Ecology, 73(6), 1992, pp. 2034–2042

PLANT AND SOIL CONTROLS ON MYCORRHIZAL FUNGAL COMMUNITIES[1]

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Abstract. A field experiment was conducted to examine the relative importance of soil factors and plant species on communities of vesicular-arbuscular mycorrhizal (VAM) fungi. Populations of VAM fungal spores were studied in 4-yr-old monocultures of five successional grass species grown in a gradient of soil mixtures ranging from pure subsurface sand to pure sandy loam topsoil. A total of 19 species of VAM fungi were found across all treatments. Of the 12 most abundant VAM fungal species, 6 species had a significant dependence on both soil mixture and host species, while 2 were dependent only on soil and 2 only on host. To our knowledge, these are the first results indicating that even closely related hosts (five grasses) may cause divergence in VAM fungal communities on initially identical soils. Cluster analysis of the similarity of fungal communities by host plant species showed the fungal communities in the two late successional grasses to be most similar to one another and least similar to the fungal communities in the early successional grass species. Cluster analysis of the similarity of fungal communities by soil mixture showed the fungal communities in the sandy end of the soil gradient diverged predictably from the fungal communities in the black soil end of the gradient. These results support the hypothesis that soil factors and plant species may be of equal importance in regulating the species composition of VAM fungal communities.

Key words: Cedar Creek; edaphic effects; host plant effects; spore populations; successional grasses; VAM fungal communities; V-A mycorrhizae.

INTRODUCTION

Vesicular-arbuscular mycorrhizae are symbiotic associations between plant roots and an ubiquitous group of zygomycetous fungi. Vesicular-arbuscular mycorrhizal (VAM) fungi are believed to be among the most abundant fungi in the soil (Gerdemann and Nicolson 1963), yet very little is known about their ecology. Nearly 150 species of VAM fungi have currently been described based on the morphology of their asexual soil-borne spores (Schenck and Pérez 1990). Some insights into the ecology of VAM fungi have been gained by studying natural distributions of their spores, but still little is understood about the factors that regulate populations of these fungi. Many species of VAM fungi are known to have worldwide distributions, and occur in a remarkable variety of habitats and climates. Nevertheless, patterns in the distributions of some VAM fungal species are beginning to emerge as more ecological studies are conducted. Distributions of certain VAM fungal species have been shown to be related to abiotic factors such as soil pH (Abbott and Robson 1977, Porter et al. 1987), soil moisture (Anderson et al. 1984), total soil C and N (Johnson et al. 1991*b*), landscape position (Day et al. 1987, Gibson and Hetrick 1988, Henkel et al. 1989), and temperature (Koske 1987).

VAM fungi are obligate root symbionts, but they are not host specific. Some studies have suggested that VAM fungal communities are not influenced by the species composition of the plant community. Liberta and Anderson (1986) found VAM fungal communities in an undisturbed prairie to be no different from those of an adjacent corn field. Conversely, adjacent agricultural fields growing the same crop were shown to contain different species of VAM fungi (Hayman 1982). Such results seem to suggest that host plant species are essentially ecologically equivalent in terms of their influence on VAM fungal communities. However, other studies of agroecosystems provide strong evidence that crop plant species may indeed influence the composition of VAM fungal communities (Schenck and Kinloch 1980, McGraw and Hendrix 1984, Johnson et al. 1991*a*).

It is important to understand the factors influencing populations of VAM fungi because species of these fungi differ greatly in their effects on plants, ranging from mutualistic to neutral to parasitic (Carling and Brown 1980, Modjo and Hendrix 1986, Schubert and Cammarata 1986). If plants can indeed influence the composition of VAM fungal communities, it suggests that there may exist a previously unrecognized positive or negative feedback mechanism that influences plant community structure. This feedback would be positive (and stabilize the plant community) if the VAM fungal

[1] Manuscript received 29 July 1991; revised 22 November 1991; accepted 8 December 1991; final version received 27 January 1992.

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species that proliferate within a particular host are the most beneficial mutualists for that host, but the feedback would be negative (and destabilize the plant community) if parasitic fungal species proliferate. We hypothesize that plant and fungal communities reciprocally influence one another, and soil fertility mediates the ultimate outcome of these interactions.

