ARBUSCULAR MYCORRHIZAL FUNGI (GLOMALES, ZYGOMYCOTA) OF THE BŁĘDOWSKA DESERT, POLAND

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ABSTRACT

The occurrence of arbuscular mycorrhizal fungi (AMF; Glomales, Zygomycetes) associated with plants growing in sand dune soils of the Błędowska Desert, Poland, was investigated in 1995-1997. A total of 134 mixtures of soils and roots were sampled. The mixtures represented 26 plant species in 14 families and one unrecognized plant. Spores of AMF were found in 118 soil-root mixtures. The AMF spore populations comprised 20 described species of the genera *Acaulospora*, *Gigaspora*, *Glomus* and *Scutellospora*, as well as two undescribed morpho-species of the genus *Glomus*. The AMF most frequently occurring in the field-collected soils were members of the genus *Scutellospora*. The AMF spore populations comprised 20 described species in the genera *Acaulospora*, *Gigaspora*, *Glomus* and *Scutellospora*, as well as two undescribed morpho-species of the genus *Glomus*. The fungal species most frequently and numerously found was *Scutellospora armeniaca*. The fungi relatively frequently present also were *A. rugosa*, *A. lacunosa*, *G. aggregatum*, an undescribed *Glomus* 142 and *Sc. dipurpurens*. The overall spore abundance of AMF averaged 69.1 and ranged from 0 to 837 in 100 g dry soil. The highest abundance of spores occurred among roots of the families Cupressaceae, followed by the Rosaceae, Asteraceae and Poaceae. Of the plant species investigated two and more times, most spores harboured *Juniperus communis*. The overall average species richness was 2.4 and ranged from 0 to 6 in 100 g dry soil. Of the plant species sampled at least two times, the highest average species diversity was found in the root zone of *Salix arenaria*. The plant species that hosted the highest overall number of species of AMF was *Festuca rubra*. Trap pot cultures with soil-root mixtures collected in 1997 revealed 10 species of AMF that were not found in field soils sampled in the same year. This suggests that a great part of AMF of Błędowska Desert is represented by rarely or non-sporulating species.

KEY WORDS: arbuscular mycorrhizal fungi, Glomales, occurrence, inland sand dunes.

INTRODUCTION

The Błędowska Desert is the largest inland sandy area of Poland (Szczypek and Wika 1984). It is located in the eastern part of the Silesian Upland and occupies 30 km². The unique character of the Błędowska Desert results also from the presence of rare plant species and fragments of natural plant communities (Mrozik and Wika 1993).

The unique plant communities of the Błędowska Desert are phytocenoses of inland sandy dunes and xerothermic swards with original psammophytic species. The plants of the greatest participation in the sward vegetation, colonizing typical dune areas, are *Corynephorus canescens* (L.) P. B., *Elymus arenarius* L. and *Koeleria glauca* (Schkuhr) DC. (Mrozik and Wika 1993). The plants occurring more rarely are *Arabis arenosa* (L.) Scop., *Arabidopsis thaliana* (L.) Heynh., *Epipactis atropurpurea* Raf. and *Rumex acetosella* L. Additionally, plant species frequently present in the Błędowska Desert are *Salix acutifolia* Willd. and *S. arenaria* L., which origin from planting and natural succession.

In the last years, an increasing diminution of water resources of the Błędowska Desert is observable due to drawing underground waters by neighbouring mines of zinc and lead (Kleczkowski 1972). Additionally, the underground surface waters are highly contaminated by a great amount of savages of the factory of cellulose in Klucze. This results in a quick disappearance of many rare and protected vegetation sites.

The soil microorganisms occurring commonly and probably associated with ca. 80% of plants of the Earth are arbuscular mycorrhizal fungi (AMF, Glomales, Zygomycetes; Gianinazzi and Gianinazzi-Pearson 1986). Literature data indicate that AMF increase the root absorptive area and hence the plant nutrition (Bielecki 1973), influence the succession of plant communities (Janos 1980), their competitiveness (Allen and Allen 1984; Fitter 1977) and phenology (Allen and Allen 1986), equalize the level of nutrition of co-existing plants by formation of hyphal bridges transferring nutrients between them (Newman 1988), and improve the soil structure through binding sand grains into

aggregates by extramatrical hyphae (Koske et al. 1975; Sutton and Sheppard 1976). Additionally, AMF increased the tolerance of plants to heavy metals (Dehn and Schüepp 1989; Griffioen and Ernst 1989), water stresses (Stahl and Smith 1984), and pathogenic fungi and nematodes (Schönbeck 1978).

The sites lacking AMF are colonized by facultatively mycorrhizal or non-mycorrhizal plant species (Miller 1979; Reeves et al. 1979). In contrast, the plants of soils containing abundant spore populations of AMF mainly are obligately mycorrhizal species. The persistence of dominance of obligate mycorrhizal plants ensures, e.g., (1) their increased ability to absorb mineral elements and water (Janos 1980), (2) the inhibition of facultative mycorrhizal plants by obligate mycorrhizal plants being more resistant to unfavourable environmental changes (Hetrick et al. 1989) and (3) higher species diversity of vegetation resulting from nutrient supplying of facultative mycorrhizal species by the better nourished obligate mycorrhizal plants through hyphal bridges (Newman 1988). Additionally, faster growing mycorrhizal plants compete more effectively with non-mycorrhizal plants for, e.g., light or place at a site (Hetrick et al. 1989).

The effectiveness of mycorrhizae in influencing a plant depends mainly on its degree of adjustment to a fungus (Dodd et al. 1990). This expresses in the extent of mycorrhizal colonization and the abundance and diversity of the AM spore population associated (Gemma et al. 1989; Scheltema et al. 1987). In effective associations, a fungus significantly increases plant growth (Abbott and Robson 1981; Raju et al. 1990), and fast growing plants usually harbour both extensive mycorrhizal colonizations and more abundant and diverse spore populations (Hetrick and Bloom 1986). The activity of AMF also highly depends on physical and chemical properties of the soil, especially on its pH, content of phosphorous and heavy metals (Koomen et al. 1987, 1990; Thomson et al. 1992). High concentrations of zinc, copper, nickel and cadmium may eliminate mycorrhizae (Gildon and Tinker 1983).

The aim of this paper was to investigate the occurrence of AMF associated with plants colonizing sandy soils of the Błędowska Desert. The presence of AMF was determined basing on both spores isolated from field mixtures of roots and rhizosphere soils collected in the years 1995–1997 and trap pot cultures established with such mixtures coming from the third year of study. The revealed spore populations of AMF were analyzed using different statistical methods of which the adequacy in characterizing the functional role of these fungi was discussed.

MATERIALS AND METHODS

Study site

The study site was the Błędowska Desert located in southern Poland. The Błędowska Desert is a flat, sandy area whose position, in relation to sea level, ranges from 325 m near Klucze (50°20'N, 19°34'E) to 302 m near Błędów (50°21'N, 19°28'E). It is divided into a smaller northern part and a larger southern one by the Biała Przemsza valley. The northern part of the Błędowska Desert is mainly of a deflation character due to stronger winds compared with those of the southern part, which is

much more diverse, comprising both deflation fields and different dune areas.

Climate

The mean sum of rainfalls in the Błędowska Desert ranges from 676 to 726 mm, and the average annual air temperature is 7.6°C.

Vegetation

The Błędowska Desert comprises 18 vegetative complexes, including five and 13 forestry and non-forestry groups, respectively. The plant communities of this area are represented by 357 vascular plant species of different trophic, thermal and moisture requirements. Only 44 taxa are indicator plants of sandy areas. Most of them are psammophytes or xerophytes, more rarely shrubs and trees. Loose sands are dominated by *Corynephorus canescens*, *Elymus arenarius*, *Salix acutifolia* and *S. arenaria*. The valley areas are colonized by plants of higher trophic and moisture requirements. Eighteen plant species of the Błędowska Desert are protected.

Collection of samples

Samples of roots and attached soils of randomly selected plants were collected on 12 August 1995, 6 September 1996 and 26 June 1997. The samples were excavated from a depth of 5–30 cm using a small trowel. About 0.3–0.5-l soil-root mixtures were placed in plastic bags and then stored at 4°C for 2–8 months until processed.

