorus budget of an individual *A. gerardii* plant and to determine what proportion of its phosphorus was acquired from different sources (Hartnett and Wilson, unpubl.). Although the results were variable, this study showed that a significant amount (an average of 17%) of the phosphorus taken up by this grass was acquired directly from its neighbor via hyphal interconnections (Figure 2). Whether similar quantities of nutrients are transferred among neighboring plants in the field is unknown. This study showed further that approximately 75% of the P acquired by an *A. gerardii* plant was acquired from its own rhizosphere via mycorrhizal hyphae, and less than 10% of its P was acquired directly from the soil without the aid of mycorrhizal fungi. These patterns underscore the overriding importance of arbuscular mycorrhizas in P acquisition by these dominant grassland plants.

The results of these various experiments indicate the potential that the movement of plant resources through hyphal interconnections may be an important mechanism influencing plant species interactions and community structure in grasslands and other plant communities. However, results to date are equivocal and much further study is needed to determine whether this mechanism plays a significant role in patterns of species abundances and diversity in natural communities. The methodological limitations and difficulties in measuring the patterns and consequences of this phenomenon in the field will be the greatest challenge.

Complex biotic interactions and indirect effects

In addition to their direct effects on their host plants, mycorrhizal fungi may influence plant communities indirectly through their effects on interactions between plants and their herbivores, pathogens, pollinators, and other microbial mutualists (e.g., Finlay and Soderstrom, 1989; Fitter and Garbaye, 1994; Gehring and Whitham, 1994; Hodge, 2000; Lussenhop, 1996; Newsham et al., 1994). In turn, these species interactions can also influence mycorrhizal fungal communities and their function (Eom et al., 2001). Because a given host plant interacts simultaneously with mycorrhizal fungi and with its herbivores, pathogens, and other symbionts, and all of these organisms jointly influence important plant resources and costs and benefits, strong interactions and indirect effects of mycorrhizal fungi in plant communities should be expected. Furthermore, because many interactions such as those between mycorrhizal fungi or belowground invertebrate herbivores and their host plants are relatively non-host-specific, many communities may be characterized by 'diffuse' mutualisms or plant-consumer interactions in which interactions occur and are best defined at the functional group level rather than between particular pairs of species (e.g., Setala, 1995). Thus, as argued for the structure of competitive relationships in natural communities (e.g., Connell, 1990), 'diffuse' and 'apparent' interactions may be a common characteristic of plant communities associated with mycorrhizal fungi.

Although the direct effects of mycorrhizas through symbiotic uptake of mineral nutrients have been well studied, accumulating evidence suggests that these strong indirect effects of mycorrhizas may be of great importance in plant communities and should not be ignored. These multiple, complex interactions remain poorly understood, as most studies of species interactions have examined them independently as binary interactions (e.g., plant–plant, plant–herbivore, plant–microbe), without considering their function and effects in the multi-species context of natural communities. A further complexity of these relationships is that effects of mycorrhizas and other organisms on their host plant are not universally positive or negative, but may vary in time and space along a mutualism-antagonism continuum (e.g., Johnson et al., 1997).

Every approach to study in ecology involves a trade-off between simplicity, realism, precision, and generality (Harper, 1982). Most studies to date have involved simple pairwise experimental study of plant–mycorrhizal fungi interactions under a single or limited set of environmental conditions. Such experimental approaches are tractable, offer simplicity and precision, and have contributed to our understanding of the range of potential effects of mycorrhizal symbiosis. However, they lack the necessary realism to draw strong conclusions about the role and function of mycorrhizas in natural communities. To accurately assess the role of mycorrhizal symbiosis in plant communities in the context of natural multi-species interactions and under the range of environmental conditions found in nature will be a significant challenge. Mycorrhizal associations play a large role in influencing other species interactions and plant community dynamics, however their population and community-level effects appear to be quite varied and their underlying mechanisms are still not well understood (Bergelson and Crawley, 1988; Crowell and Boerner, 1988; Grime et al., 1987; Hartnett and Wilson, 1999; Miller, 1987).

