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MYCORRHIZAE AND SUCCESSION IN PLANTINGS OF BEACHGRASS IN SAND DUNES[1]

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A survey of arbuscular mycorrhizal fungi (AMF), arbuscular mycorrhizae (AM), and hyphal networks of AMF was carried out in sand dune sites of different successional stages in the Province Lands Area of Cape Cod National Seashore, Massachusetts. The study focused on large-scale plantings (each of 12–20 ha) of American beachgrass (*Ammophila breviligulata*) aged 0–7 yr and five adjacent natural dune areas. Sample sites ranged in vegetative cover from barren to forested. Spores of 17 species of AMF were recovered from the dunes. Over the successional sequence, there were increases in the richness and spore populations of the AMF community, the extent of colonization of *A. breviligulata* roots, and the mycorrhizal inoculum potential of the soil. Unvegetated sites lacked propagules of AMF, but roots of planted culms of *A. breviligulata* (which carried propagules of AMF) became mycorrhizal in <1 yr after planting. Spores were recovered from previously AMF-free sites that had been planted with beachgrass for 47 wk, and five species of AMF sporulated in sites <6 yr old. Significant hyphal networks were not present in any of the planted areas (<6 yr old at the time of sampling), but did occur in natural areas. The rate of invasion of areas planted to *A. breviligulata* by later successional plant species may in part depend upon the establishment of a vigorous network of hyphae of AMF in a site.

Key words: *Ammophila breviligulata*; arbuscular mycorrhizae; hyphal network; plant succession; Poaceae; sand dunes.

Since 1959, the possible importance of arbuscular mycorrhizal fungi (AMF) in sand dune succession has been recognized, and numerous surveys have shown AMF to be routine inhabitants of temperate and tropical dune sites in coastal and inland dunes throughout the world (e.g., Nicolson, 1960; Koske and Polson, 1984; Giovannetti, 1985; Puppi and Riess, 1987; Rose, 1988; Read, 1989; Koske and Gemma, 1990, 1992, 1996; Sturmer and Bellei, 1994; Al-Agely and Reeves, 1995). In these primary successional sites, AMF arrive early, often with the first plant colonizers (Nicolson, 1960; Sylvia and Will, 1988; Gemma and Koske, 1989, 1992; Koske and Gemma, 1990).

The development of the belowground AMF community is closely linked to aboveground vegetational changes during colonization and succession. In a variety of natural sites, AMF have been found to play a vital role in plant succession, affecting the success not only of obligately mycotrophic species, but also of species that are facultatively mycotrophic and even nonmycotrophic. Depending on the level of disturbance and existing plant population in a site, the ability of plant species to become established after dispersal to the site is determined in part by the population of AMF in the soil (Miller, 1979, 1987; Reeves et al., 1979; Janos, 1980; Grime et al., 1987; Read and Birch, 1988; Gemma and Koske, 1990, 1992; Koske and Gemma, 1990; Gange, Brown, and Sinclair, 1993; Francis and Read, 1994, 1995).

Stabilization of large, mobile dune fields has concerned inhabitants of Cape Cod for more than three centuries. Prior to the arrival of European colonists in the 1600s, the area consisted of forested dunes. Destruction of the forest and damage by grazing livestock in the following century permitted the formerly stabilized dunes to become mobile again and led to the current problems with drifting sand (McCaffrey and Leatherman, 1979). Human uses of the mobile dunes for recreation have prevented re-establishment of sufficient vegetation to slow the movement of the sand. Inundation of roads, buildings, and adjacent forests and the filling in of Provincetown Harbor and Pilgrim Lake by wind-blown sand are longstanding problems in the area.

Vegetation is an effective means of slowing sand movement in dunes (e.g., Jagschitz and Bell, 1966; Ranwell, 1972; Woodhouse, 1982), and large plantings have been made on Cape Cod for this purpose since at least 1825 (Thoreau, 1865; Strahler, 1966). The most recent major plantings have been made in the Province Lands Dunes Area of Cape Cod National Seashore (CCNS). Since 1985, ≈ 75 ha of American beachgrass (*Ammophila breviligulata* Fern.) have been planted (in 1985, 1988, 1989, and 1990) in a program administered by the National Park Service (NPS).

Careful record keeping of the history of plantings in clearly identifiable areas by the NPS in The Province Lands Dunes site of CCNS offered a unique opportunity to study the dynamics of primary succession in the earliest seral stages (spanning 7 yr) in large plantings of beachgrass. The purpose of the studies reported here was to document the species of AMF present in the dunes and to identify changes occurring in the AMF community as well as the inoculum potential of the dune soil during the early stages of primary succession of the plant community.

MATERIALS AND METHODS

Study site—Studies were performed in an area measuring ≈4 × 1 km in the Province Lands Dunes region of CCNS (70°8.5′W, 42°4.0′N)

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near Provincetown, MA. The vegetation and ecological processes occurring in the Cape Cod dunes are similar to those in dunes along much of the North Atlantic seaboard of the U.S. (Godfrey, 1977; Godfrey, Leatherman and Zaremba, 1979; Woodhouse, 1982). The geology of the area is described by Strahler (1966). The Province Lands Dunes comprise a variety of dune systems in various stages of succession. Large mobile dunes up to 32 m high are interspersed among smaller, more densely vegetated areas (Strahler, 1966). In the mobile dunes, the dominant plant species is *A. breviligulata.* Early invaders of *A. breviligulata*-dominated sites are *Polygonella articulata* (L.) Meisn. and *Solidago sempervirens* L. Later successional sites are characterized by the grass *Deschampsia flexuosa* (L.) Trin., the shrubs *Myrica pensylvanica* Loisel. and *Prunus maritima* Marsh., the trees *Pinus rigida* Mill. and *Quercus ilicifolia* Wang., and other species (Svenson and Pyle, 1979; Whatley, 1988). A forest of mixed deciduous trees and shrubs is the most advanced successional stage in the area.

Our studies focused on areas planted in 1985, 1988, 1989, and 1990 (Figs. 1–4). Each planting covered 12–20 ha, and had been free of vegetation for >5 yr prior to planting. Vegetation in the planted areas had a highly regular distribution. During NPS-supervised planting on the dunes, three cleaned culms (tillers with roots and dead leaves removed) of *A. breviligulata* cv. Cape were inserted in a hole 20 cm deep, and the soil was packed around the culms. Such a group of three culms is termed a "hill." Hills in the dunes were planted 46 cm apart in rows. The rows run in an east-west direction (parallel to the shore) and are spaced 46 cm apart. Hills in adjacent rows were staggered. At the completion of each of the NPS plantings, 36 kg/ha of a pelletized 10:10:10 fertilizer were applied by broadcasting. No additional fertilizer was added.

The Province Lands plantings are located 0.5–1.3 km from the beach, and separated from it by a series of dune ridges. Movement of sand from the beaches inland to the planting sites is uneven, and most sites appear to receive very little sand deposition (Godfrey, Fowler and Stack, 1991), resulting in a gradual decline in the vigor of the plantings (Eldred and Maun, 1982; Disraeli, 1984; Godfrey, Fowler, and Stack, 1991).

