SUCCESSION OF ARBUSCULAR MYCORRHIZAL FUNGI IN A DEFLATION HOLLOW OF THE SŁOWIŃSKI NATIONAL PARK, POLAND

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(Received: February 10, 2000. Accepted: May 11, 2000)

ABSTRACT

In the years 1994-1995, the occurrence of arbuscular mycorrhizal fungi (AMF) and arbuscular mycorrhizae (AM) in eight successional stages of vegetation of a deflation hollow no. 12 of the Łeba Bar, Poland, was investigated. Early successional stages were colonized by members of the families Gramineae and Juncaceae, being gradually replaced by ericaceous plants in the middle and later stages and by trees in the most advanced stage corresponding to the *Empetro nigri-Pinetum* plant association. From the 96 soil samples collected, 21 species in three genera of AMF were recovered. The fungi most frequently found were members of the genus *Acaulospora*. The overall spore abundance, the species richness of AMF and the level of AM colonisation increased from stage 1 to reach a maximum in the middle stages and then gradually declined, being lowest in the forested stage 8. The values of the overall spore abundance and those of the abundances of the most frequently occurring AMF species strongly evidenced functioning in nature of the process of host-dependent differentiation of AMF communities. Of the five most numerous represented AMF species, the early colonizer and quickly diminishing in later successional stages was *Glomus* 107. The mid-late successor was *A. koskei*, and the latest – *Glomus aggregatum*. All measures of AMF presence negatively correlated with the content of organic C in the soil and most of them were negatively correlated with soil N-NO₃ and P concentrations. In contrast, the occurrence of AMF and AM generally was positively correlated with soil pH and the K content of the soil.

KEY WORDS: arbuscular mycorrhizal fungi, arbuscular mycorrhizae, succession, deflation hollow.

INTRODUCTION

Arbuscular mycorrhizal fungi (AMF) are common inhabitants of maritime sand dunes (Bergen and Koske 1984; Błaszowski 1993; Dalpé 1989; Giovannetti and Nicolson 1983; Koske 1975, 1987, 1988; Koske and Gemma 1997; Koske and Halvorson 1981, 1989; Mohankumar et al. 1988; Nicolson 1960; Puppi and Riess 1987; Rose 1988; Stürmer and Bellei 1994; Sylvia 1986) and the number of literature records of their crucial role in the influence of succession of vegetation is accumulating (Allen and Allen 1984, 1988; Janos 1980; Koske and Gemma 1997; Nicolson 1960; Read 1986; Rose 1988). The formation of AMF communities is closely linked to changes in the aboveground vegetation (Dalpé 1989; Koske and Gemma 1997; Koske and Halvorson 1981; Nicolson 1960; Rose 1988). On the other hand, AMF affect the succession of both obligately and facultatively mycorrhizal and nonmycorrhizal species (Allen and Allen 1988; Francis and Read 1994; Janos 1980; Koske and Gemma 1990; Reeves et al. 1979). Results of investigations carried out in various natural sites and those coming from laboratory experiments suggest that the influence of AMF on plants mainly depends on the number of their infective propagules in the soil

and abiotic and biotic environmental conditions (Allen 1991; Al-Ageley and Reeves 1995; Anderson et al. 1984; Gange et al. 1990; Jasper et al. 1989; Koske 1987; Read 1986; Sylvia 1986). The number of infective propagules of an AMF is strongly associated with its host-dependent sporulation rate (Bever et al. 1996; Hetrick and Bloom 1986). A strong influence of AMF may significantly change the quantitative and qualitative composition of vegetation (Allen and Allen 1988; Allen et al. 1989; Francis and Read 1994; Gange et al. 1990) and the performance of plant species relative to each other (Bever et al. 1996). This may result in formation of an environment more favourable to other species of plants and AMF or microorganisms associated with the plant successors (Allen 1991; Allen and Allen 1988; Koske and Gemma 1997; Read 1986).

According to Piotrowska (1991), sand dune areas best expressing the pattern of natural succession of vegetation are deflation hollows. However, no literature data exist on the succession of AMF associated with plants of these areas. Therefore, the aim of the studies reported here was to determine the succession of AMF in a deflation hollow of the Słowiński National Park.

Fig. 1. Diagrammatic representation of the nature of a deflation hollow (see Materials and methods).

MATERIALS AND METHODS

Study site

The investigations were carried out in a deflation hollow no. 12 of dimensions 300 × 150 m. The field is localized in the south-western part of the White Mountains, i.e., in ca. 500-ha range of active, mobile sands placed between the Lebsko lake and the Baltic Sea, in the center of the Łeba Bar (54°38'-54°46'N, 17°03'-17°33'E).

This field is a depressed area that originated when dry sand blew away, exposing a wet substratum saturated with ground water (Fig. 1). The newly exposed zone of wet sand is the youngest part of this field, whereas its western part is the oldest one. The succession of vegetation proceeds towards the west.

The deflation hollow considered comprises eight vegetative successional stages (Piotrowska 1991; Table 1; Figs. 2-9). Stage 1 is characterized by short-lived seedlings of *Ammophila arenaria* and *Corynephorus canescens* in dry years or *Agrostis stolonifera* and *Juncus articulatus* in wet years. Additionally, *Carex arenaria* is always present. On an average, 5 plant species are present here and they cover ca. 3% of the area of this stage. The level of ground water on an average is 20 cm, although it frequently reaches the soil surface in wet years. Stage 2 is permanently colonized by pioneer psammophytes. The most abundant plant species are *A. stolonifera* and *J. articulatus*. The secondary plants are *A. arenaria* and *C. arenaria*. The rapid expansion of pioneer mosses and the

appearance of first seedlings of ericaceous plants, *Betula pendula* and *Pinus sylvestris* distinguish stage 3. The frequency of occurrence of *J. articulatus* is higher than in stage 2, and that of *A. arenaria* and *A. stolonifera* increases. An initial layer of humus is formed. Stage 4 is characterized by the mass appearance of seedlings of ericaceous plants, mainly *Calluna vulgaris*, and the expansion of members of the family Droseraceae. The mean number of plant species is 16. A 1-cm humus layer is formed. The ground water begins a gradual dropping to reach a minimum in stage 8. In stage 5, a young heath is formed by *C. vulgaris* and *Empetrum nigrum*. The psammophytes regress and only the abundance and behaviour of *C. arenaria* and *J. balticus* remain unchanged. The number of species is similar to that of stage 4. Stage 6 is dominated by *C. vulgaris* and comprises few psammophytes. The thickness of the humus layer is ca. 2 cm. Compared with stage 5, the number of species is slightly lower and the percent of cover markedly higher in this stage. Stage 7 is an old heath with frequently occurring *P. sylvestris*. *C. arenaria* and *J. balticus* are markedly inhibited. The thickness of the humus layer is 4-5 cm. Stage 8 corresponds with the *Empetro nigri-Pinetum* plant association. The thickness of the humus layer is 5-6 cm.

Soil physical and chemical properties

The mechanical composition of the soils of all the successional stages corresponded with properties of a loose sand. pH ranged from 5.25 to 3.62 and was highest in stage 2, then gradually decreased, reaching a minimum in stage 6 (Table 1). Concentrations of N-NO₃ and P were lowest in stage 5, and highest in stages 6-8 and 1, respectively. The contents of K were markedly higher in stages 1-5 than in stages 6-8.

Climate

The climatic conditions of a deflation hollow no. 12 correspond with those earlier characterized (Tadych and Błaszowski 2000).

TABLE 1. Vegetational, physical and chemical characteristics of a deflation hollow no. 12 of the Łeba Bar.

