Plant and Soil **244:** 281–290, 2002.
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Host-specificity of AM fungal population growth rates can generate feedback on plant growth

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Key words: arbuscular mycorrhizal fungi, community dynamics, feedback, host-specificity, population growth rates

Abstract

While the mutualistic interaction between plants and AM fungi is of obvious importance to ecosystem processes, the factors influencing the ecological and evolutionary dynamics within this interaction are poorly understood. The mutual interdependence of plant and AM fungal relative growth rates could generate complex dynamics in which the composition of the AM fungal community changes due to association with host and this change in fungal composition then differentially feeds back on plant growth. I first review evidence for feedback dynamics and then present an approach to evaluating such complex dynamics. I specifically present evidence of host-specific differences in the population growth rates of AM fungi. Pure cultures of AM fungi were mixed to produce the initial fungal community. This community was then distributed into replicate pots and grown with one of four co-occurring plant species. Distinct compositions of AM fungal spores were produced on different host species. The AM fungal communities were then inoculated back onto their own host species and grown for a second growing season. The differentiation observed in the first generation was enhanced during this second generation, verifying that the measure of spore composition reflects host-specific differences in AM fungal population growth rates. In further work on this system, I have found evidence of negative feedback through two pairs of plant species. The dynamic within the AM fungal community can thereby contribute to the coexistence of plant species.

Introduction

Arbuscular mycorrhizal (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 the majority of plant species associate with AM fungi, including most agricultural plants (Smith and Read, 1997) and the presence of these fungi have been shown to influence interspecific competition (Grime et al., 1987; Hartnett et al., 1993; Hartnett and Wilson, 1999), the trajectory of succession (Allen and Allen, 1990; Janos, 1980; Medve, 1984), and the stabilization of soil aggregates (Miller and Jastrow, 2000).

AM fungi have been found to associate with plants with relatively low specificity and therefore the association is thought to be largely non-specific (Hoeksema, 1999; Law, 1985; Smith and Read, 1997). However, there is growing evidence of host-specific differences in plant response to AM fungi and in fungal response to plants. The extent of plant growth promotion by AM fungi depends upon the specific plant and fungal combinations (Adjoud et al., 1996; Streitwolf-Engel et al., 1997; Van der Heijden et al., 1998). Conversely, measures of growth of AM fungal species also depends on the associated host plant species (Bever et al., 1996; Eom et al., 2000; Johnson et al., 1992b; Sanders and Fitter, 1992).

This level of specificity of AM fungi can have important consequences on plant ecology. Specifically, as a result of the specificity of plant response to the AM fungi, the diversity and composition of the AM fungal community has been shown to exert large effects on plant diversity and composition (Van der Heijden et al., 1998). Conversely, the composition of the plant community has similar large effects on the diversity and composition of the AM fungal community (Bever et al., 1996; Eom et al., 2000; Johnson

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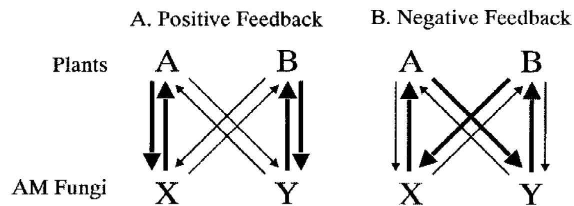

Figure 1. Representation of fitness sets that would produce positive and negative feedback within the interaction of plants and AM fungi. In these figures, the thickness and direction of the arrows represent the relative benefit that two plant types (A and B) and two AM fungal types (X and Y) receive from their association. In the case of a highly symmetric fitness relationship between plants and AM fungi (a), an initial abundance of plant A will result in an increase in representation of AM fungus X, which will increases the growth rate of plant A and thereby generate a positive feedback that can lead to the loss of diversity. Alternatively, in the case of a highly asymmetric fitness relationship (b), an initial abundance of plant A will increase the representation of AM fungus Y and thereby boost the performance of plant B, resulting in a negative feedback on plant A (redrawn from Bever et al. 1997).

et al., 1992b; Sanders and Fitter, 1992). Because of the mutual interdependence of plant and fungal growth rates, it is difficult to project the long-term dynamics and stability of the community.

