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Dynamics of vesicular-arbuscular mycorrhizae during old field succession

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Summary. The species composition of vesicular-arbuscular mycorrhizal (VAM) fungal communities changed during secondary succession of abandoned fields based on a field to forest chronosequence. Twenty-five VAM fungal species were identified. Seven species were clearly early successional and five species were clearly late successional. The total number of VAM fungal species did not increase with successional time, but diversity as measured by the Shannon-Wiener index tended to increase, primarily because the community became more even as a single species, *Glomus aggregatum*, became less dominant in the older sites. Diversity of the VAM fungal community was positively correlated with soil C and N. The density of VAM fungi, as measured by infectivity and total spore count, first increased with time since abandonment and then decreased in the late successional forest sites. Within 12 abandoned fields, VAM fungal density increased with increasing soil pH, H_2O soluble soil C, and root biomass, but was inversely related to extractable soil P and percent cover of non-host plant species. The lower abundance of VAM fungi in the forest sites compared with the field sites agrees with the findings of other workers and corresponds with a shift in the dominant vegetation from herbaceous VAM hosts to woody ectomycorrhizal hosts.

Key words: VA-mycorrhizae – Old field succession – Infectivity – Spore populations

Although there have been many studies reporting the dynamics of plant species and soil properties during old field succession, the dynamics of an important plant-soil intermediary, vesicular-arbuscular mycorrhizae, have rarely been studied. Vesicular-arbuscular mycorrhizae are symbiotic associations between plant roots and a group of ubiquitous soil zygomycetes. Most vascular plants form vesicular-arbuscular mycorrhizae, and the zygomycetes involved in these associations are frequently the most abundant fungi in the soil (Gerdemann and Nicolson 1963). Mycorrhizae often improve plant growth and survival by facilitating uptake of nutrients and increasing drought tolerance (e.g., Mosse 1973; Nelsen 1987). It has been suggested that recovery of disturbed ecosystems may depend upon the reestablishment of mycorrhizal fungi (Reeves et al. 1979; Janos 1980; Allen and Allen 1980; Perry et al. 1989). Therefore, a study of mycorrhizal dynamics during succession may provide insights into the factors and processes regulating ecosystem development.

Nearly 150 species of vesicular-arbuscular mycorrhizal (VAM) fungi have been described worldwide (Schenck and Perez 1990). Natural distributions of these species appear to be influenced by edaphic factors (Hayman 1982; Anderson et al. 1984; Porter et al. 1987; Gibson and Hetrick 1988; Henkel et al. 1989), and plant community composition (Schenck and Kinlock 1980; McGraw and Hendrix 1984; Johnson et al. 1991). Consequently, the species composition of VAM fungal communities may change in response to the changes in soil properties and plant community composition occurring during succession. Successional patterns in species of ectomycorrhizal fungi have been described (Mason et al. 1983; Gardner and Malajczuk 1985), but such patterns were not found in the VAM fungal communities studied by Benjamin et al. (1989).

We hypothesized that VAM fungal communities change during old field succession, and that these changes are related to plant species replacement and nutrient accrual. To test this hypothesis, we studied mycorrhizae in a chronosequence of old fields and forest sites in order to (1) compare the composition of VAM fungal communities of early and late successional sites and (2) assess the relationships between the density and species of VAM fungi and various soil and plant community properties.

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Methods

Study sites. VAM fungal populations were studied in 14 field sites and 3 forest sites at Cedar Creek Natural History Area, about 50 km north of Minneapolis, Minnesota (Fig. 1). The field sites included a continuously cropped rye field, a fallow field and 12 abandoned fields (ranging in age from 1 to 60 years). The rye field, fallow field and the 6 youngest abandoned fields formed a series of adjacent plots (0.2 ha) that were sequentially abandoned over the past 13 years (Delaney 1988), while the remaining 6 abandoned fields were interspersed throughout the 2200 ha natural history area (Fig. 1). The forest sites included an oak savanna, an upland pin oak (*Quercus ellipsoidalis* Hill) forest and a northern hardwood forest. Soils of the 17 sites are all well drained upland sands which occur on the same landform and have similar patterns of soil development. Although the sites do differ in soil series (Nymore, Sartell, or Zimmerman), all of them, with the exception of the 60 year old field, belong to the same taxonomic group. Soil in the 60 year old field was an Alfic Udipsamment, whereas the soil of the remaining fields and forests was a Typic Udipsamment (Grigal et al. 1974). Characteristics of these sites are summarized in Table 1. Soil series classifications in Inouye et al. (1987) differ slightly from those of this study because classifications in the former study were based on general soil maps, while classifications in the present study were based on field examination.