Isolation, trap culture establishment and identification of AMF

The methods of isolation of the AMF communities, as well as the places of deposition of vouchers of the species found, and the nomenclature and classification used were such as those previously characterized (Tadych and Błaszowski 2000). Briefly, spores of AMF were isolated from the soils by wet sieving and decanting (Gerdemann and Nicolson 1963). Both intact and crushed spores in polyvinyl/alcohol/glycerin (PVLG) and a mixture of PVLG and Melzer's reagent were investigated. The fungi were identified according to their original descriptions (Schenck and Pérez 1990), revisions (Morton 1995; Franke and Morton 1994; Stürmer and Morton 1997), informations and specimens obtained from Prof. R. E. Koske (Rhode Island University, U.S.A.), Prof. J. M. Morton (West Virginia University, U.S.A.), Prof. J. M. Trappe (Oregon State University, U.S.A.), and Dr. C. Walker (U.K.). Vouchers of all the recovered fungal species are preserved in the authors' collections. Nomenclature of the fungi mentioned in this paper follows Walker and Trappe (1993). The classification is that of Morton and Benny (1990). The nomenclature of plants is after Flora Europea (1964–1980). Literature data indicate that a high proportion of AMF in different ecosystems is represented by non-sporulating species, and an effective method initiating sporulation of these fungi is culturing of field-collected mixtures of roots and soils in trap cultures (Brundrett et al. 1999; Stutz and Morton 1996). Therefore, in 1997, investigations of the presence of AMF in soils of the Błędowska Desert were supplemented with observations of spores of these fungi produced in trap pot 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 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.

Soil characteristics

The soil chemical properties investigated in the collected samples were: pH (in H₂O), contents of nitrate nitrogen, phosphorous, potassium, calcium, magnesium, sodium, chlorine, potassium chloride (mg l⁻¹ of soil), cadmium, lead, copper, zinc (mg kg⁻¹ of soil), and organic carbon (%).

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), and the total volume of spores of each species recovered. The frequency of occurrence was calculated by determining the percentage of 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. The dominance coefficient expresses the proportion of the number of spores of a particular species in all spores of AMF recovered. The total spore volume was calculated by multiplying the total number of spores of a given species, isolated during the three years of study, by the average volume of individual spores. The average volume of spores was calculated from their average diameter and equation of a sphere.

RESULTS AND DISCUSSION

Despite the term „desert” present in the name „Błędowska Desert”, the average sum of rainfalls of the dune area ranges from 676 to 726 mm, and its average annual air temperature is 7.6°C. Thus, the soil and climatic conditions of the Błędowska Desert resemble those of maritime or inland dune areas. No literature report exists on AMF of inland dunes. Therefore, the discussion presented below will mainly regard AMF occurring in soils of maritime dunes.

General data

During the three years of study, the occurrence of AMF in the Błędowska Desert soils was determined, basing on 134 mixtures of roots and rhizosphere soils. The mixtures represented 26 plant species in 14 families and one unrecognized plant (Table 1). The plant families most frequently examined were the Poaceae, Salicaceae and Cupressaceae.

In the years 1995, 1996 and 1997, the numbers of plant species investigated were 18, 10 and 6, respectively. Additionally, in 1996, one soil and root sample came from an unrecognized plant. In 1995, the most frequently exam-

TABLE 1. Plants examined and soil samples in which the occurrence of arbuscular mycorrhizal fungi was investigated.

Plant	Number of soil sample
Asteraceae	
<i>Leontodon autumnalis</i> L.	1045
<i>Leontodon</i> sp.	764
Boraginaceae	
<i>Echium vulgare</i> L.	797
<i>Carlina acaulis</i> L.	786
Cistaceae	
<i>Helianthemum nummularium</i> (L.) Dun.	1057
Cupressaceae	
<i>Juniperus communis</i> L.	758-762, 1033, 1036, 1043, 1053, 1054-1056, 1058, 1226, 1227, 1229, 1232, 1244, 1249, 1256, 1259
Fabaceae	
<i>Oenothera biennis</i> L.	787, 1065
Lycopodiaceae	
<i>Lycopodium</i> sp.	793
Orchidaceae	
<i>Epipactis atropurpurea</i> Raf.	783, 796, 1035, 1037
Pinaceae	
<i>Pinus sylvestris</i> L.	763
Plantaginaceae	
<i>Plantago lanceolata</i> L.	778-780, 782
<i>Plantago major</i> L.	1276
Poaceae	
<i>Corynephorus canescens</i> (L.) Beauv.	768-772, 1231, 1250
<i>Deschampsia flexuosa</i> (L.) Trin.	1273
<i>Festuca rubra</i> L.	773-777, 781, 1240, 1241, 1245, 1246, 1252, 1255, 1257, 1258, 1263, 1264, 1272, 1274
<i>Holcus mollis</i> L.	1228, 1230, 1233-1239, 1242, 1243, 1247, 1248, 1251, 1253, 1260-1262, 1265-1270, 1275
<i>Elymus arenarius</i> (L.) Hochst	765, 792, 1050, 1254, 1271
<i>Molinia coerulea</i> (L.) Moench	767
Rosaceae	
<i>Sanguisorba minor</i> Scop.	1066
<i>Rubus</i> sp.	785
Salicaceae	
<i>Salix acutifolia</i> Willd.	1027, 1029, 1031, 1046, 1047, 1063
<i>Salix arenaria</i> L.	794, 795, 798,
<i>Salix rosmarinifolia</i> L.	1028, 1030, 1032, 1034, 1038, 1040-1042, 1044, 1048, 1049, 1051, 1052, 1059, 1060-1062, 1064, 1067
<i>Salix</i> sp.	788-791
Scrophulariaceae	
<i>Verbascum phlomoides</i> L.	766, 1039
Violaceae	
<i>Viola</i> sp.	784
Unrecognized plant	1068

ined plants were *F. rubra* (6 times), followed by *C. canescens* (5) and *J. communis* (5), *P. lanceolata* (4) and *Salix* sp. (4). In 1996, the plant species most frequently sampled were *S. rosmarinifolia* (19 samples), followed by *J. communis* (8) and *S. acutifolia* (6). The most frequently studied plant species in 1997 were *H. mollis* (26), then *F. rubra* (12) and *J. communis* (8). From among the plant species investigated in this study, only *J. communis* and *E. arenarius* were considered in each of the three years of investigation. In 1995 and 1997, spores of AMF were found in 100% (40 soil samples were collected) and 94.1%

(51 samples) of the field-collected soil samples, respectively. In contrast, in 1996, only 27 of the 42 (64.3%) field soils contained spores of AMF.

The high average percent (86.5% from three years) of soil samples of the Błędowska Desert containing spores of AMF confirms many earlier reports that sandy dune soils especially favour these fungi (Bergen and Koske 1984; Błaszowski 1993a; Dalpé 1989; Giovannetti and Nicolson 1983; Koske 1975, 1987, 1988; Koske and Halvorson 1981, 1989b; Koske and Tews 1987; Mohankumar et al. 1988; Puppi and Riess 1987; Stürmer and Bellei 1994). The relatively infrequent and not abundant occurrence of spores of AMF in soils collected in 1996 was probably a result of unfavourable influences of above-, and underground conditions and the vegetation of the site considered. This site was the northern part of the Błędowska Desert of a markedly deflation character and much lower species diversity of the vegetation (Szczypek et al. 1994). Windy sites usually harbour low numbers of plants due to (1) burning or decreasing their activity (Allen 1991; Allen and Allen 1988) and associated other microorganisms interacting with AMF during, e.g., root colonization and infection (Allen and McMahon 1985; Aziz and Habte 1989; Calvet et al. 1992; Will and Sylvia 1990) or because of (2) blowing away spores of AMF with the root zone sand (Allen 1991; Allen and Allen 1988). High plant-species diversity promotes species diversity of spore populations of AMF (Anderson et al. 1983; Koske and Gemma 1997; Koske and Halvorson 1981). Most of the soil samples collected in 1996 came from *S. rosmarinifolia*. In this study, the family Salicaceae ranked last in the abundance of spores harboured by plant species sampled at least two times. The family Salicaceae comprises plant species able to form both ecto-, and arbuscular mycorrhizae (Harley and Harley 1987ab, 1990). There are no literature data on mycorrhizae of *S. rosmarinifolia*. Finally, the frequency of sampling of *J. communis* was similar in each of the three years of study. *Juniperus communis*, the only member of the family Cupressaceae sampled in this study, was associated with the highest number of spores of AMF. Earlier investigations also indicated *J. communis* to harbour abundant communities of AMF (Błaszowski 1993a).

