Arbuscular Mycorrhizal Fungi: More Diverse than Meets the Eye, and the Ecological Tale of Why

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Historically, ecologists focused on interspecific competition as the critical factor structuring plant communities. Interactions between plants, however, are likely to be mediated by myriad interactions with soil organisms (Bever et al. 1997). The vast majority of plants, for example, take up nutrients through interactions with root symbionts. Of these root symbionts, arbuscular mycorrhizal (AM) fungi are perhaps the most common, likely forming associations with the majority of plant species, and are probably among the most important because they facilitate plants' uptake of phosphorus, a limiting nutrient in many soils.

While acknowledging the potential importance of AM fungi, ecologists are only beginning to understand the diversity and dynamics of these soil symbionts. Research on plant–fungal interactions has always been hampered by a basic asymmetry: Whereas plants show themselves and wait to be counted, fungi are much more cryptic. Over the past several years, we have worked intensely on the ecology of the plant–AM fungal interactions within a one-hectare field in North Carolina. This work provides a window into an underground world that is surprisingly diverse and dynamic. In this article, we describe the process of discovering this diversity, detail mechanisms that might maintain fungal diversity, and then discuss our understanding of what this diversity means for ecology as a whole.

Background on AM fungi and plant ecology

Associations with arbuscular mycorrhizal fungi increase plant access to scarce or immobile soil minerals, particularly phosphorus, and thereby increase plant growth rates. In vegetation as different as the prairies of Kansas, the dry shrublands of California, and the rich rainforests of Costa Rica, the presence of these fungi has been shown to be essential for the sustained growth and competitive ability of plants (Janos 1980a, Allen and Allen 1990, Hartnett et al. 1993, Koide et al. 1994). Moreover, the presence of these fungi has been shown to alter plant community structure, productivity (Grime et al. 1987, Klironomos et al. 2000), and the course of succession (Medve 1984, Gange et al. 1990); provide resistance to pathogens (Newsham et al. 1995a); and stabilize soil aggregates (Wright and Upadhyaya 1998, Miller and Jastrow 2000).

THE HIGH DIVERSITY OF ECOLOGICALLY DISTINCT SPECIES OF ARBUSCULAR MYCORRHIZAL FUNGI WITHIN A SINGLE COMMUNITY HAS BROAD IMPLICATIONS FOR PLANT ECOLOGY

Although evidence of the ecological importance of AM fungi in general is abundant, understanding of the distinct roles of individual AM fungal species is relatively limited. Researchers do know that the fungi are distinct. Numerous studies have shown that individual species of AM fungi differ in their ability to promote plant growth, and promotion of plant growth can depend on the particular matching of plant and fungal species (Nemec 1978, Powell et al. 1982, Adjoud et al. 1996, Streitwolf-Engel et al. 1997, van der Heijden et al. 1998a). Individual fungal species also differ in

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their growth response to plant species (Johnson et al. 1992, Sanders and Fitter 1992, Bever et al. 1996), in their response to agricultural disturbance (Schreiner and Bethlenfalvay 1997, Douds and Millner 1999), and even in their ability to bind soil particles (Wright et al. 1996). However, scientists are just beginning to incorporate this evidence of the unique ecologies of AM fungal species into a framework that makes the biology of individual fungi important to plant ecology as a whole. As a result, ecologists are starting to appreciate the importance of the diversity of mycorrhizal fungi per se. For example, two recent studies of grasslands in Europe and North America demonstrate that increasing the diversity of AM fungi may directly increase the diversity of plants (van der Heijden et al. 1998b).

Investigations of the importance of mycorrhizal fungal diversity to plant ecology are understandably rare for two reasons. First, until recently ecologists have assumed that AM fungal species are functionally redundant. This belief has been supported both by the observations that these fungi have low specificities of association (individual species can associate with a broad range of host plants) and by the perception that AM fungal communities are depauperate relative to plant communities (Law and Lewis 1983, Allen et al. 1995). Second, investigations of AM fungal diversity in plant ecology have been hampered by limitations in researchers' ability to monitor and manipulate the identity and diversity of the AM fungal community. Indeed, even measuring the species richness of the AM fungal community is fraught with difficulties. Not only can distinguishing soil-borne spores of one species from those of another be difficult, but our limited knowledge of the population ecology of individual fungal species may itself constrain the measurement of AM fungal community composition.