As a first step in testing this hypothesis, we conducted a field experiment to examine the relative importance of soil factors and plant species on communities of VAM fungi. Populations of VAM fungal spores were studied in long-term gardens containing 4-yr-old monocultures of five successional grass species grown in a gradient of soil mixtures ranging from pure subsurface sand to pure sandy loam topsoil. These experimental gardens allowed us to tease apart the effects of plant and soil factors that are normally confounded in natural systems because successional changes in plant communities generally occur simultaneously with successional changes in soil properties.

Methods

Experimental gardens

This research was performed at the Cedar Creek Natural History Area (CCNHA), located on a glacial outwash plain in Isanti and Anoka counties in east-central Minnesota, USA. Our experiment was conducted within 11 garden plots (3 × 12 m), designed to be an experimental N gradient. These gardens were established in 1985 and have been the site of numerous other experiments (Wedin 1990, Wedin and Tilman 1990, Tilman and Wedin 1991*a*, *b*). Here we will briefly describe the preparation of the subplots we sampled within the larger garden plots (refer to Tilman and Wedin [1991*a*] for a more complete description). Each plot was prepared by rototilling a different (randomly assigned) proportion of topsoil into subsurface sand, ranging from 0 to 100% topsoil. One plot, which contained 100% topsoil, was further enriched with N additions of 6.55 $g \cdot m^{-2} \cdot yr^{-1}$ as NH_4NO_3, added monthly in proportion to normal N mineralization rates at CCNHA. The topsoil, which was obtained nearby but not within CCNHA, was a sandy loam of the Hubbard-Isanti-Duelm Association containing 72% sand, 4% clay, 24% silt, 2.9% organic matter, 1200 mg/kg total soil N, 58 mg/kg Bray-1 P, 52 mg/kg K, a pH of 7.2, and a bulk density of 1.40 g/cm^3. The subsurface sand contained 93% sand, 3% clay, and 4% silt, 0.3% organic matter, 90 mg/kg total soil N, 31 mg/kg Bray-1 P, 29 mg/kg K, a pH of 6.6, and a bulk density of 1.51 g/cm^3. To ensure that N was the only nutrient limiting plant growth, each plot was fertilized annually with 12.2 g/m^2 of P_2O_5 (commercial 0-46-0 [N-P-K] fertilizer), 14.6 g/m^2 of K_2O (commercial 0-0-61 fertilizer), 42 g/m^2 of $MgSO_4$ (commercial epsom salts), 42 g/m^2 of $CaSO_4$, 1.9 g/m^2 of $ZnSO_4$, 1.12 g/m^2 of $CuSO_4$, 0.28 g/m^2 of boric acid, and 0.56 g/m^2 of $MnSO_4$. The soil pH was stable at 7.2 in all plots except the two sandiest plots, which received fine-ground lime in 1987 and 1988 to adjust their pH to 7.2.

Each 3 × 12 m garden plot was divided into 0.75 m × 0.75 m subplots using galvanized sheet metal driven into the soil to a depth of 23 cm. In May 1986, two or three randomly assigned subplots within each of the 11 plots were sown with monocultures of five different grass species. The grasses were chosen for study because they represent the five most abundant grasses in the successional grasslands at CCNHA. These species were: *Agrostis scabra* Willd., a native C_3 species common in early successional fields; *Agropyron repens* (L.) Beauv. and *Poa pratensis* L., Eurasian C_3 species common in early and mid successional sites, respectively; *Schizachyrium scoparium* (Michx.) Nash-Gould and *Andropogon gerardi* Vitm., native C_4 species common in late successional sites.

Sampling VAM fungal communities

In November 1989, soil samples were collected from each of the five grass monocultures in each of the 11 plots. These 55 samples were composites formed by combining a single core (2.2 cm diameter × 15 cm deep) from the center of each replicate monoculture of each of the grass species within each of the large garden plots. There were two replicate monocultures of *Andropogon* and three replicate monocultures of the other four species within each of the large plots. Soils were placed in Whirlpack bags and stored at 4°C until they were processed. Composite soil samples were thoroughly mixed and spores were extracted from 25 g of air-dried soil using a modification of McKenney and Lindsey's (1987) technique. We used a smaller mesh screen (25 μm) than that recommended by McKenney and Lindsey (38 μm) to minimize loss of the smallest spores. Spores were spread evenly onto a gridded membrane filter and all of the spores within 27% of the area of the filter paper were removed using a dissecting microscope (50×) and a fine forceps. These spores were mounted in both polyvinyl-alcohol and a 1:1 solution of polyvinyl-alcohol plus Melzer's solution to make permanent slides. Slides were examined using a compound microscope (100-1000×), and spores were identified to species based on wall structure (Schenck and Pérez 1990). Voucher specimens of each of the species we identified are available from the Plant Pathology Herbarium at the University of Minnesota.