Interactions between herbivores and mycorrhizal fungi are expected because both depend upon and influence important plant resources. Aboveground consumers may reduce photosynthate translocated to the root system and available to mycorrhizal fungi, resulting in a reduction in mycorrhizal colonization and reduced development of the symbiosis (Gehring et al., 1997; Hetrick et al., 1990a; Trent et al., 1988). Mycorrhizas, in turn, have many potential effects on plant–herbivore interactions. Under certain conditions, up to 40–50% of a plant's net production may be allocated to its fungal symbiont (Fogel and Hunt, 1979; Harris and Paul, 1987). Because mycorrhizal fungi both consume photosynthate and at the same time enhance mineral nutrient acquisition and growth capacity, the cost–benefit relationships among mycorrhizal fungi, herbivores and host plants are likely to be complex. Mycorrhizas may affect herbivores through alteration of plant growth or foliar chemistry (e.g., Goverde et al., 2000; Koide, 2000), and they may have large effects on plant responses to herbivores by influencing anti-herbivore defenses and/or herbivory tolerance (regrowth capacity). Mycorrhizas may significantly enhance grazing tolerance in grassland plants because their regrowth capacity following defoliation is often limited by the availability of nutrients such as phosphorus or nitrogen, or because mycorrhizas alter biomass allocation patterns in ways that promote persistence under grazing (Chapin and McNaughton, 1989; Coughenour et al., 1985; McNaughton et al., 1983).

Evidence from several grasslands indicates a strong relationship between mycorrhizal symbiosis and plant–grazer interactions. In east African grasslands dominated by *Panicum coloratum*, Wallace (1981) found a positive correlation between grazing intensity and mycorrhizal colonization, and in North American grasslands Reece and Bonham (1978) found that grazing increased vesicle density in *Bouteloua gracilis* roots. In tallgrass prairie, mycorrhizal *Andropogon gerardii* plants showed higher clipping tolerance than non-mycorrhizal plants, although repeated defoliation decreased mycorrhizal root colonization (Hetrick et al., 1990a). Gange and Brown (1992) similarly reported an interaction of mycorrhizal fungi and plant responses to belowground herbivores in a successional community. Effects of experimental herbivore reductions on the abundance of perennial grasses disappeared when mycorrhizal fungi were also suppressed. Based on patterns observed in various grasses, we hypothesize that the effect of mycorrhizas on plant responses to defoliation will vary in both direction and magnitude with the intensity of herbivory (Figure 3). Under light to moderate herbivory, when mineral nutrient availability limits plant regrowth rates, mycorrhizal symbiosis will increase grazing tolerance (compensatory growth capacity) by increasing nutrient supply. However, under intense or repeated defoliation, regrowth of aboveground tissue and mycorrhizal fungi may become competing sinks for limited photosynthate. This switch from nutrient limitation to carbon limitation as herbivory increases results in a switch in the cost–benefit balance to the plant and mycorrhizas may become detrimental rather than beneficial by reducing the plants ability to tolerate herbivory (Figure 3).

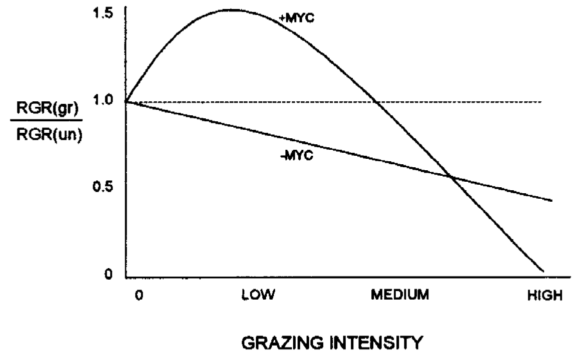

Figure 3. Hypothesized effects of mycorrhizas on the grazing tolerance of dominant tallgrass prairie grasses. +MYC, mycorrhizal symbiosis present; −MYC, mycorrhizal symbiosis absent or suppressed; gr, grazed; un, ungrazed.

We further hypothesize that this change in cost–benefit balance of mycorrhizal symbiosis as herbivory intensity increases, coupled with interspecific variation in plant responses to mycorrhizal colonization, will alter the effects of herbivore intensity on plant species diversity (Figure 4). Conceptual models such as the intermediate disturbance hypothesis and the model of Milchunas et al., (1988) predict a maximization of plant species diversity at intermediate intensities of herbivory in many grassland communities.