Soil samples. Transects were established in each of the 17 sites. The center point of each transect was randomly established and then the transect was oriented in a north-south direction. Three sample points were located at 5 m intervals along each transect. In November, 1987, six cores (2.5 cm diameter × 15 cm deep) were collected from each sample point, three cores were composited for analysis of spore populations, soil P and pH, and the remaining three cores were used for a bioassay and were placed directly into plastic growth tubes called Conetainers (Stuewe and Sons, Inc., Corvallis, Oregon USA). A sampling depth of 15 cm was chosen because VAM propagule densities are generally greatest in the surface 15 cm. In a study of the vertical distribution of VAM fungal spores, An et al. 1990 found 87% of the spores occurred in the top 15 cm and just 13% occurred at greater depths. In June, 1988, composite

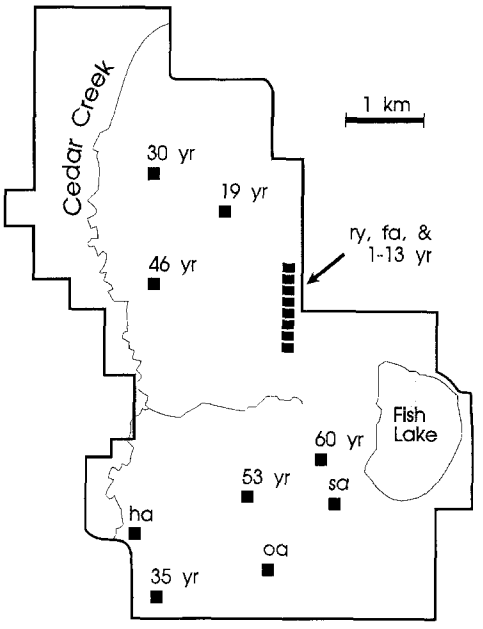

Fig. 1. Study site locations within the Cedar Creek Natural History Area. *ry* = rye field, *fa* = fallow field, *sa* = oak savanna, *oa* = upland pin oak forest, *ha* = hardwood forest, 1–60 yr = abandoned fields of various ages

Table 1. Soil and plant characteristics of the 17 sites studied

Site, or field age	Soil series[a]	Soil pH[b]	Organic C[c]	Soluble C[d]	Total N[e]	Bray–1 P[f]	Total P[g]	Root biomass[h]	Nonhost abundance[i]
			$g\ m^{-2}$			$\mu g\ g^{-1}$		$g\ m^{-2}$	%
Field sites									
rye	Ny	4.91	nd[j]	nd	nd	29.5	340.4	nd	nd
fallow	Ny	4.61	nd	nd	nd	31.5	nd	nd	nd
1 year	Ny	4.77	1170	3.3	79.6	24.0	363.1	233.8	35.0
3 years	Ny	4.97	1146	3.4	66.6	43.9	362.2	167.6	1.7
5 years	Ny	5.21	912	4.2	68.9	51.0	345.8	251.1	2.4
8 years	Ny	5.22	922	4.3	62.7	54.8	335.6	131.4	0.5
10 years	Ny	5.11	1058	3.8	62.4	53.2	329.8	93.6	0.2
13 years	Ny	5.00	nd	nd	nd	59.3	342.3	103.1	nd
19 years	Sa	5.78	1206	5.6	71.8	32.5	230.7	344.7	12.2
30 years	Sa	5.11	1580	5.9	81.1	36.8	238.3	420.2	1.4
35 years	Sa	5.47	1768	6.5	93.6	31.0	276.6	1175.1	0.5
46 years	Sa	5.55	1914	6.0	105.0	39.7	274.8	522.9	0.2
53 years	Ny	5.41	2047	6.5	109.1	31.3	288.6	681.2	0.3
60 years	Zm	5.11	2119	6.6	114.4	14.2	326.2	600.0	0.2
Forest sites									
Savanna	Sa	5.20	2883	6.3	132.3	45.0	262.3	nd	nd
Upland-pin-oak	Ny	4.60	3146	9.5	151.3	30.6	234.6	nd	nd
Hardwood	Ny	4.40	4589	10.7	188.0	56.0	395.4	nd	nd

[a] Ny: Nymore sand; Sa: Sartell sand; Zm: Zimmerman sand. Soil of the 60 year old field was an Alfic Udipsamment, whereas the soil of the remaining fields and forests was a Typic Udipsamment.
[b] pH of 1:1 soil water dilution
[c] measured by combustion
[d] H_2O-soluble C measured according to Burford and Bremner (1975)
[e] air dried soil digested with concentrated H_2SO_4 and HgO as a catalyst
[f] Available–P determined by the Bray–1 method
[g] nitric perchloric wet ashing technique
[h] determined by Gleeson and Tilman (1990)
[i] % non-host cover
[j] not determined

soil samples were collected for a second bioassay. For this bioassay, a total of 15 cores (6 cm diameter × 10 cm deep), five cores from each of the three sample points, were collected from each transect and composited.

Spore populations. Spores were extracted, counted, and identified from composite soil samples collected from each of the three sample points along 15 of the 17 transects (spore populations in the 3 and 8 year old fields were not analyzed). Spores were extracted from 25 ml aliquots of soil by wet-sieving followed by sucrose centrifugation (McGraw and Hendrix 1984). Spores were placed in a gridded petri dish and counted using a dissecting microscope (40×). Permanent slides of randomly selected sub-samples (10 to 20%) of these spores were made and examined at 400× to 1000×. Spores were identified based on wall structure (Walker 1983; Schenck and Perez 1990) and comparison with holotypes, paratypes and collections obtained from the Oregon State University herbarium. Voucher numbers were assigned to representative specimens of each of the species we identified. These voucher specimens can be obtained upon request. Spore counts from the three sample locations in each transect were added together (so spore populations were analyzed from a total of 75 ml of soil from each site). An aliquot of each soil sample was air dried, and bulk density was determined. Total spore counts were expressed as spores per gram dry soil. The relative abundance (%), of each species at each site, 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 from the site. Mycorrhizal fungal diversity (at each site) was calculated by the Shannon-Wiener index. This index combines two components of diversity: numbers of species and the evenness of allotment of individuals among the species (Krebs 1985). The percentage dissimilarity of the VAM fungal community in each site compared to the rye field was computed as in Olff and Bakker (1991): $D = 100 \times (1-(2c/(a+b)))$; a = the sum of species abundances in the site; b = the sum of species abundances in the rye field; c = the sum of the minimum abundances of species common to both sites.