Stage	Most important plant species	No. of plant species		Cover (%)	Level of ground water (cm)	pH	org C (%)	N-NO ₃ mgdm ⁻³	P	K
		maximum	Mean							
1	<i>Ammophila arenaria</i> , <i>Agrostis stolonifera</i>	9	5	3	20	4.12	0.20	21.09	27.31	30.16
2	<i>Agrostis stolonifera</i> , <i>Juncus articulatus</i>	18	6	10	20	5.25	0.19	20.03	23.25	35.87
3	<i>Juncus articulatus</i> , <i>J. balticus</i> , <i>Polytrichum commune</i> var. <i>perigoniale</i>	30	11	22	30	4.77	0.18	24.32	19.22	28.73
4	<i>Juncus balticus</i> , <i>Drosera rotundifolia</i> , <i>Polytrichum commune</i> var. <i>perigoniale</i>	44	16	35	32	4.54	0.22	24.13	23.88	26.09
5	<i>Drosera rotundifolia</i> , <i>Calluna vulgaris</i> , <i>Polytrichum commune</i> var. <i>perigoniale</i>	38	16	29	38	4.24	0.19	19.66	15.10	27.19
6	<i>Calluna vulgaris</i> , <i>Empetrum nigrum</i>	29	13	75	42	4.11	0.29	25.12	24.40	8.57
7	<i>Calluna vulgaris</i> , <i>Empetrum nigrum</i> , <i>Pinus sylvestris</i>	23	11	65	42	3.84	0.27	25.49	22.90	9.74
8	<i>Pinus sylvestris</i> , <i>Empetrum nigrum</i> , <i>Pleurozium schreberi</i>	37	16	58	52	3.62	0.40	26.63	20.78	6.59

Figs 2-9. The 1-8 successional stages of vegetation, respectively (see Materials and methods).

Sampling

Roots and rhizosphere soils (ca. 0.8-2 l taken from a depth of 5-30 cm) of six dominating plant species of the eight successional stages were collected in the periods of 29 July-1 August of 1994 and 27-29 July of 1995. These plants were *A. stolonifera*, *A. arenaria*, *C. canescens*, *F. rubra* subsp. *arenaria*, *J. articulatus*, and *J. balticus*. The soils were placed in plastic bags, then air-dried and stored at 4°C for 2-8 months until processed.

Identification of AMF communities

The methods of isolation of the AMF communities, as well as the places of the deposition of vouchers of the species found and the nomenclature and classification used are as those previously characterized (Tadych and Błazkowski 2000). The AMF present in a deflation hollow no. 12 were identified based on both spores recovered from the field-collected samples and those produced in pot trap cultures. One part of each field-collected sample was used to determine the abundance of spores and richness of species produced in the field. The second part of each sample was bulked with the other samples representing the same successional stage of vegetation and mixed with an autoclaved sand of maritime dunes adjacent to Świnoujście (pH 6.7; 12 and 6 mg L⁻¹ P and K, respectively). The mixtures were placed in 0.5-L plastic pots and seeded with *Plantago lanceolata* L. as the host plant. The cultures were grown for 4-14 months in a greenhouse at 18-30°C with supplemental 16-h lighting provided by one SON-T AGRO sodic lamp (Philips Lighting Poland S. A.) placed 1 m above pots. The maximum light intensity was 180 µE m⁻² s⁻¹ at pot level. Plants were watered 2-3 times a week. To observe all morphological structures of spores, they were harvested at ca 30-day intervals.

Mycorrhizal status of plants

Mycorrhizae were determined based on 1-1.5-cm root fragments stained with 0.05% trypan blue (Phillips and Hayman 1970). The percent length of roots with arbuscules, vesicles

and hyphae was calculated based on 50 root fragments examined under a light microscope (McGonigle et al. 1990).

The nomenclature of plants is after Flora Europea (1964-1980).

Soil characteristics

Soil chemical and physical measurements included the determinations of pH (in H₂O), contents of nitrate nitrogen, phosphorous, potassium, (mg/cm³ of soil), organic carbon (%) and bulk density (kg l⁻¹ of soil).

Statistical analysis

Differences in the structure of arbuscular fungal communities were investigated by determining the frequency of occurrence of species, spore abundance and species richness and by calculating dominance coefficients (Górny and Gruma 1981). Frequency of occurrence was calculated by determining the percentage of field-collected samples from which spores of a particular species were recovered. Spore abundance and species richness were defined by determining the number of spores and species, respectively, occurring in 100 g dry soil. Dominance coefficient expresses the proportion of the number of spores of a particular species in all spores of AMF recovered.

Spore count data and root colonization data were transformed prior to two-way ANOVA. Spore counts were transformed by the formula sqrt(x+1), and those of root colonization underwent an arcsin(x) transformation (Green 1979). Means were separated using Tukey's HSD test at P<0.05. Relationships between spore count data, values of mycorrhizal colonization and soil chemical and physical properties were assessed by a Pearson correlation analysis.

RESULTS

AMF community

During the two years of investigation, the occurrence of AMF and mycorrhizae in eight plant successional stages of a deflation hollow no. 12 of the Łeba Bar was determined

TABLE 2. Plant species sampled for the presence of AMF and AM in light successional stages of a deflation hollow no. 12 of the Łeba Bar in 1994 and 1995.

Stage	Plant species	
	1994	1995
1	<i>Agrostis stolonifera</i> , <i>Ammophila arenaria</i> , <i>Juncus articulatus</i>	<i>Agrostis stolonifera</i> , <i>Ammophila arenaria</i> , <i>Juncus articulatus</i>
2	<i>Agrostis stolonifera</i> , <i>Ammophila arenaria</i> , <i>Juncus articulatus</i> , <i>Juncus balticus</i>	<i>Agrostis stolonifera</i> , <i>Ammophila arenaria</i> , <i>Juncus articulatus</i> , <i>Juncus balticus</i>
3	<i>Agrostis stolonifera</i> , <i>Ammophila arenaria</i> , <i>Corynephorus canescens</i> , <i>Juncus articulatus</i> , <i>Juncus balticus</i>	<i>Agrostis stolonifera</i> , <i>Ammophila arenaria</i> , <i>Juncus articulatus</i> , <i>Juncus balticus</i>
4	<i>Ammophila arenaria</i> , <i>Corynephorus canescens</i> , <i>Juncus articulatus</i> , <i>Juncus balticus</i>	<i>Ammophila arenaria</i> , <i>Corynephorus canescens</i> , <i>Juncus articulatus</i> , <i>Juncus balticus</i>
5	<i>Ammophila arenaria</i> , <i>Festuca rubra</i> subsp. <i>arenaria</i> , <i>Juncus balticus</i>	<i>Ammophila arenaria</i> , <i>Corynephorus canescens</i> , <i>Festuca rubra</i> subsp. <i>arenaria</i> , <i>Juncus balticus</i>
6	<i>Juncus balticus</i>	<i>Ammophila arenaria</i> , <i>Festuca rubra</i> subsp. <i>arenaria</i> , <i>Juncus balticus</i>
7	<i>Ammophila arenaria</i> , <i>Corynephorus canescens</i> , <i>Festuca rubra</i> subsp. <i>arenaria</i> , <i>Juncus balticus</i>	<i>Ammophila arenaria</i> , <i>Festuca rubra</i> subsp. <i>arenaria</i> , <i>Juncus balticus</i>
8	<i>Juncus balticus</i>	<i>Festuca rubra</i> subsp. <i>arenaria</i> , <i>Juncus articulatus</i> , <i>Juncus balticus</i>

TABLE 3. Arbuscular mycorrhizal fungi isolated from eight successional stages of vegetation of a deflation hollow no. 12 of the Leba Bar.

Species	Frequency of occurrence	Dominance
	(%)	
<i>Acaulospora koskei</i> Błaszk.	47.92	25.46
<i>Acaulospora lacunosa</i> Morton	8.33	2.32
<i>Acaulospora paulineae</i> Błaszk.	4.17	0.16
<i>Acaulospora polonica</i> Błaszk.	2.08	0.09
<i>Acaulospora rugosa</i> Morton	18.75	7.90
<i>Acaulospora trappei</i> Ames et Linderman	3.13	0.19
<i>Glomus aggregatum</i> Schenck et Smith emend. Koske	22.92	11.67
<i>Glomus constrictum</i> Trappe	2.08	0.03
<i>Glomus corymbiforme</i> Błaszk.	1.04	0.07
<i>Glomus deserticola</i> Trappe, Bloss et Menge	2.08	0.10
<i>Glomus etunicatum</i> Beck. et Gerd.	2.08	0.04
<i>Glomus fasciculatum</i> (Thaxter) Gerd. et Trappe emend. Walker et Koske	1.04	0.01
<i>Glomus laccatum</i> Błaszk.	1.04	0.01
<i>Glomus macrocarpum</i> Tul. et Tul.	1.04	0.01
<i>Glomus pustulatum</i> Koske, Friese, Walker et Dalpé	3.13	0.57
<i>Glomus</i> 107	20.83	33.58
<i>Glomus</i> 111	1.04	0.30
<i>Glomus</i> sp.	7.29	0.35
<i>Scutellospora armeniaca</i> Błaszk.	2.08	0.05
<i>Scutellospora dipurpureus</i> Morton et Koske	33.33	17.06
Unrecognized	1.04	0.02

based on 96 soil and root samples collected from under 6 most frequently occurring plants (Table 2).