The 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, 1999; Bever et al., 1997, in press). Positive feedback is generated by symmetric fitness relations between plant and AM fungi while highly asymmetric fitness relations will generate negative feedback (Figure 1). 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).

Evidence of negative feedback through the AM fungal community

Currently, there is little evidence of such complex community feedback dynamics between plants and AM fungi, or within any other mutualism. Several studies have identified patterns consistent with negative feedback through the AM fungal community (Bever, 1994; Bever et al., in press; Johnson et al., 1991; Kiers et al., 2000). Johnson et al. (1991) identified a shift in AM fungal spore composition due to cropping sequence in the midwestern United States. Specifically, different species of AM fungi increased with repeated cropping of corn compared to repeated cropping of soybeans. Corn and soybeans are regularly rotated in the Midwestern US because of yield decline following repeated monocropping. This yield decline could result from the shift in AM fungal community composition (Johnson et al., 1992a). A similar correlation has been observed between host-specific degradation of the soil community and shifts in the AM fungal composition in old field weeds in North Carolina (Bever, 1994; Bever et al., 1996, 1997). However, in both of these cases, the plant growth effects could result from accumulation of host-specific root pathogens. In the case of the corn–bean rotation host-specific root feeding nematodes are known to be a potential driver of the yield decline (Agrios, 1997). In the North Carolina system, both host-specific accumulation of root pathogens in the genus *Pythium* (Mills and Bever, 1998) and host-specific shifts in the composition of rhizosphere bacteria have been shown to be potential agents of negative feedback (Westover and Bever, 2001).

Two studies, one in the North Carolina old field (Bever, 1994) and the second in a tropical forested system (Kiers et al., 2000), observed negative feedback in experiments that attempted to separate the effects of soil pathogens from other components of the soil community by inoculating with roots and controlling for non-mycorrhizal species with microbial washes. Specifically, they found that plants grew more poorly when grown with their own live roots than when grown with each other's roots. The microbial wash, however, is unlikely to equalize the density of root pathogens and, since root pathogens are known to have strong effects in both of these systems (Augspurger and Kelley, 1984; Mills and Bever, 1998; Westover and Bever, 2001), these studies cannot eliminate the possibility that the differential effects of root inocula on plant growth was due to root pathogens.

A third approach to investigating the feedback dynamics through the AM fungal community is to make inference into the dynamics from measures of the interdependence of plant and fungal growth rates. While measurement of specificity of plant response to AM fungi is common, concurrent measurement of AM fungal growth response is rare. This likely reflects the difficulties that measurement of AM fungal

growth presents. 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. AM fungal community composition therefore has been inferred from counts of the spores, an imperfect measure. One such study compared the growth responses of six plants and five AM fungi that co-occur within an old field in North Carolina (Pringle, 2001). In this study, plant growth and fungal sporulation were measured over a 5-month period. In reanalysis of this data in the context of the feedback model (Bever, 1999), we found evidence of highly asymmetric fitness relations between plants and AM fungi that would generate negative feedback (Bever et al., in press). Because this study started with pure cultures of AM fungi, it avoids the problems of separating the effects of pathogens from that of mycorrhizal fungi. However, the prediction of negative feedback depends upon the accuracy of counts of spores as estimates of fungal population growth rates.

Clearly, evaluation of feedback effects through the AM fungal community is made difficult both by the separation of effects of AM fungi from the effects of other soil organisms and by the measurement of the relative growth rates of AM fungal populations. Here, I present an approach to testing AM fungal community feedback that overcomes these difficulties. I do this by first manipulating replicate laboratory AM fungal communities and then testing the consequences for plant growth (Bever et al., in press). Specifically, a diverse community of AM fungi was reconstructed from pure cultures to eliminate plant pathogens. The initial AM fungal community was then trained on individual plant hosts and then the growth responses of these plant species were evaluated in response to inoculation by the trained fungal communities. The inoculum in this test experiment includes both the spores and hyphal structures of AM fungi and therefore accurately represents the entire fungal community. I test the interactions between four plant species and co-occurring AM fungi from an old field in North Carolina (Bever et al., 1996, 2001, in press). Through this work, I have demonstrated negative feedback through two pairs of plant species (Bever, unpublished ms.). In the present paper, I detail the evidence of host-specificity of AM fungal population growth rates and the resulting differentiation of the AM fungal community.