Mean species abundances were square root × 10 transformed prior to the computation of dissimilarity.

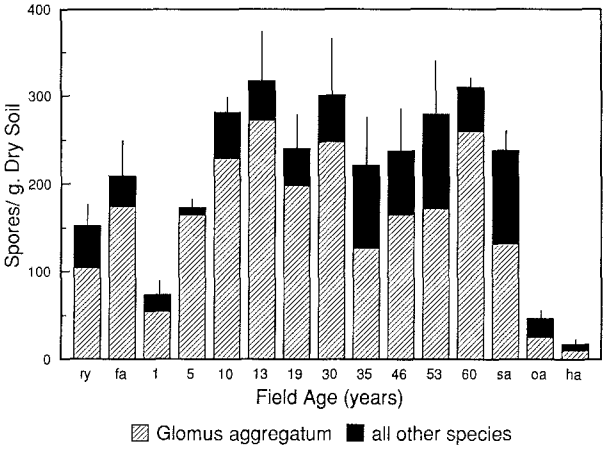

Fig. 2. Total spore count and counts of *Glomus aggregatum* in the chronosequence soils (lines above bars represent standard errors). ry = rye field, fa = fallow field, sa = oak savanna, oa = upland pin oak forest, ha = hardwood forest

VAM infectivity. A modification of Moorman and Reeves' (1979) infectivity bioassay was used to quantify the relative soil densities of infective propagules of VAM fungi (including spores, mycelium, and infected root fragments). Soil samples were collected from the transects, placed in surface sterilized Conetainers, and planted with a single surface sterilized corn seed (hybrid A639 × A676, University of Minnesota Agronomy Department). It has been shown that early in the colonization process the level of root infection is linearly related to soil densities of VAM fungal propagules (Carling et al. 1979; Smith and Walker 1981). Thus, we assumed that the level of mycorrhizal infection of 30 day old corn roots was proportional to the density of VAM fungal propagules in the soil.

This bioassay was conducted twice, first with samples collected in November, 1987 and again with samples collected in June, 1988. All 17 sites were analyzed in the 1987 bioassay, but the three forested sites were not included in the 1988 bioassay. The two bioassays differed slightly in the sampling and cultural methods used. In the 1987 bioassay, nine intact soil cores (three cores from three sample points) from each transect were placed into small (50 ml) Conetainers, loosely covered with plastic, and stored at 11° C. After 48 days of cold treatment, the Conetainers were sown with corn and maintained in a growth chamber: 16 h, 25° C "days" (ca. 340 microeinsteins $m^{-2}\ s^{-1}$ PAR), and 8 h, 15° C nights. Plants were watered daily with one-tenth strength Hoaglands solution (Hoagland and Snyder 1933) minus phosphorus. In the 1988 bioassay, composite soil samples from each transect were thoroughly mixed by hand for 3 min, subsamples were placed in 160 ml Conetainers, and were sown with corn within 24 h following collection. Plants were kept in a greenhouse (20–32° C) and watered daily with deionized water.

Corn plants were harvested in the same manner for both harvests. After 30 days, shoots were cut from roots, oven dried at 70° C and weighed. Root systems were washed, cut into 2.5 cm segments,

Table 2. Correlations between VAM indices, field age, soil properties and plant properties in the 14 field sites. Pearson product-moment correlation coefficients

	Spore count	Infectivity	Age	Soil pH	Soil org–C	Soil sol–C	Soil total–N	Soil Bray–P	Soil tot–P	Root biomass
Infectivity	+0.39	–	–	–	–	–	–	–	–	–
Age	+0.66*	+0.75**	–	–	–	–	–	–	–	–
pH	+0.38	+0.93***	+0.70**	–	–	–	–	–	–	–
Org–C	+0.46	+0.44	+0.84***	+0.29	–	–	–	–	–	–
Sol–C	+0.71*	+0.80**	+0.96***	+0.65*	+0.81**	–	–	–	–	–
Tot–N	+0.25	+0.45	+0.76**	+0.24	+0.95***	+0.76**	–	–	–	–
Bray–P	+0.21	−0.08	−0.13	+0.08	−0.65*	−0.43	−0.72**	–	–	–
Tot–P	−0.45	−0.79**	−0.60*	−0.76**	−0.43	−0.71**	−0.28	+0.12	–	–
Roots	+0.24	+0.64*	+0.73**	+0.46	+0.84***	+0.84***	+0.85***	−0.58*	−0.52	–
Non-hosts	−0.85***	−0.29	−0.68*	−0.41	−0.27	−0.53	−0.16	−0.28	+0.25	−0.19

* $P<0.05$; ** $P<0.01$; *** $P<0.001$

and 0.5 g of randomly selected segments were stained with trypan blue in lactoglycerin (Phillips and Hayman 1970). Percent root length containing vesicles and/or arbuscules was assessed using a gridline intersect method (Giovannetti and Mosse 1980).