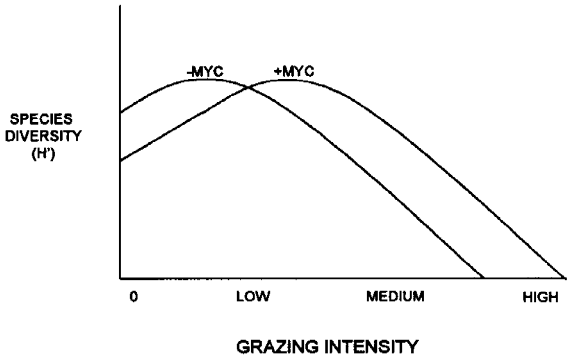

Figure 4. Hypothesized relationship between tallgrass prairie plant species diversity and grazing intensity under mycorrhizal and non-mycorrhizal conditions. +MYC, mycorrhizal symbiosis present; −MYC, mycorrhizal symbiosis absent.

The interaction of mycorrhizal symbiosis and plant–herbivore interactions is predicted to shift this relationship and influence the grazing intensity at which diversity is maximized (Figure 4).

Mycorrhizal fungi may also alter effects of belowground grazers of plant roots (Bakhtiar et al., 2001; Bonkowski et al., 2000). Currently, we are examining effects of above- and belowground grazing and their potential interactions on plant community composition, using experimental microcosms (0.4 × 0.52 × 0.32 m) planted with an assemblage of eight tallgrass prairie grass and forb species growing in native prairie soil. These microcosms are maintained under mycorrhizal and nonmycorrhizal conditions, with and without native soil nematodes, and with and without aboveground herbivory (clipping treatments and grasshopper herbivory) to elucidate the interactions and effects of these key species interactions. Preliminary results indicate that belowground herbivory by nematodes reduces biomass production of mycorrhizal C_4 grasses, and nonmycorrhizal C_3 grasses, while having variable effects on the forb species. Greater compensatory above- and belowground biomass production was observed in defoliated plants under mycorrhizal conditions than under nonmycorrhizal conditions, whether foliage removal was accomplished by clipping or by grasshopper herbivory. These preliminary results support our hypothesis that mycorrhizal symbiosis may enhance grazing tolerance under light to moderate grazing in grasslands. These results also underscore the importance of above-and belowground linkages and indicate that alterations in mycorrhizal and rhizosphere processes can have large indirect effects on plant communities through their effects on plant responses to above- and belowground consumers.

A comment on experimental approaches

One of the greatest difficulties in attempting to assess the role of mycorrhizas in natural plant communities is that all of the various approaches for experimentally manipulating mycorrhizal colonization and symbiotic function have limitations. Suppression of mycorrhizas with fungicides may result in non-target effects on other fungi or soil processes, however both target and potential non-target effects of the fungicide can be quantified and dealt with as co-variates in statistical analyses (e.g., Smith et al., 2000). The fungicide approach also provides greater realism than approaches using soil sterilization (which alters numerous soil processes), artificial growing media, and/or the use of one or only a few AM fungal species obtained from a source other than the native community under study. These latter approaches provide some insight into potential effects and mechanisms, but they lack the realism necessary to draw strong conclusions about the role and functioning of mycorrhizas in nature.

The fungicide benomyl has been used successfully in our studies and by several other workers to experimentally vary mycorrhizal activity (Carey et al., 1992; Fitter, 1986; Fitter and Nichols, 1988; Jacobson et al., 2001; Kahiluoto et al., 2000; Merryweather and Fitter, 1986; Schweiger and Jakobson, 1999). Several studies suggest that it is effective in reducing AM fungal colonization, has no direct effects on a wide range of plants in the absence of fungi, and has the fewest drawbacks of all potential methods of AM fungal suppression in the field (Fitter and Nichols, 1988; Paul et al., 1989; Sukarno et al., 1993; Wilson and Hartnett, 1997). In addition, several lines of evidence indicate that, in tallgrass prairie ecosystems, the use of benomyl is a conservative approach and its *primary*, although not exclusive effect is suppression of mutualistic mycorrhizal associations and their symbiotic function (Carey et al., 1992; Hartnett and Wilson, 1999; Hetrick et al., 1990b; Smith et al., 2000). Thus, in our view suppression of mycorrhizal fungi with fungicides remains the best approach currently available to assess the roles and function of mycorrhizas in natural communities, and indeed the only approach practical for field situations and large-scale experiments.

Summary

Although their specific effects vary, it is clear that mycorrhizas exert a significant influence on plant community structure and dynamics in grasslands and other terrestrial ecosystems. The effects of mycorrhizal fungi on patterns of plant diversity and their underlying mechanisms are quite varied. In one community type AM fungi may increase local plant diversity, whereas in another they may maintain the stability of the local community by maintaining the competitive balance among dominant and subordinate species. The structure of some plant communities may be regulated simply by the presence and abundance of mycorrhizal fungi and the patterns of variation in mycorrhizal dependency among co-occurring species. In others the taxonomic or genotypic composition of the fungal community may also be important. The role of mycorrhizas in patterns of diversity at larger scales has not been examined.