In the three years of investigations, a total of 9196 spores of AMF were isolated. The spores represented four of the six existing genera of the order Glomales (Table 2). None of the examined soil samples contained spores of the genera *Entrophospora* and *Sclerocystis*. However, in 1995 and 1997, the numbers of recovered spores were 20.6 and 18.7 times, respectively, greater than the number of spores revealed in 1996.

The AMF spore populations comprised 20 described species of the genera *Acaulospora*, *Gigaspora*, *Glomus* and *Scutellospora* and two undescribed *Glomus* morpho-species (Table 2).

The AMF of the highest constancy of occurrence in the field-collected soils of the Błędowska Desert were members of the genus *Scutellospora*. The fungi of this genus were present in 65.4% of samples and constituted 20.9% of all the AMF spores recovered. The members of the genus *Acaulospora* occurred in 45.1% of the soils sampled, and their proportion relative to all the spores found was 40.6%. *Glomus* spp. were encountered in 58.6% of soils, in which their spores constituted 35.7% of all the spores revealed.

TABLE 2. Arbuscular mycorrhizal fungi isolated from among the roots of plants of the Błędowska Desert.

Fungal species	Frequency of occurrence	Dominance	Total spore volume $\mu\text{m}^3 \times 10^6$
	%		
<i>Acaulospora lacunosa</i>	21.6	41.17	2637.2
<i>Acaulospora mellea</i>	6.7	1.79	12.3
<i>Acaulospora polonica</i>	0.8	0.02	2.6
<i>Acaulospora rugosa</i>	24.6	17.50	655.7
<i>Acaulospora trappei</i>	3.0	0.27	2.3
<i>Gigaspora gigantea</i>	3.0	0.61	3818.1
<i>Glomus aggregatum</i>	29.9	5.60	237.0
<i>Glomus clarum</i>	3.7	2.82	162.1
<i>Glomus constrictum</i>	2.2	0.73	143.6
<i>Glomus etunicatum</i>	4.5	0.81	11.8
<i>Glomus fasciculatum</i>	8.2	6.81	143.8
<i>Glomus intraradices</i>	1.5	0.67	14.8
<i>Glomus macrocarpum</i>	2.2	0.08	7.2
<i>Glomus microcarpum</i>	2.2	12.71	17.6
<i>Glomus mosseae</i>	0.8	0.01	2.1
<i>Glomus pustulatum</i>	1.5	0.18	4.2
<i>Glomus rubiforme</i>	1.5	3.15	21.3
<i>Glomus 111</i>	0.8	0.72	15.3
<i>Glomus 142</i>	24.6	14.09	341.5
<i>Scutellospora ameniaca</i>	59.7	27.22	9866.9
<i>Scutellospora dipurpurens</i>	32.1	2.37	1846.4
<i>Scutellospora pellucida</i>	0.8	0.02	1.3

Additionally, not abundant spores of *Gigaspora gigantea* were found in four soil samples.

The high stability of occurrence of the large-spored *Scutellospora* spp. and their low spore productivity in the field found in this study agrees with the finding of Brundrett et al. (1999) revealed in a pot culture experiment. Moreover, most spores isolated in this study came from relatively small-spored species of *Acaulospora* and *Glomus*. This inverse relationship probably resulted from the need to use more energy to produce rather large than small spores and to retain vitality by species of AMF forming spores with only one wall (all *Glomus* spp.) or with two or three walls (all *Acaulospora* spp.), but being more delicate as compared with those of *Scutellospora* spp. According to Morton and Benny (1990), the inner flexible walls form a considerable barrier against parasitism or some other disruptive extrinsic biotic and abiotic factors.

Frequency of occurrence

The species of AMF most frequently found in soils of the Błędowska Desert was *S. ameniaca* (Table 2). The fungi relatively frequently present were also *A. rugosa*, *A. lacunosa*, *G. aggregatum*, *Glomus 142* and *S. dipurpurens*.

This study and earlier investigations of the first author of this paper suggest that *S. ameniaca*, a species found in the greatest number of soil samples collected from the Błędowska Desert, is adapted only to dune sites. This fungus has not been present in any of the more than 1600 soil samples coming from over 200 cultivated and non-dune uncultivated sites distributed in the former 25 voivodeships of Poland. *Scutellospora ameniaca* was originally described based on spores isolated from dune soils of the Hel Peninsula (Błaszowski 1992). This species has also been many times encountered in maritime dunes adjacent to Świnoujście in north-western Poland (Błaszowski 1993a). Further studies

are needed to determine the range of occurrence of *S. armeniaca*.

Spore abundance

The overall spore abundance of AMF in the Błędowska Desert averaged 67.8±123.2 (±S.D.) and ranged from 0 to 837 in 100 g dry soil. The highest abundance of spores was found in rhizosphere soils of plants of the families Cupressaceae, followed by Rosaceae, Asteraceae and Poaceae (Table 3). However, the Rosaceae and Asteraceae were represented by only two and three plant species, respectively.

Both the overall average and the range of spore abundance of AMF in dune soils of the Błędowska Desert are similar to those recorded in maritime dunes of the Baltic Sea (0-1006; Błaszowski 1993a), the Hel Peninsula (1-547; Błaszowski 1994a), the Słowiński National Park (0-1523; Tadych and Błaszowski 2000), Florida (0-667; Sylvia 1986; Sylvia and Will 1988) and Lake Huron (0-632; Koske et al. 1975). Lower spore abundances of these fungi were found in dunes of Pakistan (1-29; Khan 1974), Italy (0-250; Puppi and Riess 1987), New South Wales, Australia (0-110; Koske 1975), Massachusetts (0.2-16.2; Bergen and Koske 1984), Rhode Island (101-336; Koske and Halvorson 1981) and Santa Catarina, Brazil (0-69; Stürmer and Bellei 1994).

The difference between the spore abundance of AMF of the Błędowska Desert and those of other sites mentioned above may have resulted from differences in (1) the mycorrhizal affinity of the plant species considered (Harley and Harley 1987ab, 1990); (2) the number of plant species and the degree of the cover of dunes by them (Anderson et al. 1984); (3) climatic conditions of these sites (Koske 1987) and physical, chemical and microbiological properties of their soils (Anderson et al. 1984; Koske 1988), as well as (4) the number of soil samples examined and the period of their collection (Gemma et al. 1989; Tews and Koske 1986).

Of the plant species investigated two and more times, most spores harboured *J. communis*.

Species richness

The overall average species richness in 100 g dry soil of the Błędowska Desert was 2.3±1.8 (±S.D.), and ranged from 0 to 6. Among the plant species sampled two and

TABLE 3. Spore abundance* and species richness* of arbuscular mycorrhizal fungi among roots of 15 plant families of the Błędowska Desert ±S.D.

Family	n	Spore abundance	Species richness
Asteraceae	2	101.7±101.0	2.3±1.2
Boraginaceae	2	41.0	6
Cistaceae	1	0.0	0.0
Cupressaceae	21	177.0±241.8	2.5±1.8
Leguminosae	2	0	0
Lycopodiaceae	1	29.0	5.0
Orchidaceae	4	0.5±0.7	0.5±0.7
Pinaceae	1	16.00	3.00
Plantaginaceae	5	20.8±27.6	2.0±1.6
Poaceae	57	73.8±114.1	3.0±1.5
Rosaceae	2	120.0±169.7	1.5±2.1
Salicaceae	32	24.1±51.2	1.3±1.6
Scrophulariaceae	2	0.0	0.0
Violaceae	1	60.0	3.0

* in 100 g dry soil
n – number of soil samples examined

more times, the highest average species diversity was found in roots of *S. arenaria*, then in roots of *C. canescens*, *Salix* sp. and *H. mollis* (Table 4).

The overall average species richness found in this study corresponds with that found in the Słowiński National Park (av. 2.4) and the Szczecin coast (av. 2.2) examined by Błaszowski (1993a), New South Wales, Australia (av. 1.5-2.4; Koske 1975) and Hawaii (av. 2.0 and 2.4; Koske 1988; Koske and Gemma 1996, respectively). Lower richness values were recorded in dunes of the Słowiński National Park investigated by Tadych and Błaszowski (2000). Higher richness data were noted in dunes of the Gdańsk coast (av. 3.6; Błaszowski 1993a), the Hel Peninsula (av. 3.9; Błaszowski 1994a), Rhode Island (av. 3.1; Koske and Halvorson 1981), New Jersey to Virginia (av. 4.9; Koske 1987) and Santa Catarina, Brazil (av. 5.9; Stürmer and Bellei 1994).