Basics of arbuscular mycorrhizal fungal biology and taxonomy

Arbuscular mycorrhizal fungi get their name from their characteristic formation of branching structures called *arbuscules* within the cortical cells of roots (Figure 1). Arbuscules increase the contact area between plant and fungus and are thought to be the primary sites of exchange of the plant's carbon for the fungus's phosphorus. One suborder of these fungi, Glomineae, also forms vesicles, or sack-like reservoirs, within plant cortical cells (Figure 1c). Consequently, AM fungi are also known as vesicular–arbuscular mycorrhizal, or VAM, fungi.

AM fungi are believed to propagate via infective hyphae, hyphal fragments, or asexual spores (Figure 2). A generalized life history begins with colonization of a root and the development of arbuscules from branch hyphae within the root. Hyphae may extend from one infected root to another, or from an infected root to the root of another plant. Spores form in the root cortex or in the soil. These spores may be dormant for a period, but they will eventually germinate and colonize another root. Spores may be dispersed away from the site in which they were formed. Viable spores are generally ephemeral (some spores of *Acaulospora* species are exceptions), and viability is limited by dormancy, susceptibility to pathogens, and other factors. Although the morphology and architecture of external hyphae and internal mycorrhizal structures can differ between families of AM fungi (e.g., Figure 1c, 1d), there are few differences between species within each genus. Therefore, taxonomy of these fungi is based on the discrete characters of the spore subcellular structure, which can vary from simple to very complex for a single multinucleate cell (e.g., Figure 1a, 1b; Morton 1988, Morton and Bentivenga 1994). On the basis of spore wall characters and spore ontogeny, AM fungi are grouped into genera that encompass approximately

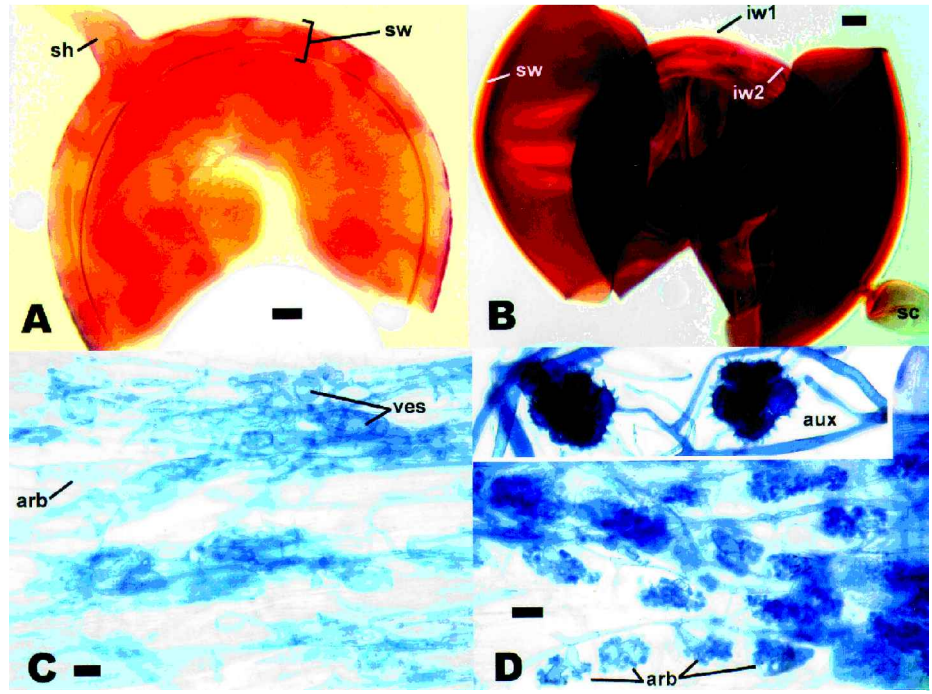

Figure 1. Examples of spores and colonization by arbuscular mycorrhizal fungi. (a) Subcellular structure of a* Glomus clarum *spore broken and mounted in Melzer's reagent. (b) Subcellular structure of a* Scutellospora pellucida *spore broken and mounted in Melzer's reagent. (c) Typical mycorrhizae of* Acaulospora morrowiae *stained in 0.05% trypan blue. (d) Typical mycorrhizae of* Gigaspora rosea *stained in 0.05% trypan blue; inset shows auxiliary cells. Abbreviations: sw = spore wall, sh = subtending hyphae, sc = sporogenous cell, iw1 = first inner wall, iw2 = second flexible inner wall, arb = arbuscule, ves = vesicle, aux = auxillary cells. Scale bar = 20 µm.