Each of the various methodological approaches to studying the ecological roles of mycorrhizal symbiosis has limitations, and each represents a compromise of generality, simplicity, precision and realism. Finding solutions to some of these methodological limitations is a significant challenge. Glasshouse experiments typically lack the realism necessary to draw conclusions about the functioning of mycorrhizas in natural communities, and field studies alone rarely reveal underlying mechanisms and controls. We suggest that both field studies and complementary glasshouse experiments, conducted together in different communities, have the greatest potential to provide a better understanding of the patterns and mechanisms of mycorrhizal effects and the role of this symbiosis in natural plant communities.

Recent empirical and theoretical approaches indicate that the greatest or most frequent effects of mycorrhizal fungi may be indirect rather than direct, as mycorrhizas influence interactions between plants and their competitors, herbivores, and other microorganisms. Because mycorrhizal fungi and these other organisms all influence important plant resources, they are unlikely to have independent effects on their host plants, and each is likely to alter the cost-benefit relationships of the other to the plant. Furthermore, in many grassland ecosystems which are characterized by non-equilibrium dynamics, the relative importance and limitation of different plant resources changes greatly over space and time (Knapp et al., 1998). Thus, the effects of mycorrhizas, their interactions at the community level, and the cost–benefit relationships among mycorrhizal fungi, other organisms, and host plants are likely to be complex and are likely to vary considerably spatially and from year to year. Long-term field studies will be essential to elucidate the dynamic consequences of mycorrhizal symbiosis in native plant communities.

References

Allen E B and Allen M F 1984 Competition between plants of different successional stages: mycorrhizae as regulators. Can. J. Bot. 62, 2625–2629.

Allen E B and Allen M F 1990 The mediation of competition by mycorrhizae in successional and patchy environments. *In* Perspectives on Plant Competition. Ed. J B Grace and D Tilman. pp. 367-389. Academic Press, San Diego, CA.

Allen M F 1991 The Ecology of Mycorrhizae. Cambridge University Press, Cambridge, UK.

Bakhtier Y, Miller D, Cavagnaro T and Smith S 2001. Interactions between two arbuscular mycorrhizal fungi and fungivorous nematodes and control of the nematode with fenamifos. Appl. Soil Ecol. 17, 107–117.

Bengtsson J, Fagerstrom T and Rydin H 1994 Competition and coexistence in plant communities. Trends Ecol. Evol. 9, 246–250.

Bergelson J M and Crawley J M 1988 Mycorrhizal infection and plant species diversity. Nature 334, 202.

Bethlenfalvay G J, Ulrich J M and Brown M S 1982 Plant response to mycorrhizal fungi: host, endophyte, and soil effects. Soil Sci. Soc. Am. J. 49, 1164–1168.

Bonkowski M, Cheng W, Griffiths B S, Alphei J and Scheu S 2000 Microbial-faunal interactions in the rhizosphere and effects on plant growth. Eur. J. Soil Biol. 36, 135–147.

Brown J H 1995 Macroecology. University of Chicago Press, Chicago, IL.

Callaway R M 1995 Positive interactions among plants. Bot. Rev. 61, 306–349.

Carey P D, Fitter A H and Watkinson A R 1992 A field study using the fungicide benomyl to investigate the effect of mycorrhizal fungi on plant fitness. Oecologia 90, 550–555.

Chapin F S III and McNaughton S J 1989 Lack of compensatory growth under phosphorus deficiency in grazing-adapted grasses from Serengeti Plains. Oecologia. 79, 551–557.

Chiariello N, Hickman J C and Mooney H A 1982 Endomycorrhizal role for interspecific transfer of phosphorus in a community of annual plants. Science 217, 941–943.

Clay K and Holah J 1999 Fungal endophyte symbiosis and plant diversity in successional fields. Science 285, 1742–1744.

Connell J H 1990 Apparent versus ‘real’ competition in plants. *In* Perspectives on Plant Competition. Eds. J B Grace and D Tilman. pp. 9–26. Academic Press, San Diego, CA.

Connell J H and Lowman M D 1989 Low-diversity tropical rain forests: some possible mechanisms for their existence. Am. Nat. 134, 88–119.

