

Negative feedback within a mutualism: host-specific growth of mycorrhizal fungi reduces plant benefit

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A basic tenet of ecology is that negative feedback on abundance plays an important part in the coexistence of species within guilds. Mutualistic interactions generate positive feedbacks on abundance and therefore are not thought to contribute to the maintenance of diversity. Here, I report evidence of negative feedback on plant growth through changes in the composition of their mutualistic fungal symbionts, arbuscular mycorrhizal (AM) fungi. Negative feedback results from asymmetries in the delivery of benefit between plant and AM fungal species in which the AM fungus that grows best with the plant *Plantago lanceolata* is a poor growth promoter for *Plantago*. Growth of *Plantago* is, instead, best promoted by the AM fungal species that accumulate with a second plant species, *Panicum sphaerocarpon*. The resulting community dynamic leads to a decline in mutualistic benefit received by *Plantago*, and can contribute to the coexistence of these two competing plant species.

Keywords: mutualism; mycorrhizae; maintenance of diversity; negative feedback; coexistence; plant–microbe interactions

1. INTRODUCTION

A basic tenet of ecology is that negative feedback on abundance (i.e. negative density dependence) plays an important part in the regulation of population density and, therefore, in the coexistence of species within guilds (Levins 1974; May 1974). This negative feedback has generally been thought to result from antagonistic interactions such as competition, predation and parasitism (Tilman & Pacala 1993; Chesson 2000). Mutualistic interactions in which both participants benefit from their association, while known to be common (Boucher 1985), have not been thought to generate negative feedback and therefore were not expected to contribute to the coexistence of species (May 1974). While mutualism can be defined as a positive feedback process in density, it is possible that the community dynamics between mutualistically interacting guilds of species can generate net negative feedback on the relative abundance of species within these guilds (Bever 1999). In this study, I use a series of manipulative experiments to demonstrate negative feedback on plant growth through changes in the composition of their mutualistic fungal symbionts, arbuscular mycorrhizal (AM) fungi. This negative feedback results from the asymmetry in the delivery of benefit between plant and mycorrhizal fungal species.

AM fungi can facilitate plant growth by increasing access to soil resources. The interaction is a well-established mutualism, as the fungus, in turn, is wholly dependent on carbohydrates from the plant. The ecological importance of this interaction is broadly appreciated, as most plant species, including most agricultural plants, associate with AM fungi (see Smith & Read 1997). While the association is thought to be largely non-specific, there is growing evidence of host-specific differences in plant response to fungi and in fungal response to plants. The extent of plant growth promotion by AM fungi depends

upon the specific plant and fungal combinations (see Streitwolf-Engel *et al.* 1997; van der Heijden *et al.* 1998). Conversely, the growth response of AM fungal species also depends on the associated host-plant species (see Johnson *et al.* 1992; Bever *et al.* 1996; Eom *et al.* 2000).

This mutual interdependence of plant and AM fungal population growth rates could generate complex community dynamics between the plant and fungal guilds. Host-specific changes in the AM fungal community could lead to increases in the relative growth rates of the most abundant plant (i.e. positive feedback) or to decreases in the relative growth rates of the most abundant plant species (i.e. negative feedback) (Bever *et al.* 1997; Bever 1999). These two dynamics lead to very different predictions for the community. Positive feedback causes a strengthening of the mutualism between plant and fungal guilds, but a decline in species diversity. Negative feedback causes a weakening of the mutualism, but can contribute to the coexistence of competing plant species (Bever 1999).

Currently, there is little evidence of such complex community feedback dynamics between plants and fungi, or within any other mutualism. Several studies have identified patterns consistent with negative feedback through the AM fungal community (Johnson *et al.* 1991; Bever 1994; Kiers *et al.* 2000). However, in each case, accumulation of host-specific root pathogens provides a likely alternative mechanism (Mills & Bever 1998; Bever 2002). An additional study indicates a decline in crop yield due to the accumulation of an AM fungal species (Modjo & Hendrix 1986), but the accumulation of this fungus was probably driven as much from the fertilization treatments as from host-specificity of fungal growth rates. Experimental tests of plant and fungal growth rates using pure cultures have indicated highly asymmetric relative growth rates between plants and AM fungi that would generate negative feedback (Pringle 2001; Bever *et al.* 2002).