Soil analysis. Composite soil samples collected in November, 1987 were analyzed for pH (1:1 water slurry) and P. Bray-1 P ($NH_4F + HCl$ extractable P) was measured following the procedure of Dahnke (1988), and total P was measured as in Tandon et al. (1988). Total soil N, organic C and H_2O soluble organic C are summarized from Zak et al. (1990). However, they did not study the rye field, fallow field and 13 year old field. Total N was determined by digesting air dried soil in a block digester with concentrated H_2SO_4 and HgO as a catalyst. Organic C was determined by combustion in a LECO automatic C analyzer (LECO Corp. St. Joseph, MI USA) and H_2O soluble organic C was measured following the procedure of Burford and Bremner (1975).

Root biomass. Root biomass was measured along transects ca. 5 m from those used for VAM analysis (Gleeson and Tilman 1990). Between 13 and 30 July, 1987, three soil cores (4.8 cm diameter × 30 cm deep) were taken from five 100 m transects in each of the field sites except the rye field, fallow field and 13 year old field. Cores were placed on a screen and soil was gently rinsed from the roots. Roots were sorted from litter and adhering debris, but no attempt was made to distinguish between living and dead roots. Roots were oven dried at 70° C for 24 h and weighed (Gleeson and Tilman 1990).

Plant communities. Detailed studies of plant species composition have been conducted across the chronosequence (Delaney 1988; Inouye et al. 1987), and we used this information in the present study. Plant species' cover data from these two studies were coded according to the putative mycorrhizal status of their families. Species from four families: Brassicaceae, Caryophyllaceae, Chenopodiaceae, and Polygonaceae, reported to contain a large proportion of nonmycorrhizal species (Newman and Reddell 1987), were coded as "non-hosts". Non-host abundance, calculated as (relative cover of non-host plants/relative cover of host plants), was determined for 11 of the 12 old field sites (no plant community data were available for the 13 year old field).

Statistical analysis. Spearman rank correlation analysis was used to relate abundances of VAM fungal species with age, or successional rank, and soil or plant properties of the 15 field and forest sites in which spores were analyzed (spore populations were not analyzed in the 3 year and 8 year old fields). The oak savanna, upland pin oak forest and northern hardwood forest were assigned successional ranks of 13, 14, and 15, respectively. Simple and partial correlation analyses were used to examine the relationships between infectivity, total spore counts, field age, soil properties, below-ground biomass, and non-host abundance of the 14 field sites. Prior to statistical analysis, root infection data were arcsine square root transformed and soil C, soil P, soil N and root biomass were ln transformed. Significance of the correlations were accepted at alpha = 0.05. Correlation analyses were performed using Statgraphics (STSC, IN., USA 1986). Plant community data was coded and collated using SAS (SAS IN., USA 1988). Percentage dissimilarity was calculated using VEGROW (Fresco 1989).

Results

VAM fungal communities

Total counts of VAM fungal spores ranged from 17 to 316 spores/g dry soil, and were lowest in the 1 year field, the oak forest and the hardwood forest (Fig. 2). Within the 12 abandoned fields, total spore count was positively

Table 3. VAM fungal species observed from 15 Cedar Creek sites, their mean abundance and frequency

Voucher Number[a]		Frequency[b]	Mean relative abundance[c]
			%
cc1	*Acaulospora appendicula*, Spain, et al.	7	0.24
cc2	*Acaulospora elegans*, Trappe and Gerd.	2	0.01
cc3	*Acaulospora laevis*, Gerd. and Trappe	13	0.86
cc4	*Acaulospora morrowae*, Spain and Schenck	13	0.50
cc5	*Acaulospora scrobiculata*, Trappe	14	1.16
cc6	*Acaulospora spinosa*, Walker and Trappe	9	0.28
cc7	*Entrophospora infrequens*, (Hall) Ames and Schneider	11	0.15
cc8	*Gigaspora albida*, Schenck and Smith	2	0.01
cc9	*Gigaspora gigantea*, (Nicol. and Gerd.) Gerd. and Trappe	15	2.29
cc10	*Gigaspora margarita*, Becker and Hall	3	0.07
cc11	*Gigaspora sp.*	13	1.77
cc12	*Glomus aggregatum*, Schenck and Smith emend. Koske	15	76.20
cc13	*Glomus albidum*, Walker and Rhodes	6	0.09
cc14	*Glomus ambisporum*, Smith and Schenck	15	6.09
cc15	*Glomus etunicatum*, Becker and Gerd.	8	0.27
cc16	*Glomus fasciculatum*, (Thaxter) Gerd. and Trappe emend. Walker and Koske	12	0.32
cc17	*Glomus geosporum*, (Nicol. and Gerd.) Walker	6	0.14
cc18	*Glomus halonatum*, Rose and Trappe	1	0.006
cc19	*Glomus intraradix*, Schenck and Smith	5	0.13
cc20	*Glomus microcarpum*, Tul. and Tul.	8	5.05
cc21	*Glomus mosseae*, (Nicol. and Gerd.) Gerd. and Trappe	3	0.03
cc22	*Glomus occultum*, Walker	15	1.52
cc23	*Scutellospora calospora*, (Nicol. and Gerd.) Walker and Sanders	14	2.38
cc24	*Scutellospora erythropa*, (Koske and Walker) Walker and Sanders	11	0.28
cc25	*Scutellospora persica*, (Koske and Walker) Walker and Sanders	6	0.13

[a] voucher numbers assigned to representative specimens of each species

[b] number of sites, of 15 sampled, in which species occurred

[c] mean relative abundance across all 15 sites was calculated as:

$$\frac{\text{Total spores of Sp.i observed from all 15 sites}}{\text{Total spores of all Spp. observed from all sites}} \times 100$$