Coughenour M B, McNaughton S J and Wallace L L 1985 Responses of an African graminoid (*Themeda traindra* Forsk.) to frequent defoliation, nitrogen and water: a limit of adaptation to herbivory. Oecologia 68, 80–86.

Crowell H F and Boerner R E J 1988 Influences of mycorrhizae and phosphorus on belowground competition between two old-field annuals. Environ. Exp. Bot. 28, 381–392.

Davidson D E and Christiansen M 1977 Root-micofungal and mycorrhizal associations in a shortgrass prairie. *In* The Belowground Ecosystem: a Synthesis of Plant-Associated Processes. Ed. J K Marshall. pp. 279–287. Colorado State University Press, Fort Collins, CO.

Eissenstat D M 1990 A comparison of phosphorus and nitrogen transfer between plants of different phosphorus status. Oecologia 82, 342–347.

Eissenstat D M and Newman E I 1990 Seedling establishment near large plants: effects of vesicular-arbuscular mycorrhizas on the intensity of plant competition. Funct. Ecol. 4, 95–100.

Eom A H, Wilson G W T and Hartnett D C 2001 Effects of ungulate grazers on arbuscular mycorrhizal symbiosis and fungal community composition in tallgrass prairie. Mycologia 93, 233–242.

Finlay R D and Soderstrom B 1989 Mycorrhizal mycelia and their role in soil and plant communities. *In* Ecology of Arable Land. Ed. M Clarholm and L. Bergstrom. pp. 139–148. Kluwer, Amsterdam.

Fischer Walter L E, Hartnett D C, Hetrick B A D and Schwab A P 1996 Interspecific nutrient transfer in a tallgrass prairie plant community. Am. J. Bot. 83, 180–184.

Fitter A H 1986 Effect of Benomyl on leaf phosphorus concentration in alpine grassland: a test of mycorrhizal benefit. New Phytol. 103, 767–776.

Fitter A H and Garbaye J 1994 Interactions between mycorrhizal fungi and other soil organisms. Plant Soil 159, 123–132.

Fitter A H and Nichols R 1988 The use of Benomyl to control infection by vesicular-arbuscular mycorrhizal fungi. New Phytol. 110, 201–206.

Fitter A H, Graves J D, Watkins N K, Robinson D and Scrimgeour C M 1998 Carbon transfer between plants and its control in networks of arbuscular mycorrhizas. Funct. Ecol. 12, 406–412.

Fogel R and Hunt G 1979 Fungal and arboreal biomass in a western Oregon Douglas-fir ecosystem: distribution patterns and turnover. Can. J. Forest Res. 9, 245–256.

Francis R and Read D J 1984 Direct transfer of carbon between plants connected by vesicular-arbuscular mycorrhizal mycelium. Nature 307, 53–56.

Francis R and Read D J 1995 Mutualism and antagonism in the mycorrhizal symbiosis, with special reference to impacts on plant community structure. Can. J. Bot. 73, 1301–1309.

Francis R, Finlay R D and Read D J 1986 Vesicular-arbuscular mycorrhiza in natural vegetation systems IV. Transfer of nutrients in inter- and intra-specific combinations of host plants. New Phytol. 102, 103–111.

Frank D A, McNaughton S J and Tracy B 1998 The ecology of the earth's grazing ecosystems. Bioscience 48: 513–521.

Frey B and Schuepp H 1992 Transfer of symbiotically fixed nitrogen from berseem (*Trifolium alexandrinum* L.) to maize via vesicular-arbuscular mycorrhizal hyphae. New Phytol. 122, 447–454.

Gange A C and Brown V K 1992 Interactions between soil-dwelling insects and mycorrhizas during early plant succession. *In* Mycorrhizas in Ecosystems. Eds. D J Read, D H Lewis, A H Fitter and I J Alexander. pp. 177–182. C A B Int. Cambridge University Press, Cambridge.

Gange A C, Brown V K and Sinclair G S 1993 Vesicular-arbuscular mycorrhizal fungi: a determinant of plant community structure in early succession. Funct. Ecol. 7, 616–622.

Gehring C A and Whitham T G 1994 Interactions between aboveground herbivores and the mycorrhizal mutualists of plants. TREE 9, 251–255.

Gehring C A, Cobb N S and Whitham T G 1997 Three-way interactions among ectomycorrhizal mutualists, scale insects, and resistant and susceptible pinyon pines. Am. Nat. 149, 824–841.