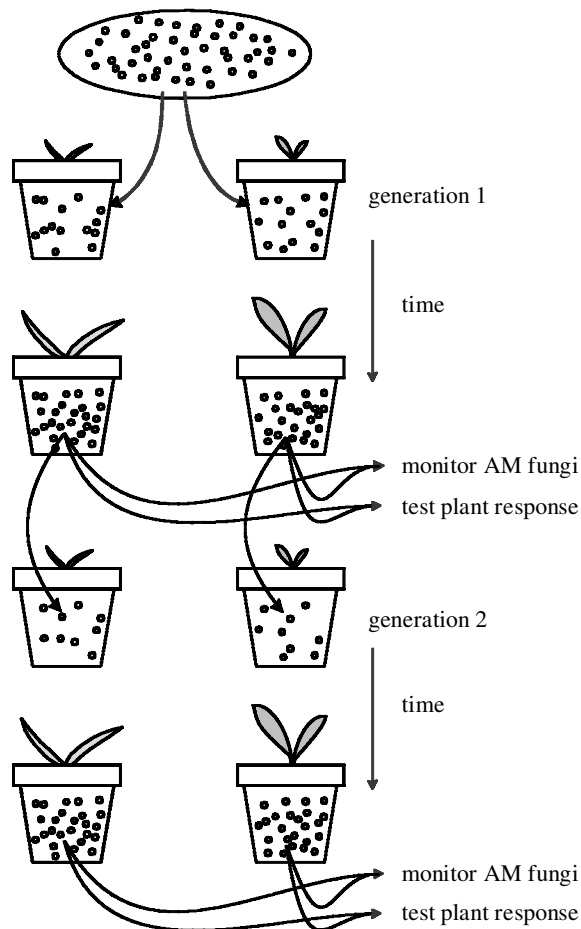


Figure 1. Design of feedback experiment. The initial AM fungal community was created by mixing equal volumes of pure cultures of eight fungal species. This community was then grown with four host species (two are shown) for a five month growing season (generation 1). The fungal communities were then harvested, assayed, and then re-inoculated onto their same plant host species at the start of the second growing season (generation 2). At the end of each growing season, the composition of the AM fungal community was monitored and the fungal communities were used as inoculum in a separate test experiment that evaluated the growth response of the plant species in association with each of the fungal communities.

Predictions of fungal dynamics in this study, however, are dependent upon counts of spores, an incomplete measure of AM fungal population growth rate.

Evaluating the nature of the plant-AM fungal community dynamics is complicated by the difficulties in measuring relative rates of population growth of AM fungi. AM fungi can reproduce vegetatively through hyphal extension and by the production of resting propagules in the form of asexual spores. The hyphal structures, which are embedded in the root and soil, cannot be identified morphologically and are hard to quantify. Monitoring of the AM fungal community composition therefore often depends on counts of spores, an imperfect measure. In this study, I circumvented the difficulties in measurement of AM fungal population growth rates by manipulating and monitoring replicate laboratory AM fungal communities (figure 1). Follow-up tests indicated negative feedback

through the soil community and the AM fungal causal mechanism was confirmed in an independent assay of plant growth response.

2. METHODS

Two complementary approaches were used to test negative feedback through the AM fungal community. First, I manipulated and evaluated AM fungal communities that were constructed by mixing pure cultures of individual AM fungal species. Specifically, replicate AM fungal communities were grown on individual host plants for a growing season, during which time the composition of the fungal community may have differentiated due to host-specific differences in fungal population growth rates (figure 1). These fungal communities were then used as inoculum in a separate test experiment evaluating plant growth response. The inoculum in this test experiment includes both the spores and hyphal structures of AM fungi and therefore accurately represents the entire AM fungal community. The second approach confirms the AM fungal mechanism of negative feedback by monitoring the host-specific differentiation of the AM fungal community during the feedback experiment (figure 1). The causal relationship between the feedback on plant growth and the changes in the AM fungal community composition was then tested by an independent assessment of plant growth in response to inoculation with the original pure cultures of AM fungi.