Spores of AMF were found in 63 (65.63%) of the soil samples. A total of 9658 spores representing three of the six existing genera of AMF of the order Glomales were recovered. More spores were isolated in 1994 (5101) than in 1995 (4557). The spore populations comprised 17 species and 3 apparently undescribed morphotypes (Table 3). Additionally, trap cultures established based on mixtures of root-soil samples representing all the successional stages considered revealed *Scutellospora persica* (Koske & Walker) Walker & Sanders, whose spores were not isolated from field-collected samples. However, the proportion of spores of this fungus in the population of spores of all the fungi sporulating in the trap culture conditions was very low (2.7%). Therefore, *S. persica* was excluded from further analyses presented in this paper.

The spores most frequently occurring in the soil samples examined were members of the genus *Acaulospora* (present in 55.21% of soils). Relatively frequently isolated spores were those of the genus *Glomus* (50.50%). Spores of the genus *Scutellospora* were found in 33.33% of the soil samples. None of the soil samples contained spores of the genera *Entrophospora*, *Gigaspora* or *Sclerocystis*. The fungi dominating in the spore populations of AMF encountered were members of the genus *Glomus* constituting 46.76% of all the spores. Relatively numerous isolated spores were those of *Acaulospora* (36.12%). The proportion of spores of the genus *Scutellospora* in the communities of AMF recovered was 17.12%.

The species of AMF most frequently found was *A. koskei* (present in 47.92% of the soils examined; Table 3), followed by *S. dipurpureus* (33.33%), *G. aggregatum* (22.92%), *Glomus* 107 (20.83%), and *A. rugosa* (17.71%). The other 15 species and morphotypes occurred in 1.04% to 8.33% of the soils.

The eudominants (with a dominance coefficient at and above 10%) were *Glomus* 107 (33.58%), *A. koskei* (25.46%), *S. dipurpureus* (17.06%), and *G. aggregatum* (11.67%;

Table 3). The dominant was only *A. rugosa* (7.89%), and the subdominant *A. lacunosa* (2.32%).

Spore abundance

A two-way ANOVA indicated that the spore abundance of AMF in the deflation hollow examined differed significantly depending on both the successional stages compared ($df=7.80$; $F=9.95$; $P<0.001$) and the plant species investigated ($df=5.84$; $F=5.01$; P ; Fig. 10).

The spore abundance was higher ($P<0.05$) in stages 2, 4 and 5 than in stages 1 and 6-8. Most ($P<0.05$) spores were found among roots of *A. stolonifera* (av. 270.43), and least in the root zone of *J. balticus* (38.91).

Species richness

The species richness of AMF depended on both the vegetative successional stage ($df=7.80$; $F=18.03$; $P<0.01$) and the plant species compared ($df=5.84$; $F=3.74$; $P<0.001$; Fig. 10).

The highest species richness occurred in stages 3-5, and the lowest in stages 1 and 8. Greatest richness ($P<0.05$) occurred in the root zones of *A. arenaria* (3.24) and *C. canescens* (2.63), and least richness with *J. balticus* (1.31) and *J. articulatus* (1.19).

The abundance of spores of the most frequently occurring species *Acaulospora koskei*

A two-way ANOVA showed significant differences in the spore abundance (number of spores in 100 g dry soil) of *A. koskei* in the vegetative successional stages of the deflation hollow ($df=7.80$; $F=5.84$; $P<0.001$) and the root zones of the plant examined ($df=5.84$; $F=3.50$; $P<0.01$; Fig. 11).

The highest spore abundance of *A. koskei* was in stage 5 (58.25; $P<0.05$), and the lowest in stage 7 (1.50). Stages 1 and 8 did not contain *A. koskei* spores. The plant species associated with the greatest ($P<0.05$) number of spores of *A. koskei* was *C. canescens* (83.38). The other plant species harboured significantly less spores; the spore count data ranged from 5.11 (*J. balticus*) to 37.29 (*A. stolonifera*).

Fig. 10. Spore abundance (no. of spores · 100 g⁻¹ dry soil) and species richness of AMF in eight successional stages of vegetation and in the root zone of 6 plant species. Values followed by the same letter did not differ significantly at $P < 0.05$.

Acaulospora rugosa

The spore abundance of *A. rugosa* differed in the vegetative successional stages of the deflation hollow ($df = 7.80$; $F = 3.51$; $P < 0.01$; Fig. 11). Most ($P < 0.05$) spores occurred in stage 3 (25.92); soils of stages 1 and 6-8 did not contain spores of this fungus. Despite the lack of significance of the influence of the plants investigated on the 1994 and 1995 spore counts, the plant harbouring the highest number of *A. rugosa* spores was *A. stolonifera* (39.00 and 17.25 spores in 100 g dry soil, respectively).

Glomus aggregatum

The spore abundance of *G. aggregatum* depended on the vegetative successional stage of the deflation hollow (S) and the year of study (Y) considered ($df = 7.80$; $F = 4.83$; $P < 0.001$ for SxY; Fig. 11). Additionally, the abundance of *G. aggregatum* differed among roots of the plants compared ($df = 5.84$; $F = 5.12$; $P < 0.001$).

Most ($P < 0.05$) spores of this fungus were recovered from stage 5 in 1995 (92.00). Relatively numerous spore populations of *G. aggregatum* occurred in stages 3-5 in 1994. In the two years, in the other vegetative successional stages, *G. aggregatum* either occurred rarely or not at all. The plants associated with the greatest number ($P < 0.05$) of *G. aggregatum* spores were *C. canescens* (39.63) and *F. rubra* subsp. *arenaria* (38.88); least spores came from under *J. articulatus* (0.24). *Glomus aggregatum* was absent among roots of *A. stolonifera*.

Glomus 107

The spore abundance of *Glomus* 107 was different in the successional stages ($df = 7.80$; $F = 6.23$; $P < 0.001$) and depended on the plant species (P) and the year of study (Y) compared ($df = 5.84$; $F = 2.77$; $P < 0.05$ for PxY; Fig. 11).

It was highest (P) in stage 2 (207.08). In stages 3-6, the spore abundance of *Glomus* 107 gradually declined from

33.58 to 1.83. No spore of this fungus was found in stages 1, 7 and 8. *Glomus* 107 was more abundant in the root zone of *A. stolonifera* (422.33) in 1994 than in that of the other plant species (av. 0.00 to 57.67) in the two years of investigations.

Scutellospora dipurpurea

The spore abundance values regarding *S. dipurpurea* varied depending on both the successional stage ($df = 7.80$; $F = 8.34$; $P < 0.001$) and the plant species ($df = 5.84$; $F = 9.40$; $P < 0.001$) compared (Fig. 11).

Scutellospora dipurpurea occurred most abundantly in stages 4 and 5. Relatively numerous spore populations were revealed in stage 3. The least spore numbers came from stages 2, 6 and 7; stages 1 and 8 were free from spores of this fungus. The plant harbouring most ($P < 0.05$) spores of *S. dipurpurea* was *C. canescens* (76.63 in 100 g dry soil), and *J. articulatus* and *A. stolonifera* were associated with the fewest spores (0.76 and 3.57 spores, respectively).

Arbuscular mycorrhizae

Arbuscules

The percent of root length with arbuscules of the plants investigated differed depending on the vegetative successional stage (S) and the year (Y) of study ($df = 7.80$; $F = 2.37$; $P < 0.05$ for SxY), as well as on the plant species and the year of study ($df = 5.84$; $F = 5.09$; $P < 0.001$ for PxY; Fig. 12).

The highest ($P < 0.05$) root arbuscular colonization values regarded stage 5 in 1995 (3.00% of root length). In 1995, the level of root colonization by arbuscules was higher ($P < 0.05$) in *C. canescens* (3.67%) than in *F. rubra* subsp. *arenaria*, *J. balticus*, *J. articulatus* and all the plants investigated in 1994.

Vesicles

The incidence of root vesicles depended on the successional stage from which a plant came ($df = 7.80$; $F = 5.74$; $P < 0.001$),

Fig. 11. Spore abundance (no. of spores $\cdot 100 \text{ g}^{-1}$ dry soil) of five species of AMF in eight successional stages of vegetation and in the root zone of 6 plant species. Values followed by the same letter did not differ significantly at $P < 0.05$.