In addition to the plantings of 1985–1990, we also sampled some nearby natural areas of the dunes (Sites 1–5) in different seral stages for comparison. These areas were naturally vegetated, but had not been planted by the NPS. Site 1 (Fig. 5) was a vigorous stand of *A. breviligulata* located between NPS planting areas of 1988 and 1989. This area had been previously identified by Godfrey, Fowler, and Stack (1991) as a native stand of beachgrass. Sand accretion was high at this site, organic matter was low, and invading species were very rare. Sites 2 and 3 (Fig. 6) were dominated by declining stands of *A. breviligulata* and represented slightly later successional stages. In addition to *A. breviiligulata,* areas 2 and 3 were very sparsely colonized by *Achillea millefolium* L., *Aster linariifolius* L., *Deschampsia flexuosa, Myrica pensylvanica, Prunus maritima, Polygonella articulata, Quercus ilicifolia, Rosa rugosa* Thunb., *Solidago nemoralis* Ait., *S. odora* Ait., and *S. sempervirens.* Site 4 (Fig. 7) had 98% cover by *A. breviligulata* and numerous vigorously invading species (e.g., *Myrica pensylvanica, Rosa rugosa, Artemisia borealis* Pall., *Deschampsia flexuosa, Daucus carota* L., *Hieracium canadense* Michx., and *Kalmia angustifolia* L., *Pinus rigida,* and *Q. ilicifolia*). Site 5 was forested with *Acer rubrum, Quercus* spp., *Sassafras albidum,* and an understory of shrubs (e.g., *Clethera*


1


2


3


4

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Figs. 1–4. Plantings of *Ammophila breviligulata* on Province Lands Dunes. **1.** 1990 planting (age 1 yr). Sparse area near center was planted with one culm per hill instead of the usual three per hill. **2.** 1989 planting (age 2 yr). This planting suffered extensive winterkill a few months after planting. Note many dead individuals in some rows. **3.** 1988 planting (age 3 yr). 4. 1985 planting (age 6.5 yr). Note low vigor and cover in this declining stand.

Figs. 5–7. Natural dune areas in the Province Lands Dunes. **5.** Site 1. A vigorous, flowering stand of *Ammophila breviligulata* is shown. Light band at top of dune indicates the numerous inflorescences. **6.** Site 2. *Ammophila* in decline, some invading species present. **7.** Site 4. Note high cover. *Ammophila* dominates, but other species are common.

alnifolia L., *Gaylussacia baccata* (Wang.) K. Koch). Soil organic matter and diversity were high. The natural sites were ranked 1, 2, 3, 4, and 5 from earliest to latest in a successional sequence on the basis of soil organic matter, incidence of invading species, and vigor of *A. breviligulata* (Koske and Gemma, 1992).

Sampling—Sampling for AMF, arbuscular mycorrhizae (AM), vegetation, and soil characteristics was carried out in 1990 and 1991 using stratified random sampling techniques (Mueller-Dombois and Ellenberg, 1974; Koske and Gemma, 1992). The most extensive sampling was carried out in the planted areas that were of known age. Sampling of natural areas was less comprehensive, and those data were gathered mainly for comparison to results from the planted sites.

To ensure that any changes in vegetative cover, vigor, etc. were not the result of pathogens or pests, we had Dr. Noel Jackson, a plant pathologist at the University of Rhode Island, examine *A. breviligulata* plants from the NPS plantings and from some natural areas in November 1990, February 1991, March 1991, and August 1991. He looked specifically for chinch bugs, root cyst nematodes, striped smut, and root aphids. No significant occurrences of any of these pests were found.

Soil characteristics—Most soil samples were collected in October 1990 for physical analysis. Samples at the 1990 planting site were collected a few days before planting (October) and just after planting and fertilization (November). The upper 15 cm of sand at each sampling point was scraped away, and a sample (≈ 1 L) was collected by inserting a clean trowel to a depth of 15 cm and removing the soil. Thus the sample included only soil that occurred in the zone between 15 and 30 cm below the original soil surface. Soil pH was measured in a soil: water slurry (1:2) with a pH meter after a 20-min equilibration, organic matter was measured by loss-on-ignition at 400°C for 6 h, and the other parameters were measured by the Soil Testing Service, University of Rhode Island Cooperative Extension Service.

AMF community—The AMF community present in the soil at the time of sampling was assessed by direct counts of spores from each area in the dune system. Fifteen soil samples were collected on 12 October 1990 from each of the four planting sites (1985–1990) and from area 2. The collections from the 1990 planting area were taken before the planting occurred. In October 1991 additional samples were collected from the following sites: 1990 planting area (12 samples), site 3 (eight samples), site 4 (13 samples), and site 5 (five samples). Samples were collected in the fall because spore populations in New England dunes typically reach their maximum in fall/winter (Gemma and Koske, 1988; Gemma, Koske and Carreiro, 1989).

Prior to collection of root zone samples, the upper ≈ 20–25 cm of soil in which few roots occur were removed and discarded. A trowel was then used to excavate soil (≈ 1 L) and roots from the bottom of the hole. Spores of AMF were recovered from soil samples by wet-sieving and centrifugation (Walker, Mize, and McNabb, 1982). All the spores contained in an 85-mL soil sample were placed on a 5.5 cm filter paper after centrifugation and then transferred to glass microscope slides. Spores were mounted in a polyvinyl alcohol mounting solution (Koske and Tessier, 1983) and identified at 400-1000×. Species identities were confirmed by comparison to authenticated specimens. Vouchers have been preserved in the authors' collections. All spore counts were converted to number of spores per 100 mL soil.

Mycorrhizal status of plants—The extent of mycorrhizal colonization in plantings of *A. breviligulata* and in invading species of plants was measured. Four field surveys were carried out to assess the extent of AM in *A. breviligulata* in sites of different ages and to determine when plantings form mycorrhizae. The first two studies included only established plants, and the second two focused on seedlings. On 12 October 1990, five root samples were collected from each of the 1985, 1988, and 1989 planting areas and from native area 2. At each sampling point, a root sample (50–80 cm long) was collected at a depth of ≈ 25 cm beneath the surface. The second survey was carried out at the 1990 planting site on 18 October 1991 (47 wk after planting). Ten root samples were collected.

In the seedling surveys, ten plants (3–5 cm high) were collected from the 1988 area in October 1990, and ten from the 1990 planting site in

June 1992. Because seedlings were infrequent, samples were collected haphazardly from the areas and not by the stratified random sampling procedure.

Root samples were cleared in hot (65°C) 2.5% KOH and stained in an acidic glycerol solution of trypan blue (Koske and Gemma, 1989). Extent of arbuscular mycorrhizae (AM) development in the roots was quantified by calculating a Mycorrhizal Index (MI), in which colonization was assessed at 30–60× on a scale of 0–3, where 0 = no colonization, 1 = up to 25% of the root length containing hyphae, arbuscules, vesicles, or coils of AMF, 2 = 25–50% colonized, and 3 = >50% of length colonized. Portions of each root system were observed at 400×. Roots were considered to have functional vesicular-arbuscular (VA) mycorrhizae only if arbuscules were observed (Gemma and Koske, 1990).

To estimate mycorrhizae in invading species, root samples were collected in April 1992 from 13 species of plants invading the 1985, 1988, and 1990 plantings or occurring in natural areas 3 and 4. Care was taken to ensure that only the roots of the invading species were assessed for colonization. Invading species were rare in the youngest plantings, and the collecting reflected this. Roots were treated as described above. Ectomycorrhizae were rated visually only for presence or absence.

Mycorrhizal inoculum potential of soils and assessment of the hyphal network—An assay of mycorrhizal inoculum potential (MIP) (Moorman and Reeves, 1979; Gemma and Koske, 1988) was employed to assess the relative population of infective units (i.e., spores, hyphae, pieces of mycorrhizal roots) in soils from various sites.