Methods

The overall approach involved the reconstruction of an AM fungal community free of plant pathogens, followed by the training of this fungal community on plant hosts and finally testing the growth response of these plants to inoculation by these trained fungal communities (Bever et al., in press). Specifically, replicate AM fungal communities were grown on individual host plants for one growing season, during which time the composition of the fungal community may differentiate due to host-specific differences in fungal growth rates (Figure 2). I monitored this differentiation by examining the production of AM fungal spores. To confirm these inferences into the AM fungal community differentiation, I reinoculated the AM fungal communities on their own hosts and monitored AM fungal differentiation after a second growing season (Figure 2). If the differentiation observed after the first growing season is enhanced during this second growing season, this confirms that the spore counts do reflect the differentiation of the AM fungal community.

Isolation of plants and AM fungi

These experiments were performed using co-occurring plants and AM fungi from a North Carolina grassland. The site has a diverse community of plants and fungi (Bever et al., 2001). Four plant species and eight AM fungal species were used in this study, all of which were isolated from within a 75-m^{-2} area (Bever et al., 1996). 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 described in (Bever et al., 1996). Clones of *Allium* were replicated with their asexually produced bulbils and clones of *Plantago* were grown from leaf cuttings dipped in IAA.

The eight fungal species included *Acaulospora morrowiae*, *Archaeospora trappei*, *Gigaspora gigantea*, *Gi. decipiens*, *Scutellospora calospora*, *S. pellucida*, *S. reticulata*, and an undescribed species of *Glomus* (identified as *Gl. D1* in Bever et al. (1996)). Each of these species has been deposited in the *International Culture Collection of Arbuscular and Vesicular–Arbuscular Mycorrhizal Fungi* (INVAM) as described in (Bever et al., 1996). All fungal cultures