The relative density (percent) of each of the species in each composite sample was calculated as: $(n_i/N_t) \times 100$; where n_i = number of spores from the i^{th} species and N_t = total number of spores examined in the sample (N_t averaged 935 spores). Total spore counts of each species were estimated by multiplying relative spore densities by the total count of spores on the filter paper. Diversities of VAM fungal communities were calculated by the Shannon-Wiener index (Krebs 1985). Percent similarity of VAM fungal communities by host

plant and by soil mixture were computed and cluster analysis performed using MVSP Plus, version 2.0 (Kovach 1990).

It is important to note that relative spore density does not necessarily reflect the functional importance of individual species within the VAM fungal community because some species may be prolific sporulators even when they are in relatively low abundance within plant roots. Spores of *Glomus aggregatum* and *Glomus leptotichum* were significantly more abundant than spores of all other species across all combinations of host plants and soil mixtures. Spore densities of these two species were omitted from the similarity analysis because their overdominance obscured the distribution patterns of less abundant but potentially equally important species in the VAM fungal community.

Analysis of the soil gradient

Total soil N and C of the 55 samples were measured with a Carlo-Erba NA1500 Analyzer. The percent black soil in each sample was estimated as: $(M - S)/(B - S) \times 100$, where M = total N of the sample, S = total N of pure sand, and B = total N of pure black soil. The 11 experimental plots were divided into five soil mixture levels based on the percent black soil they contained: level 1 contained 0–15% black soil, level 2 contained 20–40% black soil, level 3 contained 50–75% black soil, level 4 contained 75–100% black soil, and level 5 contained 100% black soil and was fertilized monthly with NH_4NO_3. Levels 1 and 2 each included three plots, levels 3 and 4 each included two plots, and level 5 included a single plot.

Statistical analysis

Two-way ANOVA for unbalanced designs was used to evaluate the effects of host species and soil mixture on total spore densities, species richness, and species diversity of the VAM fungal communities. Relative spore densities were arcsine-square-root transformed (Zar 1984) and then two-way ANOVA was used to evaluate the effects of host species and soil mixture on the densities of 12 VAM fungal species that occurred in 25% or more of the plots. Tukey's test was used to make multiple comparisons of means. Spearman rank correlation analysis was conducted to examine the relationships between spore densities of individual VAM fungal species and total soil C (which was highly correlated with both total N and percent organic matter) and successional ranking. *Agrostis, Agropyron, Poa, Schizachyrium,* and *Andropogon* were assigned successional rankings of 1 through 5, respectively, based on their relative abundance in the successional grasslands at CCNHA (Tilman 1988). ANOVA and correlation analyses were performed using STATGRAPHICS (STSC 1986).

TABLE 1. Spore populations of vesicular-arbuscular mycorrhizal (VAM) fungi observed in the experimental plots.

VAM fungal species	Fungal spores: Mean density* (spores/25 g soil)	Fungal spores: Frequency† (%)
Acaulospora foveata Trappe & Janos	4	4
A. morrowiae Spain & Schenck	12	14
A. scrobiculata Trappe	9	20
Entrophospora infrequens (Hall) Ames & Schneider	10	40
Gigaspora gigantea (Nicol. & Gerd.) Gerd. & Trappe	5	42
Gigaspora sp.	12	71
Glomus aggregatum Schenck & Smith emend. Koske	976	100
G. etunicatum Becker & Gerd.	1	74
G. fasciculatum (Thaxter) Gerd. & Trappe emend. Walker & Koske	109	20
G. geosporum (Nicol. & Gerd.) Walker	5	5
G. intraradix Schenck & Smith	22	18
G. leptotichum Schenck & Smith	992	100
G. macrocarpum Tul. & Tul.	40	87
G. microaggregatum Koske, Gemma, Olexia	96	40
G. mosseae (Nicol. & Gerd.) Gerd. & Trappe	7	69
G. occultum Walker	107	78
Scutellispora calospora (Nicol. & Gerd.) Walker & Sanders	15	73
S. erythropa (Koske & Walker) Walker & Sanders	4	4
S. persica (Koske & Walker) Walker & Sanders	5	65

* Mean of the total spore counts from the subplots in which the species was observed.

† Percentage of the 55 subplots in which the species was observed.