Assay of 1990 planting area prior to planting—A MIP assay of the soil from the 1990 planting area was performed to check for the presence of viable propagules of AMF. Fifteen soil samples were collected on 12 October 1990 using a stratified random sampling plan. At each collection point, the upper 15 cm of soil was removed and a 1-L soil sample (≈ 6 cm diameter) was collected. Soil samples were returned to the greenhouse at the University of Rhode Island, and 70 mL of each sample were mixed with an equal amount of Terra-Green®, a calcined clay (Oil Dri Corp., Chicago, IL 60611), and the mix was placed in a Cone-tainer® (a tapering, cylindrical plastic growth tube, 20.5 × 4.0 cm of 150 mL capacity, Stuewe and Sons, Corvallis, OR 97331). Two seeds of *Zea mays* L. were sown in each of the 15 Cone-tainers, and the material was placed in a heated greenhouse (avg. 26°C). Sunlight was supplemented for 16 h/d with high-pressure Sodium vapor lamps giving an intensity at the leaf surface of 350–1375 μmol photons$\cdot$m$^{-2}\cdot$s^{-2}. After seed germination, Cone-tainers were thinned to contain a single plant. Plants were watered as required, but not fertilized, and harvested after 60 d. Roots were cleared, stained, and assessed for colonization by the line-intercept method (Giovannetti and Mosse, 1980).

Assay of soils from vegetated sites—Undisturbed soil samples (see below) were used for the MIP assays, and disturbed and undisturbed samples were used to estimate the extent of the hyphal network in the different sites. Soil samples were collected on 3 September 1991 from plantings of *A. breviligulata* (1985, 1988, 1989, and 1990 sites) and from sites 1 and 4. Samples were collected by driving a PVC (polyvinyl chloride) tube (20 cm long × 5.1 cm inside diameter; the top of the tube covered with a piece of fiberglass window screen glued to it) into the soil. The tube was then carefully withdrawn, with the core of sand remaining inside. Before the tube was driven into the ground, the upper 8 cm of soil had been removed. After their removal from the soil, the tubes were inverted (screen now at bottom) and used as pots for growing plants in the greenhouse (see below). At each of the six collecting sites, five hills (in the planted areas) or locations (sites 1 and 4) were selected randomly, and two cores were taken. The distance between the center of the plant and the cores was 15–20 cm, so that portions of the root zone were included in each sample. The contents of one member of each pair of cores were emptied into a plastic bag. When five cores from a site were in the bag, the bag was shaken vigorously for 30 s, and the soil was transferred back into the five original PVC tubes. These shaken samples were the "disturbed" cores. The intact cores were termed "undisturbed." Thus, ten cores were obtained from each of the six sites, and half of the cores were undisturbed and half were disturbed.

Disturbed and undisturbed cores were placed on the mist bench in the greenhouse, and one pregerminated seed of *Z. mays* was added to each tube. After 1 wk, tubes were removed from the mist bed and transferred to the greenhouse benches and grown as described above. At 8.5 wk after sowing, the entire root system was removed from each tube, cleared, stained, and assessed for mycorrhizae as described above.

In addition to the standard MIP assay which measures the amount of root colonization, two other parameters were measured. When the plants were harvested at 8.5 wk, the length of the longest leaf in each Cone-tainer was recorded and shoot dry mass was determined by drying in a 60°C oven for 48 h.

Statistical methods—Data were analyzed using t tests, chi-squared tests, and one-way ANOVA. Means were separated with Scheffé's test. Spore count data and root colonization data typically are not normally distributed (Sylvia, 1986; St. John and Koske, 1988) and were transformed prior to analysis. Spore counts were transformed by adding 0.5 to the abundance value and taking the square root of the sum (Little and Hills, 1978), and colonization values underwent a log $(x+1)$ transformation (St. John and Hunt, 1983). A confidence level of $P = 0.05$ was used to determine statistical significance.

RESULTS

Physical characteristics of soils—Soils in all sites were nearly pure quartz sand. With few exceptions, all soils had very low levels of organic matter, nitrate, phosphorus, and potassium, and were acidic (Table 1). In the planted areas (of known age), organic matter and age of the stand were positively correlated (organic matter = 0.51 × age in yr + 0.123, $r = 0.56$; $P = 0.02$). When all sites were compared (planted and natural), organic matter was higher in site 5 and nitrate was higher in site 4 than elsewhere.

AMF community—Spores of 17 species of AMF were isolated from the 98 samples collected from root zones (i.e., excluding the 12 samples collected from the barren 1990 planting area before the planting had been made). Five of the species apparently are undescribed and are identified by number and are informally described below. Terminology follows that recommended by Walker (1983, 1986) and Morton (1986). No spores were present in the 1990 planting area prior to planting. Frequency of occurrence and spore abundance of the more important species are shown for each site in Fig. 8. In the notes that follow, reference to the frequency of occurrence of particular species in all of the samples does not include the 12 samples collected from the 1990 planting area prior to planting.

1. *Acaulospora lacunosa* Morton

Spores of *A. lacunosa* were recovered significantly more frequently in sites ≥ the 1985 planting in age ($P = 0.01$) (Fig. 8). They occurred in 15% of all samples. This species is relatively common in dunes of the U.S. Atlantic coast from Massachusetts to Virginia (R. E. Koske, personal observation). Until its description in 1986, spores

TABLE 1. Some physical and vegetational characteristics of sampling sites.

Site	Age of planting (yr)	Cover (%)	(N)[a]	pH	NO_3 (mg/kg)	P (mg/kg)	K (mg/kg)	Organic matter (%)[b]
1990[c]	0	0E[d]	2	6.0A	1.5B	14.5A	5.0A	0.12B (N = 14)
1990[c]	1	33C	6	5.4A	2.1B	24.5A	5.4A	n.d.[e]
1989	1	15D	2	5.8A	1.4B	13.9A	5.0A	0.12B (N = 15)
1988	2	34C	2	6.1A	1.5B	14.3A	5.0A	0.14B (N = 13)
1985	5	26C	2	6.2A	1.6B	15.1A	5.0A	0.15B (N = 13)
1	n.a.[f]	59B	5	5.8A	1.4B	22.8A	10.5A	0.13B (N = 5)
2	n.a.	28C	2	5.6A	1.4B	13.2A	6.3A	0.13B (N = 13)
3	n.a.	25C	3	5.8A	3.9B	22.6A	13.3A	0.23B (N = 4)
4	n.a.	98A	3	5.8A	9.1A	30.6A	13.3A	0.38B (N = 12)
5	n.a.	n.d.	3	5.2A	3.0B	22.8A	25.8A	1.91A (N = 5)

[a] N = no. of samples analyzed for pH, nitrate, phosphorus and potassium.

[b] Mean percentage organic matter. N = no. of samples analyzed for organic matter.

[c] The 1990 area was planted and fertilized in November 1990. It was sampled immediately after and 1 yr later.

[d] Mean of samples. Values in columns followed by the same uppercase letter did not differ significantly.

[e] Not determined.

[f] Age of the vegetation of the natural areas was not determined.

of this species would have been identified as *A. scrobiculata* Trappe.

2. *Acaulospora mellea* Spain & Schenck

Spores of *A. mellea* were recovered from 16% of all samples. Like *A. lacunosa,* it was absent from the 1988–1990 plantings, but occurred in all other areas (Fig. 8). Maximum spore abundance occurred in the 1985 planting (avg. 4.9 spores/100 mL).

3. *Acaulospora scrobiculata* Trappe

A common species in dunes of the Atlantic coast of the U.S. including other areas of Cape Cod, *A. scrobiculata* (e.g., Bergen and Koske, 1984; Koske, 1987; Gemma, Koske, and Carreiro, 1989) was recovered only from site 2 in this study. It was present in 20% of the samples from this site, averaging 2.7 spores/100 mL.

