Original papers

Mycorrhiza and root-associated fungi in Spitsbergen

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Summary. Roots of 76 plant species collected in West Spitsbergen (Svalbard), in the middle-northern Arctic zone, were examined for mycorrhiza and root-associated fungi. *Dryas octopetala*, *Pedicularis dasyantha* and *Salix polaris* were ectomycorrhizal and *Cassiope tetragona* and *Empetrum hermaphroditum* ericoid mycorrhizal. *Pedicularis dasyantha* was only slightly infected. Structures resembling vesicular-arbuscular mycorrhizal (VAM) fungi were not found in the roots, and soil samples screened for VAM fungi contained only one spore. Root endophytic fungi commonly occurred in Spitsbergen, but only *Olpidium brassicae*, *Pleospora herbarum*, *Papulaspora*, *Microdochium bolleyi* and *Rhizoctonia solani* were identified with reasonable certainty. A sterile endophytic dark-septate fungus (DSF) was in 39.5% of the flowering-plant species examined, especially in the *Brassicaceae*, *Caryophyllaceae*, *Saxifragaceae* and *Poaceae*. DSF were categorized into four slightly overlapping groups. Sterile endophytic hyaline septate fungi were rare. In the literature it is suggested that at least some of the DSF species or the hyaline septate fungi are functionally mutualistic rather than saprophytic or pathogenic. The literature on ectomycorrhizal fungi and plants in Spitsbergen is reviewed, including about 50 species, mainly of the genera *Cortinarius*, *Hebeloma*, *Inocybe*, *Laccaria*, *Lactarius* and *Russula*. These are symbiotic with the above-mentioned ectomycorrhizal plants. Four further ectomycorrhizal plants (*Betula nana*, *Salix* spp.) are very rare in the area.

Key words: Arctic – Mycorrhiza – Endophytic fungi – Dark-septate fungi

Introduction

Only a few surveys of arctic, subantarctic or alpine mycorrhiza are available, e.g. studies by Russian scientists in the low Arctic of Siberia (Katenin 1964, 1972), and by

American scientists in Alaska (Laursen and Chmielewski 1982). In the high Arctic, studies were made of the Canadian Devon and Ellesmere Islands (Stutz 1972; Kohn and Stasovski 1990). Alpine mycorrhiza have been studied in the High Tatra Mountains (Nespiak 1953), in the European Alps (Read and Haselwandter 1981; Haselwandter and Read 1982; Fitter 1986; Blaschke 1991), in Otago Province, southern New Zealand (Crush 1973), in the northern Rocky Mountains of Montana and Wyoming (Lesica and Antibus 1986), and in the Alberta Rocky Mountains (Stoyke and Currah 1991); those of the Antarctic and Subantarctic have been studied by Christie and Nicolson (1983) and Smith and Newton (1986).

The results of investigations on mycorrhizae share some common features, for example the percentage of flowering plants with vesicular-arbuscular (VA) mycorrhiza and the percentage of infection decrease towards polar sites and higher altitudes. However, ectomycorrhiza and ericoid mycorrhiza seem to be ubiquitous in arctic and alpine woody shrubs. Many species in high-alpine plant communities typically have endomycorrhizal colonization of the VA type, while another typical feature is sterile dark septate fungi (DSF) or hyaline septate fungi in the roots of arctic and alpine plants (Read and Haselwandter 1981; Haselwandter and Read 1982; Kohn and Stasovski 1990; Blaschke 1991; Stoyke and Currah 1991).

Although many other groups of micromycetes have been studied in detail, root-associated microfungi have not been investigated on Spitsbergen. Soil microfungi examined by Kobayasi et al. (1968) were presented in a review concerning the Arctic zone (Kobayasi 1982), and Zabawski (1976) isolated a total of 108 fungal taxa from peat bog in West Spitsbergen. The arctic actinomycetes were studied by Krzywy et al. (1961) and Wieczorek et al. (1964) and parasitic microfungi on leaves and stems by Lind (1928). In view of this sparsity of investigations, especially at middle and high arctic sites, we analysed the mycorrhizal status of roots in Spitsbergen as well as other root endophytic fungi.

Materials and methods

The native flora of Spitsbergen consists of 162 species (Rønning 1979). Roots (Table 1) were collected on West Spitsbergen (Svalbard) (Fig. 1) of 76 species representing 47.5% of the native taxa; 86% were common species (37 out of 43), 55% widespread but less common (34 out of 62) and 11% were rare (6 out of 54) as classified by Rønning (1979). The roots were collected on Spitsbergen by Eurola in 1969. Voucher specimens for most species, including all the critical taxa, are preserved in the Botanical Museum, University of Oulu. The habitats of each studied species are given in Fig. 1.