145 species described to date. Undoubtedly the majority of AM fungal species remains undescribed. The International Culture Collection of Arbuscular and Vesicular Arbuscular Mycorrhizal Fungi (INVAM) at West Virginia University, for example, currently maintains approximately 40 isolates that do not belong to currently described species (Morton et al. 1993). For more information on this collection, see the INVAM Web site at *http://invam.caf.wvu.edu*.

Measurement of diversity within a community

We initiated our work on AM fungal community dynamics at an abandoned 1-ha agricultural field. Agriculture ended at this site approximately 60 years ago, and it has been maintained as a grassland by mowing ever since. We chose the site because it was close at hand (on the Duke University campus) and because the plant community was well studied. (Research for more than 10 doctoral dissertations on plant population biology and community ecology had been conducted at the site by graduate students of Dr. Janis Antonovics [e.g., Fowler and Antonovics 1981]). Despite the long history of research at this site, the field is rather unspectacular. It is composed of a mixture of native and exotic annual and perennial grasses and forbs—largely lawn and pasture weeds, which represent a relatively high diversity of approximately 50 plant species.

Figure 2. Spores of arbuscular mycorrhizal fungi from our study site. The central picture is a composite of spores from nine species of AM fungi. Around this composite photo, we have arranged pictures of individual species. Starting in the upper left corner and moving clockwise around the composite photo, these species are* Scutellospora calospora, S. pellucida, S. heterogama, Archaeospora trappei, Gigaspora gigantea, Gi. rosea, Acaulospora colossica, *and* Ac. morrowiae. *Scale bar = 200 µm.

We launched this project with the goal of finding multiple species of AM fungi in the field. We expected that diversity would be limited. In our initial examination of AM fungal spores from freshly collected field soil in 1992, we recognized 11 species. However, we were aware that viable, identifiable spores are ephemeral and that direct examination of spores in field soil at any one time may not reveal all of the fungal species present in that soil. We were also aware that some spores were so altered by soil conditions that species differences might not have been detected. In order to identify other species of AM fungi in the field, we "trapped" the fungi in pots, thereby promoting growth and inducing sporulation in a variety of, as yet, unseen species. By *trapping* we mean a process of amplifying the fungi from a site by growing them on a host plant within the greenhouse for 4 or 5 months. During this time, the fungi infect the plants and sporulate. These freshly produced spores greatly facilitate identification. Over subsequent years through a series of research projects, we examined the fungal community at our site by extensive sampling of field soil and an assortment of trapping approaches (Bever et al. 1996).

As a result of this effort, we now know that there are at least 37 different species of AM fungi at this site, and one-third of these species have not previously been described. This species richness within a one-hectare field is remarkable, given that it is higher than that previously recorded from entire countries (Morton et al. 1995) and is roughly the same magnitude as the diversity of plants at this site. Moreover, we continue to find additional species (Figure 3a). Our discoveries owe as much to perspiration and persistence as inspiration. It is clear that the previously held generalization that arbuscular mycorrhizal fungal communities are depauperate relative to their associated plant communities needs to be reevaluated.

The manner in which we discovered this diversity reflects the unique ecologies of individual AM fungal species. No single sampling methodology was able to reveal all of the species at the site (Figure 3b, Schultz 1996). In fact, it seems that each

variant on the sampling methodology, whether it be greenhouse conditions of the trap cultures, species of plant host used in the traps, treatment of soil prior to trapping, or season of sampling field soil, would reveal additional fungal species. For example, *Glomus fasciculatum*, a small-spored species whose thick wall exhibits a distinctive staining reaction in response to Melzer's reagent, was observed only when mature *Plantago* plants were dug from the field, had their roots washed free of soil, and were then planted in sterile soil and grown in a cool greenhouse (Bever et al. 1996). Other species, such as *Acaulospora colossica* (the large red spore in Figure 2) sporulated in traps only after being grown under conditions typical of the cool winter and spring months in North Carolina (Schultz et al. 1999). The distinct conditions favorable to successful growth and sporulation reflect differences in AM fungal ecologies. There are undoubtedly additional fungal species present at the site for which we have not yet adequately met growth and sporulation requirements.