4. *Acaulospora* 3106A (Fig. 9)

This species is similar to *A. lacunosa,* but spores possess a more finely dimpled laminated wall. Spores were found only in three of the samples from site C.

Spores globose, 72–88 μm diameter, yellow-brown. Spore wall structure consisting of six walls. Wall 1 membranous, wrinkling, hyaline, 0.5 μm thick, appressed to wall 2. Wall 1 was difficult to observe in most specimens, apparently disappearing during exposure to the soil. Wall 2 laminated, yellow, 2.0–3.0 μm thick, ornamented with hemispherical depressions 2–3 μm diameter × 1–2 μm deep, closely spaced, separated from each other by ridges ≈ 2 μm wide. Walls 3 and 4 paired, membranous, hyaline, each 0.5–0.6 μm thick. Wall 5 membranous, beaded, 0.5–1.0 μm thick. Wall 6 amorphous, hyaline, attached to wall 5, 1.5–2.0 μm thick, up to 8 μm thick in crushed spores, staining dark red-brown in Melzer's reagent. Circatrix 12 μm diameter.

Acaulospora 3106A is a a member of the group of small-spored *Acaulospora* species that include *A. lacunosa* and *A. mellea,* which have a common wall structure (Morton, 1994). The ornamentation of the laminated wall is sufficient to distinguish *A.* 3106A from other ornamented species in this group, but sufficient quantities of material and stages of development were not available to prepare a formal description.

5. *Acaulospora* 7034 (Figs. 10, 11)

Spores of this species were common in the midsuccessional sites in our study, and were especially abundant in the 1985 planting and in site 2 (Fig. 8). Spores of *A.* 7034 were the most frequently recovered of any species, occurring in 31% of all the root zone samples. No spores were isolated from the 1-yr-old 1990 planting and sites 4 and 5 (i.e., the youngest and oldest sites).

Spores globose to subglobose, 120–160 μm diameter, brownish-yellow. Spore wall structure complex, consisting of six walls. Walls 1 and 2 evanescent, hyaline, adherent to each other and to wall 3. Wall 1 0.5–0.8 μm thick; wall 2 1.5–2.0 μm thick. Wall 3 laminated, colored, ornamented by craniform folds, 5.6–7.5 μm thick. Wall 4 membranous, wrinkling, hyaline, 1.0 μm thick. Wall 5 coriaceous, hyaline, 1.0–2.2 μm thick. Wall 6 appressed to wall 5, membranous, hyaline, 0.5 μm thick. Circatrix 12–14 μm diameter.

Spores of *A.* 7034 are similar to those of *A. rehmii* Sieverding & Toro in their surface ornamentation, but differ in wall structure.

6. *Entrophospora infrequens* (Hall) Ames & Schneider

Spores were found in a single sample from area 4. This species has not previously been recovered from sand dunes of the Atlantic coast of the U.S., although it is known from dunes in the west coast (Koske and Halvorson, 1989).

7. *Gigaspora gigantea* (Nicol. & Gerd.) Gerd. & Trappe

Spores of *G. gigantea* were recovered from the 5-yr-old site and natural areas 2, 3, and 4 (Fig. 8). Spores were present in 18% of all samples. The species is common in *A. breviligulata*-dominated dunes of the Atlantic coast of North America from Quebec to Virginia (Koske and Halvorson, 1981; Bergen and Koske, 1984; Koske,

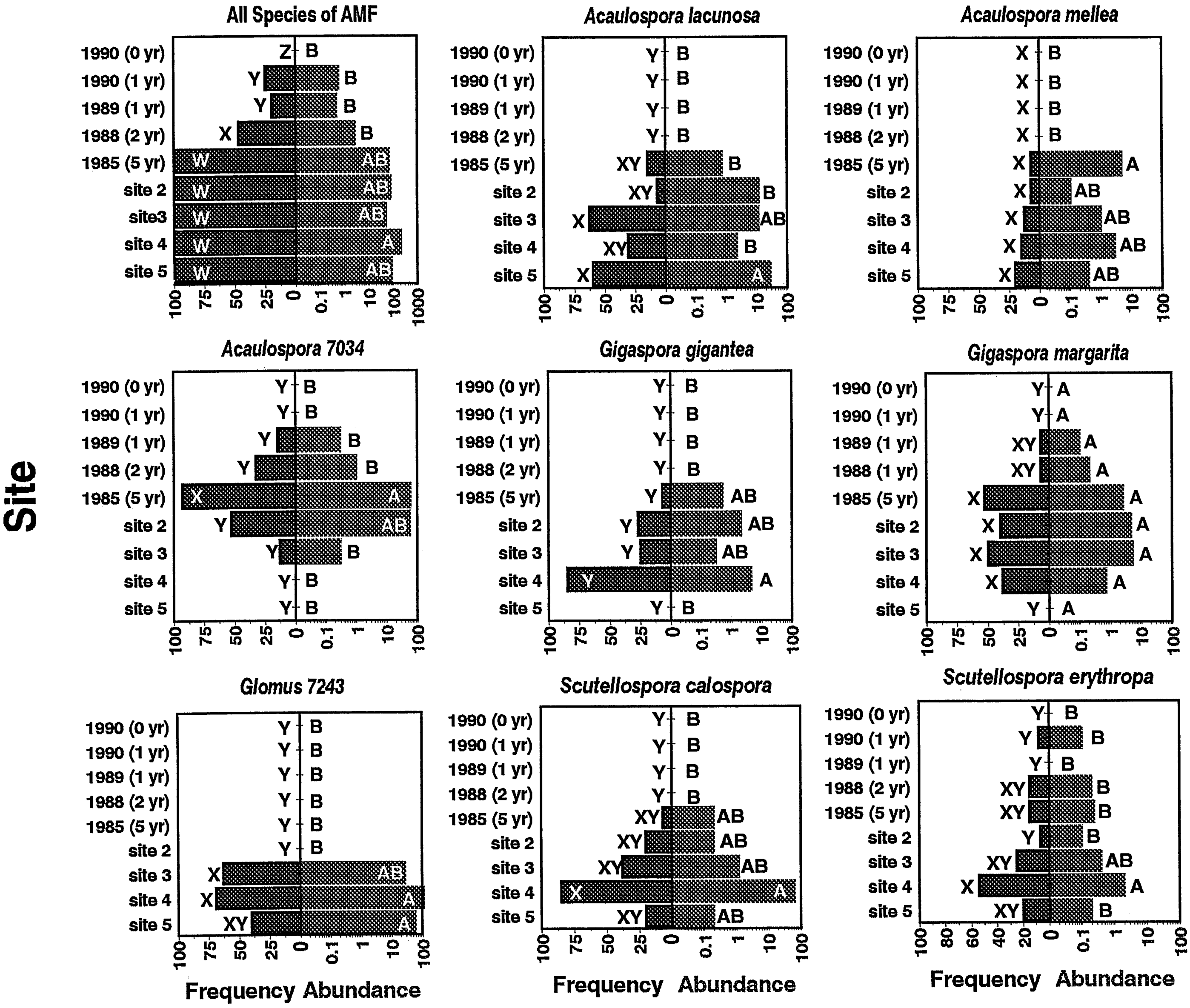


Fig. 8. Plots of frequency of occurrence and average spore abundance (spores/100 mL soil) of the species of AMF present in ≥15% of all samples. Nine additional species were recovered, but their distributions are not illustrated. Frequency and abundance of all 17 species are combined in the first graph.