(a) *Study system*

Four plant species and eight AM fungal species were used in this study, all of which were isolated from within a 75 m² area of a North Carolina grassland (Bever *et al.* 1996, 2001). The four plant species included two herbs, *Allium vineale* and *Plantago lanceolata* and two grasses, *Anthoxanthum odoratum* and *Panicum sphaerocarpon*. Six genotypes of each of the plant species used in this study were clonally propagated. *Anthoxanthum* and *Panicum* were cloned and cleaned as previously described (Bever 1994). Clones of *Allium* were replicated with their asexually produced bulbils, and clones of *Plantago* were grown from leaf cuttings dipped in indoleacetic acid. All fungal cultures were started from a single spore and maintained in isolation in a growth chamber within the Duke University Phytotron to avoid contamination by soil pathogens. These eight pure cultures were mixed in equal proportion to create the initial AM fungal communities used for the feedback experiments. The eight AM fungal species were: *Acaulospora morrowiae*, *Archaeospora trappei*, *Gigaspora gigantea*, *Gi. decipiens*, *Scutellospora calospora*, *S. pellucida*, *S. reticulata* and an undescribed species of *Glomus* (identified as *Gl. D3* (Bever *et al.* 1996)). Each of these species has been deposited in an international culture collection (INVAM) as previously described (Bever *et al.* 1996). Cultures were propagated on a common host, *Sorghum vulgare*, and grown in a growth chamber for four and a half months at which time there was abundant sporulation. The cultures were then stored dry for several months in the refrigerator to break the dormancy of the spores prior to use.

(b) *AM fungal community training experiment*

Replicate 600 cc pots were filled with 400 cc 1 : 1 mixture of sterile soil and sand mix and inoculated with 200 cc of the initial mixture of pure cultures of eight AM fungal species. Into these pots were planted soil-microbe free plants of one of six geno-

types of each of the four plant species (three replicates of each of the six genotypes of each of the four plant species). The plants were grown in a growth chamber with conditions set to mimic Spring in North Carolina (12 h day length; 27 °C during the day and 20 °C during the night). After four months, when the perennial plants began to die back, watering was reduced and AM fungi sporulated (Bever *et al.* 1996). These soils were stored dry in the refrigerator for several months before use to break the dormancy of the spores. The second generation of the experiment was started as the first with each AM fungal community being grown with its same plant genotype. The composition of the AM fungal community within each pot was monitored as previously described (Bever *et al.* 1996). Host-specific differentiation of AM fungal communities was evaluated using multivariate profile analysis on ranks of spore densities as previously detailed (Bever *et al.* 1996).

(c) Tests of feedback on plant growth

To test for feedback, the effect of the differentiated AM fungal communities on plant growth was evaluated by growing replicates of the six genotypes of each plant species with individual fungal communities. In the test experiment for generation 1, each plant genotype was grown in an uninoculated control and with the AM fungal community from its own genotype, from a second genotype of its own species and from one genotype of each of the other species. This design was repeated for two replicate cultures for each genotype. The test experiment after the second generation focused on the *Panicum-Plantago* comparison. The design was as in generation 1, with balanced replication of each species in their own and each other's fungal communities. In both test experiments, soil-microbe free plants were planted into 400 cc pots of sterile soil and sand mix inoculated with 50 cc of inoculum from the cultures. They were grown in growth chambers as above for 10 weeks after which they were harvested, dried and weighed. Feedback was tested using a series of pairwise home versus away contrasts as previously derived (Bever *et al.* 1997).

(d) Plant growth response to AM fungal isolates

To confirm the mycorrhizal mechanism of the feedback between *Panicum* and *Plantago*, I evaluated the growth response of these species to inoculation with three AM fungal species that showed host-specific growth rates. *Panicum* and *Plantago* seedlings were grown in 500 cc sterile soil and sand mix (1 : 1 v/v) with seven inoculation treatments: the three AM fungal species, a separate control treatment for each AM fungal inoculum, and a fourth un-amended control. AM fungal treatments received 50 cc of inoculum. The controls for each AM fungal species received equal amounts of heat-pasteurized inoculum plus a drench of non-AM fungal filtrate from the inoculum, thereby controlling for potential mineral and non-mycorrhizal microbial components of the inoculum. AM fungal treatments, microbial controls and the sterile control were replicated 11, 9 and 7 times, respectively. The plants were grown and harvested as in the previous growth experiments. Microscopic examination of roots confirmed infection of mycorrhizal treatments and the absence of mycorrhizae in the controls. There were no statistical differences in plant growth between the four controls. Therefore, the differences in growth between inoculated and control treatments can be attributed to the different AM fungal species.