RESULTS

Spores of 19 species of VAM fungi were found in the experimental plots (Table 1). Two species, *Glomus aggregatum* and *Glomus leptotichum,* clearly dominated the spore communities and were found in high densities in every plot. More total spores and more fungal species were recovered from monocultures of *Andropogon* and *Schizachyrium* than from monocultures of the other three grasses, however the five grasses did not differ significantly in the diversity of their VAM fungal communities as measured by the Shannon-Wiener index (Fig. 1a, c, e). Total spore counts and species richness were constant across the soil gradient, however the Shannon-Wiener index was higher at the black soil end of the gradient compared to the sand end of the gradient (Fig. 1b, d, f). Relative densities of eight species were significantly influenced by host plant species and a slightly different set of eight species were significantly influenced by soil mixture (Table 2). There was also a significant plant × soil interaction for two species, *Glomus etunicatum* and *Glomus macrocarpum* (Table 2). *Glomus aggregatum* spores were most abundant in monocultures of *Agropyron* and *Poa,* while *Glomus leptotichum* spores were most abundant in

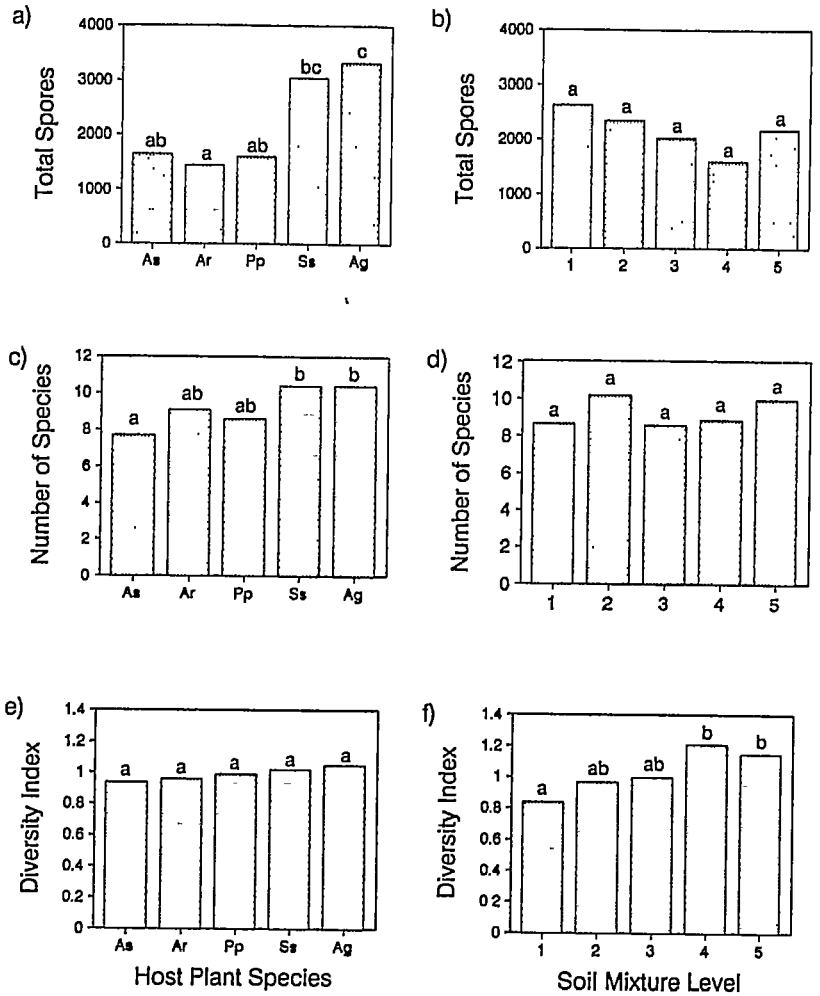

FIG. 1. Total spores (in 25 g dry soil), species richness, and Shannon-Wiener diversity by host plant (a, c, e) and by soil mixture (b, d, f). Within each graph, bars with different letters indicate the means are significantly different ($P \leq .05$). Host plant abbreviations: *Agrostis scabra* = As, *Agropyron repens* = Ar, *Poa pratensis* = Pp, *Schizachyrium scoparium* = Ss, and *Andropogon gerardi* = Ag. Soil mixture levels indicate relative abundance of top (black) soil, topsoil abundance increasing from 0–15% (level 1) to 100% plus added N (level 5).

TABLE 2. *F* values from ANOVA tests of host and soil effects on relative spore densities of vesicular-arbuscular mycorrhizal (VAM) fungal species that occurred in >25% of the plots. *F* values that are significant ($P \leq .05$) are underlined.