The number of AM fungal species within the community provides only a cursory look at the true level of ecological diversity present at this site. Within populations of single AM fungal species, we have found evidence of abundant genetic variation, in spite of the asexual nature of these species. We found that variation in spore shape of *Scutellospora pellucida* (the large white spores in Figure 2), for example, was highly heritable (Bever and Morton 1999). Moreover, investigations of the ITS region of *Ac. colossica* demonstrated that abundant molecular genetic variation exists not only within the population at this site but within single spores of this species as well (Pringle et al. 2000). Clearly, we are just beginning to discover the extent of genetic and ecological diversity among clones, as well as species, of these fungi. In the discussion that follows, we focus on ecological variation among species; we note, however, that our discussion could apply equally well to species or intraspecific clones of AM fungi.

Maintenance of AM fungal diversity

How do so many species of AM fungi coexist within a single community? Classical ecological theory posits two possible explanations for the maintenance of high diversity within our study site. All of the species could be ecologically equivalent. That is, they are competitively equivalent within a single niche, which is the cortical cells of plant roots. In this case, diversity is sustained by random drift processes. This hypothesis of functional redundancy has been implicitly assumed when biologists, limited by the availability of funds and fungi, try to generalize results of experiments that test the effects of single isolates of AM fungi. These fungi are, in fact, in some ways equivalent or redundant, given that a particular plant species can be colonized by a wide range of fungal species. However, these fungi have been repeatedly shown to differ in their effects on plant hosts (e.g., Nemec 1978, Powell et al. 1982, Streitwolf-Engel et al. 1997). Further, the manner in which we discovered the fungal species within our field suggests that the local isolates of these species differ in ecologically important traits.

A second hypothesis for the high diversity of AM fungi in our field site is that fungal species are ecologically distinct and occupy different niches. Individual fungi would therefore be competitively superior in their specific niche, and the presence of multiple niches in a habitat results in the active maintenance of a speciose fungal community. The manner in which we discovered this diversity at our study site, with different fungi predominating in various trap cultures under dif-

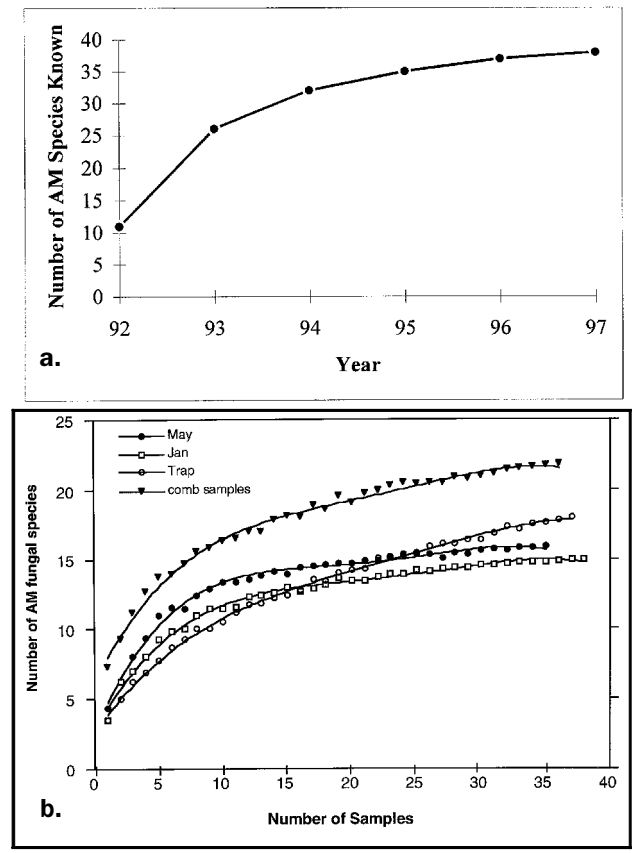

Figure 3. Sampling effort curves depicting the rate of discovery of arbuscular mycorrhizal fungal species at our site against years and number of samples. (a) The number of species that we knew were present increased from 11 in our first year of work to 37 in our last year of field sampling. (b) The species sampling effort curve for paired sampling of more than 35 sites using three methods: field sampling in May as represented by solid circles, field sampling in January as represented by open squares, and trap cultures as represented by open circles (from Schultz 1996). The triangles represent the diversity found when the three methods are combined. The curves present the means of estimates obtained by jackknifed resampling of the data (Schultz 1996). Note that the combined results are always higher than any those from any one sampling strategy, indicating that no single sampling approach allowed the discovery of the total diversity known at these sites. This pattern results from the unique ecologies of the individual species of AM fungi.

ferent environmental conditions, strongly supports this second hypothesis. While questions remain as to the importance of individual environmental variables on which AM fungi differentiate, further work at our study site suggests several candidates, namely plant hosts, seasonality, and edaphic factors.