3. RESULTS

(a) Tests of feedback on plant growth

After the first generation of training, the plants generally grew better with each other's AM fungal community than with their own ($F_{1,236} = 9.0$, $p < 0.003$). This overall effect was due to significant negative feedback between two of the six pairs of plant species. After adjusting for multiple comparisons, there was weak evidence for negative feedback between *Allium* and *Panicum* ($F_{1,236} = 6.03$, $p < 0.05$) and strong evidence for negative feedback between *Panicum* and *Plantago* ($F_{1,236} = 17.04$, $p < 0.0001$). With this strong evidence of negative feedback between *Panicum* and *Plantago*, I focused the rest of this study on these two plant species.

In specifically comparing *Plantago* and *Panicum*, *Plantago* was more responsive than *Panicum* to AM fungal inoculation in general, and was specifically more responsive to the AM fungal community developed in association with *Panicum* relative to that developed with itself (figure 2a). These two patterns of the greater responsiveness of *Plantago* to inoculation and the negative feedback between *Plantago* and *Panicum* were also significant after the second generation of training (figure 2b).

(b) Host-specificity of AM fungal population growth rates

I found strong evidence of host-specific differences in the AM fungal population growth rates. These results have been previously described in full (Bever 2002). Here, I present analyses of the differentiation between *Panicum* and *Plantago*. While the total biovolume of AM fungal spores produced in either generation was not significantly different between *Panicum* and *Plantago*, the AM fungal community composition was highly divergent. For both hosts, the biovolume was largely made up of four AM fungal species: *Ac. morrowiae*, *Ar. trappei*, *Gi. gigantea* and *S. calospora*. Three of these species showed strong differences in growth with the two hosts. The fungi *Ac. morrowiae* and *Ar. trappei* sporulated more strongly with *Panicum* than *Plantago*, while *S. calospora* sporulated more strongly in association with *Plantago* than *Panicum* (figure 3).

While it is possible that these differences in sporulation rates reflect host-specific differences in fungal phenology, two lines of statistical evidence strongly indicate the existence of underlying host-specificity in AM fungal population growth rates. First, host-specific divergence between the AM fungal communities became stronger through time as tested by the species effect within multivariate profile analysis (generation 1: Wilks' $\lambda F_{9,151} = 8.97$, $p < 0.0001$; generation 2: Wilks' $\lambda F_{3,148} = 14.78$, $p < 0.0001$). Second, for each fungal species, when spore abundance in the first generation is included as a covariate predictor of spore abundance in the second year, both spore abundance in year 1 and host in year 2 are significant predictors of spore abundance in the second generation. Both of these analyses indicate that spore density for these species accurately represents their relative population growth rates and therefore the host-specific differences in sporulation that we measured reflect underlying host-specific differences in AM fungal population growth rates.