Dominance

The eudominants were *A. lacunosa*, *A. rugosa*, *G. microcarpum*, *Glomus* 142 and *S. armeniaca* (Table 2). The dominants were *G. aggregatum* and *G. fasciculatum*. *Glomus clarum*, *G. rubiforme* and *S. dipurpurescens* represented the subdominants.

Total spore volume

The greatest total spore volume attained *S. armeniaca*, followed by *Gi. gigantea*, *A. lacunosa* and *S. dipurpurescens* (Table 2).

The analysis of the frequency of occurrence, dominance and the total volume of spores of the AMF found leads to

TABLE 4. Spore abundance* and species richness* of arbuscular mycorrhizal fungi among roots of 31 plant species ±S.D.

Plant species	n	Spore abundance	Species richness
<i>Carlina acaulis</i>	1	204.0	3.0
<i>Corynephorus canescens</i>	7	46.0±41.6	3.4±1.0
<i>Deschampsia flexuosa</i>	1	3.0	1.0
<i>Echium vulgare</i>	1	41.0	6.0
<i>Epipactis atrorubens</i>	4	10.8±14.9	1.8±1.7
<i>Festuca rubra</i>	18	70.6±76.3	2.9±1.6
<i>Helianthemum nummularium</i>	1	0	0
<i>Holcus mollis</i>	25	52.5±79.8	3.1±1.6
<i>Juniperus communis</i>	21	177.0±241.8	2.5±1.8
<i>Leonthodon autumnalis</i>	1	2	1
<i>Leonthodon</i> sp.	1	99.0	3.0
<i>Leymus arenarius</i>	5	113.6±109.3	2.8±1.8
<i>Lycopodium</i> sp.	1	29.0	5.0
<i>Molinia coerulea</i>	1	97.0	2.0
<i>Oenothera biennis</i>	2	7±9.9	1.0±1.4
<i>Pinus sylvestris</i>	1	16.0	3.0
<i>Plantago lanceolata</i>	4	26.0±28.9	2.5±1.3
<i>Plantago major</i>	1	0.0	0.0
<i>Rubus</i> sp.	1	240.0	3.0
<i>Salix acutifolia</i>	6	42.0±7.3	0.7±1.2
<i>Salix arenaria</i>	3	147.3±93.2	3.7±1.5
<i>Salix rosmarinifolia</i>	19	7.5±17.8	0.7±1.0
<i>Salix</i> sp.	4	40.0±35.6	3.3±1.5
<i>Sanguisorba minor</i>	1	0	0
<i>Verbascum phlomoides</i>	2	0.0	0.0
<i>Viola</i> sp.	1	60.0	3.0
Unrecognized plant	1	0	0

* in 100 g dry soil
n – number of soil samples examined

three conclusions. First, the fungus of the decidedly highest importance in the Błędowska Desert soils was *S. armenica*. This fungus was revealed over two-fold more frequently than other frequently found species and ranked second in respect of the dominance and first when the total volume of spores produced was considered. Second, another important fungal species also was *A. lacunosa* mainly due to its high number of spores formed. Third, an importance of an AM fungus in a site determined based only on the total volume of produced spores may be inadequate to its real played role. For example, during three years of this study, only 55 spores of *Gi. gigantea* were isolated, which were encountered only in 3.0% of the soil samples collected. Meanwhile, this fungus ranked second among AMF of the greatest volume of the spore produced. This resulted from the fact that *Gi. gigantea* produces the largest spores of all AMF recognized to date.

Plant-AM fungal species associations

Considering the total number of spores of AMF isolated from the root zone of the sampled plant species, most species of AMF were isolated from the root zone of *F. rubra* (17 species), followed by *J. communis* (14) and *H. mollis* (12). No sporulation of AMF was revealed in soils from under *H. nummularium*, *S. minor*, *P. major* and the unrecognized plant species. Unfortunately, the rhizosphere soils and roots of these plants were not used to establish trap cultures to initiate sporulation of non-sporulating AMF in the field conditions.

Grasses are generally considered better host plants of AMF than other hosts (Brundrett et al. 1999; Simpson and Daft 1990; Douds 1994). This study and earlier investigations (Błaszowski 1993a) indicate that *J. communis* hosts also abundant and diverse populations of AMF.

Field vs. trap culture AMF species composition

Among the 51 trap cultures established in 1997, AMF sporulated in 41. The AMF species revealed in trap cultures, but earlier not found in the field-collected soil samples, were *A. trappei*, *G. clarum*, *G. clarioideum*, *G. lamellosum*, *G. occultum*, *G. etunicatum*, *G. pustulatum*, *Glomus* 129, *Glomus* 144 and *Glomus* 145. The species found only in the field soils were *A. rugosa*, *G. aggregatum*, *G. constrictum*, *G. microcarpum*, *G. macrocarpum*, *Glomus* 111, *Gi. gigantea* and *S. pellucida*.

The disclosure in trap cultures of 10 species of AMF not found in the field soils indicates that a high proportion of AMF associated with plants of the Błędowska Desert do not sporulate in the field. A high participation of non-sporulating fungi has several times been recorded in soils of different ecosystems (Brundrett et al. 1999; Stutz and Morton 1996). In Stutz and Morton's (1996) investigations, 75% of the species found after three culture cycles were not detected in the first generation trap cultures with soils of arid sites. Gazey et al. (1992) observed that sporulation of AMF began only after root colonization levels built up to threshold values. Thus, the absence of sporulation does not indicate the absence of the fungal organism. Therefore, further culture cycles will probably reveal next species of AMF functioning in soils of the Błędowska Desert.

The lack of eight species of AMF in trap cultures found to occur in field soils may have resulted from: (1) expulsion or suppression of these fungi by species more compet-

itive or faster to adjust to the new soil conditions of the trap cultures; (2) the absence or low vitality of their spores due to the influence of parasites; (3) incompatibility of these fungi to above-, and underground conditions and the host plant used in trap cultures, and (4) delayed germination of spores of these fungi and, thereby, colonization of roots of the host plant below the minimum threshold level needed to trigger sporulation at harvest.

The very similar averages of spore abundance (112.02 ± 148.7 and 80.8 ± 131.5) and those of species richness (3.4 ± 1.3 and 3.0 ± 1.5) found in the south part of the Błędowska Desert investigated in 1995 and 1997, respectively, indicated that the communities of AMF in this part of the area are very homogenous and stable.

THE OCCURRENCE OF ARBUSCULAR MYCORRHIZAL FUNGI IN THE BŁĘDOWSKA DESERT AND NOTES ON THEIR GENERAL OCCURRENCE

Acaulospora lacunosa Morton (Fig. 1)

$n=29$, $\underline{n}=2$, $\underline{\underline{n}}=5$: 758, 762, 766, 773, 776, 780, 784, 785, 786, 788, 789, 794, 797, 798, 1054, 1226, 1229, 1232, 1236, 1238, 1244, 1245, 1249, 1256, 1260, 1261, 1266, 1268, 1270, 1271, 1272.

Acaulospora lacunosa has been a very frequent inhabitant of dune soils adjacent to the Baltic Sea (Błaszowski 1993a, 1994a; Tadych and Błaszowski 2000). This fungus has also many times been found in different other uncultivated and cultivated sites of Poland (Błaszowski 1991a). Koske and Gemma (1997) found this species to be relatively common in dunes of the U.S. Atlantic coast from Massachusetts to Virginia. *Acaulospora lacunosa* was originally described based on spores recovered from under *Andropogon virginicus* L. growing in West Virginia (Morton 1986).

Acaulospora mellea Spain & Schenck

$n=9$, $\underline{n}=1$, $\underline{\underline{n}}=1$: 758, 765, 766, 769, 1045, 1239, 1248, 1257, 1260, 1263.

Koske and Gemma (1997) recovered *A. mellea* spores from sand dunes of the Province Lands Area of Cape Cod National Seashore, Massachusetts.

Acaulospora polonica Błaszki

$n=1$, $\underline{n}=0$, $\underline{\underline{n}}=0$: 759.

To date, *A. polonica* has been revealed in dune soils of the Słowiński National Park and the Hel Peninsula (Błaszowski 1991a, 1994a; Tadych and Błaszowski 2000).