Host specificity. AM fungi are considered to have low specificities of association with plant host species, but these conclusions are based almost exclusively on experiments in which individual isolates of species are grown separately, apart from competitive interactions. When fungi are examined as a community, we find abundant evidence that AM fungal growth rates are highly host specific. In an experiment in which AM fungi were trapped on different plant hosts, isolates of different fungal species sporulated differentially, with the relative dominance of fungal species being reversed, depending on the plant species with which they were associated (Bever et al. 1996). For example, *Acaulospora colossica* was dominant in association with *Allium vineale*, field garlic, but this fungus was a minor component of the community associated with *Plantago lanceolata* (Figure 4). Alternatively, *Scutellospora calospora* (the medium-sized white spore in Figure 2) sporulated profusely with *Plantago*, but was a minor component in association with *Allium* (Figure 4). We found the distribution of fungi in the field to be similarly host specific (Bever et al. 1996, Schultz 1996). As this pattern of host specificity of growth rates in this nonspecific association has been observed in many other systems, including tallgrass prairie (Johnson et al. 1992), sand dunes (Koske 1981), California grasslands (Nelson and Allen 1993), chalk grasslands (Sanders and Fitter 1992), and agricultural fields (Douds and Millner 1999), this appears to be a general property of this interaction. This specificity of fungal response could contribute to the maintenance of diversity within the AM fungal community.

Seasonality. We have also found evidence that AM fungi differ in their seasonality, with some fungi sporulating in late spring and others sporulating at the end of summer (Figure 5; Schultz et al. 1999). As the spores represent the dormant state of the fungus, the physiologically active state is most likely the mirror image of the seasonal spore counts. Therefore, *Gigaspora gigantea* (the large yellow spore in Figure 1), which sporulates most abundantly in the fall and appears to overwinter as spores, is likely to be physiologically active during the warm season. Similar patterns have been seen for *Gi. gigantea* in a sand dune on the coast of Rhode Island (Gemma et al. 1989, Lee and Koske 1994). Alternatively, *Ac. colossica*, which sporulates most profusely at the beginning of summer and oversummers as spores, is physiologically active with the cool season plant community (e.g., *Allium vineale*).

Abiotic factors. Arbuscular mycorrhizal fungi are also known to vary in their response to the mineral environment of the soil. At our site, about 30% of the variation in the spatial distribution of AM fungi could be explained by variation in aspects of the mineral soil (Schultz 1996). Again, individual fungi showed opposite associations with certain soil parameters. For example, the distribution and abundance of *Ac. colossica* was negatively associated with soil phosphorus concentration, while the reverse was true for *Gi. gigantea* (Schultz 1996). This dependence of fungal spatial distributions on edaphic factors is consistent with observations in other communities, including tallgrass prairie (Johnson et al. 1992) and sand dunes (Koske 1981).

Other factors. Arbuscular mycorrhizal fungi at our field site also appear to differ in life history characters, including duration of dormancy, germination requirements, and sporulation requirements. These fungi may also differ in their palatability and resistance to grazing by belowground herbivores. The external hyphae of these fungi have been shown to be less palatable in general than hyphae of soil-borne conidial fungi (Klironomos and Kendrick 1995), although the diverse and numerous fungivorous nematodes found in soils of Kansas prairies are thought to feed predominantly on AM fungal hyphae (Todd 1996). Species-specific differences in palatability have been observed in ectomycorrhizal hyphae (Schultz 1991), and similar patterns are likely to occur among the arbuscular mycorrhizal fungi as well. Such ecological differences may also contribute to the maintenance of diversity within communities of AM fungi.

Our study site is a single small field, and, even so, we are far from understanding the ecology of individual AM fungal species within it. We cannot assign a relative importance to