1987; Gemma and Koske 1988; Gemma, Koske, and Carreiro, 1989; Dalpe, 1989) where it frequently is a co-dominant member of the AMF community.

8. *Gigaspora margarita* Becker & Hall

Spores of *G. margarita* were recovered from 26% of all samples, including the 1-yr-old 1989 planting area but were not significantly more abundant at any particular site (Fig. 8). This was the second most frequently recovered species.

9. *Glomus clarum* Nicol. & Schenck

This species was one of the earliest appearing pioneers, showing up in the 1-yr-old planting (1989), apparently originating in the planting stock (see below). Spores were present in only 6% of the samples and were absent from the 1985 planting as well as areas 3, 4, and 5. *Glomus clarum* also is known from sand dunes of eastern Canada (Dalpe, 1989).

10. *G. microaggregatum* Koske, Gemma & Olexia

Another common inhabitant of coastal dunes of eastern North America and the Great Lakes (Koske, Gemma, and Olexia, 1986; Koske, 1987; Koske and Tews, 1987; Dalpe, 1989), *G. microaggregatum* was recovered only from the more advanced seral stages (sites 3, 4, and 5) in this study, and its abundance never exceeded 2 spores/100 mL. Spores of this species typically form within dead spores of other AMF, and we tended to find them more abundantly in areas of the dunes where the *A. breviligulata* was in decline and organic matter was higher that near the dune crest (personal observation).

11. *Glomus* 7099

Spores of this undescribed species occurred in one sample from site 3 and one from site 4.

Spores globose to subglobose, 60–80 μm diameter, hyaline. Spore wall 2–3 μm thick, laminated. Spores surrounded by a hyaline peridium 10–30 μm thick composed of loosely organized hyaline hyphae. Peridial hyphae 2–5 μm broad, with walls up to 1.0 μm thick. Walls of thickest hyphae roughened.

12. *Glomus* 7243 (Fig. 12)

This was another of the species that was limited to more advanced seral stage, and spores were recovered only from sites 3, 4, and 5 (Fig. 8). In some samples, spores occurred in great abundance (up to 600 spores/100 mL in a sample from site 4).

Spores globose to subglobose, 80–90 (–115) μm diameter, red-brown to orange-brown. Spore wall relatively thick, 8–12 μm thick, laminated. Attachment hypha yellow-brown, 10–12 μm wide, constricted to 4–6 μm at base of spore. The species is very similar to *G. etunicatum* Becker & Gerd. but differs in the smaller size of the spores and the more robust attachment hypha. Spores of *G.* 7243 occurred only in the soils with high organic matter and frequently were found inside dead spores of *Gigaspora* and *Scutellospora* spp.

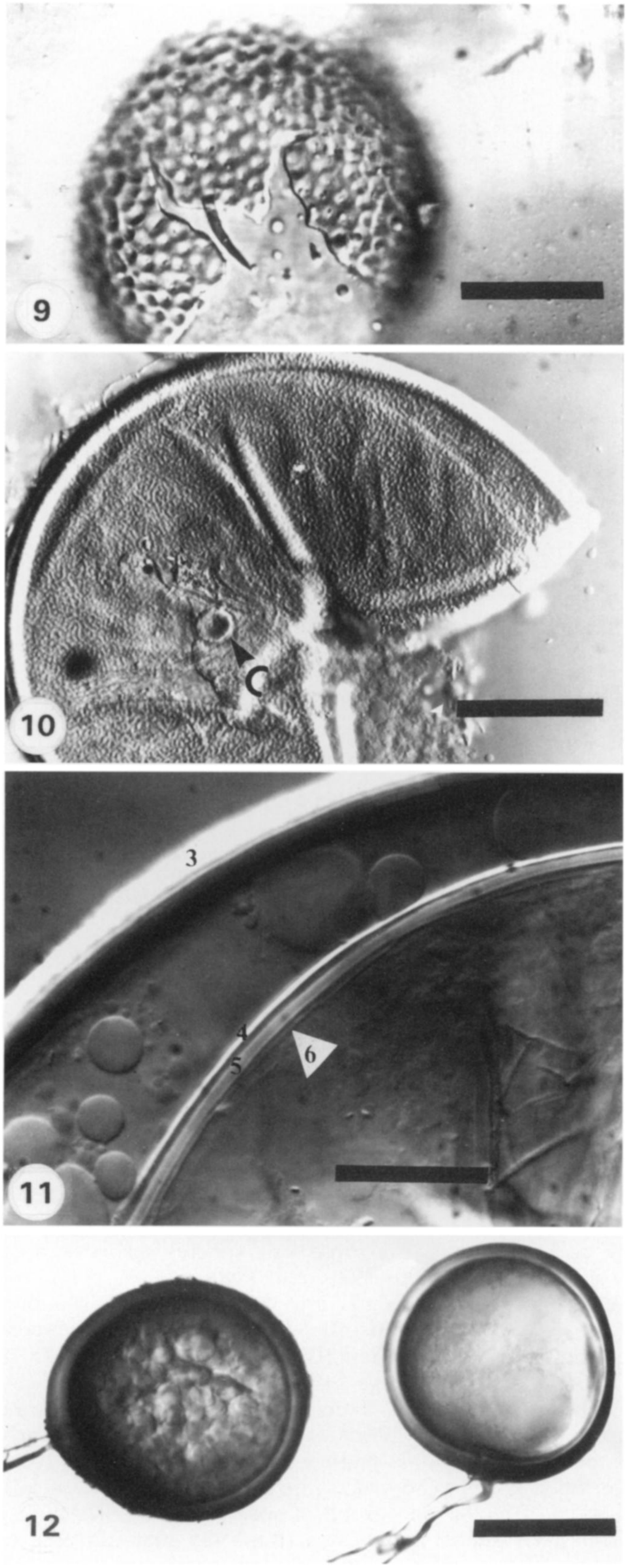
13. *Scutellospora calospora* (Nicol. & Gerd.) Walker & Sanders

Spores of *S. calospora* were present only in the older sites (i.e., the 1985 planting and in all of the natural areas) (Fig. 8). Highest abundance and frequency occurred in site 4. The species was recovered from 19% of all samples.

Scutellospora calospora is a common member of the dune community of the Atlantic coast of North America and the Great Lakes (Koske and Halvorson, 1981; Bergen and Koske, 1984; Koske, 1987; Gemma, Koske, and Carreiro, 1989; Gemma and Koske 1988; Dalpe, 1989).

14. *S. erythropa* (Koske & Walker) Walker & Sanders

Spores of *S. erythropa* occurred in sites ranging from the 1-yr-old planting of 1990 to site 5 (Fig. 8). It seldom was present in abundance, but was a consistent member of most sites. It was found in 16% of all samples. This is another common member of the sand dunes of the Atlantic coast of the U.S.



Figs. 9–12. Spores of unnamed AMF from Province Lands Dunes. **9.** Surface of spore of *Acaulospora* 3106A. Bar = 40 μm. **10.** Surface of spore of *Acaulospora* 7034. Note fine-textured ornamentation and prominent circatrix ("C"). Bar = 60 μm. **11.** Spore of *Acaulospora* 7034. Walls 3-6 are indicated. Walls 1 and 2 are not visible in this photograph. Bar = 30 μm. **12.** Spores of *Glomus* 7243. Note thick laminated wall of spore and stout attachment hypha. Bar = 50 μm.