Roots were collected during the period 6 June to 12 August 1969, fixed in formalin acetic acid alcohol (FAA) for 1 h and stored in the cold (5° C) in 70% ethanol. Despite the long storage period, the root structures were well preserved. The number of replicates examined is indicated in Table 1. The formation of mycorrhiza in *S. polaris* was monitored for a longer period (June 19, 22, 27 and 30) at the depth of 0 cm, 2 cm, 5 cm, 10 cm and 15 cm at site no. 3 (Fig. 1), a meltwater-influenced *S. polaris* heath.

Preparation of roots for microscopy

Plant roots stained in acid fuchsin (Kormanik et al. 1980) were examined for VA mycorrhiza and other endophytic fungi by light microscopy. A total of 205 samples was studied, each on two mi-
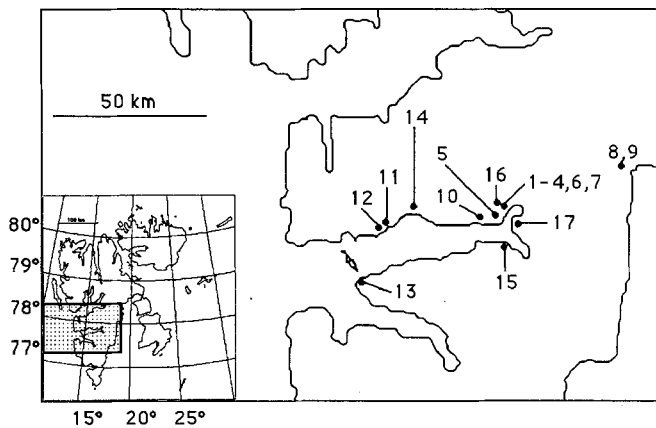

Fig. 1. The location of sites studied on Spitsbergen in 1969. The *numbers* refer to the following habitats. *1*, Van Mijenfjorden, Sveagruva, a grass field influenced by trampling (19.–22. 6., 14. 7. and 12. 8.). *2*, As above, but a *Dryas* heath W of village (20. 6., 14. 7. and 28. 7.). *3*, As above, but a melt-water influenced *Salix polaris* heath (19.–27. 6.). *4*, Van Mijenfjorden, Sveagruva, NW site of Braganzavågen in front of Mt. Deinbolltoppen, 20 m the seashore on bare till (21. 6.). *5*, Van Mijenfjorden between Sveagruva and Slettvika (26. 6.). *6*, As no. 1, but in front of a talus slope W of the village (26. 6.). *7*, Van Mijenfjorden, Sveagruva, Barryneset, on bare till (24. 6., 14. 7. and 10. 8.). *8*, Junction of the valley Agardhdalen and Bellsunddalen, Mt. Friedrichfjellet, its lower SE slope (4.–8. 7.). *9*, As no. 8, but a water-filled depression (14. 7.). *10*, Van Mijenfjorden, Slettvika, on moist to wet habitats (17.–19. 7.). *11*, Van Mijenfjorden, Camp Morton, Kolfjellet, a dry bird cliff talus (22. 7.). *12*, Van Mijenfjorden, Berzeliusdalen (22. 7.). *13*, Van Mijenfjorden, Midterhuken, a bird cliff talus (23. 7.). *14*, Van Mijenfjorden, Reindalen, different heath and mire habitats (25. 7.). *15*, Van Mijenfjorden, Fagerstaneset, a shore meadow (2. 8.). *16*, Van Mijenfjorden, Liljevalchfjellet, meadows (5. 8.). *17*, Van Mijenfjorden, Mt. Torellfjellet, heath vegetation (10. 8.)