Acaulospora rugosa Morton (Fig. 2)

$n=33$, $\underline{n}=0$, $\underline{\underline{n}}=0$: 770, 771, 773, 777, 780, 785, 787, 789, 790, 791, 793, 794, 795, 797, 798, 1040, 1059, 1232, 1236,

Abbreviations

n – the number of field-collected soil samples in which a fungal species was found

$\underline{n}$ – the number of soil samples with a fungal species sporulating only in trap pot cultures

$\underline{\underline{n}}$ – the number of soil samples with a fungal species sporulating in both the field and trap pot cultures. The numbers following are those of soil samples given in Table 1.

Figs 1-16. Selected species of AMF found in soils of the Błędowska Desert. Fig. 1. *Acaulospora lacunosa*. Spore wall layers 1+2 (spl1+2) and two-layered (L1+2) inner walls (iw) 1 and 2; pits in the laminate spore wall layer 2 and granules of layer 1 of the innermost wall 2 are visible. Fig. 2. *Acaulospora rugosa*. Structure of spore wall (sp) and inner walls (iw). Fig. 3. Cluster of *Glomus aggregatum* spores with extramatrical hyphae (eh). Fig. 4. Sporocarp of *Glomus mosseae* with spores (sp) enclosed by peridium (p). Fig. 5. Funnel-shaped subtending hypha of *Glomus mosseae*. Fig. 6. Three layers of spore wall (spl1-3) of a young *Glomus* 111 spore. Fig. 7. Spore wall layer 3 (spl3) and subtending hypha (sh) occluded by a septum (s) of mature spore of *Glomus* 111; layers 1 and 2 are sloughed. Fig. 8. Two permanent spore wall layers 1 and 2 (spl1, spl2) and subtending hypha of mature spore of *Glomus* 123.

Figs 1 (×313); 2-4, 15, 16 (×250); 5, 7, 10, 12, 13 (×1000); 6 (×500); 8, 14 (×800); 9 (×625); 11 (×400); all differential interference contrast.

Fig. 9. Separated spore wall layers 1 and 2 (spl1, spl2) of vigorously crushed spore of *Glomus* 123. Fig. 10. Three-layered spore wall (spl1-3) of *Glomus* 129. Fig. 11. Two spore wall layers (spl1, spl2) and subtending hypha (sh) of a pitted (p) spore of *Glomus* 142. Fig. 12. Permanent spore wall layer 1 (spl1) separated from spore wall layer 2 (spl2); pits on the inner surface of spore wall layer 2 are seen. Fig. 13. Pits of mature spore seen through the outer surface and on the inner surface of spore wall layer 2. Fig. 14. Spore wall layers 1 and 2 (spl1, spl2) of *Glomus* 145. Fig. 15. Crushed spore of *Scutellospora armeniaca* with spore wall (sw) and two adherent inner walls (iw1+2). Fig. 16. The innermost layer of the innermost wall stained purple in spore of *Scutellospora dipurpurescens* crushed in Melzer's reagent.

1238, 1239, 1241, 1242, 1244, 1247, 1249, 1251, 1254, 1255, 1259, 1260, 1262, 1271.

In Poland, *A. rugosa* has earlier been found associated with roots of *Calamagrostis arundinacea* (L.) Roth growing in a forest (Błaszowski 1990a) and with roots of many plant species colonizing maritime dunes of the Słowiński National Park (Tadych and Błaszowski 2000). *Acaulospora rugosa* was described based on spores isolated from among roots of *A. virginicus* growing in West Virginia (Morton 1986).

Acaulospora trappei Ames & Linderman

$n=4$, $\underline{n}=26$, $\underline{\underline{n}}=0$: 776, 1028, 1029, 1033, 1226, 1230, 1232, 1235, 1236, 1238, 1239, 1241, 1242, 1244, 1245, 1247, 1248, 1250, 1251, 1252, 1253, 1256, 1257, 1258, 1264, 1265, 1267, 1268, 1272, 1275.

There is only one earlier report of *A. trappei* in maritime sandy dunes (Tadych and Błaszowski 2000). However, observations of trap pot cultures with both dune and non-dune soils suggest that *A. trappei* is adapted to a wide range of ecological conditions. Spores of this fungal species consist of very delicate and impermanent layers. They probably undergo a rapid decomposition by soils microorganisms. Therefore, this fungus is rarely reported to occur in other regions of the world.

The original description of *A. trappei* was prepared based on spores recovered from the root zone of *Lilium longiflorum* Thunb. colonizing southern Oregon and northern California coastal areas (Ames and Linderman 1976).

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

$n=4$, $\underline{n}=0$, $\underline{\underline{n}}=1$: 784, 1248, 1249, 1251.

Gigaspora gigantea has earlier been found in many Polish maritime dune sites distributed along the Baltic Sea coast (Błaszowski 1990b, 1991a, 1994a; Tadych and Błaszowski 2000). This fungus commonly occurred in dunes of the Atlantic coast of North America from Quebec to Virginia (Bergen and Koske 1984; Dalpé 1989; Gemma and Koske 1988; Gemma et al. 1989; Koske 1987; Koske and Halvorson 1981). Rose (1980) and Sylvia and Will (1988) found this fungus in dunes of Florida, and Koske and Tews (1987) and Koske (1975) encountered it in dunes of Wisconsin and New South Wales, Australia, respectively.

Glomus aggregatum Schenck & Smith emend. Koske (Fig. 3) $n=40$, $\underline{n}=0$, $\underline{\underline{n}}=0$: 758, 759, 762, 763, 764, 765, 766, 769, 773, 774, 777, 781, 782, 789, 794, 796, 797, 1031, 1032, 1052, 1053, 1229, 1231, 1235, 1241, 1242, 1243, 1244, 1249, 1250, 1251, 1254, 1255, 1259, 1260, 1262, 1265, 1266, 1270, 1275.

In Poland, *G. aggregatum* has earlier been identified in different dune sites of the Baltic Sea shore (Błaszowski 1991b; Tadych and Błaszowski 2000), the Hel Peninsula (Błaszowski (1994a) and sands of the bank of the Odra river (Błaszowski 1991b). This fungus is a stable inhabitant of dunes of the eastern coast of North America (Dalpé 1989; Friese and Koske 1991; Gemma and Koske 1989; Koske 1987; Sylvia 1986; Sylvia and Will 1988), Wisconsin (Koske and Tews 1987), Florida (Sylvia 1986; Sylvia and Will 1988), San Miguel Island (Halvorson and Koske 1987; Koske and Halvorson 1989a) and Hawaii (Koske 1988).

Glomus aggregatum forms exceptionally extensive extramatrical hyphae binding sand grains into aggregates.

Therefore, this fungus probably plays an important role in stabilization of dunes and sandy river banks.

Glomus claroideum Schenck & Smith

$n=0$, $\underline{n}=2$, $\underline{\underline{n}}=0$: 1228, 1242.

Mohankumar et al. (1988) encountered *G. claroideum* in sandy beach soils of Madras coast, India.

Glomus clarum Nicol. & Schenck

$n=5$, $\underline{n}=12$, $\underline{\underline{n}}=0$: 765, 768, 774, 791, 798, 1226, 1233, 1237, 1251, 1255, 1257, 1258, 1259, 1261, 1264, 1269, 1274.

Other dunes sites with plants harbouring *G. clarum* have been located in the Province Lands Area of Cape Cod National Seashore, Massachusetts (Koske and Gemma 1997), Someshwara, Mangalore Coast of Karnataka, India (Kulkarni et al. 1997), and Quebec, New Brunswick and New Scotia, Canada (Dalpé 1989).

Glomus constrictum Trappe

$n=3$, $\underline{n}=0$, $\underline{\underline{n}}=0$: 765, 781, 1272.

Glomus constrictum has earlier been found associated with roots of different dune plants of the Baltic Sea shore (Błaszowski 1993a, 1994a; Tadych and Błaszowski 2000). This fungus has also been revealed in dunes of Quebec, New Brunswick and New Scotia, Canada (Dalpé 1989) and dunes from New Jersey to Virginia (Koske 1987), Koske (1988) and Stürmer and Bellei (1994) recovered *G. constrictum* from Hawaii (Koske 1988) and Santa Catarina, Brazil, respectively.

Glomus etunicatum Becker & Gerd.

$n=6$, $\underline{n}=3$, $\underline{\underline{n}}=0$: 772, 775, 783, 1028, 1034, 1042, 1251, 1263, 1268.