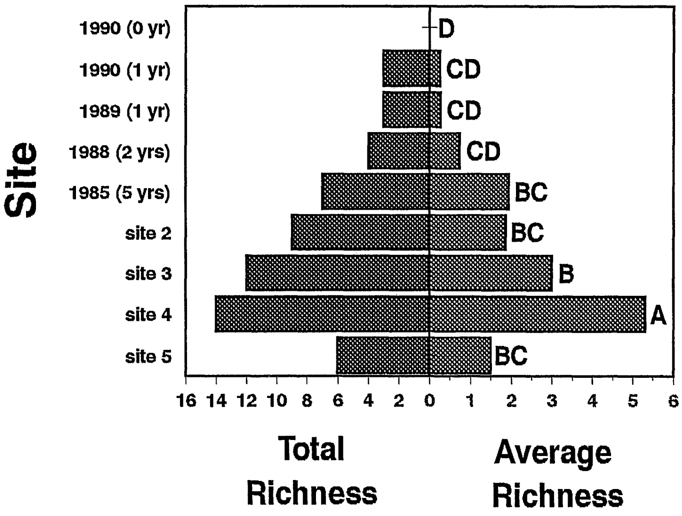


Fig. 13. Species richness in different successional sites. "Total richness" indicates the total number of species recovered from each site, and "average richness" is a measure of the average number of species in each sample. The 1990 planting was sampled before planting and 1 yr later.

15. *S. pellucida* (Nicol. & Schenck) Walker & Sanders

Spores of *S. pellucida* occurred in the 1-yr-old 1990 planting and in sites 3 and 4. It was recovered from 6% of all samples and never in abundance. It is a common species in maritime dunes of the eastern U. S. and Canada.

16. *S. persica* (Koske & Walker) Walker & Sanders

This species was isolated only from sites 3 and 4. It occurred in 7% of all samples. *Scutellospora persica* is another common member of the AMF community in sand dunes of the eastern coast of the U.S.

17. *S. reticulata* (Koske, Miller & Walker) Walker & Sanders

Spores of this species were isolated only from four of the 13 soil samples collected at site 4. Its abundance was low (avg. 0.6 spores/100 mL at this site). *Scutellospora reticulata* is an infrequently recovered species in U.S. dunes (Koske, Miller, and Walker, 1983; Koske, 1987), and its spores seldom occur in abundance. Spores of *S. reticulata* typically are found in dunes of the North Atlantic coast of the U.S. where organic matter is higher than in accreting areas (personal observation).

Increases in the richness and complexity of the AM fungal community accompanied the development and succession in the plant community. Spores were absent prior to planting, but were recovered from areas that had been vegetated for <1 yr (Fig. 8). The species richness (total number of AMF species present in a site) increased with increasing stabilization of the dunes and then declined in the oak/maple forest (Fig. 13). Average richness per sample at different sites showed a similar pattern. Maximum richness occurred in site 4, where spores of 14 species were isolated. In some individual samples from site 4, spores of nine species of AMF were present. Average species richness in site 4 was 5.3, a value significantly higher than values from other sites. Spores of only five species of AMF were isolated from the 1-yr-old sites. In the planted areas (for which the age was known), the average species richness per sample was highly correlated with age of the planting ($r = 0.699$, $P = 0.0001$), as was the percentage of samples that contained spores of AMF ($r = 0.996$, $P = 0.003$) (Fig. 14A).

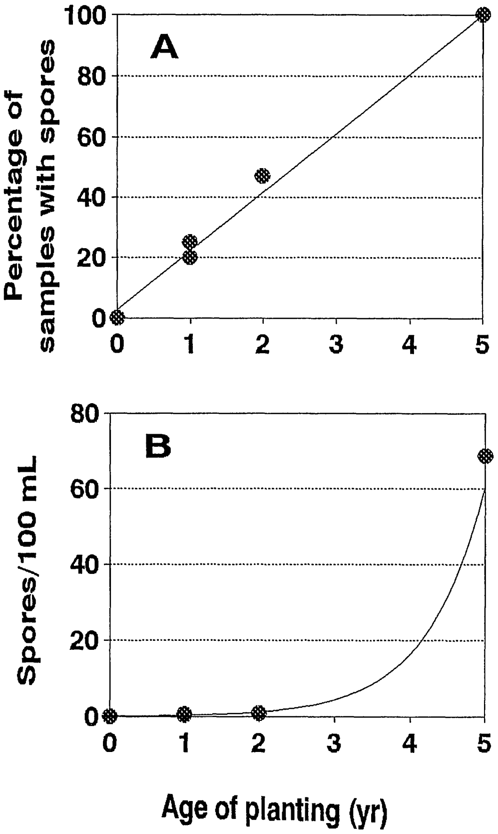


Fig. 14. Changes in the populations of AMF in association with plantings of *Ammophila breviligulata* over a 5-yr-period. The percentage of samples from which spores were recovered (A) showed a significant linear trend over the time period ($r = 0.996$, $P = 0.003$), and spores abundance (B) showed a significant exponential trend ($r = 0.964$, $P = 0.008$).

The abundance of spores of AMF in the different sites (Fig. 8) generally mirrored the species richness data. Youngest sites (1990, 1989, and 1988 plantings) had the fewest spores per 100 mL, and site 4 had the most spores (avg. 208.9 spores/100 mL). In the planted areas, spore abundance was significantly correlated with age ($r = 0.964$, $P = 0.008$) (Fig. 14B).

Based upon when their spores were first recovered from the sites, two groups of AMF were identified. Early invaders (present 1–2 yr after planting) included *A.* 7034, *Gl. clarum, Gi. margarita, S. erythropa, and S. pellucida.* Spores of the second group of species were isolated only from later successional sites (the 1985 planting area or older). This second group included the majority of AMF species, including *A. lacunosa, A. mellea, Gi. gigantea, Gl.* 7243, and *S. calospora. Scutellospora erythropa* was unique in sporulating in all seral stages.

TABLE 2. Mycorrhizae in *Ammophila* roots from different aged stands.

Site and age of planting	Plant type	*N*	Mycorrhizal index	Percentage of samples mycorrhizal
1990 (47 wk)	Mature	9	1.0C[a]	78A
1990 (1.5 yr)	Seedling	10	0.0D	0B
1989 (1 yr)	Mature	5	1.2B	80AB
1988 (2 yr)	Mature	5	1.9A	100A
	Seedling	10	0.0D	0B
1985 (5 yr)	Mature	5	1.8A	100A
Natural area 2 (age unknown)	Mature	5	2.0A	100A

[a] Values in columns followed by the same uppercase letter did not differ significantly.

Mycorrhizal status of plants—

A. breviligulata—Most plants became mycorrhizal in the 1st yr after planting, and all mature plants were mycorrhiza within 2 yr after planting (Table 2). Greatest colonization occurred in the 1985 and 1988 plantings and in site 2 and least in the 1990 area (sampled 47 wk after planting). No mycorrhizae were present in any of the seedlings.

Invading species—The incidence of mycorrhizae in invading species appeared to increase with succession, but an insufficient number of samples was recovered to identify trends in the planted areas (Table 3). The majority of species and specimens in natural areas 3 and 4 were mycorrhizal, and half of the six species from the 1985 planting were mycorrhizal. In the 1988 site, only one species, the nonmycorrhizal *Polygonella articulata,* was found. No invaders were located in the 1989 area, and a single, nonmycorrhizal seedling of *Prunus maritima* with red, puckered leaves was present in the 1.5-yr-old 1990 planting.

Mycorrhizal inoculum potential of soils—No AM were observed in any of the 15 roots systems examined from the MIP assays set up using soil from the 1990 planting area prior to planting, indicating that viable propagules of AMF were not present in the sampling area.