Fungal species	Source of variation					
	Host plant		Soil mixture		Plant × soil	
	F (4 df)	*P*	*F* (4 df)	*P*	*F* (16 df)	*P*
Entrophospora infrequens	5.65	.002	5.28	.002	1.67	.11
Gigaspora gigantea	4.27	.007	2.16	.10	0.82	.65
Gigaspora sp.	1.17	.34	4.12	.009	0.26	.99
Glomus aggregatum	8.96	.0001	8.91	.0001	0.84	.63
G. etunicatum	0.51	.73	2.17	.10	2.47	.02
G. leptotichum	7.83	.0002	9.97	.00001	1.25	.29
G. macrocarpum	4.72	.004	9.76	.00001	2.70	.009
G. microaggregatum	1.12	.32	0.24	.91	0.89	.59
G. mosseae	1.94	.13	7.90	.0002	0.88	.59
G. occultum	5.61	.002	4.16	.008	0.67	.80
Scutellispora calospora	6.64	.0006	6.47	.0007	1.77	.08
S. persica	4.50	.006	1.70	.17	0.96	.52

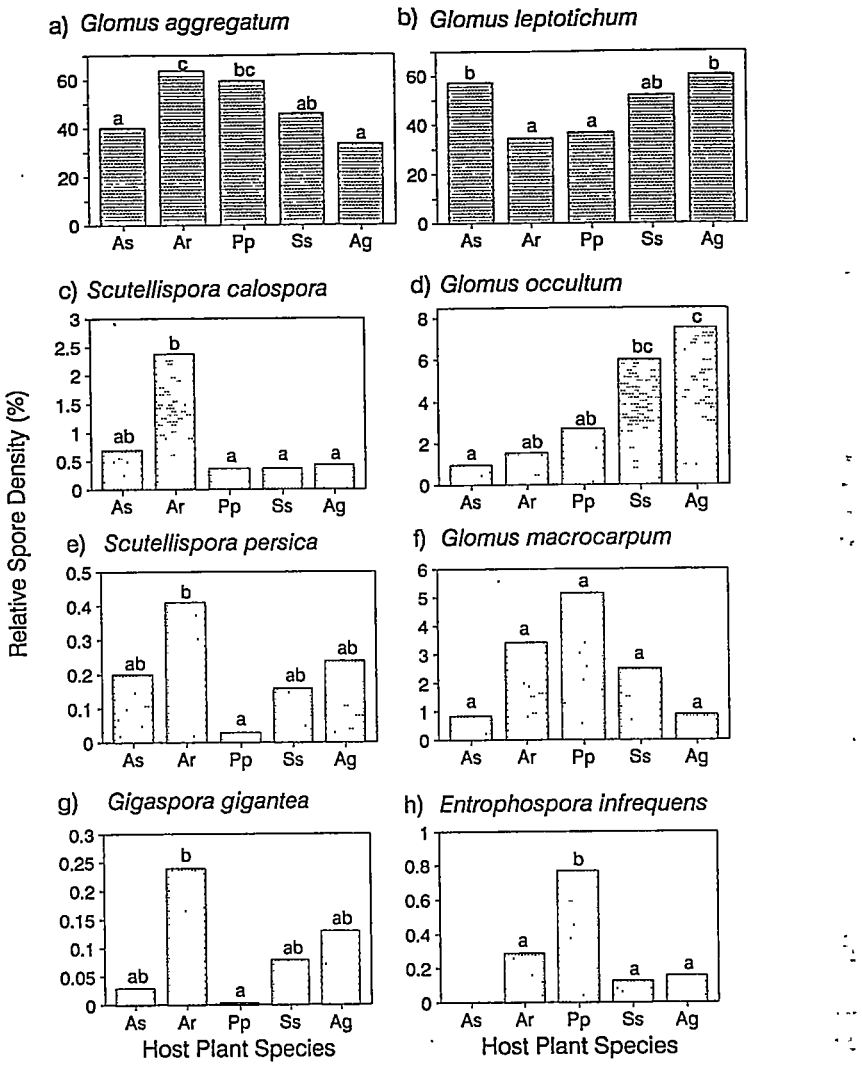

FIG. 2. Relative spore abundances of eight vesicular-arbuscular mycorrhizal (VAM) fungal species according to host plant species. Within each graph, bars with different letters indicate the means are significantly different ($P \leq .05$). Host plants are abbreviated as in Fig. 1.