Table 4. Spearman rank correlations between abundances of VAM fungal species and successional rank, soil properties and plant properties of the 15 field and forest sites in which spores were analyzed

	Rank correlation with:								
	Successional rank[a]	Soil pH	Soil org–C	Soil sol–C	Soil tot–N	Soil Bray–P	Soil tot–P	Root biomass	Non–host abundance
Early Successional									
A. laevis	−0.63**	−0.25	−0.14	−0.56*	−0.60*	+0.11	−0.09	−0.80*	+0.35
A. scrobiculata	−0.55*	−0.10	−0.49	−0.50	−0.47	+0.05	−0.002	−0.45	+0.51
A. spinosa	−0.72**	−0.53*	−0.72**	−0.49	−0.45	+0.24	+0.59*	−0.60	+0.44
G. aggregatum	−0.54*	+0.11	−0.45	−0.53*	−0.66*	+0.02	+0.24	−0.46	+0.11
S. calospora	−0.78**	−0.16	−0.13	−0.81**	−0.62*	−0.10	+0.06	−0.77*	+0.37
S. erythropa	−0.57*	−0.50	−0.58*	−0.36	−0.34	−0.03	+0.70**	−0.64	+0.21
S. persica	−0.76**	−0.47	−0.38	−0.66*	−0.56	+0.06	+0.37	−0.70	+0.10
Late Successional									
A. elegans	+0.59*	−0.59*	+0.06	+0.64*	+0.64*	+0.08	+0.007	na[b]	na
Gi. gigantea	+0.53*	+0.07	+0.57*	+0.45	+0.55	−0.31	−0.33	+0.65	−0.20
G. ambisporum	+0.56*	−0.23	+0.72**	+0.69*	+0.76**	−0.43	−0.15	+0.72*	−0.22
G. fasciculatum	+0.55*	−0.30	+0.11	+0.39	+0.56	+0.30	+0.03	+0.05	−0.16
G. microcarpum	+0.70**	+0.23	+0.58*	+0.60*	+0.64*	−0.23	−0.21	+0.80*	−0.34

* $P<0.05$; ** $P<0.01$

[a] The oak savanna, upland-pin-oak forest and northern-hardwood forest sites were assigned successional ranks of 13, 14, and 15 respectively

[b] root biomass and plant community data were not available for the sites in which *A. elegans* was observed

Table 5. Spearman rank correlations between characteristics of VAM fungal communities and successional rank, soil properties, and plant properties of the 15 field and forest sites in which spores were analyzed. Refer to the materials and methods for descriptions of the statistics used to characterize the VAM fungal communities

Community statistic	Rank correlation with:								
	Successional rank[a]	Soil pH	Soil org–C	Soil sol–C	Soil tot–N	Soil Bray–P	Soil tot–P	Root biomass	Non-host abundance
Species Richness	−0.16	−0.10	−0.32	−0.34	−0.37	+0.19	+0.04	−0.44	+0.08
Diversity	+0.45	−0.27	+0.28	+0.60*	+0.73**	−0.10	−0.04	+0.45	−0.20
% Dissimilarity with rye field	+0.78**	+0.18	+0.27	+0.68*	+0.67*	+0.10	−0.13	+0.69*	−0.20

* $P<0.05$; ** $P<0.01$

[a] The oak savanna, upland-pin-oak forest, and northern-hardwood forests were assigned successional ranks of 13, 14 and 15 respectively

correlated with field age and H_2O soluble C, and negatively correlated with non-host abundance (Table 2). Total spore count was not significantly correlated with infectivity (Table 2).

A total of 25 different VAM fungal species in 5 genera were identified from the 15 sites examined (Table 3). We were uncertain of the identity of a thick walled *Gigaspora* species (*Gigaspora* sp.) which resembled *Gigaspora margarita* in wall structure, but ranged in color from yellow to orange. *Glomus aggregatum* was the most abundant species, comprising between 54% and 95% of the spores from each site (Fig. 2). Relative abundance of some species were unrelated to successional rank, but other species were distinctly more abundant early, or late in the chronosequence (Fig. 3). Of the 25 species observed, seven were significantly negatively correlated to successional rank (early successional) and five were significantly positively correlated to successional rank (late successional) (Table 4). Spore abundance of early successional species were negatively correlated to organic and H_2O soluble soil C, soil N and root biomass, while late successional species were positively correlated to these parameters (Table 4).

Between 12 and 22 different VAM fungal species were observed per site (Fig. 4a). Species richness did not increase with successional rank; however, diversity tended to increase ($P=0.08$), primarily because *G. aggregatum* became relatively less abundant in the older sites (Table 5). Percent dissimilarity with the rye field increased significantly with successional rank (Fig. 4b). Diversity and dissimilarity with the rye field were also positively correlated to H_2O soluble C and total N (Table 5).