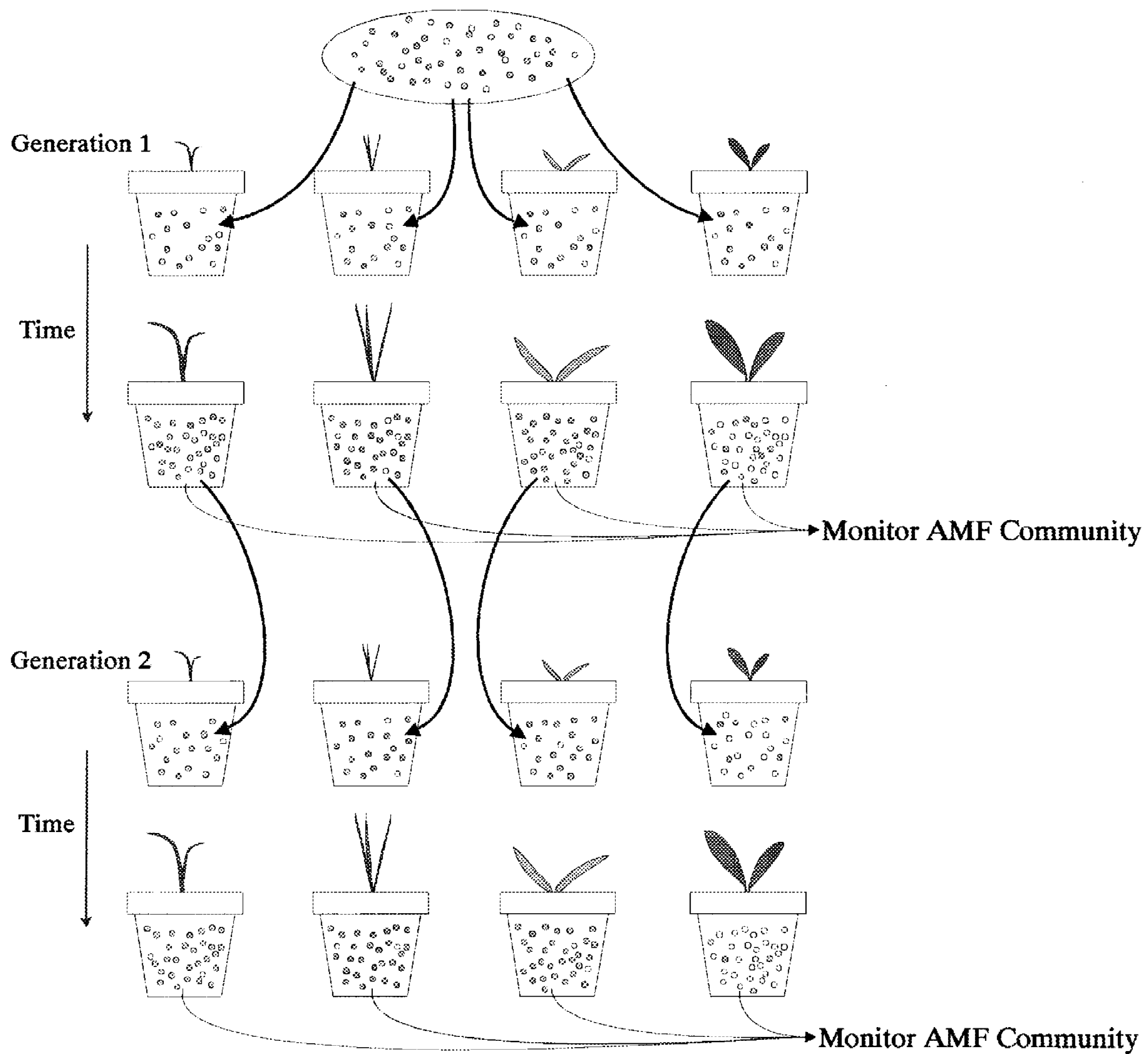

Figure 2. Experimental design. Pure cultures of AM fungi were mixed to produce the initial fungal community. This community was then distributed into replicate pots into which soil-microbe free replicates of four plant species were planted. These were grown for 4.5 months during which the AM fungal species infected their hosts' roots, proliferated, and then sporulated. At the end of this time, the AM fungal spore composition was monitored. To verify that the differentiation observed after the first generation reflects differences in AM fungal growth rates, the AM fungal communities were inoculated back onto their own host genotype and grown for a second growing season, after which the AMF community composition was monitored.

were started from a single spore to ensure that they were free of pathogens. The cultures were grown on Sorghum in autoclaved 1:1 mixture of field soil and sand for 4.5 months in a growth chamber at which time there was abundant sporulation. The cultures were then dried and stored for several months in the refrigerator to break dormancy of spores prior to use.

Laboratory microcosms

The overall design of the microcosm experiment is as depicted in Figure 2. The initial AM fungal community was created by mixing the eight pure cultures in equal proportion. Replicate 600-cc pots were filled with 400 cc 1:1 mixture of sterile soil and sand and inoculated with 200 cc of the initial AM fungal community. Into these pots were planted single, soil-microbe-free plants of one of six genotypes of each of

P. lanceolata, A. odoratum and *P. sphaerocarpon*, each replicated three times. For *Allium* there were 5 genotypes three of which were replicated five times and two replicated four times (for a total of 77 AM fungal communities). The plants were grown in a growth chamber with conditions set to mimic Spring in North Carolina (12 h day length, 27 and 20 °C day and night). After 4 months, when the perennial plants begin to dieback, watering was reduced and AM fungi sporulated (Bever et al., 1996). This pattern of sporulation is consistent with the seasonal patterns of spore production observed in the field at this site (Bever et al., 2001; Pringle, 2001; Schultz, 1996). The reduced watering and subsequent harvest was staggered, with the water being reduced in the first replicate at 4 months and the watering of the second replicate reduced after 4.5 months and the watering of the third replicate reduced after 5 months. The three times of harvest allow testing of whether AM fungal sporulation patterns reflect shifts in the phenology of sporulation of individual AM fungal species. These soils were stored dry in the refrigerator for several months prior to use in order to break dormancy of spores. The second generation of the experiment was started as the first, with each AM fungal community being grown with its same plant genotype.

Monitoring of the AM fungal community composition

The composition of the AM fungal community within each pot was monitored through the extraction, identification and enumeration of freshly produced spores, as in (Bever et al., 1996). Spore biovolume was then estimated from spore counts of individual fungal species by weighting these counts by the average volume of individual spores.