Agrostis, Schizachyrium, and *Andropogon monocultures* Fig. 2a, b). *Glomus occultum* spores were also most abundant in the two late successional C_4 hosts (Fig. 2d). *Glomus macrocarpum* and *Entrophospora infrequens* spores were most abundant in monocultures of *Poa,* while *Scutellispora persica* and *Gigaspora gigantea* spores were least abundant with this host (Fig. 2e–h). *Agropyron* appeared to be the favored host for *Glomus aggregatum, S. calospora, S. persica,* and *Gigaspora gigantea* (Fig. 2a, c, e, g). *Glomus aggregatum* and *Gigaspora* sp. were most abundant in the sandy end of the gradient, *Glomus leptotichum* and *Glomus macrocarpum* were most abundant in the intermediate portion of the soil gradient, and *Entrophospora infrequens, G. mosseae, G. occultum,* and *S. calospora* were most abundant in the black soil end of the gradient (Fig. 3).

Rank correlation could be used to divide the species into roughly two groups: sand species and black soil species. Spore densities of sand species were correlated negatively, and spore densities of black soil species were correlated positively with soil C (Table 3). Only *G. occultum* and *S. calospora* correlated significantly with host rank.

Cluster analysis of the similarity of the fungal communities by host plant species showed the *Andropogon* community be the most similar to the *Schizachyrium* community (74% similarity), the *Agropyron* community most similar to the *Poa* community (65% similarity), and the *Agrostis* community only 40% similar to the other four communities (Fig. 4). Cluster analysis of the similarity of fungal communities by soil mixture showed that the fungal communities in soil mixture 1 were 76% similar to soil mixture 2 but only 47% similar

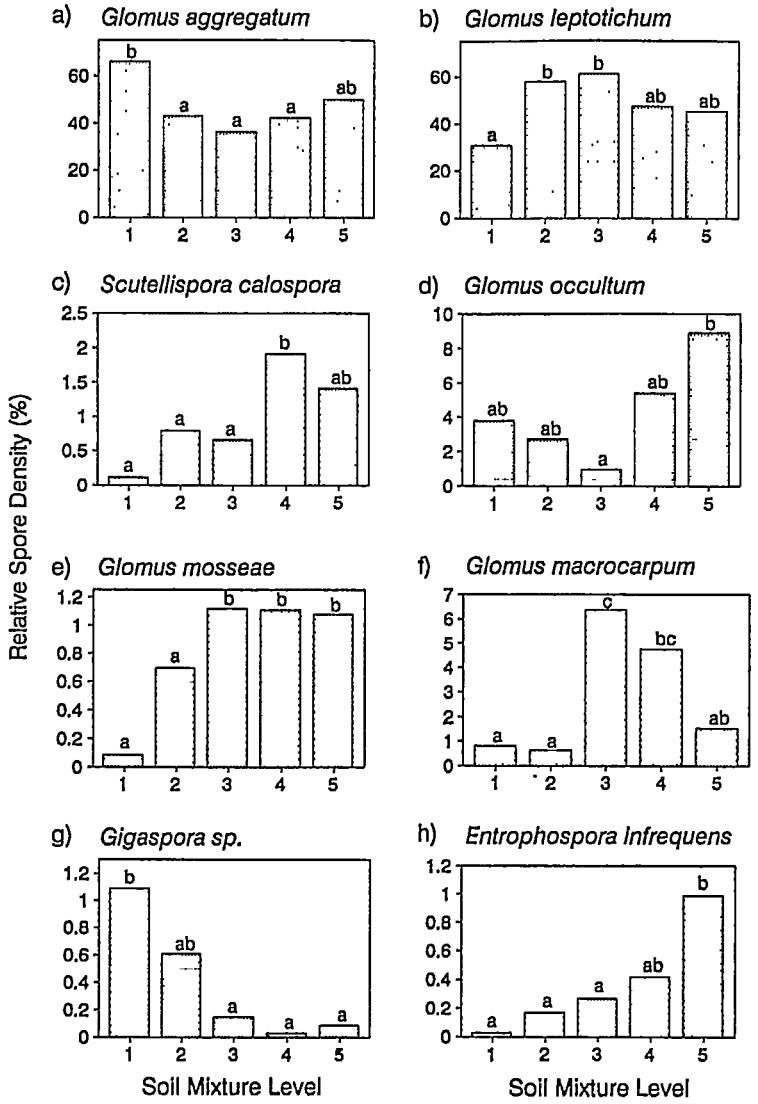

FIG. 3. Relative spore abundances of eight vesicular-arbuscular mycorrhizal (VAM) fungal species according to soil mixture level. Within each graph, bars with different letters indicate the means are significantly different ($P \leq .05$). Soil mixture levels are as in Fig. 1.

to the communities in the other three soil mixtures. Fungal communities in soil mixtures 3 and 4 were 62% similar to each other but only 52% similar to the community in mixture 5 (Fig. 5).