Fig. 12. Percent of root length with arbuscules, vesicles and intraradical hyphae in eight successional stages of vegetation and in 6 plant species. Values followed by the same letter did not differ significantly at $P < 0.05$.

as well as the plant species (P) and the year (Y) of study considered ($df = 5.84$; $F = 5.66$; $P < 0.001$ for $P \times Y$; Fig. 12).

The highest ($P < 0.05$) percent of root length with vesicles was found in plants of stage 5 (9.08%), and the lowest in plants of stages 1 (0.33%), 7 and 8 (each 0.08%). The highest ($P < 0.05$) vesicular infections were recorded in *C. canescens* sampled in 1995 (17.67%). The lowest values of this property regarded the 1995 and 1996 *J. articulatus* and *J. balticus* collections, *A. arenaria* and *C. canescens* sampled in 1994, as well as *A. stolonifera* and *F. rubra* subsp. *arenaria* representing the year 1995.

Hyphae

The colonization of roots by hyphae varied in the vegetative successional stages ($df = 7.80$; $F = 4.08$; $P < 0.001$) and the year of study ($df = 1.80$; $F = 22.94$; $P < 0.001$; Fig. 12). The incidence of hyphae in roots also differed when the plant species ($df = 5.84$; $F = 4.09$; $P < 0.01$) and the study year ($df = 1.84$; $F = 16.68$; $P < 0.001$) were compared.

The percent of root length with hyphae was highest ($P < 0.05$) in plants of stages 3-5, and lowest in plants of stage 7. More ($P < 0.05$) roots containing hyphae came from plants of the 1995 collection (10.42%) than from that of 1994

TABLE 4. Succession of AMF in eight successional stages of vegetation of a deflation hollow no. 12 of the Łeba Bar.

Stage	Fungal species	No. of spores	Frequency	Dominance
			%	
1	<i>Glomus</i> sp.	5	16.67	100.00
2	<i>Glomus</i> 107	2485	83.33	81.91
	<i>A. koskei</i>	391	75.00	12.89
	<i>A. rugosa</i>	117	8.33	3.86
	<i>S. dipurpurescens</i>	24	25.00	0.79
	<i>G. pustulatum</i>	16	8.33	0.53
	<i>A. trappei</i>	1	8.33	0.03
	<i>G. deserticola</i>	1	8.33	0.03
	<i>Glomus</i> sp.	1	8.33	0.03
3	<i>A. koskei</i>	516	75.00	29.27
	<i>Glomus</i> 107	403	41.67	22.86
	<i>S. dipurpurescens</i>	400	50.00	22.69
	<i>A. rugosa</i>	311	33.33	17.64
	<i>G. aggregatum</i>	99	25.00	5.62
	<i>A. trappei</i>	17	16.67	0.96
	<i>A. lacunosa</i>	15	8.33	0.85
	<i>A. paulineae</i>	1	8.33	0.06
	<i>G. constrictum</i>	1	8.33	0.06
4	<i>A. koskei</i>	642	83.33	33.37
	<i>S. dipurpurescens</i>	512	83.33	26.61
	<i>A. rugosa</i>	210	66.67	10.91
	<i>G. aggregatum</i>	189	50.00	9.82
	<i>Glomus</i> 107	160	25.00	8.32
	<i>A. lacunosa</i>	144	16.67	7.48
	<i>G. pustulatum</i>	38	8.33	1.98
	<i>A. paulineae</i>	12	8.33	0.62
	<i>A. polonica</i>	9	16.67	0.48
	<i>S. armeniacae</i>	3	8.33	0.16
	<i>G. constrictum</i>	2	8.33	0.10
	<i>G. etunicatum</i>	2	8.33	0.10
	<i>G. laccatum</i>	1	8.33	0.05
5	<i>G. aggregatum</i>	810	83.33	31.64
	<i>S. dipurpurescens</i>	700	83.33	27.34
	<i>A. koskei</i>	699	75.00	27.30
	<i>Glomus</i> 107	173	8.33	6.76
	<i>A. rugosa</i>	124	33.33	4.84
	<i>Glomus</i> 111	29	8.33	1.13
	<i>A. lacunosa</i>	9	16.67	0.35
	<i>G. corymbiforme</i>	7	8.33	0.27
	<i>Glomus</i> sp.	5	8.33	0.20
	<i>A. paulineae</i>	2	16.67	0.08
	<i>G. fasciculatum</i>	1	8.33	0.04
	<i>G. pustulatum</i>	1	8.33	0.04
6	<i>A. koskei</i>	193	75.00	77.20
	<i>Glomus</i> 107	22	8.33	8.80
	<i>A. lacunosa</i>	20	8.33	8.00
	<i>S. dipurpurescens</i>	11	16.67	4.40
	<i>G. aggregatum</i>	4	8.33	1.60
7	<i>A. lacunosa</i>	36	16.67	30.77
	<i>G. aggregatum</i>	25	16.67	21.37
	<i>S. dipurpurescens</i>	23	25.00	19.66
	<i>A. koskei</i>	18	8.33	15.38
	<i>G. deserticola</i>	9	8.33	7.69
	<i>G. etunicatum</i>	2	8.33	1.71
	<i>S. armeniacae</i>	2	8.33	1.71
	<i>G. macrocarpum</i>	1	8.33	0.85
	<i>Glomus</i> sp.	1	8.33	0.85
8	<i>A. rugosa</i>	1	8.33	100.00

(2.63%). The plant of the highest root hyphal colonisations was *A. stolonifera* (15.29%). Least hyphae in roots were found in *J. balticus* (2.17%). The level of root colonisation by hyphae was higher ($P < 0.05$) in 1995 (12.39%) compared with that of 1994 (4.18%).

Succession of fungi

Taking into account the place of the first record of a particular species of AMF and its behaviour in the succeeding vegetative successional stages, the succession of AMF in the deflation hollow considered in this study was as follows. The single inhabitant of stage 1 and the causal agent of mycorrhizal colonisations of seedlings of *Agrostis stolonifera*, *Ammophila arenaria* and *Juncus articulatus* was *Glomus* 107 (Table 4), because most of the few spores of this undescribed *Glomus* sp. recovered were parasitized and seemed to be dead. Because of the low level of these colonisations and the short-lived plants, no sporulation of *Glomus* 107 occurred. However, *Glomus* 107 was the only AMF abundantly sporulating in trap cultures with soils coming from stage 1. Sporulation is dependent on a threshold level of mycorrhizal colonization (Gazey et al. 1992), which apparently was barely achieved by *Glomus* 107 in the greenhouse conditions.

The fungus dominating in the two years and, thereby, being the most important in the establishment of the plant and AMF communities of stage 2 was *Glomus* 107, although its 1994 spore abundance was significantly higher than that of 1995 (Fig. 11). The secondary species were *A. koskei*, *A. rugosa*, *S. dipurpureus*, and *G. pustulatum*. Apart from *Glomus* sp. of stage 1, stage 2 was also inhabited by not numerous spores of *A. trapei* and *G. deserticola*. In stages 3 and 4, the leadership took over *A. koskei*. *Glomus* 107 being second in stage 3 was outstripped by *S. dipurpureus*, *A. rugosa* and *G. aggregatum* in stage 4. Compared with stage 3, *A. lacunosa* highly increased its abundance. Of the other fungi that appeared for the first time in stage 3, the abundance of *A. paulineae* spores increased from 1 to 12, and that of *G. constrictum* remained almost unchanged in stage 4. Four new inhabitants, i.e., *A. paulineae*, *G. etunicatum*, *G. laccatum* and *S. armeniaca*, appeared in this stage; however, they were represented by not numerous spores. Additionally, *G. pustulatum* occurred again, being earlier found only in stage 2. *Acaulospora trapei* disappeared. In stage 5, the leading group of fungi of similar spore abundances was formed by *G. aggregatum*, *S. dipurpureus*, and *A. koskei*. The fungi relatively abundantly sporulating also were *Glomus* 107 and *A. rugosa*. *Glomus* 111, *G. corymbiforme* and *G. fasciculatum* invaded. *Acaulospora polonica*, *S. armeniaca*, *G. constrictum*, *G. etunicatum* and *G. laccatum* disappeared. The soils of stage 6 were dominated by *A. koskei*, although its spore abundance decreased by 72.3% compared with that of stage 5. Of the five species of AMF recovered, least spores came from *G. aggregatum*. Many spores were parasitized. No new inhabitant appeared. *Acaulospora rugosa*, *Glomus* 111, *G. corymbiforme*, *Glomus* sp., *A. paulineae*, *G. fasciculatum* and *G. pustulatum* disappeared. In stage 7, *A. lacunosa* ranked first before *G. aggregatum*, *S. dipurpureus* and *A. koskei*. However, only single spores of this species seemed to be alive. Most spores had perforated structural wall and contained hyphae. Single spores of *G. deserticola*, *G. etunicatum*, *S. armeniaca* and *Glomus* sp. occurred again. Additionally, one spore of *G. macrocarpum* was present. *Glomus* 107 disappeared. Only one dead spore of *A. rugosa* was present in soils of stage 8.