Statistical analysis

Differences in production of total spore biovolume were tested using univariate analysis of variance using the general linear models procedure in SAS (SAS, 1990). Host-specific differentiation of AM fungal communities was evaluated using multivariate profile analysis on rank of spore densities as detailed in Bever et al. (1996). The conversion to ranks improves the homogeneity of variance of the skewed distribution of spore counts. Profile analysis directly tests for shifts in the spore composition of the AM fungal community through the significance of the interaction term between plant species and response profile (Bever et al., 1996). The strong interaction terms of profile, plant species and harvest would suggest that sporulation patterns are sensitive to harvest date and may reflect shifts in AM fungal phenology rather than host-specific shifts in population growth rates (Bever et al. 1996). For all multivariate analyses, Wilk's Λ was used for testing hypotheses, though all of the multivariate tests gave similar results. The multivariate analyses were followed by univariate analyses of variances of the ranks of spore counts of individual fungal species. All analyses tested the effects of plant species, harvest dates and the interaction of plant species and harvest date. Comparisons of means after the univariate analyses were corrected for multiple comparisons using the Tukey–Kramer method (Sokal and Rohlf, 1995).

The consistency of the differentiation of spore composition between the two generations was tested using two approaches. First, an increase in the value of the Wilk's Λ F statistic for the interaction of the plant species and response profile indicates that differentiation is larger in the second generation than the first. Secondly, I conducted analyses of covariance including spore counts from the first generation (and the interaction of these spore counts and plant species) as predictors of the spore counts in the second generation. As I knew that these spore counts were correlated with plant species, I used backward elimination of predictors to identify which predictors were strongest. I started with the full model of predictors and eliminated the predictor with the highest F value and reran the analysis until all predictors were significant at $p \leq 0.1$.

Results

AM fungal community differentiation: generation 1

After the first generation of training, I found strong evidence of host-specific differences in the AM fungal communities. The total biovolume of AM fungal spores produced after the first generation was greatest with *Allium* and least with *Anthoxathum*, but was not different between *Panicum* and *Plantago*. For all hosts, spore biovolume was largely made up by four fungal species, *Acaulospora morrowiae*, *Archaeospora trappei, Gigaspora gigantea* and *Scutellospora calospora.* Spores of *Gi. decipiens*, *Gl.* D1, *S. pellucida* and *S. reticulata* were encountered infrequently and made up a negligable component of the total biovolume. Because of their low level of sporulation, I

Table 1. Multivariate profile analysis of AM fungal community composition for generation 1 and generation 2. The compositions of the AM fungal communities were highly different between hosts as indicated by the strong effect of plant species. This differentiation of the AM fungal communities increased from generation 1 to generation 2, indicating that host-specific differences in spore abundance reflects host-specific differences in relative rates of AM fungal population growth

Source	Generation 1 Interaction with Profile			Generation 2 Interaction with Profile		
	No. d.f.	Den. d.f.	Wilk's Λ F	No. d.f.	Den. d.f.	Wilk's Λ F
Plant species	9	150	8.97****	9	150	14.78****
Harvest	6	124	2.98*	6	124	3.52**
Plant species × harvest	18	175	1.57	18	175	1.21

Significance conventions: * P<0.05, ** P<0.01, *** P<0.001, **** P<0.0001.

was not able to analyze the abundance of these species statistically and analyses of composition focus on the four dominant species.

The composition of the AM fungal community was highly divergent between plant species as revealed by the high significance of the interaction of AM fungal sporulation profile with plant species (Table 1). The host specific differences in sporulation were similar across the three harvests as indicated by the insignificant and small interaction term of plant species and harvest (Table 1). This suggests that the shifts in sporulation reflect host-specific differences in population growth rates rather than host-specific differences in the phenology of sporulation.

Gi. gigantea sporulated most abundantly with *Allium* and least abundance with *Anthoxanthum* (Table 2 and Figure 3). *S. calospora* also sporulated most abundantly with *Allium*, followed by *Plantago*, and then *Panicum* and *Anthoxanthum* (Table 2 and Figure 3). *Ar. trappei* sporulated most abundantly with *Allium* and *Panicum,* followed by *Plantago* and then *Anthoxanthum* (Table 2 and Figure 3). *Ac. morrowiae* sporulated most abundantly with *Panicum*, followed by *Allium*, *Plantago* and *Anthoxanthum* (Table 2 and Figure 3).