DISCUSSION

A previous study at CCNHA showed a significant change in the composition of VAM fungal communities across a natural successional sequence of 17 old-field and forest sites (Johnson et al. 1991*b*). These successional changes in VAM fungi occurred concomitantly with changes in plant community composition, primary production, and nutrient accrual. Thus, it was impossible to separate the influences of soil and plant factors on VAM fungal communities. Results of the present study clearly indicate that both soil factors and plant species influence VAM fungal communities. Of the 12 most abundant species, spore densities of six species had a significant dependence on both soil mixture and host species, while two were dependent only on soil and two only on host. Only one species did not show a significant dependence on either host species, soil mixture, or their interaction. Thus, our results do not support the hypothesis that soil factors are more important than host plant species in regulating sporulation by VAM fungi (Koomen et al. 1987). Rather, we hypothesize that the two factors may often be of equal importance, as we observed here.

Initially, both black soil and subsurface sand contained infective propagules of VAM fungi (N. C. Johnson, *personal observations*). Thus, we assume that at the onset of this experiment VAM fungal populations

TABLE 3. Spearman rank correlations between abundances of vesicular-arbuscular mycorrhizal (VAM) fungal species and soil and plant variables.

VAM fungus	Total C	Host rank†
Sand species		
Gigaspora gigantea	−.27*	+.16
Gigaspora sp.	−.61***	+.07
Glomus aggregatum	−.36**	−.24
Scutellispora erythropa	−.29*	−.06
S. persica	−.27*	+.03
Black soil species		
Entrophospora infrequens	+.34**	+.24
Glomus leptotichum	+.22	+.19
G. macrocarpum	+.46***	+.05
G. mosseae	+.60***	+.13
G. occultum	+.23	+.49***
S. calospora	+.43***	−.29*

* $P \leq .05$, ** .01, and *** .001 (significance of correlation coefficients).

† Hosts were ranked according to their successional dominance: 1 = *Agrostis*, 2 = *Agropyron*, 3 = *Poa*, 4 = *Schizachyrium*, 5 = *Andropogon*.

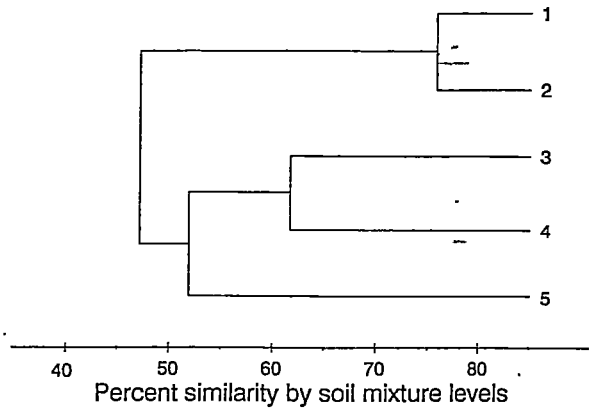

FIG. 5. Cluster analysis of the percent similarity of VAM fungal communities by soil mixture. Soil mixture levels are as in Fig. 1.

in the five soil mixtures were controlled by the proportions of black soil and sand within the mixture. We also assume that the black soil and sand initially contained different VAM fungal communities and thus the varying composition of VAM fungal communities across the gradient of soil mixtures was expected. Less expected, however, was the striking divergence in the composition of the VAM fungal communities in monocultures of the five different grass species after only 4 yr. Previous studies have shown that VAM fungal communities differ in monocultures of unrelated crop plants (Schenck and Kinloch 1980, McGraw and Hendrix 1984, Johnson et al. 1991*a*), but to our knowledge, these are the first results indicating that even closely related hosts (five grasses) may cause divergence in VAM fungal communities on initially identical soils.