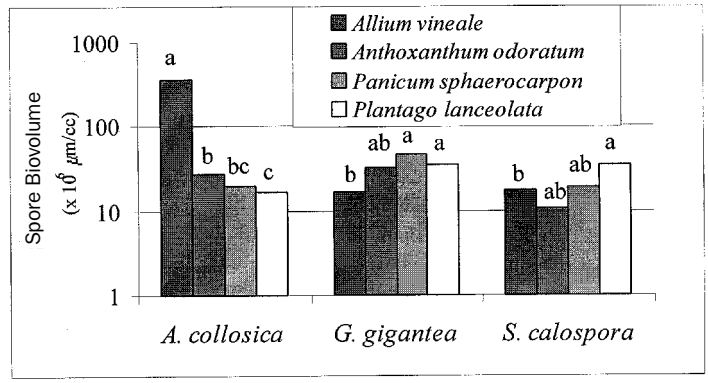

Figure 4. Host specificity and arbuscular mycorrhizal fungi response (drawn from Bever et al. 1996). The figure presents the sporulation rates of three fungal species,* Acaulospora colossica, Gigaspora gigantea, *and* Scutellospora calospora *in association with four co-occurring host plants,* Allium vineale, Anthoxanthum odoratum, Panicum sphaerocarpon, *and* Plantago lanceolata. Acaulospora colossica *grew best with* Allium, *while* Gi. gigantea *and* S. calospora *grew poorly with* Allium *relative to their performance with* Plantago. *Letters indicate significant differences within analyses based on ranked data (Bever et al. 1996).

plant host, mineral soil factors, or higher trophic factors in the maintenance of AM fungal diversity. Nevertheless, we can suggest that each of the many fungal species are ecologically distinct and that these distinct ecologies contribute to the maintenance of high diversity of AM fungi at this site.

Implications of AM fungal diversity for plant ecology

How does the evidence of a diverse community of fungi with distinct ecologies alter understanding of the impacts of mycorrhizal fungi on plant community processes? There are many possibilities. Newsham and colleagues (1995b), for example, suggest that individual fungal species may provide different services to the plant community, such as facilitation of phosphorus uptake versus pathogen protection. Therefore, a full complement of fungi would improve plant community productivity. We address the potential mechanisms by which the diversity of AM fungi could contribute to the maintenance of diversity within the plant community, as observed by van der Heijden et al. (1998b). We then discuss the potential importance of AM fungal community diversity and dynamics for plant community change and for plant and ecosystem responses to anthropogenic disturbance.

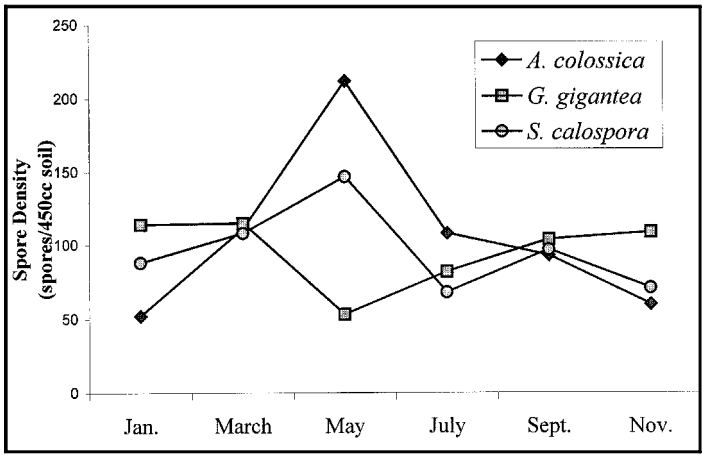

Figure 5. AM fungi differed significantly in their seasonality within our field site. The data present the mean spore densities from nine sites sampled every other month during 1996 (Pringle 2001).* Acaulospora colossica *reaches its maximal density in late spring, while* Gigaspora gigantea *peaks at the end of summer. These fungi sporulate after their period of physiological activity, much like many herbaceous plants within this community set seed at the end of their growing season. These differences in sporulation patterns within this field, therefore, quite likely reflect distinct differences in seasonal activity of these fungal species. In fact, further work on these fungi confirms the distinct seasonal behavior of these species (Schultz et al. 1999), with* Ac. colossica *being physiologically active during the cool season and dormant during the summer months, while* Gi. gigantea *is physiologically active during the warm season.

Maintenance of plant diversity. Plant growth promotion by these fungi varies with fungal identity. Not only are some fungi generally more effective at growth promotion, but growth promotion depends upon particular plant–fungal combinations. This is also true at our study site. Therefore, specific fungi may be essential for the establishment of some plant species. By way of illustration, it is possible that the successful establishment of the cool-season herb *A. vineale* depends upon the presence of the cool-season fungus *Ac. colossica*. We note that this singular dependence may appear unlikely, given that many fungal species have been shown to associate with the roots of individuals of this plant species (Bever et al. 1996), but the possibility remains that plant performance is highly dependent on an abundance of this fungal species. Other species of AM fungi may allow additional plant species to establish, and diversity and spatial structure within the fungal community may generate a heterogeneous environment that contributes to the maintenance of plant diversity. Therefore, the successful restoration of plant diversity within a highly disturbed site may depend not solely on the presence of mycorrhizal fungi but also on the functional and taxonomic diversity of these fungi. Recent results support this hypothesis (van der Heijden et al. 1998b); however, the mechanism generating this effect remains to be identified. It is also important to remember that plant community structure may have its own impact on fungal community composition, which can be critical to the resulting outcome.