AM fungal community differentiation: generation 2

The sporulation patterns observed in the first generation were reinforced during the second generation. The species of AM fungi that were infrequently observed after the first generation were even more infrequent after the second generation. Spores of *S. reticulata* and *G. decipiens* were not found and only a few spores of *S. pellucida* and *Gl.* D1 were observed. The differences in spore volume remained as in the first generation. The differentiation of the AM fungal communities was enhanced as demonstrated by the increased *F* value and significance of the interaction of AM fungal sporulation profile with plant species (from 8.97 to 14.78, Table 1). Again, the interaction of host species and harvest was not significant. The specific patterns of sporulation were generally similar to that observed in the first generation (Table 2 and Figure 3).

The continual decline of the rare fungal species and the increased differentiation of the common fungal species both indicate that the differentiation observed in the AM fungal community does reflect host-specific differences in AM fungal population growth rates. This interpretation is reinforced by re-analysis of spore abundance in the second generation using spore abundance in the first generation as a covariate. For each of the four common fungal species both spore abundance in generation 1 and host in generation 2, or the interaction of these two factors are significant predictors of spore abundance in the second generation (Table 3). The significance of previous generations' spore counts in predicting spore counts in future generations demonstrates that spore counts in generation 1 do indeed reflect fungal population growth rates.

Discussion

In this report, I demonstrate that AM fungal species, though associating with all hosts, have host-specific differences in their population growth rates. All four of the common AM fungal species showed host-specific differences in their sporulation rates after the first growing season resulting in differentiation of the AM fungal spore composition (Table 1 and Figure 3). Previous studies have also found host-specific differentiation of spore composition (Bever et al., 1996; Eom et al., 2000; Johnson et al., 1992b; Sanders and Fitter, 1992). The present study, however, is the first to demonstrate that such differentiation is increased over successive growing seasons (Table 1 and Figure 3), thereby providing strong evidence that changes in spore composition reflect underlying differences in AM fungal population growth rates. Moreover, both species of plant host and spore abundance in the previous generation are good predictors of AM fungal spore composition in the second generation (Table 3). These patterns cannot be explained under the alternative hypotheses of host-specific differences in phenology of

Table 2. Analysis of variance of spore counts. This table presents the analyses of the rank of the spore counts for the four common fungal species. The *F* value is presented.

Source	d.f.	Generation 1				Generation 2			
		Gi. gig.	*S. cal.*	*Ac. mor.*	*Ar. trap.*	*Gi. gig.*	*S. cal.*	*Ac. mor.*	*Ar. trap.*
Plant species	3	35.4****	31.9****	53.3****	43.8****	113.7****	25.5****	20.5****	19.5****
Harvest	2	0.1	1.8	12.6****	8.7***	0.6	0.4	10.3****	3.0
Plant species × harvest	6	1.8	0.4	0.5	3.1*	1.7	0.9	1.5	1.2

Significance conventions: * $P<0.05$, ** $P<0.01$, *** $P<0.001$, **** $P<0.0001$.