Other dune sites inhabited by *G. etunicatum* have been those of the Baltic Sea coast (Błaszowski 1991a, 1993a, 1994a; Tadych and Błaszowski 2000), Rhode Island (Koske and Halvorson 1981), Wisconsin (Koske and Tews 1987), San Miguel Island (Koske and Halvorson 1989a) and Santa Catarina, Brazil (Stürmer and Bellei 1994).

Glomus fasciculatum (Thaxter) Gerd. & Trappe emend. Walker & Koske

$n=11$, $\underline{n}=1$, $\underline{\underline{n}}=0$: 758, 764, 774, 792, 793, 1230, 1236, 1239, 1245, 1265, 1269, 1274.

Earlier reports of the presence of *Glomus fasciculatum* in dune soils include those regarding dunes of the Baltic Sea coast and the Hel Peninsula (Błaszowski 1991a, 1993a, 1994a; Tadych and Błaszowski 2000), as well as the eastern and western shores of North America (Dalpé 1989; Bergen and Koske 1984; Gemma and Koske 1989; Koske and Halvorson 1981; Rose 1988).

Glomus intraradices Schenck & Smith

$n=2$, $\underline{n}=5$, $\underline{\underline{n}}=0$: 1238, 1240, 1256, 1258, 1260, 1263, 1274.

This fungus has been found associated with dune plants of Poland (Błaszowski 1995; Tadych and Błaszowski 2000), Madras, India (Mohankumar et al. 1988), Canada (Dalpé 1989), San Miguel Island (Halvorson and Koske 1987; Koske and Halvorson 1989), and Hawaii (Koske 1988; Koske and Gemma 1996).

Glomus lamellosum Dalpé et al.

$n=0$, $\underline{n}=7$, $\underline{\underline{n}}=0$: 1235, 1238, 1251, 1260, 1267, 1271, 1272.

Dalpé et al. (1992) found *G. lamellosum* in the rhizosphere of *Ammophila breviligulata* Fern colonizing sandy shore of Nottawasaga Bay in Georgian Bay, Ontario, Canada and sand dunes of Baile's Harbor, Wisconsin, U.S.A.

Glomus macrocarpum Tul. & Tul.

$n=3$, $\underline{n}=0$, $\underline{\underline{n}}=0$: 1227, 1256, 1260.

Glomus macrocarpum has also occurred in dunes of the Baltic Sea coast (Błaszowski 1991a, 1993b, 1994a; Tadych and Błaszowski 2000), Italy (Puppi and Riess 1987), Canada (Dalpé 1989) and Wisconsin (Koske and Tews 1987).

Glomus microcarpum Tul. & Tul.

$n=3$, $\underline{n}=0$, $\underline{\underline{n}}=0$: 1226, 1238, 1263.

Earlier literature data inform of the presence of this fungus in dunes of the Baltic Sea coast (Błaszowski 1993a, b, 1994a), Madras, India (Mohankumar et al. 1988), and Italy (Puppi and Riess 1987).

Glomus mosseae (Nicol. & Gerd.) Gerd. & Trappe (Figs 4, 5)

$n=1$, $\underline{n}=1$, $\underline{\underline{n}}=0$: 762, 1276.

Kulkarni et al. (1997) recognized *G. mosseae* among spores of AMF recovered from coastal sand dunes located at Someshwara, Mangalore Coast of Karnataka, India.

Glomus occultum Walker

$n=0$, $\underline{n}=3$, $\underline{\underline{n}}=0$: 1236, 1256, 1257.

Other dune sites containing spores of *G. occultum* have been those of New Jersey to Virginia (Koske 1987), Madras coast, India (Mohankumar et al. 1988), and Moonstone Beach, Rhode Island (Friese and Koske 1991).

Glomus pustulatum Koske, Friese, Walker & Dalpé

$n=2$, $\underline{n}=0$, $\underline{\underline{n}}=1$: 1262, 1263.

Polish records of this fungus in dune soils comprise those from the Słowiński National Park (Błaszowski 1994b; Tadych and Błaszowski 2000) and the areas adjacent to Świnoujście (Błaszowski 1995). *Glomus pustulatum* also inhabited dunes of Canada (Dalpé 1989) and the eastern U.S. coast (Koske et al. 1986), as well as dunes of the Madras coast, India (Mohankumar et al. 1988).

Glomus rubiforme (Gerd. & Trappe) Almeida & Schenck

$n=2$, $\underline{n}=0$, $\underline{\underline{n}}=0$: 766, 792.

Błaszowski (1991a) and Tadych and Błaszowski (2000) listed this fungus as an associate of dune plants of the Gdańsk coast and the Słowiński National Park, respectively. Dalpé (1989) recorded *G. rubiforme* in maritime dunes of Canada and Friese and Koske (1991) encountered it in dune sites of Rhode Island.

Glomus 111 (Figs 6, 7)

$n=1$, $\underline{n}=0$, $\underline{\underline{n}}=0$: 1272.

Sporocarps unknown. Spores borne singly in the soil or sometimes in roots; orange to raw umber; globose to subglobose; (55-)97(-120) μm diam; sometimes ovoid; 65-105 $\times$ 95-140 μm ; with a single subtending hypha, rarely two. Subcellular structure of spores consists of one wall with three layers (layers 1-3). Outermost layer 1 hyaline, (0.5-)0.9(-1.5) μm thick before disintegration, closely adherent

to layer 2, smooth in juvenile spores, gradually deteriorating and sloughing at the end of formation of layer 2, always absent in mature spores. Layer 2 hyaline, smooth, (0.7-)1.1(-1.5) μm thick, semiflexible (folding when separated from the laminated layer 3), sloughing with age, rarely present in mature spores. Layers 1 and 2 are continuous with a two-layered subtending hypha of juvenile spores. Layer 3 laminate, smooth, orange to raw umber, (2.0-)6.1(-8.8) μm thick in mature spores, formed by gradual synthesis of very thin, approximately 0.5 μm thick, laminae in the spore and its subtending hypha; the first lamina is highly flexible and frequently separates from layer 2 in crushed spores. Spore wall layers not reacting in Melzer's reagent. Layers 1 and 2, when not deteriorated, swell in lactic acid-based mountants. Layer 3 then appears to be covered with blisters or surrounded with an aureola. Subtending hypha hyaline to yellowish white; straight or recurvate; cylindrical or funnel-shaped, rarely constricted; (3.7-)4.9(-8.1) μm wide at the spore base. Wall of subtending hypha hyaline to yellowish white; (0.7-)1.1(-1.7) μm thick at the spore base; continuous with spore wall layers 1-3 in juvenile spores, then consisting of a single layer continuous with spore wall layer 3. Pore occluded by a septum, 2.3-4.7 μm wide, continuous with the innermost lamina of spore wall layer 3.

The only one described species of the genus *Glomus* resembling *G. arenarium* is *G. etunicatum*. The two fungi form spores similar in color, size and shape with a narrow subtending hypha, whose wall is much lighter-colored than the wall of its spore. Examination of the spore wall structure easily separates these fungi. The spore wall of *G. etunicatum* consists of a mucilaginous outer layer tightly adherent to a laminate inner layer (Stürmer and Morton, 1997). In contrast, the wall of *G. arenarium* spores is composed of a sloughing outermost layer closely associated with a semiflexible middle layer that easily separates from a laminate innermost layer. Although the outermost layers of the two fungi are similar in appearance and quickly slough, the mucilaginous layer of *G. etunicatum* spores stains dark pinkish to reddish purple and that of spores of *G. arenarium* does not react in this reagent. Additionally, the subtending hypha of *G. arenarium* spores is persistent and almost always present in mature spores, whereas that of spores of *G. etunicatum* frequently breaks at the spore base.

Glomus 123 (Figs 8, 9)

$n=0$, $\underline{n}=1$, $\underline{\underline{n}}=0$: 1275.

Sporocarps unknown. Spores single in the soil or in loose clusters; hyaline; globose to subglobose; (75-)95(-120) μm diam. Spore wall structure of one wall with two hyaline, permanent layers (layers 1 and 2). Outermost layer 1 0.5-0.8 μm thick before disintegration. Layer 2 laminate, smooth, (1.5-)2.6(-3.8) μm thick. No layers react in Melzer's reagent. Subtending hypha hyaline; straight or recurvate; cylindrical or slightly flared, (2.0-)2.8(-3.3) μm wide at the spore base. Wall of subtending hypha hyaline, (0.7-)0.9(-1.2) μm thick at the spore base, usually continuous only with spore wall layer 2. Pore occluded by a straight or curved septum, 0.9-1.3 μm wide, continuous with the innermost lamina of spore wall layer 2.