Correlations

Of the 361 comparisons made, 324 were statistically significant. Of them, the most important (Table 5) are the positive correlations between the overall spore abundance, the species richness, the spore abundances of *A. koskei*, *A. rugosa*, *G. aggregatum*, *Glomus* 107, *S. dipurpureus* and the percent root length with arbuscules, vesicles and intramatrical hyphae. Most of the characteristics compared were positively correlated with soil pHs and the content of K in the soil. In contrast, all the characteristics regarding the presence of AMF and AM were negatively correlated with the content of organic C in the soil. The occurrence of AMF and AM was generally negatively associated with the soil contents of N-NO_3 and P. Additionally, the overall spore abundance, the species richness, the abundance of spores of the genus *Glomus* and that of *Glomus* 107 were negatively linked to the level of ground water.

DISCUSSION

Although maritime sand dunes highly favour AMF, the occurrence of their spores in 65.63% of the soil samples examined in this study generally is lower than that reported from other dune sites (Błaszowski 1993a, 1994c; Koske 1975; Koske and Gemma 1990, 1996, 1997; Logan et al. 1989; Mohankumar et al. 1988; Puppi and Riess 1987). This probably resulted from the uniqueness of the above- and underground conditions and the plant community composition of the site investigated. This site is a small deflation hollow with (1) soils of pHs ranging from 3.62–5.25 and containing both nearly pure quartz sand in its initial and middle stages and large amounts of more-humus in the last stages, (2) plants typical of maritime dunes (*A. arenaria*), very wet soils (*J. articulatus*, *J. balticus*), heaths (*C. vulgaris*) and forests (*P. sylvestris*) and (3) very difficult atmospheric conditions due to the strong winds (Ostrowski and Symonides 1994). High amounts of mor-humus and water inhibit the activity of AMF (Al-Ageley and Reeves 1995; Anderson et al. 1984; Read 1986). Members of the family Juncaceae rarely form AMF (Harley and Harley 1987, 1990). Ericaceous plants and *P. sylvestris* mainly associate with fungi producing ericoid and ecto- or ectendomycorrhizae (Harley and Harley 1987, 1990). Strong winds may directly affect AMF by blowing away their spores with the root zone sand and indirectly by burying the host plants or decreasing their activity (Allen 1991; Allen and Allen 1988) and associated other rhizosphere microorganisms interacting with AMF during, e.g., root colonization and infection (Allen and MacMahon 1985; Aziz and Habte 1989; Calvet et al. 1992; Will and Sylvia 1990).

The presence of members of *Acaulospora*, *Glomus*, and *Scutellospora* in the spore populations recovered generally agrees with literature data indicating that these fungi are common inhabitants of sand dune soils (Bergen and Koske 1984; Błaszowski 1993a; Fries and Koske 1991; Gemma et al. 1989; Giovannetti and Nicolson 1983; Koske 1987, 1988; Koske and Gemma 1996; Koske and Halvorson 1981, 1989; Koske and Tews 1987; Nicolson and Johnston 1979; Mohankumar et al. 1988; Dalpé 1989; Sylvia 1986). However, the lack of the fungi of the genus *Gigaspora* in soils of the deflation hollow investigated contradicts most of these reports. *Gigaspora* spp. prefer dry and warm soils with a high amount of sand (Koske 1981; Schenck et al. 1975), thus soils unlike those of the deflation hollow investigated in this study. Fungi of the genera

TABLE 5. Correlation between arbuscular spore, mycorrhiza and soil chemical variables.

OSA	OSA																			
SR	+0.85	SR																		
Aac	+0.87	+0.75	AAc																	
Agl	+0.83	+0.64	+0.54	AGl																
Asc	+0.66	+0.69	+0.56	+0.41	Asc															
Ak	+0.74	+0.60	+0.90	+0.44	+0.41	Ak														
Ar	+0.55	+0.53	+0.57	+0.33	+0.53	+0.27	Ar													
Ga	+0.54	+0.54	+0.40	+0.50	+0.69	+0.28	+0.35	Ga												
G107	+0.55	+0.29	+0.36	+0.75	NS	+0.31	NS	NS	G107											
Sd	+0.66	+0.69	+0.55	+0.42	+0.99	+0.41	+0.53	+0.69	NS	Sd										
A	+0.35	+0.35	+0.32	+0.22	+0.40	+0.27	+0.28	+0.38	NS	+0.40	A									
V	+0.5	+0.48	+0.53	+0.33	+0.52	+0.51	+0.33	+0.37	NS	+0.52	+0.70	V								
H	+0.39	+0.29	+0.42	+0.32	NS	+0.45	NS	NS	+0.29	NS	+0.31	+0.33	H							
PH	0.54	+0.49	+0.46	+0.50	NS	+0.42	+0.25	+0.25	+0.54	NS	NS	NS	+0.30	pH						
OrgC	-0.50	-0.50	-0.40	-0.43	-0.32	-0.35	-0.25	-0.26	-0.28	-0.32	-0.21	-0.28	-0.26	-0.73	orgC					
N-NO3	-0.37	-0.31	NS	-0.45	-0.22	NS	NS	NS	-0.29	-0.22	NS	-0.22	NS	-0.55	+0.75	N-NO3				
P	-0.38	-0.37	-0.27	-0.32	-0.40	-0.21	NS	-0.45	NS	-0.40	-0.22	-0.36	NS	NS	NS	NS	P			
K	+0.47	+0.42	+0.36	+0.46	+0.27	+0.33	+0.24	NS	+0.39	+0.27	NS	+0.23	+0.27	+0.82	+0.82	-0.82	NS	K		
LGW	-0.25	-0.21	NS	-0.28	NS	NS	NS	NS	-0.35	NS	NS	NS	-0.21	-0.75	+0.82	+0.71	-0.37	-0.90	LGW	

Probability level: P<0.01, NS=P>0.05; OSA=overall spore abundance, SR=species richness, AAc, Agl, ASc=abundances of *Acaulospora*, *Glomus* and *Scutellospora* spp., respectively, Ak=*A. koskei*, Ar=*A. rugosa*, Ga=*G. aggregatum*, G107=*Glomus* 107, Sd=*S. dipurpurens*, A, V, H=percent of root length with arbuscules, vesicles and hyphae, respectively, LGW=level of ground water.

Entrophospora and *Sclerocystis* rarely occur in dunes (Błaszkowski and Tadych pers. observ.; Koske and Gemma 1997).

The dominance of fungi of the genera *Acaulospora* and *Glomus* in the populations of fungi found in this study supports the findings of Haas and Menge (1990), Klironomos et al. (1993) and Porter et al. (1987) that *Acaulospora* spp. prefer acid soils, Anderson et al. (1984), Haas and Menge (1990), Grey (1991) and Porter et al. (1987) that members of the genus *Glomus* are adapted to a wide range of host plants and soil conditions and Daniels and Trappe (1980) that the optimum temperature for *Glomus* spp. is 14-22°C, i.e., a temperature range typical of SNP (Ostrowski and Symonides 1994).

Except for *A. trappei* and *Glomus* 107, the other species of AMF recovered from a deflation hollow no. 12 have been previously reported from other dune sites of both Poland and the world (Tadych and Błaskowski 2000). *Glomus* 107 seems to be an endemic fungus of SNP, because over 1200 other soil samples collected in ca. 170 other sites of Poland did not contain spores of this fungus.