Goverdr M, van der Heijden M G A, Wiemken A, Sandres I R and Erhardt A 2000 Arbuscular mycorrhizal fungi influence life history traits of a lepidopteran herbivore. Oecologia 125, 362–369.

Grace J B and Tilman D G (Eds.) 1990 Perspectives on Plant Competition. 484 pp. Academic Press, San Diego, CA.

Grime J P, MacKey J M Hillier S H and Read D J 1987 Floristic diversity in a model system using experimental microcosms. Nature 328, 420–422.

Hamel C and Smith D L 1992 Mycorrhizae-mediated ^{15}N transfer from soybean to corn in field-grown inter-crops: effect of component crop spatial relationships. Soil Biol. Biochem. 24, 499–501.

Harper J L 1982 After description. *In* The Plant Community as a Working Mechanism. Ed. E I Newman. pp. 11–26. Blackwell Scientific Publications, Oxford, UK.

Harris K K and Paul E A 1987 Carbon requirements of vesicular-arbuscular mycorrhizae. *In* Ecophysiology of VA Mycorrhizal Plants. Ed. G R Safir. pp. 93–105. CRC Press, Boca Raton, FL.

Hartnett D C and Wilson G W T 1999 Mycorrhizal influence plant community structure and diversity in tallgrass prairie. Ecology 80, 1187–1195.

Hartnett D C, Hetrick B A D Wilson G W T and Gibson D J 1993 VA-mycorrhizal influence on intra- and interspecific neighbour interactions among co-occurring prairie grasses. J. Ecol. 81, 787–795.

Hartnett D C, Samenus R J Fischer L E and Hetrick B A D 1994 Plant demographic responses to mycorrhizal symbiosis in tallgrass prairie. Oecologia 99, 21–26.

Haystead A, Malajczuk N and Grove T S 1988 Underground transfer of nitrogen between pasture plants infected with vesicular-arbuscular mycorrhizal fungi. New Phytol. 108, 417–423.

Heap A J and Newman E I 1980 Links between roots by hyphae of vesicular-arbuscular mycorrhizas. New Phytol. 85, 169–171.

Hetrick B A D, Kitt D G and Wilson G W T 1986 The influence of phosphorus fertilization, drought, fungal species, and nonsterile soil on mycorrhizal growth response in tallgrass prairie plants. Can. J. Bot. 64, 1199–1203.

Hetrick B A D, Wilson G W T and Hartnett D C 1989 Relationship between mycorrhizal dependence and competitive ability of two tallgrass prairie grasses. Can. J. Bot. 67, 2608–2615.

Hetrick B A D, Wilson G W T and Owensby C E 1990a Mycorrhizal influences on big bluestem rhizome regrowth and clipping tolerance. J. Range Manag. 43, 286–290.

Hetrick B A D, Wilson G W T and Todd T C 1990b Differential responses of C_3 and C_4 grasses to mycorrhizal symbiosis, phosphorus fertilization, and soil microorganisms. Can. J. Bot. 68, 461–467.

Hetrick B A D, Hartnett D C Wilson G W T and Gibson D J 1994 Effects of mycorrhizae, phosphorus availability, and plant density on yield relationships among competing tallgrass prairie grasses. Can. J. Bot. 72, 168–176.

Hodge A 2000 Microbial ecology of the arbuscular mycorrhiza. Micro. Ecol. 32, 91–96.

Huston M A 1994 Biological Diversity: The Coexistence of Species on Changing Landscapes. 681 pp. Cambridge University Press, Cambridge.

Jakobsen I, Gazey C and Abbott L K 2001 Phosphate transport by communities of arbuscular mycorrhizal fungi in intact soil cores. New Phytol. 149, 95–103.

Johnson N C, Graham J H and Smith F A 1997 Functioning of mycorrhizal associations along the mutualism-parasitism continuum. New Phytol. 135, 575–585.

Kahiluoto H, Ketoka E and Vestberg M 2000 Creation of a non-mycorrhizal control for a bioassay of AM effectiveness. Mycorrhiza 9, 241–258.

Knapp A K, Briggs J M, Hartnett D C and Collins S L (eds) 1998 Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie. 364 pp. Oxford University Press, New York.

Koide R T 2000 Mycorrhizal symbiosis and plant reproduction. *In* Arbuscular Mycorrhizas: Physiology and Function. Eds. Y Kapulnik and D D Douds. pp. 19–46. Kluwer Academic Publishers, Dordrecht.