In the planted sites the MIP of dune soils showed a significant logarithmic trend ($\ln[x+1] = -0.308 + 0.526 \times \text{age in yr}$; $r = 0.701$, $P = 0.0006$), increasing with age (Fig. 15A). Greatest root colonization occurred in the samples from site 4. Variation was greater for MIPs from soil collected from youngest planted areas than from the older, more established sites, indicating a very uneven distribution of AMF propagules in the former. For example, root colonization values in the five MIPs from the 1988 planting site were 7, 52, 39, 4, and 5%, while values from site 4 were 33, 32, 30, 33, and 40%. The average MIP from the native areas (26.4%) was significantly higher (*t* test, $P = 0.002$) than the average MIP (8.6%) of the 1985–1990 planting sites.

TABLE 3. Incidence of mycorrhizae in seedlings of plant species invading areas of the Province Lands dunes collected April 1992.[a]

Species	Plantings of *Ammophila*			Natural areas		
	1990 (1.4 yr)[b]	1988 (3.4 yr)	1985 (7 yr)	Area 3	Area 4	All sites
Asteraceae						
Achillea millefolium				0/3[c]		0/3
Artemisia borealis			0/2			0/2
Aster linariifolius				2/4		2/4
Solidago sempervirens			0/2	1/5		1/7
Solidago odora			2/2	2/2		4/4
Solidago nemoralis			1/3			1/3
Myricaceae						
Myrica pensylvanica				0/1		0/1
Poaceae						
Deschampsia flexuosa			3/5	2/3		5/8
Pinaceae						
Pinus rigida					3/3	3/3
Polygonaceae						
Polygonella articulata		0/4	0/1			0/5
Rosaceae						
Prunus maritima	0/1[d]			3/3		3/4
Rosa rugosa				1/1	1/1	2/2
Fagaceae						
Quercus ilicifolia				3/3	3/3	6/6
Totals						
specimens[e]	0/1AB	0/4B	6/15B	14/25AB	7/7A	27/52
species[e]	0/1A	0/1A	3/6A	7/9A	3/3A	9/13

[a] Mycorrhizae, if present, were of the arbuscular type except in *Quercus* and *Pinus,* which had ectomycorrhizae.

[b] Age of planting site at time that samples were collected.

[c] First value indicates how many samples possessed mycorrhizae; second indicates no. of samples examined at a site.

[d] This seedling had red, distorted leaves and appeared stunted.

[e] Values in rows followed by the same uppercase letter did not differ significantly.

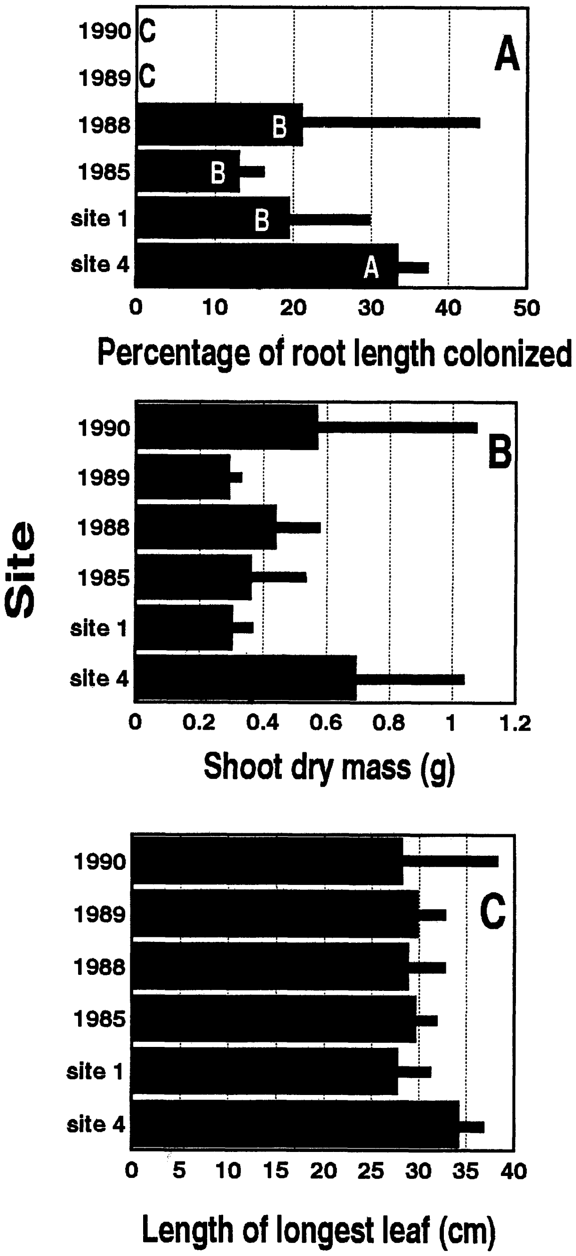


Fig. 15. Measurements of MIP from undisturbed soil cores from sites differing in successional stage. Cores were collected in September 1991. Three parameters were measured: root colonization, shoot dry mass, and length of the longest leaf. Narrow bars represent standard deviation. Note great variation in the data from the youngest planted areas. Bars in 15A sharing a common letter did not differ significantly. No significant differences were detected in the data for Fig. 15 B, C.

Shoot growth and leaf length were not correlated with the age of the site in the planted sites, and no significant differences were noted between growth made in soil cores from natural sites and planted sites. (Fig. 15B, C).

Extent of the hyphal network—Soil disturbance reduced the MIP of the soil cores from sites 1 and 4, indicating that significant hyphal networks had developed only in these sites (Fig. 16). Similar reductions were observed in shoot mass and the length of the longest leaf in disturbed soil cores. Disturbance of cores from the planted areas did not result in significant reduction in root colonization or growth of plants.

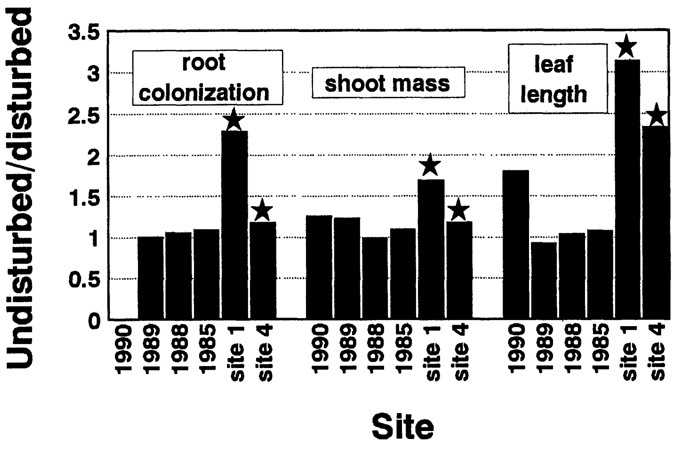


Fig. 16. Effect of destruction of the hyphal network on root colonization and growth of *Zea mays* plants grown in soils from different seral stages of the dunes. *Y*-axis values were calculated by dividing the response of plants grown in undisturbed soil cores by the response in disturbed cores. Values >1.0 are indicative of a hyphal network present in undisturbed cores. Bars marked by a star indicate significant differences between colonization or growth in disturbed and undisturbed samples.