In the deflation hollow examined, the parameters of mycorrhizal presence increased from stage 1 to reach the highest values in the middle stages and then gradually declined, being lowest in the last stage 8. A similar pattern of AMF and AM distributions were found in dunes of Scotland (Nicolson 1960), the Pacific coast of the U.S.A. (Rose 1988), Mexico (Corkidi and Rincón 1997) and the Province Lands Area of Cape Cod National Seashore, Massachusetts (Koske and Gemma 1997). However, none of these sites was a deflation hollow with its distinctive physical and chemical soil properties and the unique plant communities. Rose (1988) found no AMF spores in the hollows distributed along a transect of the Lamphere-Christensen sand dunes in Northern California.

The low presence of AMF in stage 1 probably mainly resulted from the high instability of its soil and the high level of ground water, frequently reaching the soil surface (Piotrowska 1991). The vegetation of this stage consisted of seedlings of *A. stolonifera*, *A. arenaria* and *J. articulatus* harbouring low levels of mycorrhizal colonisations. However, these plants are short-lived due to their damage by transported sand

grains (Piotrowska 1991). AMF are known to increase the vitality of plants by increasing their resistance to abiotic and biotic stresses (Allen 1991; Habte et al. 1988; Hayman 1983; Moorman and Reeves 1979) and their mycorrhizae are considered to be a main source of inoculum for new host plants (Read et al. 1977). Thus, the presence of mycorrhizae in roots of the seedlings suggests that these plants played an important role in maintaining and increasing colonisation propagules of AMF and creating more favourable conditions for the plants of this and the next stage by, e.g., retarding wind and transported sand, as Allen and Allen (1988) suggested.

The reason for the gradual increase of the presence of AMF and AM in stages 2-4(-5) probably were increases in the number of host plants of these fungi (Table 1) and the content of organic matter in the soil, as well as the decreasing level of ground water. Spore abundance and species richness of AMF are usually higher when plant cover and species diversity of vegetation are greater (Anderson et al. 1984; Koske and Gemma 1997; Koske and Halvorson 1981). In Anderson et al. (1983) and Dickman et al. (1984) investigations, soil moisture was the dominant factor associated with spore population density of AMF; more spores occurred in drier soils. According to Piotrowska (1991), the major factor influencing the quantitative and qualitative composition of plant communities of the deflation hollows of the Łeba Bar is the level of ground water. A moderate increase of organic matter in the soil has been shown to increase the abundance and activity of both AMF (Hepper and Warner 1983) and other soil microflora beneficially interacting with these fungi (Calvet et al. 1992).

The culmination of most of the measures of AMF presence in stage 5 harbouring a great number of plants in the soil of the lowest contents of N-NO₃ and P (Table 1) complements the finding of Fitter (1977) that mycorrhizal activity increases under competitive conditions.

The sharp declining of the occurrence of AMF in the next vegetative successional stages was probably mainly caused by the increasing content of mor-humus in the soil (Table 1; Piotrowska 1991) and the lowering soil pH, earlier found to inhibit both AMF and their host plants (Read 1986). Addition-

ally, the high amount of parasitized spores isolated from soils of these stages indicate a high activity of antagonistic and parasitic microflora associated with the loss of vitality of these fungi. Lee and Koske (1994) found many soil microorganisms significantly reducing the inoculum potential of AMF.

The statistical analysis of the spore counts of all and the most frequently recovered species of AMF associated with 6 plant species of the deflation hollow provided strong evidence of functioning in nature of the process of host-dependent differentiation of AMF communities. For example, irrespective of the year of study, the overall sporulation of these fungi was significantly highest among roots of *A. stolonifera*, and greatest AMF species richness was associated with *A. arenaria*, *Acaulospora koskei*, *G. aggregatum* and *S. dipurpureus* sporulated most abundantly in association with *C. canescens*, and *A. rugosa* with *A. stolonifera*. Although such host-dependence has earlier been found in laboratory microcosm experiments, it has operated weakly in the field, probably due to the too-close placement of plants of the meadow considered (Bever et al. 1996). Vegetation of meadows usually is much more diverse and dense than that sampled in this study. The strong predominance of the *A. stolonifera*-*Glomus* 107 association found in 1994 may have resulted from collection of a highly aggregated spore population of this fungus or seasonality of its sporulation. Clumped spatial distribution of AMF and seasonal dependence of their sporulation have been frequently observed (Friese and Koske 1991; Gemma et al. 1989; Hetrick et al. 1984; St. John and Koske 1988).

The pattern of succession of AMF in the deflation hollow considered most corresponds with the tolerant model defined by Connell and Slatyer (1977). This model assumes that species are replaced by other ones better tolerating limiting factors and the succession takes place due to either the invasion of late species or diminishing the early colonizers. Of the most frequently recovered AMF in this study, the early colonizer and quickly diminishing fungus in later successional stages was *Glomus* 107. The mid-late successor was *A. koskei*, and the latest – *G. aggregatum*, which became dominant in stage 5. Although *A. koskei* again predominated in stage 6, many of its spores and those of the other accompanying AMF were parasitized. This stage was absolutely dominated by *C. vulgaris* (Piotrowska 1991), and hence the successors certainly became fungi forming ericoid mycorrhizae, then being gradually replaced by ecto- and ectendomycorrhizal fungi, including *Complexipes moniliformis* and *Endogone* spp. recovered in this study, associated with the predominating *P. sylvestris* in stages 7 and 8.

The transitional stage for *A. koskei*, *G. aggregatum* and *S. dipurpureus* was stage 5, whereas the decline of *A. rugosa* began in stage 4. Stage 4 is characterized by the mass appearance of *C. vulgaris* and the increased significance of *J. balticus* (Piotrowska 1991), which probably did not favour *A. rugosa*, although these plants are facultative hosts of AMF (Harley and Harley 1987, 1990). Stage 5 is a phase of expansion of *C. vulgaris* and only *C. arenaria* and *J. balticus* are stable and relatively numerous plants. Thus, the reason for the highest overall spore abundance and that regarding *A. koskei*, *G. aggregatum* and *S. dipurpureus* likely was the severe competition of the more mycorrhizal-dependent *C. arenaria* and *J. balticus* with the highly invasive *C. vulgaris* which prefers ericoid mycorrhizal fungi. AMF are known to increase the vitality and competitiveness of their host plants (Fitter 1977; Hetrick et al. 1989; Janos 1980).

Comparing the degree of the decline of the spore abundances of the five leading species of AMF in the stage pro-

ceeding the stage of their maximal abundance and the presence of these fungi in the eight successional stages, the fungus with the highest competitive efficiency was *A. koskei* (a decline of 72.4%, present in 6 stages), followed by *S. dipurpureus* (98.4%, 6 stages). The highest sensitivity to the changing abio- and biotic conditions showed *A. rugosa* (41.0%, 4 stages) and *G. aggregatum* (99.5%, 5 stages).

Changes in the level of AM colonisations generally mirrored those of the occurrence of spores of these fungi in the deflation hollow considered. These colonisations peaked in the middle stages and were lowest in the early and the most advanced stages. This agrees with the distribution of AM in other dune sites (Koske and Gemma 1997; Koske and Halvorson 1981; Nicolson 1960; Rose 1988).

The high number of statistically proved correlations indicate that AMF, plants and abiotic factors of this relatively small deflation hollow strongly collaborated with each other. However, the links found between the overall spore abundance and the components of AM, as well as between the two characteristics and the spore counts of *A. koskei*, *A. rugosa*, *G. aggregatum*, *Glomus* 107, and *S. dipurpureus* evidence the leading role of these five species in the succession of both AMF and plants of the deflation hollow. This also indicates that the spore populations of these fungal species were uniformly distributed in the particular successional stages, which has been rarely found in other dune sites (Friese and Koske 1991; Koske and Gemma 1997; Koske and Halvorson 1981; St. John and Koske 1983).

ACKNOWLEDGMENTS

This study was supported in part by The State Committee of Scientific Research, grant no. 6.P04C.015.13.