When observed under a stereoscope microscope, spores of *Glomus* 123 resemble those of *G. diaphanum* Morton & Walker, *G. laccatum* Błasz., *G. occultum* Walker, *G.*

spurcum Pfeiffer et al. and *G. viscosum* T.H. Nicolson (Błaszkowski 1988; Kennedy et al. 1999; Morton 1998; Morton and Walker 1984; Pfeiffer et al. 1996; Walker 1982; Walker et al. 1995). All species form hyaline spores and the largest spores of *Glomus* 123 attain the lower level of the spore size range of the other species listed above. However, only *G. viscosum* produces spores in loose clusters as *Glomus* 123 does.

Examination of *Glomus* 123 spores under a light microscope readily separates this fungus from the species considered in this comparison. While the spore wall of *Glomus* 123 consists of two layers, that of *G. diaphanum* and *G. occultum* comprises three layers. The outermost layer of *Glomus* 123 spore wall is permanent, semiflexible in mature spores and adheres to the innermost laminate layer. In contrast, the outermost spore wall layer of *G. diaphanum* and *G. occultum* sloughs with age and is rarely present in mature spores. Additionally, this sloughing layer is associated with either a middle permanent layer (*G. occultum*) or a middle laminate layer (*G. diaphanum*). *Glomus* 123 also lacks the innermost semiflexible layer of *G. diaphanum* and the innermost permanent layer of *G. occultum*.

Glomus spurcum produces spores with two permanent wall layers, of which, however, the outer one may be darker coloured (hyaline to pale yellow-brown) and thicker (0.4-1.2 μm) than that of *Glomus* 123 remaining hyaline and being not thicker than 0.7 μm . Additionally, the outer layer of *G. spurcum* spores easily wrinkles and separates from the neighbouring laminate layer (vs. it usually tightly adheres to a laminate layer in *Glomus* 123), which is much thicker than that of the new fungus described here (1.4-4.2 μm vs. 0.5-1.2 μm thick).

Glomus viscosum also has a spore wall structure with two layers. However, its outer spore wall layer is thicker, more plastic and separates more readily from the laminate layer. Additionally, the outer layer of *Glomus* 123 spores does not exude a mucigel-like substance as found in *G. viscosum*.

The features distinguishing *Glomus* 123 and *G. laccatum* are properties of their spore wall and subtending hypha. The outermost spore wall layer of the latter species sloughs with age and usually is absent in mature specimens, and its laminate layer is composed of easily separating and thick (ca 0.5-2.2 μm) laminae (vs. inseparable and very thin in *Glomus* 123). The subtending hypha of *G. laccatum* compared with that of *Glomus* 123 is much wider (7.4-12.9 μm vs. 4.2-8.1 μm), and its wall is less compact, because it is formed from loose laminae continuous with those of the laminate spore wall layer.

Glomus 129 (Fig. 10)

$n=0$, $\bar{n}=2$, $\underline{n}=0$: 1232, 1235.

Sporocarps unknown. Spores produced singly in the soil; light yellow to yellow brown; globose to subglobose; (75-) 135(-160) μm diam; with a single subtending hypha. Spore wall structure of one wall with three layers (layers 1-3). Outermost layer 1 permanent, hyaline, 0.5-0.9 μm thick. Layer 2 laminate, smooth, light yellow to yellow brown, (4.5-)6.8(-9.8) μm thick. Layer 3 flexible, hyaline, 0.5-0.8 μm thick. Subtending hypha light yellow; straight or recurvate; cylindrical to slightly flared; (3.4-)07(-9.6) μm wide at the spore base. Wall of subtending hypha light yellow; (1.2-)1.9(-3.5) μm thick at the spore base; continuous with

spore wall layers 1-3. Pore occluded by a curved septum, 2.2-7.1 μm wide, continuous with the innermost spore wall layer 3.

Glomus 129 most resembles *G. claroideum*, because spores of both fungi are similar in size, colour, and have a flexible innermost spore wall layer. The main differences between the two fungi result from the number and properties of the outer layers adherent to a laminate layer. In *Glomus* 129, the laminate layer is overlaid with one permanent layer, whereas the laminate layer of *G. claroideum* spores is covered with two layers sloughing with age (Stürmer and Morton 1997).

Glomus 142 (Figs 11-13)

$n=33$, $\bar{n}=4$, $\underline{n}=4$: 761, 767, 768, 769, 773, 778, 781, 783, 786, 788, 791, 793, 797, 798, 1229, 1230, 1231, 1234, 1235, 1236, 1241, 1245, 1250, 1252, 1255, 1256, 1257, 1259, 1260, 1261, 1262, 1263, 1264, 1265, 1271, 1272, 1276.

Sporocarps unknown. Spores borne singly in the soil; yellowish white to golden yellow; globose to subglobose; (50-)71(-85) μm diam; sometimes ovoid; 55-60 $\times$ 80-85 μm ; with a single subtending hypha. Subcellular structure of spores consists of one wall with two layers (layers 1-2). Outermost layer 1 hyaline, ca. 0.5 μm thick, continuous with a one-layered subtending hypha of the most juvenile spores, then darkening to pale yellow and thickening to (0.9-)1.1(-1.5) μm . Layer 2 laminate, yellowish white to golden yellow, (3.2-)4.4(-6.1) μm thick, with a smooth outer surface and an evenly pitted inner surface; pits round, (1.2-)1.6(-2.0) μm diam, 1.2-2.0 μm deep, separated by ridges, (0.7-)1.1(-1.7) μm wide; in the most juvenile spores, the inner surface frequently is smooth; in young spores, it contains shallow pits that may be difficult to see. No spore wall layers react in Melzer's reagent. Subtending hypha hyaline to pale yellow; straight or recurvate; cylindrical or slightly flared, rarely constricted; (2.9-)5.2(-6.9) μm wide at the spore base. Wall of subtending hypha hyaline to pale yellow; (0.7-)1.3(-2.9) μm thick at the spore base; continuous with spore wall layers 1 and 2; spore wall layer 2 present in the subtending hyphal wall only up to 5.6 μm below the spore base. Pore occluded by a straight or curved septum, 1.5-2.7 μm wide and 0.5-0.7 μm thick, continuous with the innermost lamina of spore wall layer 2.

When observed under a dissecting microscope, spores of *Glomus* 142 resemble small-spored isolates of *G. etunicatum* Becker & Gerd., *G. pustulatum* Koske et al., and *G. trimurales* Koske & Halvorson. All four species form globose to subglobose and yellow-coloured spores, whose mean size range overlaps (Becker and Gerdemann 1977; Koske and Halvorson 1989b; Koske et al. 1986; Stürmer and Morton 1997).

Examination of subcellular structure and phenotypic properties of layers in the spore wall of specimens crushed in Melzer's reagent readily separates the fungi. Only *Glomus* 142 forms spores with a pitted inner surface of their laminate spore wall layer. However, in young spores, their inner surface either is smooth or the pits are very shallow and difficult to see. Even then, *Glomus* 142 is distinguishable from the species considered in this comparison based on the following divergences. Although *Glomus* 142 and *G. etunicatum* have a spore wall composed of two layers, the outer layer of the former species is permanent

and, thereby, always present in mature specimens and that of the latter fungus sloughs and usually occurs only in young spores (Stürmer and Morton 1997). Additionally, the outer layer of *Glomus* 142 spores is nonreactive in Melzer's reagent, but it stains dark pinkish red to reddish-purple in *G. etunicatum* (Stürmer and Morton 1997). Finally, in contrast to the two-layered subcellular spore wall structure of *Glomus* 142, that of *G. pustulatum* and *G. trimurales* comprises three layers.

Glomus 144

n=0, $\underline{n}=1$, $\underline{\underline{n}}=0$: 1242.

Sporocarps unknown. Spores produced singly in the soil; yellowish white; globose to subglobose; (60-)85(-100) μm diam; with a single subtending hypha. Subcellular spore structure of one wall with two permanent layers (layers 1 and 2). Outer layer 1 hyaline, 0.5-0.7 μm thick. Layer 2 laminate, smooth, yellowish white, (1.9-)3.1(-4.8) μm thick. No layer stains in Melzer's reagent. Subtending hypha yellowish white; straight or recurved; slightly flared; (3.1-)5.0(-6.2) μm wide at the spore base. Wall of subtending hypha yellowish white; (1.8-)2.2(-3.3) μm thick at the spore base; continuous with spore wall layers 1 and 2. Pore occluded by a curved septum, 1.5-2.0 μm wide, continuous with the innermost lamina of spore wall layer 2.