DISCUSSION

AMF are common members of the biota of sand dune systems throughout the world where they appear to play an important role in the development of plant community structure (e.g., Nicolson, 1960; Koske and Polson, 1984; Puppi and Riess, 1987; Dalpe, 1989; Koske and Gemma, 1996). The simultaneous arrival of AMF and plant colonists in primary successional sites, represented by the planted areas in this study, allows the fungi to interact with the developing plant community from the earliest seral stage (Nicolson, 1960; Sylvia and Will, 1988; Gemma and Koske, 1989, 1992; Koske and Gemma, 1990). In the Cape Cod dunes, most measures of mycorrhizal presence (e.g., spore abundance, species richness, root colonization, and MIP) increased from the 1st yr in the planted areas, and these increases generally continued in the later successional sites represented by naturally colonized areas 2–4. These increases in the early- and mid-successional sites and their subsequent decline in the forested site agree with previous studies of sand dunes in Scotland (Nicolson, 1960), the Pacific coast of the U.S. (Rose, 1988), and Mexico (L. Corkidi and E. Rincon, University of Mexico, personal communication).

Most of the species of AMF occurring in the Province Lands have been previously reported from sand dunes of the mid-Atlantic coast of the U.S. (e.g., Koske, 1987). Values for species richness and spore abundance in the natural areas and the 1985 planting site are similar to values reported in earlier surveys of AMF in naturally vegetated dunes on or adjacent to Cape Cod (Bergen and Koske, 1984; Gemma, Koske, and Carreiro, 1989).

The identification of early- and later sporulating species of AMF in the dune sites suggested an apparent succession of AMF. While this may be, the evidence is confounded by the possibility that not all species of AMF present in the roots had sporulated at the time of collection and by uncertainty of the origin of the pioneer AMF. Three of the five species isolated from the youngest sites (*Gl. clarum, S. erythropa,* and *S. pellucida*) apparently arrived on the *A. breviligulata* planting stock (Koske and Gemma, 1992), a common occurrence with rhizomatous dune pioneers (Sylvia and Will, 1988; Gemma and Koske, 1989, 1992; Koske and Gemma, 1990). Because the planting stock was raised in a nursery in sandy agricultural soil (Church's Garden Center, Cape May, NJ), it cannot be concluded that the AMF species present on the stock are necessarily pioneer species, although they are capable of sporulation in pioneer sites.

Further, the primary vegetative succession on the planted sites differs considerably from natural succession occurring in sand dunes that are not managed (Hewett, 1970; Ranwell, 1972). The very rapid and uniform colonization of ≥12 ha of bare sand by a a single pioneer species that results from a planting of beachgrass has no parallel in nature. Thus, the rate of development and the complexity of the AMF community described in this study may differ from that occurring in a natural succession.

The formation of the AMF community is closely linked to changes in the aboveground vegetation. In a variety of natural sites, AMF have been found to play a vital role in plant succession, affecting the success not only of obligately mycotrophic species, but also of those that are facultatively mycotrophic or nonmycotrophic. Essentially, obligately mycotrophic plant species are prevented from colonizing a site if the fungi are absent or if their abundance is below a critical level (Miller, 1979, 1987; Reeves et al., 1979; Janos, 1980; Grime et al., 1987; Read and Birch, 1988; Gemma and Koske, 1990, 1992; Koske and Gemma, 1990; Miller and Jastrow, 1992; Gange, Brown, and Sinclair, 1993). The stunted seedling of *Prunus maritima* (an obligate mycotroph [Koske and Gemma, 1992]) that was found in the 1990 CCNS planting site illustrates this phenomenon. Some nonmycotrophic and facultatively mycotrophic species may be actively excluded when the inoculum potential is greater than a minimal level (Francis and Read, 1994, 1995).

It is the hyphal network of AMF that first exerts these beneficial or antagonistic effects on the seedlings of potential invaders. Studies in pasture soils and mine spoils have shown that the hyphal network is responsible for the preponderance of initial contacts with roots of seedlings (Evans and Miller, 1988; Fairchild and Miller, 1988; Read and Birch, 1988; Jasper, Abbott and Robson, 1989a, b; Gange, Brown, and Sinclair, 1993; Francis and Read, 1994, 1995). A similar role for the hyphal network appears to exist in the succession on the dunes of CCNS. Of the two sites (1 and 4) in the CCNS study area that had significant hyphal networks, widespread invasion was occurring only in the later succesional site (site 4). However, as the failure of plants to invade site 1 shows, the formation of a hyphal network is but one factor that is necessary during succession to permit colonization by nonpioneer, obligately mycotrophic plant species. Other site changes accompanying succession in dunes include improved soil conditions (e.g., soil structure, organic matter, soil nutrients, and a larger population of soil microorganisms) and an ameliorated microclimate (e.g., Oosting, 1954; Olson, 1958; Koske, Sutton, and Sheppard, 1975; Baldwin and Maun, 1983; Rose, 1988), and these improvements contribute significantly to the high plant diversity in site 4. The lack of invading species in site 1 probably results from the high rate of sand accretion in this area. Few plant species can tolerate burial by sand, and rapidly accreting dune sites (such as site 1) typically have impoverished soils with very low organic matter and are dominated by a single species (Ranwell, 1972).

The extent of of hyphal networks estimated from the "undisturbed" cores in the present study may have been underestimated because of possible damage to the network when the cores were collected. However, the difference in root colonization between disturbed and undisturbed samples from site 4 were very similar to reports from other soils (e.g., Read and Birch 1987; Evans and Miller, 1988), suggesting that little disruption occurred in the undisturbed cores. The lack of AM in seedlings of *A. breviligulata* collected from 1- and 2-yr-old planting sites also indicates that no significant network is present in very young sites. All three parameters used to assess the extent of the hyphal network (viz., root colonization, shoot dry mass, and length of longest leaf) produced similar results. The latter two techniques permit a more rapid assessment and warrant further study.

In contrast to the slow rate of invasion by obligately mycotrophic species in highly disturbed secondary successional sites where the AMF population has been destroyed (Miller, 1979, 1987; Reeves et al., 1979; Allen, 1988; Miller and Jastrow, 1992), dune sites are invaded relatively quickly. The difference is explained by the codispersal of AMF with the planting or colonizing stock (Gemma and Koske, 1989, 1992; Koske and Gemma, 1990) and the resultant rapid increase in populations of spores and other inocula of AMF.

In the Cape Cod dunes, some of the earliest invading species of stands of *A. breviligulata* are incapable of forming mycorrhizae (e.g., *Polygonella articulata*) or do not require mycorrhizae but may benefit from the symbiosis if the fungi are present (e.g., *Solidago sempervirens, Deschampsia flexuosa, Achillea millefolium*) (Koske and Gemma, 1992). An important function such facultatively mycotrophic species may be in maintaining and increasing the MIP in the dunes as the *A. breviligulata* stands lose vigor. These species can establish in areas where there is a minimal hyphal network (as seen in the older, planted areas). In time, their roots can support a population of AMF, paving the way for later invasion by plant species that require mycorrhizae. The role of such mycorrhizal "facilitators" in secondary successional sites has been described previously (e.g., Miller, 1979, 1987; Reeves et al., 1979; Janos, 1980; Allen, 1988; Miller and Jastrow, 1992).

The great variation in the MIP data from the planted areas reflected the very uneven (aggregated) distribution of AMF propagules (e.g., Sylvia, 1986; Tews and Koske, 1986; St. John and Koske, 1988) in these young soils. Such a distribution will further limit the number of sites that are amenable to invasion by plants that require AM (Allen, 1991).

Results from this study agree with Miller's (1985) observation that restoration of the aboveground plant community must include restoration of the belowground components of the site. In primary succession in sand dunes AMF fungi are an important component of the complex belowground system.

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