LITERATURE CITED

- AL-AGELY A.K., REEVES F.B. 1995. Inland sand dune mycorrhizae: effects of soil depth, moisture, and pH on colonization of *Oryzopsis hymenoides*. *Mycologia* 87: 54-60.
- ALLEN E.B., ALLEN M.F. 1984. Competition between plants of different successional stages: mycorrhizae as regulators. *Can. J. Bot.* 62: 2625-2629.
- ALLEN E.B., ALLEN M.F. 1988. Facilitation of succession by the non mycotrophic colonizer *Salsola kali* (Chenopodiaceae) on a harsh site: effects of mycorrhizal fungi. *Am. J. Bot.* 75: 257-266.
- ALLEN M.F. 1991. The ecology of mycorrhizae. Cambridge University Press.
- ALLEN M.F., ALLEN E.B., FRIESE C.F. 1989. Responses of the non-mycotrophic plant *Salsola kali* to invasion by vesicular-arbuscular mycorrhizal fungi. *New Phytol.* 111: 45-49.
- ALLEN M.F., MACMAHON J.A. 1985. Impact of disturbance on cold desert fungi: comparative microscale dispersion patterns. *Pedobiol.* 28: 215-224.
- ANDERSON R.C., LIBERTA A.E., DICKMAN L.A. 1984. Interaction of vascular plants and vesicular-arbuscular mycorrhizal fungi across a soil moisture-nutrient gradient. *Oecologia* 64: 111-117.
- AZIZ T., HABTE M. 1989. The sensitivity of three vesicular-arbuscular mycorrhizal species to stimulated erosion. *J. Plant Nutrition* 12: 859-869.
- BERGEN M., KOSKE R.E. 1984. Vesicular-arbuscular mycorrhizal fungi from sand dunes of Cape Cod, Massachusetts. *Trans. Br. Mycol. Soc.* 83: 157-158.
- BEVER J.D., MORTON J.B., ANTONOVICS J., SCHULTZ P.A. 1996. Host-dependent sporulation and species diversity of arbuscular mycorrhizal fungi in a mown grassland. *J. Ecol.* 84: 71-82.

- BLASZKOWSKI J. 1993. The occurrence of arbuscular fungi and mycorrhizae (Glomales) in plant communities of maritime dunes and shores of Poland. *Bull. Pol. Ac. Sci. Biol.* 41: 377-392.
- BLASZKOWSKI J. 1994. Arbuscular fungi and mycorrhizae (Glomales) of the Hel Peninsula, Poland. *Mycorrhiza* 5: 71-88.
- CALVET C., BAREA M., PERA J. 1992. In vitro interactions between the vesicular-arbuscular mycorrhizal fungus *Glomus mosseae* and some saprophytic fungi isolated from organic substrates. *Soil. Biol. Biochem.* 24: 775-780.
- CONNELL J.H., SLATYER R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Amer. Naturalist* 111: 1119-1144.
- CORKIDI L., RINCÓN E. 1997. Arbuscular mycorrhizae in a tropical sand dune ecosystem on the Gulf of Mexico. I. Mycorrhizal status and inoculum potential along a successional gradient. *Mycorrhiza* 7: 9-15.
- DALPÉ Y. 1989. Inventaire et repartition de la flore endomycorhizienne de dunes et de rivages maritimes du Québec, du Nouveau-Brunswick et de la Nouvelle-Ecosse. *Naturaliste Can. (Rev. Ecol. Syst.)* 116: 219-236.
- DANIELS B.A., TRAPPE J.M. 1980. Factors affecting spore germination of the vesicular-arbuscular mycorrhizal fungus, *Glomus epigaeus*. *Mycologia* 72: 457-471.
- DICKMAN L.A., LIBERTA A.E., ANDERSON R.C. 1984. Ecological interaction of little bluestem and vesicular-arbuscular mycorrhizal fungi. *Can. J. Bot.* 62: 2272-2277.
- FITTER A.H. 1977. Influence of mycorrhizal infection on competition for phosphorus and potassium by two grasses. *New Phytol.* 79: 119-125.
- FLORA EUROPEA (1964-1980) Vol. 1-5. Cambridge University Press, Cambridge.
- FRANCIS R., READ D.J. 1994. The contribution of mycorrhizal fungi to the determination of plant community structure. *Plant Soil* 159: 11-25.
- FRIESE C.F., KOSKE R.E. 1991. The spatial dispersion of spores of vesicular-arbuscular mycorrhizal fungi in a sand dune: microscale patterns associated with the root architecture of American beachgrass. *Mycol. Res.* 95: 952-957.
- GANGE A.C., BROWN V.K., FARMER L.M. 1990. A test of mycorrhizal benefit in an early successional plant community. *New Phytol.* 115: 85-91.
- GAZEY C., ABBOTT L.K., ROBSON A.D. 1992. The rate of development of mycorrhizas affects the onset of sporulation and production of external hyphae by two species of *Acaulospora*. *Mycol. Res.* 96: 643-650.
- GEMMA J.N., KOSKE R.E., CARREIRO M. 1989. Seasonal dynamics of selected species of VA mycorrhizal fungi in a sand dune. *Mycol. Res.* 92: 317-321.
- GERDEMANN J.W., NICOLSON T.H. 1963. Spores of mycorrhizal *Endogone* species extracted from soil by wet sieving and decanting. *Trans. Br. Mycol. Soc.* 46: 235-244.
- GIOVANNETTI M., NICOLSON T.H. 1983. Vesicular-arbuscular mycorrhizas in Italian sand dunes. *Trans. Br. Mycol. Soc.* 80: 552-557.
- GÓRNY M., GRUMA L. 1981. Metody stosowane w zoologii gleby. PWN, Warszawa.
- GREEN R.H. 1979. Sampling design and statistical methods for environmental biologists. John Wiley & Sons, New York.
- GREY W.E. 1991. Influence of temperature on colonization of spring barleys by vesicular-arbuscular mycorrhizal fungi. *Plant and Soil* 137: 181-190.
- HAAS J.H., MENGE J.A. 1990. VA-mycorrhizal fungi and soil characteristics in avocado (*Persea americana* Mill.) orchard soils. *Plant and Soil* 127: 207-212.
- HABTE M., FOX R.L., AZIZ T., EL-SWAIFY S.A. 1988. Interaction of vesicular-arbuscular mycorrhizal fungi with erosion in an Oxisol. *Appl. Environ. Microbiol.* 54: 945-950.
- HARLEY J.L., HARLEY E.L. 1987. A check-list of mycorrhiza in the British flora. *New Phytol.* 105: 1-102.
- HARLEY J.L., HARLEY E.L. 1990. A check-list of mycorrhiza in the British flora – second addenda and errata. *New Phytol.* 115: 699-711.
- HAYMAN D.S. 1983. The physiology of vesicular-arbuscular endomycorrhizal symbiosis. *Can. J. Bot.* 61: 944-963.
- HEPPER C., WARNER A. 1983. Role of organic matter in growth of a vesicular-arbuscular mycorrhizal fungus in soil. *Trans. Br. Mycol. Soc.* 81: 155-156.
- HETRICK B.A.D., BLOOM J. 1986. The influence of host plant on production and colonization ability of vesicular-arbuscular mycorrhizal spores. *Mycologia* 78: 32-36.
- HETRICK B.A.D., WILSON G.W.T., HARNETT D.C. 1989. Relationship between mycorrhizal dependence and competitive ability of two tallgrass prairie grasses. *Can. J. Bot.* 67: 2608-2615.
- JANOS D.P. 1980. Mycorrhizae influence tropical succession. *Biotropica* 12: 56-64.
- JASPER D.A., ABBOTT L.K., ROBSON A.D. 1989. Soil disturbance reduces the infectivity of external hyphae of VA mycorrhizal fungi. *New Phytol.* 112: 93-99.
- KLIRONOMOS J.N., MOUTOGLIS P., KENDRICK B., WIDDEN P. 1993. A comparison of spatial heterogeneity of vesicular-arbuscular mycorrhizal fungi in two maple-forest soils. *Can. J. Bot.* 71: 1472-1480.
- KOSKE R.E. 1975. *Endogone* spores in Australian sand dunes. *Can. J. Bot.* 53: 668-672.
- KOSKE R.E. 1981. A preliminary study of interactions between species of vesicular-arbuscular mycorrhizal fungi in a sand dune. *Trans. Br. Mycol. Soc.* 76: 411-416.
- KOSKE R.E. 1987. Distribution of VA mycorrhizal fungi along a latitudinal temperature gradient. *Mycologia* 79: 55-68.
- KOSKE R.E. 1988. Vesicular-arbuscular mycorrhizae of some Hawaiian dune plants. *Pacific Sci.* 42: 217-229.
- KOSKE R.E., GEMMA J.N. 1990. VA mycorrhizae in vegetation of the Hawaii: evidence for codispersal of plants and fungi. *Am. J. Bot.* 77: 466-474.
- KOSKE R.E., GEMMA J.N. 1997. Mycorrhizae and succession in plantings of beachgrass in sand dunes. *Amer. J. Bot.* 84: 118-130.
- KOSKE R.E., GEMMA J.N. 1996. Arbuscular mycorrhizal fungi in Hawaiian sand dunes: Island of Kauai. *Pacific Sci.* 50: 36-45.
- KOSKE R.E., HALVORSON W.L. 1981. Ecological studies of vesicular-arbuscular mycorrhizae in a barrier sand dune. *Can. J. Bot.* 59: 1413-1422.
- KOSKE R.E., HALVORSON W.L. 1989. Mycorrhizal associations of selected plant species from San Miguel Island, Channel Islands National Park, California. *Pacific Sci.* 43: 32-40.
- KOSKE R.E., TEWS L.L. 1987. Vesicular-arbuscular mycorrhizal fungi of Wisconsin sandy soils. *Mycologia* 79: 901-905.
- LEE P.-J., KOSKE R.E. 1994. *Gigaspora gigantea*: parasitism of spores by fungi and actinomycetes. *Mycol. Res.* 98: 458-466.
- LOGAN V.S., CLARKE P.J., ALLAWAY W.G. 1989. Mycorrhizas and root attributes of plants of coastal sand-dunes of New South Wales. *Aust. J. Plant Physiol.* 16: 141-146.
- MCGONIGLE T.P., MILLER M.H., EVANS D.G., FAIRCHILD C.L., SWAN J.A. 1990. A new method which gives an objective measure of colonization of roots by vesicular-arbuscular mycorrhizal fungi. *New Phytol.* 115: 495-501.
- MOHANKUMAR V., RAGUPATHY S., NIRMALA C.B., MOHADEVAN A. 1988. Distribution of vesicular-arbuscular mycorrhizae (VAM) in the sandy beach soils of Madras coast. *Cur. Sci.* 57: 367-368.
- MOORMAN T., REEVES F.B. 1979. The role of endomycorrhizae in revegetation practices in the semi-arid west. II. A bioassay to determine the effect of land disturbance on endomycorrhizal populations. *Amer. J. Bot.* 66: 14-18.
- MORTON J.B., BENNY G.L. 1990. Revised classification of arbuscular mycorrhizal fungi (Zygomycetes): a new order, Glomales, two new suborders, Glomineae and Gigasporineae, and two new families, Acaulosporaceae and Gigasporaceae, with an emendation of Glomaceae. *Mycotaxon* 37: 471-491.