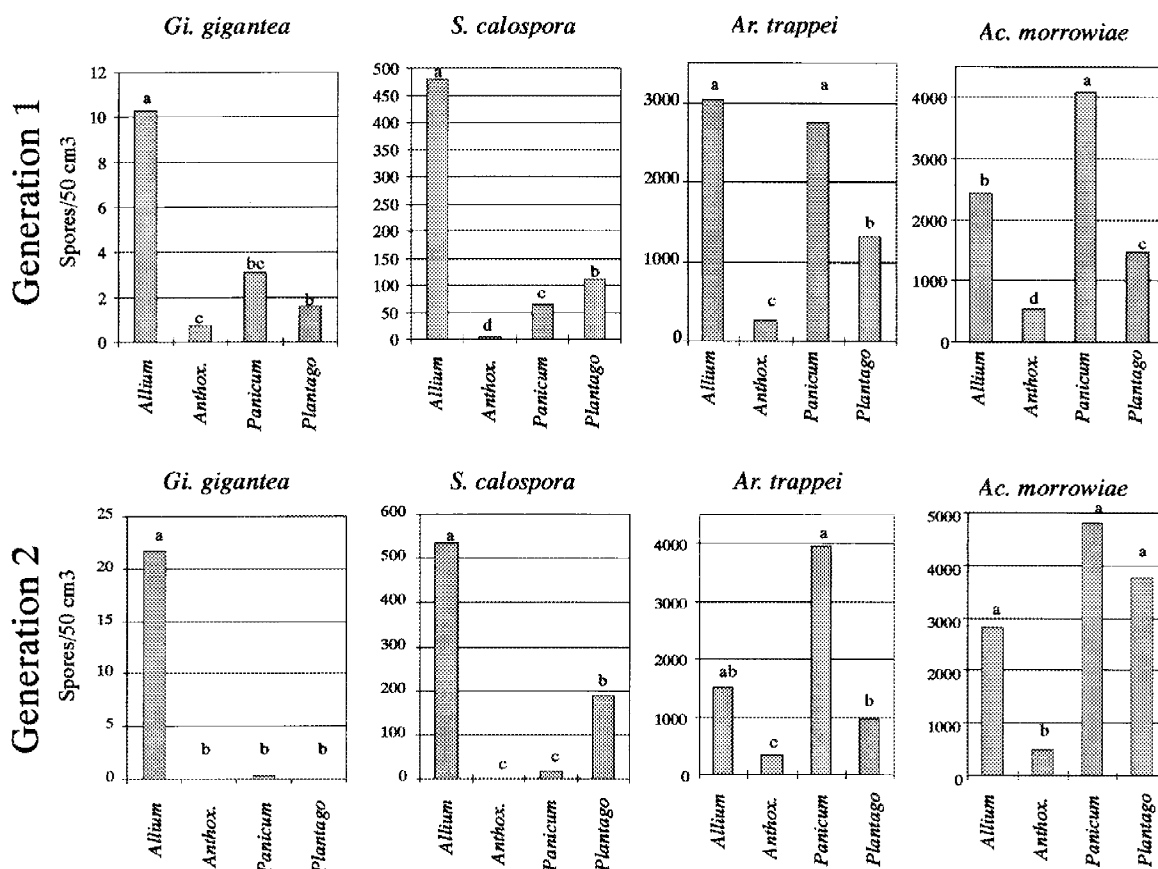

Figure 3. Spore composition after the first and second generation of training. The top row of figures give the average spore abundance of the four common AM fungal species after the first generation of training. The second row of figures gives the average spore abundance for these species after the second generation of training. Within each individual histogram, different letters indicate significant differences between means ($P<0.05$).

sporulation or of sporulation being meaningless to AM fungal population growth.

We note that confidence in the relationship between changes in spore composition and underlying differences in AM fungal population growth rate may be system specific. Species of *Acaulospora*, *Gigaspora* and *Scutellospora* from our field site have shown consistent sporulation pattern over successive years, that is likely associated with the seasonal behavior of their hosts (Bever et al., 2001; Pringle, 2001; Schultz, 1996), suggesting that, for these fungi at this site, sporulation is an important part of their life history. Other AM fungi at this site, namely species of *Glomus*, do not show this consistent pattern (Pringle, 2001). It is possible that for these species or in other

Table 3. Analysis of co-variance of spore counts from the second generation. This table presents the analyses of the rank of the spore counts from the second generation for the four common fungal species. For each fungal species the spore counts in the previous generation (indicated by the species name followed by 1) are used as covariates. The model that resulted from the backward elimination of predictors is presented. A significant effect of prior spore density supports hypothesis that spore counts reflect population growth rates. With both prior spore density and plant species predicting sporulation in generation 2, the results support the idea that differentiation continued between generations, a result that is only consistent with the hypothesis of host-specific differences in population growth rates.

Source	d.f.	*F*
Gi. gigantea (Generation 2)		
Gi. gig. 1	1	2.6†
Plant species	3	77.0****
S. calospora (Generation 2)		
S. cal. 1	1	28.8****
Plant species	3	2.2†
S. cal. 1 × Plant species	3	3.4*
Ac. morrowiae (Generation 2)		
Ac. mor. 1	1	1.3
Plant species	3	6.6***
Harvest	2	8.4***
Ac. mor. 1 × Plant species	3	4.1*
Ar. trappei (Generation 2)		
Ar. trap. 1	1	2.9†
Plant species	3	5.1**

Significance conventions: †$P<0.1$, *$P<0.05$, **$P<0.01$, ***$P<0.001$, ****$P<0.0001$.

systems, sporulation may not correlate as strongly with population growth rates.