Because the relative growth rates of plant and fungal populations are mutually interdependent (i.e., depend upon the specific plant–fungal combination), the interaction of plant and fungal communities may result in complex dynamics (Bever 1999). Both plant and fungal perspectives would need to be incorporated to predict the stability of the plant and fungal community. To illustrate, we have developed a simple model of community dynamics that takes into account mutually interdependent plant and fungal growth rates (Bever 1992, 1999). Using this model, we identify conditions for two strikingly different outcomes: positive and negative feedback (Figure 6). In the case of positive feedback, the fungus that promotes the growth of a given plant is also the fungus that has the highest growth rate on that plant host. As a result, an initially high frequency of one plant type will result in an increased frequency of its preferred fungus, which thereby increases the plant's growth rate relative to that of other plants (Figure 6). This dynamic between plant and fungus ultimately leads to a loss of diversity in the community on a local scale—in spite of the initial presence of two fungal types (Bever 1999). Because plants and AM fungi interact and disperse at highly localized scales, however, positive feedback can contribute to the spatial structuring of the plant and fungal population. This spatial structure can be relatively stable and thereby contribute to the maintenance of plant diversity at large scales (Bever et al. 1997, Molofsky et al. 1999), for example, the scale of our study site.

In the case of positive feedback, the plant and fungal combinations may be thought of as superorganisms, and the dy-

namics within the fungal community will not directly contribute to the maintenance of plant diversity at a local scale. Local scale diversity may be maintained by other processes, such as abiotic niche differentiation. The possibility remains, however, that mycorrhizal fungi *enable* the coexistence of plants if the realization of a plant's abiotic niche depends on the plant–fungus superorganism relationship. If one imagines that *Allium*, for example, has a distinct niche because of a particularly high demand and scavenging ability for mineral phosphate, and if one imagines that *Allium*'s access to this mineral is enabled by its specific association with *Ac. colossica*, then *Ac. colossica* may enable the *Allium*'s coexistence with other plants. Although in this case the local-scale coexistence of the plant species is not caused by community dynamics within the plant–fungus interaction, it is dependent on the presence of particular fungal species.

Alternatively, the dynamics between plants and fungi can actively contribute to the maintenance of plant and fungal diversity at all scales when the fungus that promotes the growth of a given plant has the highest growth rate on a second plant species (i.e., negative feedback; Bever 1992, 1999, Bever et al. 1997). In this case, an initial high frequency of the first plant type will result in a change in the mycorrhizal community that decreases this plant's growth rate relative to that of other plant species (Figure 6). That is, the benefit that the plant receives from its community of mycorrhizal fungi may decrease over time (see Johnson et al. 1997 for a discussion of other deleterious effects of AM fungi). Although the possibility of negative feedback through changes in a community of mutualists has not been widely recognized, we found evidence of just such a dynamic between two common plants at our study site, *Plantago lanceolata* and *Panicum sphaerocarpon* (Bever, unpublished data). In this case, the fungus *Scutellospora calospora* accumulates under *Plantago*. However, while *Plantago* benefits from association with *S. calospora*, *Plantago* benefits more from association with two other species of fungi, *Archaeospora trappei* and *Ac. morrowiae* (Figure 2), and these fungi accumulate under *Panicum*. As a result, *Plantago* grows best with the fungi that accumulate under *Panicum*. Therefore, the dynamics within the AM fungal community can directly contribute to the maintenance of local-scale plant species diversity.

Implications for ecological processes. Our observations of the diversity of AM fungi within a single community have broad implications for the role of these fungi in ecological processes such as succession. As described earlier, the presence of these fungi is already known to have a strong effect on the direction of succession (Janos 1980b, Medve 1984, Allen and Allen 1990, Gange et al. 1990, Allen 1991). In disturbed habitats, where the density of infective fungal parts (spores, hyphae, etc.) are drastically reduced, nonmycotrophic plants dominate (Medve 1984). As the fungi invade, facultatively and then obligately mycorrhizal plants are expected to succeed (Janos 1980b). As a result of the dependence of plant community dynamics on the presence of AM fungi, inoculation with these fungi has been shown to be an important tool in the restoration of plant communities in disturbed areas (Smith et al. 1998). It is also possible that plant succession is paralleled by succession in the associated fungal communities. Evidence of such succession was found in old-field succession in Minnesota (Johnson et al. 1991) and in gap dynamics in tropical forests of Cuba (Herrera et al. 1997).