VAM Infectivity

Results of the bioassays indicate that densities of infective propagules were relatively low in the fallow field and

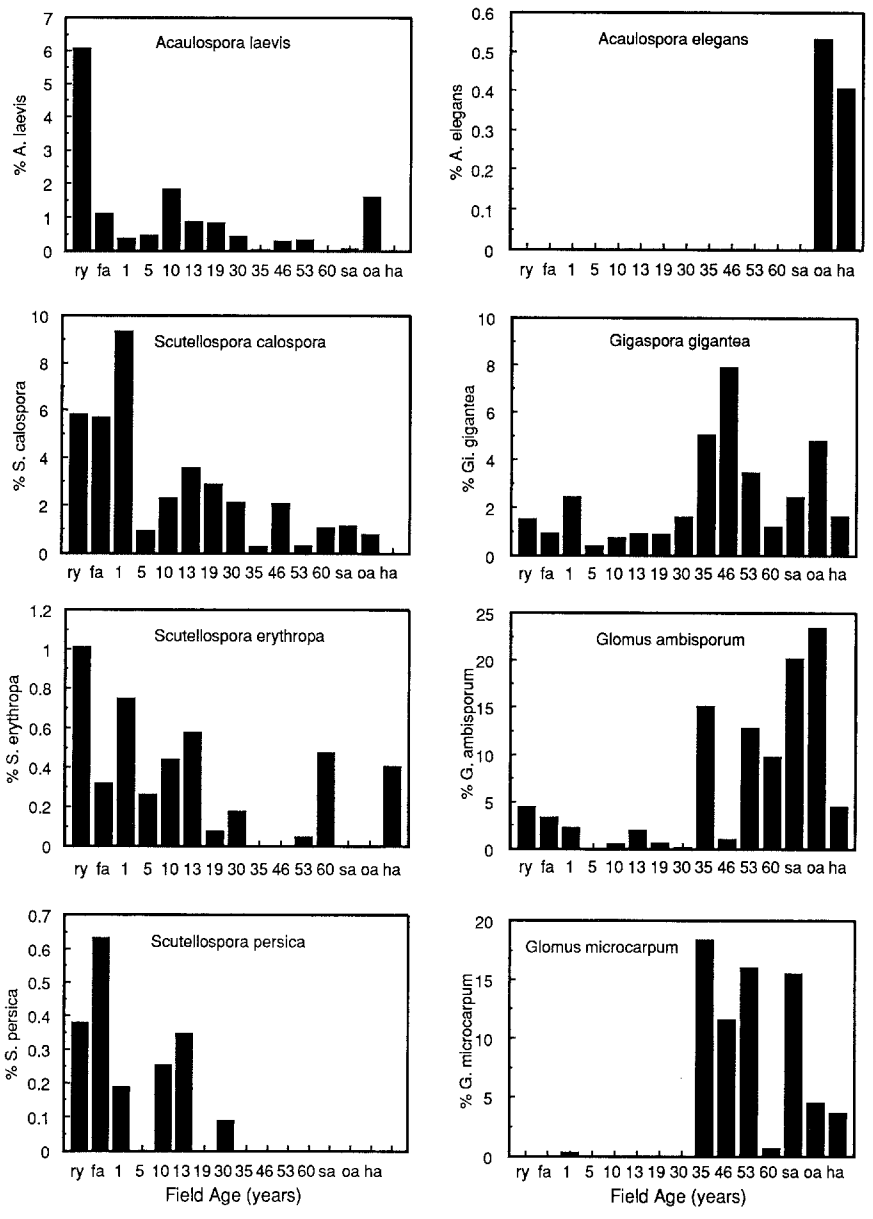

Fig. 3. Relative abundance of eight VAM fungal species in chronosequence soils. Some species were clearly more abundant early or late in the chronosequence. Sites are abbreviated as in Fig. 1

rye field and generally increased with field age up to 53 years following abandonment. Infectivity was lower in the 60 year old field and in the savanna, and was very low in the upland pin oak and northern hardwood forest sites (Fig. 5). Separate analysis of the 1987 and 1988 bioassays gave the same results. Therefore, data sets were combined [(1987 VAM root length + 1988 VAM root length)/(1987 root length + 1988 root length)] for the final correlation analysis. Infectivity was not correlated with either corn shoot weight or corn root weight ($r = 0.23$ and $r = 0.22$ respectively, $N = 14$, $P \geq 0.05$). Infectivity was positively correlated with field age, soil pH, H_2O soluble C and root biomass, and negatively correlated with total P (Fig. 6). Since these five variables were highly autocorrelated (Table 5), we used partial correlation analysis to examine each of their relationships with infectivity while holding constant the other four variables. Using this approach, pH, and H_2O soluble C were still positively correlated with infectivity ($r_p = 0.88$, $P \leq 0.001$; $r_p = 0.62$, $P \leq 0.05$ respectively), but age, root biomass, and total P were no longer significantly correlated with infectivity ($r_p = -0.36$; $r_p = -0.25$; and $r_p = 0.10$ respectively).

Discussion

Successional dynamics of VAM fungal communities

We observed a significant change in the composition of the VAM fungal communities across the Cedar Creek chronosequence. Relative spore densities of some VAM fungi were clearly more abundant in the youngest sites while other species were more abundant in the older sites. This contrasts with the findings of Benjamin et al. (1989) who observed no change in VAM fungal species throughout an Illinois prairie-forest chronosequence. A major difference between our two studies is that there was little edaphic variation in the prairie-forest gradient studied by