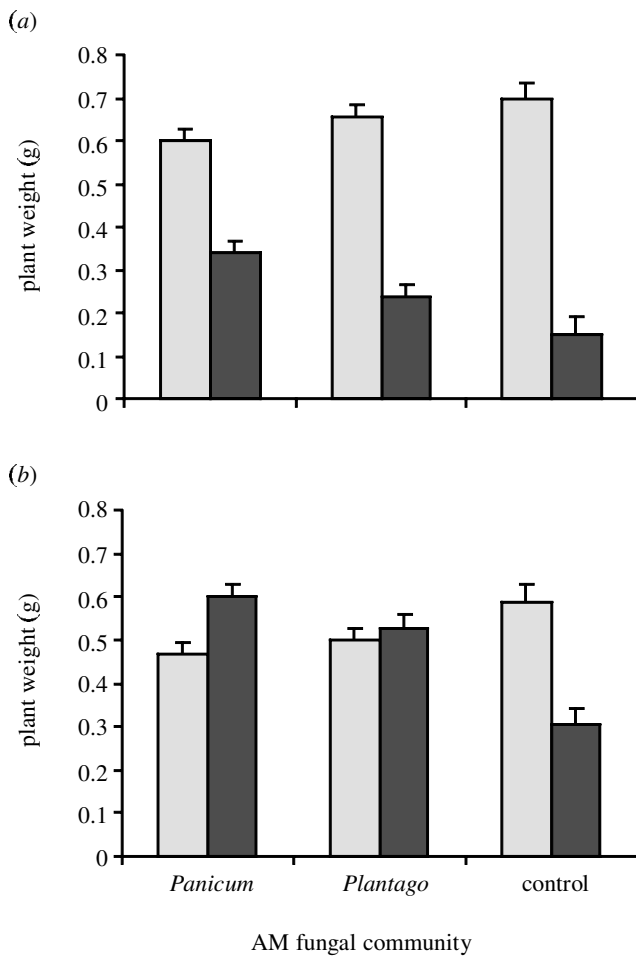


Figure 2. Plant growth responses to AM fungal communities in (a) generation 1 and (b) generation 2. Grey bars represent *Panicum* and black bars *Plantago*. *Panicum* and *Plantago* responded differently to their AM fungal communities. *Plantago* was more responsive than *Panicum* to AM fungal inoculation in general (generation 1: $F_{1,78} = 30.13$, $p < 0.0001$; generation 2: $F_{1,96} = 36.16$, $p < 0.0001$). *Plantago* was particularly responsive to the fungal community from *Panicum* as tested by a home versus away contrast (Bever *et al.* 1997) (generation 1: $F_{1,78} = 17.04$, $p < 0.0001$; generation 2: $F_{1,96} = 3.75$, $p = 0.05$). Statistics were performed on square-root transformed values of total plant biomass.

(c) *Plant growth response to individual AM fungal species*

Given the host-specific differentiation observed in the AM fungal communities (figure 3), the negative feedback on *Plantago* growth could result from differential responses of *Panicum* and *Plantago* to association with *Ac. morrowiae*, *Ar. trappei* or *S. calospora*. This interpretation was supported in independent evaluation of *Panicum* and *Plantago* growth responses to inoculation by these three AM fungal species. *Plantago*, again, was more responsive to AM fungal inoculation than *Panicum*. Most importantly, *Plantago* was particularly responsive to inoculation with *Ac. morrowiae* and *Ar. trappei* relative to *S. calospora*, while *Panicum* grew better with *S. calospora* than with *Ac. morrowiae* and *Ar. trappei* (figure 4). Therefore, the independent test of plant response to these AM fungal isolates corroborates the AM fungal mechanism for the observed negative feedback on plant growth (figure 2).