The two dominant species in the garden plots, *G. aggregatum* and *G. leptotichum*, both produce many tiny spores within tangled masses of hyphae. *Glomus*

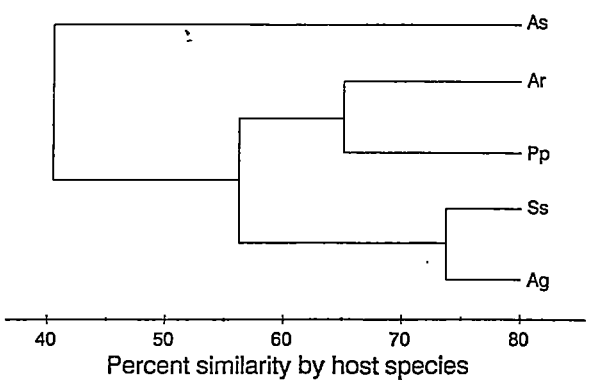

FIG. 4. Cluster analysis of the percent similarity of VAM fungal communities by host plant species. Host plants are abbreviated as in Fig. 1.

aggregatum also dominated spore communities in the natural successional sequence (Johnson et al. 1991*b*). In both the previous study and the present study spore densities of *G. aggregatum* were negatively correlated with both soil C and the successional ranking of the site or the host plant. The second dominant species, *G. leptotichum*, had never previously been observed at CCNHA, and it is likely that it was introduced to the site with the black topsoil when the garden plots were established in 1985.

Three *Scutellispora* species, *S. calospora*, *S. erythropa*, and *S. persica*, were observed in both the natural successional sequence and in the garden plots. In the previous study all three species were early successional, and their spore densities were negatively correlated with successional rank of the site and soil C. Results of the present study both support and contradict this pattern. Densities of *S. erythropa* and *S. persica* spores were negatively correlated with soil C. Furthermore, densities of *S. calospora* spores were negatively correlated with host rank (i.e., were most abundant in early successional hosts), but unlike the previous study, *S. calospora* spores were positively correlated with soil C. Soil fertility and plant species were confounded in the previous study but not in this study. Perhaps *S. calospora*'s affinity for early successional host plants (namely *Agropyron*) resulted in a spurious negative correlation with soil C in the previous study of the natural successional sequence.

We suggest that plant species are an important selective force on populations of VAM fungi, either directly, through their internal root environments, or indirectly, through their influence on the soil. Plants can modify edaphic properties relatively quickly. Wedin and Tilman (1990) have shown that within just 3 yr these five grasses caused N mineralization, and consequently N availability, to diverge by a factor of 10 in the experimental monocultures. Thus, there cannot always be a clear separation between the influence of

plant species and the influence of soil factors on VAM fungal communities.

Many studies have linked the spread of mycorrhizae with the supply of soluble sugars in root exudates (Schwab et al. 1991). Soil fertility mediates this plant control of mycorrhizal spread because the nutrient status of plants influences the amount of soluble sugars released in root exudates. Douds and Schenck (1990) found that fertilization of bahia grass (*Paspalum notatum* Flügg) with different concentrations of macronutrients influenced the concentrations of soluble sugars in roots and tissue N:P ratios. Furthermore, they found that VAM fungal species differ in their responses to varying root concentrations of soluble sugars and tissue nutrients. It is likely that the five grasses in our study differ in the soluble sugar concentrations of their root exudates and the N:P ratios of their tissues.

Perhaps patterns of root exudation have evolved as a mechanism to control VAM fungal populations. It would be adaptive for plants to exert control over VAM fungal populations if by doing so they could select the best mutualists. On the other hand, plants and fungi might be engaged in a coevolutionary arms race. When soil fertility is high plants may allocate less carbon to root exudates and perhaps select VAM fungi that require less carbohydrate. Whether or not there is any relationship between the carbohydrate requirements of VAM fungi and their effects on plants has not yet been experimentally addressed.

The results of this study support the hypothesis that plant communities influence VAM fungal communities. If there is a relationship between the species of VAM fungi selected by a particular plant species and the effects those fungi have on that plant species, then VAM fungal communities may potentially influence plant communities through either a stabilizing or destabilizing feedback mechanism. Future studies need to be conducted to determine whether proliferating fungal species are more or less beneficial than nonproliferating species and how soil fertility might influence these relationships.

ACKNOWLEDGMENTS

We wish to thank Rick Johnson, F. L. Pfleger, Anna Shoeman, Lisa Vogel, and Don Faber-Langendoen for their technical assistance. Financial support was provided by the National Science Foundation (grant BSR-8811884 for Long-term Ecological Research on CCNHA) and a University of Minnesota Dissertation Fellowship awarded to N. C. Johnson.

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