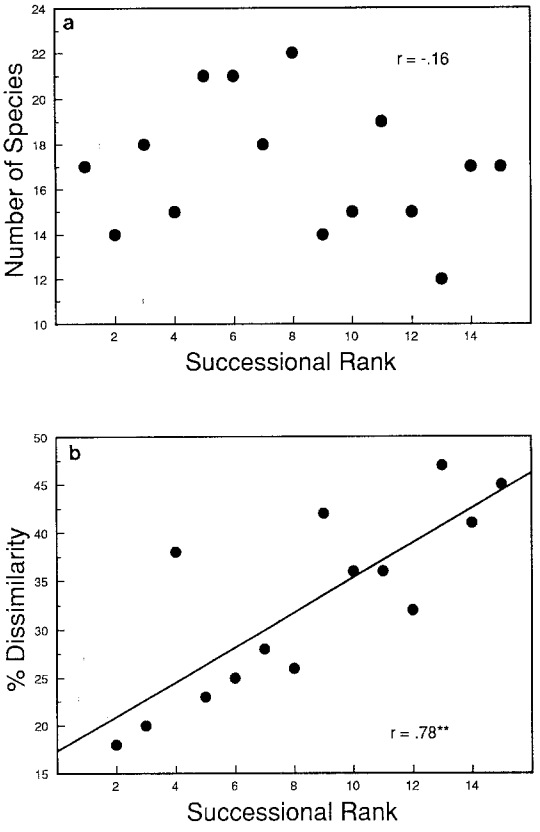

Fig. 4a, b. Two statistics of the VAM fungal communities in the chronosequence soils: species richness (**a**), and % dissimilarity with the rye field (**b**)

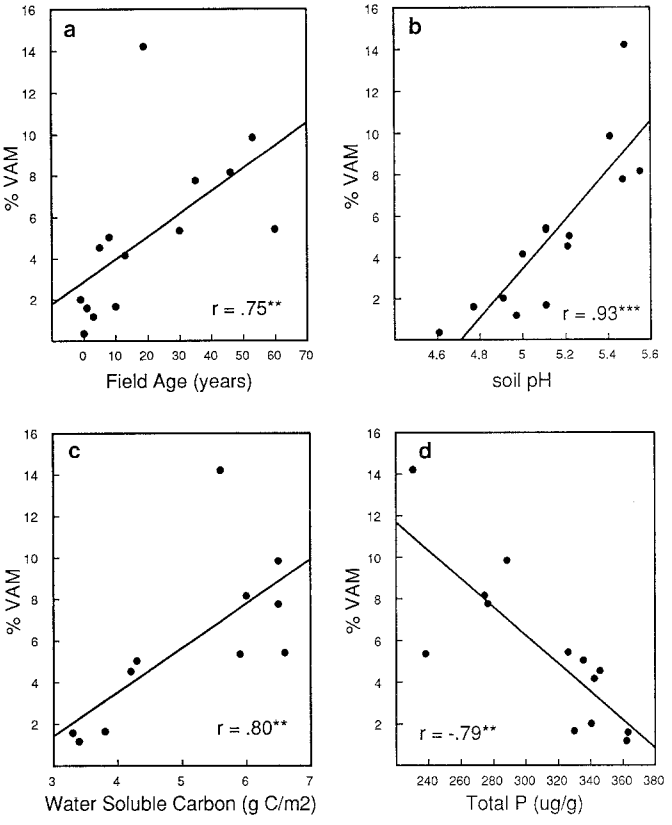

Fig. 6a–d. Simple correlations of infectivity with field age (**a**), soil pH (**b**), H_2O soluble soil C (**c**), and total soil P (**d**)

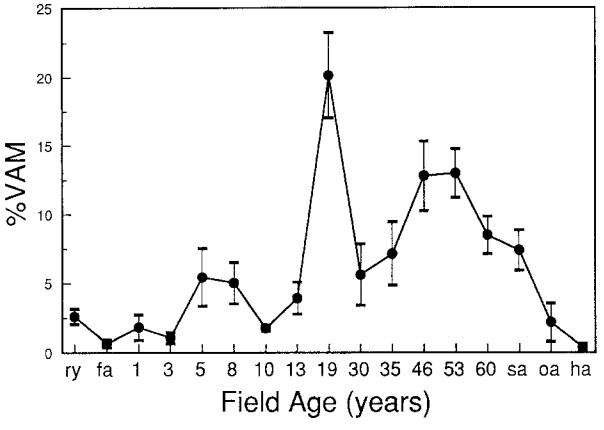

Fig. 5. Infectivity of the chronosequence soils measured by % mycorrhizal root length of bioassayed corn (bars represent standard errors). Sites are abbreviated as in Fig. 1

Benjamin et al. (1989) while there was a significant accrual of organic C and N across the Cedar Creek chronosequence. This suggests that edaphic factors may be very important in structuring VAM fungal communities.

Spore abundance of late successional VAM fungi tended to be positively related to soil C and N while spore abundance of early successional fungi tended to be inversely related to these parameters. It should be noted that closely related species of fungi often responded similarly to soil factors. For example, members of the genus *Scutellospora* were consistently inversely related to soil pH, soil C and soil N. These fungi are common sand dune inhabitants (Koske and Walker 1985), and thus may be expected to do well in early successional soils at Cedar Creek. Abundance of all four *Acaulospora* species were also inversely related to soil pH. High densities of *Acaulospora* spores have been reported in acid environments (Morton 1986; Porter et al. 1987) suggesting that members of this genus tend to be well adapted to low pH soils.