Koide R T, Huenneke L F, Hamburg S P and Mooney H A 1988 Effects of applications of fungicide, phosphorus and nitrogen on the structure and productivity of an annual serpentine plant community. Funct. Ecol. 2, 335–344.

Lussenhop J 1996 Collembola as mediators of microbial symbiont effects upon soybean. Soil Biol. Biochem. 28, 363–369.

Mader P, Vierheilig H, Streitwolf-Engel R, Boller T, Frey B, Christie P and Wiemken A 2000 Transport of ^{15}N from a soil compartment separated by a polytetrafluoroethylene membrane to plant roots via the hyphae of arbuscular mycorrhizal fungi. New Phytol. 146, 155–161.

McNaughton S J, Wallace L L and Coughenour M B 1983 Plant adaptation in an ecosystem context: effects of defoliation, nitrogen, and water on growth of an African C_4 sedge. Ecology 64, 307–318.

Merryweather J and Fitter A H 1996 Phosphorus nutrition of an obligately mycorrhizal plant treated with the fungicide benomyl in the field. New Phytol. 132, 307–311.

Milchunas D G, Sala O E and Lauenroth W K 1988 A generalized model of the effects of grazing by large herbivores on grassland community structure. Am. Nat. 132, 87–106.

Miller R M 1987 The ecology of vesicular-arbuscular mycorrhizae in grass- and shrublands. *In* The Ecophysiology of VA Mycorrhizal Plants. Ed. G R Safir. pp. 136–163. CRC Press, Boca Raton, FL.

Miller S L and Allen E B 1992 Mycorrhizae, nutrient translocation, and interactions between plants. *In* Mycorrhizal Functioning. Ed. M F Allen. pp. 301–332. Chapman and Hall, New York.

Newman E I 1988 Mycorrhizal links between plants: their functioning and ecological significance. Adv. Ecol. Res. 18, 243–270.

Newman E I and Reddell P 1988 Relationship between mycorrhizal infection and diversity in vegetation: evidence from the Great Smokey Mountains. Funct. Ecol. 2, 259–262.

Newman E I and Ritz K 1986 Evidence on the pathways of phosphorus transfer between vesicular-arbuscular mycorrhizal plants. New Phytol. 104, 77–87.

Newman E I, Devoy C L N Easen N J and Fowles K J 1994 Plant species that can be linked by VA mycorrhizal fungi. New Phytol. 126, 691–693.

Newsham K K and Watkinson A R 1998 Arbuscular mycorrhizas and the population biology of grasses. *In* Population Biology of Grasses. Ed. G P Cheplick. pp. 286–312. Cambridge University Press, Cambridge.

Newsham K K, Fitter A H and Watkinson A R 1995 Multi-functionality and biodiversity in arbuscular mycorrhizas. TREE. 10, 407–411.

O'Connor P J, Smith S E and Smith F A 2001 Arbuscular mycorrhizas influence diversity and structure in a semi-arid plant community. *In* Diversity and Integration in Mycorrhizas. Proc. 3rd International Conference on Mycorrhizas. Ed. S E Smith. Adelaide, South Australia.

Paul N D, Aryes P G and Wyness L E 1989 On the use of fungicides for experimentation in natural vegetation. Funct. Ecol. 3, 759–769.

Perez C A and Frangi J L 2000 Grassland biomass dynamics along an altitudinal gradient in the Pampa. J. Range Manag. 53, 518–528.

Pickett S T A and White P S (Eds.) 1985 The Ecology of Natural Disturbance and Patch Dynamics. 472 pp. Academic Press, Orlando, FL.

Poiani K A, Richter B D, Anderson M G and Richter H E 2000 Biodiversity conservation at multiple scales: functional sites, landscapes, and networks. Bioscience 50, 133–146.

Read D J, Francis R and Finlay R D 1985 Mycorrhizal mycelia and nutrient cycling in plant communities. *In* Ecological Interactions in Soil. Eds. A H Fitter, D Atkinson D J Read and M B Usher. pp. 193–217. Blackwell, Oxford UK.

Reece P E and Bonham C D 1978 Frequency of endomycorrhizal infection in grazed and ungrazed blue grama plants. J. Range Manage. 31, 149–154.

Ricklefs RE and Schluter D (Eds.) 1993 Species Diversity in Ecological Communities. University of Chicago Press, Chicago, IL.

Ritz K and Newman E I 1984 Movement of ^{32}P between intact grassland plants of the same age. Oikos, 43, 138–142.