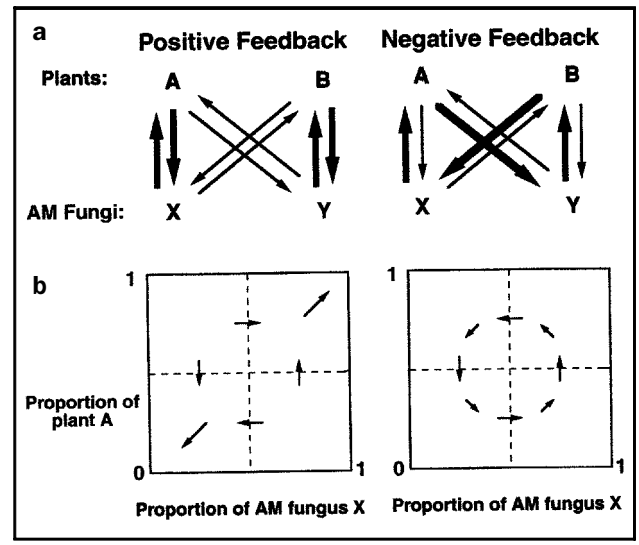

Figure 6. Two distinct dynamics resulting from the mutual interdependence of plant and fungal relative rates of growth (the full range of dynamics was analyzed in Bever 1999). The direction of benefit delivered between two plant species, A and B, and their arbuscular mycorrhizal fungal mutualists, X and Y, are indicated by the arrows, with the thickness of the arrows indicating the magnitude of benefit. When the delivery of benefit is symmetric between plants and fungi (as presented in the figure on the left in panel a), a positive feedback dynamic results, as depicted in the phase plane diagram below the fitness representation. In this diagram, the arrows represent the direction of change over time. With an initial abundance of plant A relative to plant B, fungus X will increase its representation in the fungal community, thereby enhancing the growth rate of plant A and ultimately leading to the exclusion of plant B. Positive feedback through changes in the AM fungal community therefore can contribute to the loss of diversity within the plant community. A very different dynamic results when the delivery of benefit between the plants and fungi is strongly asymmetric, as depicted in the figure on the right in panel a. In this case, an initial abundance of plant A in the plant community leads to a reduction in the abundance of fungus X in the fungal community, thereby reducing the growth rate of plant A relative to that of plant B. This negative feedback on plant growth rates through changes in the composition of the AM fungal community can directly contribute to coexistence of plant species. A complete analysis of the conditions for positive versus negative feedback is given in Bever (1999).

Successional dynamics within the AM fungal community may play an important role in driving the later stages of succession within the plant community. Resolving this issue is of critical importance for optimal management of community restoration.

The dynamics and diversity within AM fungal communities may also be critical to plant community response to anthropogenic perturbations, such as the well-documented increase in atmospheric CO_2. Plants grown under high CO_2 have been found to increase their allocation to AM fungi (reviewed in Rillig and Allen 1999), and AM fungi appear to differ in their ability to take advantage of this additional carbon (Klironomos et al. 1998). Therefore, the composition of the AM fungal community will most likely change during CO_2 enrichment. This shift in fungal community structure may alter plant community structure, plant productivity, belowground allocation, and soil aggregate stability. These factors themselves influence the rate of ecosystem-level carbon sequestration. Therefore, understanding the nature of CO_2-induced changes in the AM fungal community and their effects on ecosystem properties is important for understanding the long-term consequences of chronic anthropogenic environmental perturbations.

Conclusion

Research on the plant–mycorrhizal fungal interaction will always be hindered by a basic asymmetry. While plants are easily counted and measured, measurements of the fungal community are elusive. Nonetheless, the observation of high diversity within a fungal community, as well as the diverse approaches required to detect them, give a glimpse of the complexity within the fungal community and dramatically illustrate the limits of our understanding of mycorrhizal fungal community processes and dynamics. As knowledge of the distinct ecologies of individual fungal species grows, simple assumptions about the influence of mycorrhizae on plant communities need to be reevaluated. Such a reevaluation will enhance our appreciation of belowground organisms as dynamic participants in plant community processes, and of belowground biodiversity as an essential component of ecosystem health.

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