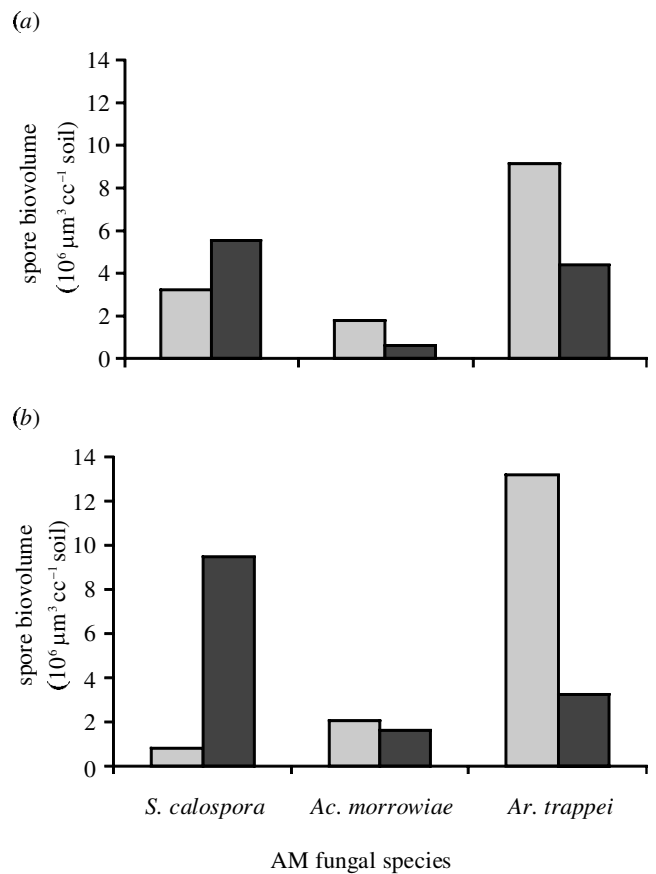


Figure 3. AM fungal spore production in (a) generation 1 and (b) generation 2. Grey bars represent *Panicum* and black bars *Plantago*. The AM fungal communities differentiated on *Panicum* and *Plantago*. *Scutellospora calospora* grew better with *Panicum* (generation 1: $F_{1,19} = 3.06$, $p < 0.1$; generation 2: $F_{1,19} = 15.95$, $p < 0.001$). *Acaulospora morrowiae* and *Archaeospora trappei* grew better with *Panicum* (for *Ac. morrowiae*, generation 1: $F_{1,19} = 50.8$, $p < 0.0001$; generation 2: not significant; for *Ar. trappei*, generation 1: $F_{1,19} = 16.17$, $p < 0.001$; generation 2: $F_{1,19} = 15.36$, $p < 0.001$). Mean spore biovolume was calculated from the average spore production weighted by the average spore volume and statistical tests were on ranks of spore abundance.

4. DISCUSSION

Negative feedback through changes in the whole soil community has been observed in previous studies of *Plantago* and *Panicum* (Bever *et al.* 1997). Previous work on soil pathogens with these two species has suggested that accumulation of soil pathogens in the genus *Pythium* that are specific to *Panicum* could contribute to the negative feedback (Mills & Bever 1998). The present study supports the operation of a second, complementary soil microbial mechanism of negative feedback between these two species: host-specific changes in the composition of the AM fungal community. Three lines of evidence come together to support the interpretation of a mycorrhizal cause of the negative feedback. First, great effort was put into excluding soil pathogens from our experimental system by starting all AM fungal cultures from single spores and then maintaining these cultures and the experimental communities away from sources of soil pathogens. Even with these efforts, a possibility of contamination of the cul-

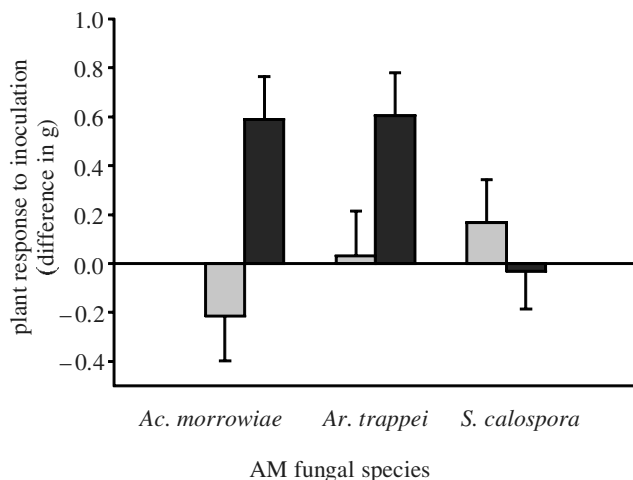


Figure 4. Plant growth response to individual AM fungal species. Grey bars represent *Panicum* and black bars *Plantago*. Differences in mean plant biomass between inoculations and controls are presented. *Plantago* was more responsive to AM fungal inoculation than *Panicum* ($F_{1,109} = 5.33$, $p = 0.02$). *Plantago* was particularly responsive to inoculation with *Acaulospora morrowiae* and *Archaeospora trappei* relative to *Scutellospora calospora* ($F_{1,109} = 5.45$, $p = 0.02$). Statistics were performed on square-root transformed values.

tures remains. However, no evidence of root pathogens was observed in the root system of the test experiments. Moreover, the plant growth responses to the individual AM fungal species (figure 4), when combined with the differentiation observed in the AM fungal community (figure 3), can explain the negative feedback observed in the test experiment (figure 2). With the internal consistency of these experiments, it is unnecessary and non-parsimonious to invoke the action of any undetected pathogens to explain the negative feedback observed in the test experiment (figure 2). The possibility remains that microorganisms that have been observed living within spores of AM fungi (see Walley & Germida 1996; Redecker *et al.* 1999) could contribute to the impact of these fungi on plant growth. However, for these microorganisms to play a part in the observed negative feedback, they would have to be stably inherited with individual AM fungal species to account for the internal consistency of these results. In such a case, the AM fungal species and its symbionts would be behaving as a single organism.