The present study does not identify the mechanism of host-specific differences in the AM fungal population growth rates. However, comparison of the patterns of differentiation of the AM fungal community observed in the present study to those patterns previously observed in an independent study of these same plant and fungal species (Bever et al., 1996) provides important clues about the factors involved in these differences. Specifically, some of the patterns are consistent between the two studies. For example, *S. calospora* sporulated in greater abundance with *Plantago* than with *Panicum* in both of these studies. However, other patterns are markedly different. *S. calospora*, for example, sporulated most abundantly with *Allium* in the present study, but sporulated poorly with *Allium* in the previous study. Such differences in specificity likely result from differences between the two studies, namely the removal of the other components of the soil community from the present study.

For example, in the earlier study, sporulation with *Allium* was dominated by *Ac. colossica* (Bever et al., 1996). Field sampling at our study site also indicate strong spatial correlation of the local abundance of *Allium* and *Ac. colossica* (Bever et al., 1996; Schultz, 1996) and the seasonalities of this plant and fungus appear to be closely matched, with both plant and fungus being physiologically active in the cool-season (Bever et al., 2001; Pringle, 2001; Schultz et al., 1999), suggesting a strong positive relationship between this species of plant and fungus. However, as *Ac. colossica* is apparently an obligately cool-season fungus, it was not easily cultured in the lab (Schultz et al., 1999) and I was therefore not able to include it in the present study. Perhaps with the absence of this fungus, or of other components of the soil community, from the present study, fungal species that had previously sporulated relatively poorly with *Allium* now sporulated most abundantly with *Allium*. *S. calospora* and *G. gigantea* sporulated more abundantly with *Plantago* than *Allium* in the presence of *Ac. collosica*, but sporulated in greater abundance with *Allium* than *Plantago* with *Ac. collosica* removed in the present study (Figure 3). This suggests that the relative growth rates of AM fungal species depends not only on the identity of the host with which they are associated, but also on the identity of the other components of the AM fungal community or other components of the soil community. That is, the host-specificity of the AM fungal population growth rates is context dependent. This context-dependence may result from the differences in interspecific competition between individual species of AM fungi.

Regardless of the mechanism, the host-specificity of AM fungal population growth rates has important consequences on our understanding of the ecology of the plant–AM fungal interaction. One simple consequence of such specificity is that the composition and diversity of the AM fungal community would be expected to change with the local composition of the plant community. The extended dominance by a single plant species might result in decreased diversity of the fungal community, due to the loss of individual fungal species that are less competitive in association with that host. Conversely, a more diverse plant community would be expected to maintain greater diversity in the fungal community. There then should be a correlation

between plant and fungal diversity, a result observed within our study site (Schultz, 1996).

As plants respond differently to individual species of AM fungi, the change in diversity and composition within the AM fungal community should feed back on plant community dynamics. In further experimentation on this system, I have found evidence of negative feedback between two pairs of plant species (Bever, unpublished ms.). Such negative feedback results from an asymmetry in the delivery of benefit between plant and fungal species (Bever, 1999; Bever et al., in press). The results of this study suggest that dynamics within the AM fungal community can contribute to the maintenance of diversity within plant communities. A positive effect of AM fungal diversity on plant diversity has recently been demonstrated in two grassland systems (van der Heijden et al., 1998; but see Wardle, 1999) and negative feedback represents one of several possible mechanisms generating this effect (Bever et al., 2001). Together with other recent demonstrations of microbial control over plant community diversity and dynamics (Clay and Holah, 1999; Mills and Bever, 1998; Packer and Clay, 2000; van der Putten et al., 1993), these studies call for heightened attention to the potential importance of microbes in plant community processes.

Acknowledgements

I thank J. Morton, J. Antonovics, P. Schultz, A. Bennett, and K. Mills for advice and assistance. This project was supported by USDA grants 92-37101-7461 and 94-37101-0354, and NSF grants DEB-9996221 and DEB-0049080.

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