- NICOLSON T.H. 1960. Mycorrhiza in Gramineae. II. Development in different habits, particularly sand dunes. Trans. Br. Mycol. Soc. 43: 132-145.
- NICOLSON T.H., JOHNSTON C. 1979. Mycorrhiza in Gramineae. III. *Glomus fasciculatum* as the endophyte of pioneer grasses in maritime sand dunes. Trans. Br. Mycol. Soc. 72: 261-268.
- OSTROWSKI M., SYMONIDES E. 1994. Słowiński National Park. SCI & ART., Warsaw.
- PHILLIPS J.M., HAYMAN D.S. 1970. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. Trans. Br. Mycol. Soc. 55: 158-161.
- PIOTROWSKA H. 1991. The development of the vegetation in the active deflation hollows of the Łeba Bar (N Poland). Fragm. Flor. et Geobot. 35: 173-215.
- PORTER W.M., ROBSON A.D., ABBOTT L.K. 1987. Field survey of the distribution of vesicular-arbuscular mycorrhizal fungi in relation to soil pH. J. Appl. Ecol. 24: 659-662.
- PUPPI G., RIESS S. 1987. Role and ecology of VA mycorrhizae in sand dunes. Angew. Botanik 61: 115-126.
- READ D.J. 1986. Non-nutritional effects of mycorrhizal infection. In: Physiological and genetical aspects of mycorrhizae. Gianinazzi-Pearson V., Gianinazzi S. (eds.). CNRS-INRA, Dijon, pp. 169-176.
- READ D.J., KIANMEHR H., MALIBARI A. 1977. The biology of mycorrhiza in *Helianthemum* Mill. New Phytol. 78: 305-312.
- REEVES F.B., WAGNER D., MOORMAN T., KIEL J. 1979. Role of endomycorrhizae in revegetation practices in the semi-arid West. 1. A comparison of incidence of mycorrhizae in severely disturbed vs. natural environments. Amer. J. Bot. 66: 1-13.
- ROSE S. 1988. Above and belowground community development in a maritime sand dune ecosystem. Plant and Soil 109: 215-226.
- SCHENCK N.C., PÉREZ Y. 1990. Manual for the identification of VA mycorrhizal fungi. Plant Pathology Department, Institute of Food and Agricultural Sciences, University of Florida, INVAM, Gainesville.
- SCHENCK N.C., GRAHAM S.O., GREEN N.E. 1975. Temperature and light effects on contamination and spore germination of vesicular-arbuscular mycorrhizal fungi. Mycologia 57: 1189-1194.
- ST JOHN T.V., KOSKE R.E. 1988. Statistical treatment of endogoneous spore counts. Trans. Br. Mycol. Soc. 91: 117-121.
- STÜRMER S.L., BELLEI M.M. 1994. Composition and seasonal variation of spore populations of arbuscular mycorrhizal fungi in dune soils on the island of Santa Catarina, Brazil. Can. J. Bot. 72: 359-363.
- SYLVIA D.M. 1986. Spatial and temporal distribution of vesicular-arbuscular mycorrhizal fungi associated with *Uniola paniculata* in Florida foredunes. Mycologia 78: 728-734.
- TADYCH M., BŁASZKOWSKI J. 2000. Arbuscular fungi and mycorrhizae (Glomales, Zygomycota) of the Słowiński National Park, Poland. Mycotaxon 74: 463-482.
- WALKER C., TRAPPE J.M. 1993. Names and epithets in the Glomales and Endogonales. Mycol. Res. 97: 339-344.
- WILL M.E., SYLVIA D.M. 1990. Interaction of rhizosphere bacteria, fertilizer, and vesicular-arbuscular mycorrhizal fungi with sea oats. Appl. Environm. Microbiol. 56: 2073-2079.

SUKCESJA ARBUSKULARNYCH GRZYBÓW MIKORYZOWYCH W POLU DEFLACYJNYM SŁOWIŃSKIEGO PARKU NARODOWEGO

STRESZCZENIE

W latach 1994-1995 badano występowanie arbuskularnych grzybów mikoryzowych (AGM) i mikoryz arbuskularnych (AM) w ośmiu strefach sukcesji roślinności 12. pola deflacyjnego Mierzei Łebskiej w Słowińskim Parku Narodowym. Wczesne stadia sukcesji zasiedlane były przez przedstawicieli rodzin Gramineae i Juncaceae, stopniowo zastępowane przez rośliny wrzosowate w środkowych i późnych stadiach sukcesji i drzewa w najbardziej rozwiniętym stadium sukcesji, które odpowiada młodemu zbiorowisku nadmorskiego boru bażnowego (*Empetro nigri-Pinetum*). Z zebranych 96 prób glebowych wyodrębniono 21 gatunków reprezentujących trzy rodzaje arbuskularnych grzybów mikoryzowych. Najczęściej znajdowanymi grzybami byli przedstawiciele rodzaju *Acaulospora*. Ogólne zagęszczenie zarodników, liczebność gatunków AGM i poziom kolonizacji AM rosły począwszy od stadium pierwszego i były najwyższe w środkowych stadiach, po czym stopniowo malały, osiągając wartości najniższe w stadium 8. Wartości ogólnego zagęszczenia zarodników i zagęszczenia zarodników najczęściej występujących gatunków AGM wyraźnie dowodzą silnego zróżnicowania zbiorowisk AGM w warunkach naturalnych w zależności od rośliny-gospodarza. Z pięciu najczęściej reprezentowanych gatunków AGM wczesnym kolonizatorem i szybko zanikającym w późniejszych stadiach sukcesji był *Glomus* 107. Średniopóźnym sukcesorem była *Acaulospora koskei*, a najpóźniejszym – *Glomus aggregatum*. Wszystkie miary obecności AGM były ujemnie skorelowane z zawartością C organicznego w glebie i większość z nich była ujemnie skorelowana z koncentracją N-NO₃ i P. Natomiast występowanie AGM i AM zazwyczaj były dodatnio skorelowane z pH gleby i zawartością K w glebie.

SŁOWA KLUCZOWE: arbuskularne grzyby mikoryzowe, mikoryza arbuskularna, sukcesja, pole deflacyjne.