Ritz K and Newman E I 1985 Evidence for rapid cycling of phosphorus from dying roots to living plants. Oikos 45, 174–180.

Ritz K and Newman E I 1986 Nutrient transport between ryegrass plants differing in nutrient status. Oecologia 70, 128–131.

Robinson D and Fitter A H 1999 the magnitude and control of carbon transfer between plants linked by a common mycorrhizal network. J. Exp. Bot. 50, 9–13.

Rogers J B, Laidlaw A S and Christie P 2001 The role of arbuscular fungi in the transfer of nutrients between white clover and perennial ryegrass. Chemosphere 42, 153–159.

Schweiger P F and Jakobsen I 1999 Direct measurement of phosphorus uptake by native arbuscular mycorrhizal fungi associated with field-grown winter wheat. Agron. J. 91, 998–1002.

Setala H 1995 Growth of birch and pine seedlings in relation to grazing by soil fauna on ectomycorrhizal fungi. Ecology 76, 1844–1851.

Smilauer P and Smilauerova M 2000 Effect of AM symbiosis exclusion on grassland community composition. Folia Geobot. 35, 13–25.

Smith M D, Hartnett D C and Wilson G W T 1999 Interacting influence of mycorrhizal symbiosis and competition on plant diversity in tallgrass prairie. Oecologia 121, 574–582.

Smith M D, Hartnett D C and Rice C W 2000 Effects of long-term fungicide application on microbial processes in tallgrass prairie soils. Soil Biol. Biochem. 32, 935–946.

Smith M R, Charvat I and Jacobson R L 1998 Arbuscular mycorrhizae promote establishment of prairie species in a tallgrass prairie restoration. Can. J. Bot. 76, 1947–1954.

Sukarno N, Smith S E and Scott E S 1993 The effect of fungicides on vesicular-arbuscular mycorrhizal symbiosis. I. The effects on vesicular-arbuscular mycorrhizal fungi and plant growth. New Phytol. 25, 139–147.

Trent J D, Wallace L L Svejcar T J and Christiansen S 1988 Effect of grazing on growth, carbohydrate pools, and mycorrhizae in winter wheat. Can. J. Plant Sci. 68, 15–120.

Van Auken O W and Brown S C 1998 Importance of arbuscular mycorrhizae to drymass production of a native Texas C_3 and C_4 grass. Texas J. Sci. 50, 291–304.

Van der Heijden M G A, Boller T Wiemken A and Sanders I R 1998a Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. Ecology 79, 2082–2091.

Van der Heijden M G A, Klironomos J N Ursic M Moutoglis P Streitwolf-Engel R Boller T Wiemken A and Sanders I R 1998b Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396, 69–72.

Wallace L L 1981 Growth, morphology and gas exchange of mycorrhizal and nonmycorrhizal *Panicum coloratum* L, a C_4 grass species, under different clipping and fertilization regimes. Oecologia 49, 272–276.

Whittingham J and Read D J 1982 Vesicular-arbuscular mycorrhiza in natural vegetation systems. III. Nutrient transfer between plants with mycorrhizal interconnections. New Phytol. 90, 277–284.

Wilkinson D M 1998 The evolutionary ecology of mycorrhizal networks. Oikos 82, 407–410.

Wilson G W T and Hartnett D C 1997 Effects of mycorrhizae on plant growth and dynamics in experimental tallgrass prairie microcosms. Am. J. Bot. 84, 478–482.

Wilson G W T and Hartnett D C 1998 Interspecific variation in plant responses to mycorrhizal colonization in prairie grasses and forbs. Am. J. Bot. 85, 1732–1738.

Wilson G W T, Hartnett D C, Smith M D and Kobbeman K 2001a Effects of mycorrhizal suppression on growth dynamics of selected tallgrass prairie forbs. Am. J. Bot. 88: 1452–1457.

Wilson G W T, Hartnett D C and Todd T C 2001b Interactions of mycorrhizal symbiosis and herbivory in tallgrass prairie. *In* Diversity and Integration in Mycorrhizas. Proc. 3rd International Conference on Mycorrhizas. Ed. S E Smith. Adelaide, South Australia.

Zobel M and Moora M 1995 Interspecific competition and arbuscular mycorrhiza: importance for the coexistance of two calcareous grassland species. Folia Geobot. Phytotax. Praha 30, 223–230.

Zobel M, Moora M and Haukioja E 1997 Plant coexistance in the interactive environment: arbuscular mycorrhizae should not be out of mind. Oikos 78, 202–208.