Spores of *Glomus* 144 most resemble those of *G. fasciculatum* due to their size and colour (Walker and Koske 1987). However, while *Glomus* 144 produces 2-layered spores not reacting in Melzer's reagent, those of *G. fasciculatum* are 3-layered and stain red in this reagent. Additionally, *G. fasciculatum* may form spores in compact clusters, and not singly in the soil as *Glomus* 144 does.

Glomus 145 (Fig. 14)

n=0, $\underline{n}=1$, $\underline{\underline{n}}=0$: 1231.

Sporocarp unknown. Spores formed singly in the soil, yellow-brown; globose to subglobose; (130-)175(-210) μm diam; sometimes ovoid; 120-145 $\times$ 190-240 μm ; with a single subtending hypha. Spore wall structure with one wall comprising two permanent layers (layers 1 and 2). Outermost layer 1 hyaline to pale yellow, 0.5-2.5 μm thick, sometimes with vesiculate swellings, 10-15 μm diam. Layer 2 laminate, yellow-brown, 10-22 μm thick. No spore wall layers react in Melzer's reagent. Subtending hypha yellow to yellow-brown; straight or recurved; cylindrical or flared, rarely constricted; 12-27 μm wide at the spore base. Wall of subtending hypha yellow to yellow-brown; 1.5-7.7 μm thick at the spore base; continuous with spore wall layers 1 and 2. Pore occluded by a curved septum, 10.5-21.5 μm wide, continuous with the innermost lamina of spore wall layer 2.

The fungus most closely related to *Glomus* 145 is *G. globiferum* Koske & Walker. Both species form spores similar in size and colour and have vesiculate swellings associated with the outermost spore wall layer. However, in contrast to the 2-layered spore wall of *Glomus* 145, that of *G. globiferum* consists of three or four layers (Koske and Walker 1986).

Scutellospora armeniaca Błasz. (Fig. 15)

n=80, $\underline{n}=1$, $\underline{\underline{n}}=9$: 758, 759, 760, 761, 762, 763, 764, 765, 766, 767, 768, 769, 771, 772, 773, 774, 775, 776, 777, 778,

780, 781, 782, 783, 784, 785, 786, 787, 789, 791, 792, 793, 794, 795, 796, 797, 798, 1031, 1032, 1037, 1042, 1043, 1052, 1059, 1226, 1227, 1228, 1230, 1231, 1232, 1234, 1235, 1236, 1237, 1238, 1240, 1241, 1242, 1243, 1244, 1248, 1249, 1250, 1251, 1253, 1254, 1255, 1256, 1257, 1258, 1259, 1261, 1262, 1263, 1265, 1266, 1267, 1268, 1269, 1270, 1271.

Scutellospora armeniaca has earlier been found to occur in spore populations of AMF of the Błędowska Desert and maritime dune soils of Poland (Błaszowski 1992, 1995; Tadych and Błaszowski 2000). Unfortunately, no report exists of the presence of this fungus in other dune sites of the world.

The exceptionally high values of the frequency of occurrence, the dominance and the total volume of spores of *S. armeniaca* found in this study indicate that abio- and biotic conditions of the Błędowska Desert highly favour the development of this fungus.

Scutellospora dipurpurescens Morton & Koske (Fig. 16)

n=43, $\underline{n}=2$, $\underline{\underline{n}}=5$: 759, 760, 763, 768, 769, 770, 771, 772, 773, 777, 778, 779, 780, 781, 783, 790, 791, 793, 797, 1031, 1042, 1227, 1228, 1229, 1230, 1232, 1235, 1236, 1237, 1240, 1241, 1242, 1244, 1248, 1250, 1253, 1256, 1258, 1261, 1262, 1264, 1265, 1270, 1273, 1274.

Scutellospora dipurpurescens dominated in soils of the Hel Peninsula (Błaszowski 1994a). This species belonged to the most frequently occurring AMF in dunes of the Słowiński National Park (Tadych and Błaszowski 2000). *Scutellospora dipurpurescens* may easily be confused with *S. calospora* (Nicol. & Gerd.) Walker & Sanders, a fungus recorded in many dune sites of the world (Dalpé 1989; Giovannetti and Nicolson 1983; Koske and Gemma 1997; Koske and Halvorson 1981, 1989a).

Scutellospora pellucida (Nicol. & Schenck) Walker & Sanders

n=1, $\underline{n}=0$, $\underline{\underline{n}}=0$: 1228.

This fungus has earlier been revealed in dunes of the Hel Peninsula, the Gdańsk and Szczecin coasts (Błaszowski 1993a), and the Słowiński National Park (Tadych and Błaszowski 2000). Other sites with dune plants associated with *S. pellucida* have been those of the eastern coast of North America from Quebec to Virginia (Bergen and Koske 1984; Dalpé 1989; Friese and Koske 1991; Gemma and Koske 1989; Gemma et al. 1989; Koske 1987). Rose (1988) identified this fungus in dunes of the California coast.

Soil chemical and physical properties

The chemical and physical properties of four randomly selected soil samples ranged: pH (in H_2O), 5.6-5.9; N-NO_3 (mg l^{-1}), 9.3-10.8; P, 3.0-5.0; K, 5.0-13.0; Ca, 66.0-196.0; Mg, 7.0-23.0; Na, 0.0-1.0; Cl, 13.7-18.2; KCl, 0.06-0.075; Cd (mg kg^{-1}), 0.24-0.49; Pb, 17.9-25.9; Cu, 20.0-23.0; Zn, 51.0-77.6; orgC (%), 0.27-0.42; bulk density (kg l^{-1}), 0.35-1.55.

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ARBUSKULARNE GRZYBY MIKORYZOWE (GLOMALES, ZYGOMYCOTA) PUSTYNI BŁĘDOWSKIEJ

STRESZCZENIE

W latach 1995-1997 badano występowanie arbuskularnych grzybów mikoryzowych (AGM; Glomales, Zygomycota) związanych z roślinami rosnącymi w glebach wydmywanych Pustyni Błędowskiej. Badania przeprowadzono na podstawie 134 prób korzeni i gleby ryzosferowej. Próby te pochodziły spod 26 gatunków roślin z 14 rodzin i jednej rośliny nie rozpoznanej. Zarodniki AGM znaleziono w 118 próbach. Wyodrębnione zbiorowiska zarodników zawierały 20 opisanych gatunków z rodzajów *Acaulospora*, *Gigaspora*, *Glomus* i *Scutellospora* oraz trzy nie opisane gatunki z rodzaju *Glomus*. Grzybami najczęściej występującymi w glebach Pustyni Błędowskiej byli przedstawiciele rodzaju *Scutellospora*. Gatunkiem znajduwanym najczęściej i najliczniej była *Scu. armeniaca*. Stosunkowo często ujawniano również *A. lacunosa*, *A. rugosa*, *G. aggregatum*, nie opisane *Glomus* 142 i *Scu. dipurpurens*. Ogólne zagęszczenie zarodników AGM wynosiło średnio 69,1 i wahało się od 0 do 837 zarodników w 100 g suchej gleby. Najwięcej zarodników występowało wśród korzeni rodziny Cupressaceae, następnie Rosaceae, Asteraceae i Poaceae. Spośród gatunków roślin badanych dwa i więcej razy, najwięcej zarodników utrzymywało *Juniperus communis*. Ogólne średnie zagęszczenie gatunków wynosiło 2,4 i wahało się od 0 do 6 gatunków w 100 g suchej gleby. Spośród gatunków roślin badanych co najmniej dwa razy, najwięcej gatunków utrzymywała *Salix arenaria*. Rośliną, która utrzymywała najwięcej gatunków AGM była *Festuca rubra*. Kultury pułpkowe utworzone z fragmentów korzeni i gleby ryzosferowej zebranych w roku 1997 ujawniły 11 gatunków AGM nie znalezionych w próbach glebowych pochodzących z tego samego roku. To sugeruje, że dużą część AGM Pustyni Błędowskiej stanowią gatunki rzadko lub nie zarodnikujące.

SŁOWA KLUCZOWE: arbuskularne grzyby mikoryzowe, Glomales, występowanie, śródlądowe wydmy piaszczyste.