The decreased benefit that *Plantago* receives from its own AM fungal community relative to that of *Panicum* appears to result from an asymmetry in delivery of benefit between plants and AM fungi. While *S. calospora* has its highest population growth rate on *Plantago*, *Plantago* does not benefit from this fungus as much as it benefits from *Ac. morrowiae* and *Ar. trappei*, which themselves accumulate with *Panicum* (figure 5). The resulting dynamic may contribute to plant species coexistence. As *Plantago* becomes increasingly common, *S. calospora* would be predicted to increase, causing *Plantago*'s growth rate to decrease and allowing *Panicum* to increase. Conversely, a high abundance of *Panicum* would be predicted to have an indirect beneficial effect on the growth of *Plantago*

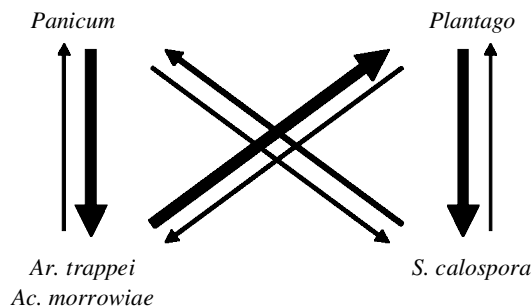


Figure 5. Asymmetric fitness relationships between plants and AM fungi generate negative feedback. The arrows indicate the direction of benefit and the thickness of the arrows indicates the relative magnitude of benefit. The presence of *Panicum* increases the relative abundance of *Acaulospora morrowiae* and *Archaeospora trappei*, thereby increasing the relative performance of *Plantago*.

through the changes in the AM fungal community. To my knowledge, this is the first demonstration of negative feedback being generated within a mutualism, and this result adds credence to previous observations indicating similar dynamics (Johnson *et al.* 1991; Bever 1994; Kiers *et al.* 2000; Bever *et al.* 2002).

It is interesting to note that *Panicum* is a native species to North Carolina while *Plantago* is exotic. In this context, the present study indicates that the presence of the native plant, *Panicum*, indirectly facilitates the establishment of the exotic plant species, *Plantago*, through changes in the composition of the AM fungal community. Mycorrhizal facilitation of invasive plant species has been suggested in several other studies (Marler *et al.* 1999; Callaway *et al.* 2001; Klironomos 2002). The AM fungal community dynamics observed in the present study could specifically contribute to an explanation of mycorrhizal mediation of competitive superiority of an invasive forb species against a native perennial grass species in the western USA (Marler *et al.* 1999; Callaway *et al.* 2001).

The observation of negative feedback through changes in the AM fungal community between *Panicum* and *Plantago* in the present study does not indicate that all feedback through the mycorrhizal fungal community should be negative. Indeed, we have circumstantial evidence of a positive feedback dynamic between other plant and AM fungal species within the same community (Bever *et al.* 2001). Rather, these results with *Panicum* and *Plantago* broaden our understanding of the range of dynamics possible within a mutualism and lead to questions of how often, and under what conditions, do dynamics between plants and AM fungi result in positive versus negative feedback. These questions are of importance beyond the plant-AM fungal interaction, as they are equally relevant to the dynamics of other mutualisms (Bronstein 1994). Moreover, as the benefit that *Plantago* receives from its AM fungal community degrades over time, a microevolutionary process of this type could lead to the dissolution of the mutualism, as has been found to occur within several mutualisms over evolutionary time (Fitter & Moyersoen 1996; Hibbett *et al.* 2000; Lutzoni *et al.* 2001). Therefore, identifying what conditions lead to positive versus negative feedback represents an important step

towards understanding the evolutionary maintenance of mutualism.

The present study uses a series of experimental manipulations to illustrate the complex dynamics possible within the plant–AM fungal mutualism. The results of this study indicate that dynamics within the AM fungal community can contribute to the maintenance of diversity within plant communities. While the generality of this mechanism awaits further experimentation, a positive effect of AM fungal diversity on plant diversity has recently been demonstrated in two grassland systems (van der Heijden *et al.* 1998). Together with other recent demonstrations of microbial control over plant community diversity and dynamics (van der Putten *et al.* 1993; Mills & Bever 1998; Clay & Holah 1999; Packer & Clay 2000; Callaway *et al.* 2001; Klironomos 2002), these studies call for heightened attention to the potential importance of microbes in community processes. These studies also raise the concern that loss of soil microbial diversity due to agriculture (Helgason *et al.* 1998; Douds & Millner 1999) and other anthropogenic disturbance (Egerton-Warburton & Allen 2000) may have unanticipated negative consequences on community functions.

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