An alternative interpretation of our results might be that VAM fungi were not early or late successional species, but were specialists on different soil series. In this study, field age was somewhat confounded with soil series because the youngest sites were aggregated in one part of Cedar Creek and occurred on Nymore sands, while the older fields and forest sites were interspersed throughout the natural history area and occurred on Sartell, Nymore and Zimmerman sands. This interpretation seems less likely than the successional interpretation however because the 53 year old field and forest sites occurred on the Nymore sands, yet they contained VAM fungal communities which were more similar to the 35, 46, and 60 year old fields than to the younger Nymore sand sites. Furthermore, the 19 and 30 year old fields occurred on Sartell sand but had VAM fungal communities more similar to the 1–13 year old fields on Nymore sand, than to the other sites on Sartell sand.

VAM fungi do not tend to be host specific. For example, *Glomus mosseae* has been shown to colonize roots of twenty different plant species belonging to twelve different families (Mosse 1973). However, there is growing evidence that VAM fungal species differ in their ability to proliferate in rhizospheres of different crop plants (Schenck and Kinlock 1980; McGraw and Hendrix 1984; Johnson et al. 1991). It is possible that VAM fungal species differ in their ability to proliferate in early versus late successional plant species, and consequently, late successional VAM fungi must await the arrival of late successional host plants before they can become abundant in the VAM fungal community. The present study illustrates that the relative cover of non-host plant taxa is negatively correlated with total counts of VAM fungal spores. Whether or not the composition of the host community influences the composition of the VAM fungal community at Cedar Creek remains to be experimentally addressed.

Successional dynamics of VAM density

We suggest that there is a close interrelationship between successional dynamics of soil properties, plant productivity and VAM density as measured by infectivity and total spore counts. Water soluble C was the only factor which correlated to both infectivity and total spore count in the 14 field sites. VAM fungi are obligate symbionts and thus it is not surprising that their densities were highly correlated with H_2O soluble C since it is a measurement of the most labile C fraction, including exudates of living roots.

The finding that infectivity was positively correlated with H_2O soluble C and negatively correlated with soil P has a physiological basis and might be expected from the results of several greenhouse studies. Colonization of roots by VAM fungi have been shown to increase with increasing quantities of soluble carbohydrates in roots and root exudates and decrease with increasing concentrations of tissue P (e.g. Schwab et al. 1983; Same et al. 1983; Thompson et al. 1986). It is thought that this P induced reduction in VAM colonization is associated with a membrane mediated decrease in root exudation (Ratnayake et al. 1978; Graham et al. 1981).

The negative correlation between total P and infectivity became insignificant when pH was held constant. This suggests that soil pH and P interact in their affects on the VAM infection process. It is well known that P solubility in the soil is highly pH dependent (Mengel and Kirkby 1982). Riley and Barber (1971) showed that P uptake by soybean decreased with increasing pH. Could plants growing in high pH soils form more VAM because they take up less P, and consequently exude more carbohydrate from their roots, compared to plants grown in low pH soils? Unlike infectivity, total spore density was not significantly correlated with soil pH, suggesting that VAM colonization of roots may be more sensitive to pH than sporulation of VAM fungi. Alternatively, the highly significant correlation between infectivity and soil pH may be an artifact of the bioassay and not a true reflection of propagule density in the soil. Such an artifact could occur if VAM colonization of the corn roots was sensitive to the pH of the soil in the Conetainers.

Plants vary greatly in the degree to which they form VAM associations, ranging from non-host species, which never form mycorrhizae, to species which always form VAM associations. Reeves et al. (1979) hypothesized that VAM fungal populations will be low and non-host plant taxa will dominate early in succession, while VAM fungal populations will be high and mycorrhizal plant taxa will dominate late in succession. Furthermore, Janos (1980) hypothesized that following disturbance in temperate regions, VAM fungal populations increase and then decrease as ectomycorrhizal fungi come to predominate with the onset of a forest community. Results from the Cedar Creek chronosequence support these hypotheses.

Both infectivity and total spore count generally increased with age in the 14 field sites but then decreased with successional rank in the 3 forest sites. Benjamin et al. (1989) also found infectivity and spore counts decreased as tree basal area increased in a sand prairie to oak hickory forest succession. We suggest that the reduced VAM densities in the savanna, oak forest and hardwood forest resulted from a shift in the plant community dominants from herbaceous, primarily VAM hosts, to woody, primarily ectomycorrhizal hosts.

Our two indices of VAM density, infectivity and total spore count, were not significantly correlated. There are several reasons to expect this result, and it agrees with the findings of others (Powell 1977; Hayman and Stovlod 1979; Abbott and Robson 1982; Scheltema et al. 1987). Spore counts assess only one type of propagule, while infectivity indirectly measures all types: spores, hyphae, and VAM roots. Consequently spore counts probably do not measure total VAM density as accurately as infectivity. Furthermore, spore formation may be unrelated to the total fungal biomass (including hyphae, vesicles and arbuscules) since different VAM fungal species do not all sporulate to the same degree. For example, *Glomus aggregatum* produce copious tiny spores in loose sporocarps, while *G. tenuis* rarely, or never, form soil-borne spores (Hall 1977). Finally, dead spores may accumulate in the soil and are often impossible to distinguish from viable spores. Consequently, the dominance of *G. aggregatum* in the spore community may or may not reflect its actual abundance within plant roots.

During old field succession at Cedar Creek, changes in plant community composition, primary production, and nutrient accrual occur in relatively predictable patterns. Previous research has demonstrated that a close interrelationship exists between the pattern of plant and microbial biomass owing to the reciprocal nature of C and N cycles (Zak et al. 1990). The results we present here suggest a concomitant interrelationship exists between soil properties, plant productivity and VAM density.

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