Table 1. Plants collected for mycorrhizal analysis on Spitsbergen, their abundance according to Rønning (1979); C, common; W, widespread but unusual; R, rare; E, ectomycorrhizal; Er, ericoid myorrhiza; NM, non-mycorrhizal

Species	Abundance	No. of replicates	Mycorrhizal status	Habitats and groups of non-VAM endophytes[a]
Sphenopsida		2		
Equisetum arvense	C	2	NM	8NI-II
Salicaceae		26		
S. polaris	C	26	E	1NI, 3DI-II, 3NI-XVII, 3MI, 5NI-VI, 5BVII
Polygonaceae		4		
Oxyria digyna	C	2	NM	1NI-II
Polygonum viviparum	C	2	NM	2NI-II
Caryophyllaceae		13		
Sagina intermedia	C	1	NM	4DI
Minuartia rubella	C	1	NM	2DI
M. biflora	C	1	NM	8DI
Stellaria crassipes	C	1	NM	1NI
Cerastium regelii	W	5	NM	1NI-II, 8DKI, 8NI-II
C. arcticum	W	2	NM	1CEI, 1NI
Melandrium apetalum	W	1	NM	10NI
Silene acaulis	W	1	NM	8DLMI
Ranunculaceae		15		
Ranunculus nivalis	W	2	NM	14DI, 15NI
R. lapponicus	W	1	NM	14NI
R. hyperboreus	C	2	NM	9NI-II
R. spitsbergensis	W	3	NM	10NI, 11NI, 14NI
R. sulphureus	C	4	NM	1DI, 1EII, 1JIII, 1LIV
R. pygmaeus	C	3	NM	1NI-III
Papaveraceae		4		
Papaver dahlianum	W	4	NM	1BKI, 1NII-III, 7NI
Brassicaceae		36		
Cardamine nymani	W	2	NM	3NI, 10DI
Cochlearia officinalis	C	2	NM	8NI, 13KI
Draba corymbosa	W	2	NM	6DI, 7NI, 8DI
D. adamsii	W	6	NM	6DI, 6NII-V, 7NI
D. alpina	C	4	NM	1DMI, 6CI, 6GII, 6NIII
D. micropetala	R	1	NM	2NI
D. fladnizensis	W	4	NM	6BMI, 6JI, 8KI, 8NII
D. subcapitata	C	7	NM	6NI-IV, 7NI, 8CEI, 8NII
D. nivalis	W	6	NM	1NI-II, 6GI, 6NII, 7NI, 11NI

Table 1 (continued)

Species	Abun-dance	No. of repli-cates	Mycor-rhizal status	Habitats and groups of non-VAM endophytes[a]
D. cf. arctogena	R	1	NM	1FI, 1NII
D. cf. arctica	R	1	NM	6NI
Saxifragaceae		33		
Saxifraga cernua	C	3	NM	1NI–III
S. oppositifolia	C	5	NM	2NI, 7NI–III, 8CI
S. hieraciifolia	W	1	NM	8JI
S. foliolosa	W	2	NM	1NI–II
S. hirculus	C	1	NM	8NI
S. nivalis	W	5	NM	1CI, 1NII–III, 1HIV, 15JI
S. rivularis	C	3	NM	12NI, 13KI, 17NI
S. hyperborea	W	5	NM	1NI–II, 8NI, 16BCFGJKI, 17NI
S. cespitosa	C	6	NM	1AI, 1DII, 1GIII, 1NIV, 6BFI, 8CI
S. flagellaris	W	2	NM	5AI, 8ADI
Rosaceae		9		
Potentilla pulchella	W	2	NM	7NI–II
P. hyparctica	C	2	NM	2DEFI, 2CEII
Dryas octopetala	C	5	E	2NI–V
Ericaceae		2		
Cassiope tetragona	C	2	Er	14NI–II
Empetraceae		2		
Empetrum hermaphroditum	R	2	Er	14NI, 16NI
Polemoniaceae		2		
Polemonium boreale	R	2	NM	2DI, 5II
Boraginaceae		2		
Mertensia maritima	W	2	NM	10DI–II
Scrophulariaceae		5		
Pedicularis dasyantha	W	3	E	2NI–II, 14DI
P. hirsuta	C	2	NM	2NI, 6FI
Campanulaceae		2		
Campanula uniflora	R	2	NM	17KI–II
Asteraceae		4		
Erigeron humilis	W	2	NM	16NI, 17NI
Petasites frigidus	C	1	NM	14NI
Arnica alpina	W	1	NM	16NI
Cichoriaceae		2		
Taraxacum arcticum	W	2	NM	2NI, 6DJMI
Juncaceae		12		
Juncus biglumis	C	2	NM	3NI, 11NI
Luzula confusa	C	6	NM	1NI–III, 10NI, 15NI, 17MI
L. arctica	W	4	NM	1NI, 2CI, 8NI, 17NI

Table 1 (continued)

Species	Abun-dance	No. of repli-cates	Mycor-rhizal status	Habitats and groups of non-VAM endophytes[a]
Cyperaceae		4		
Eriophorum scheuchzeri	W	1	NM	10FI
Carex ursina	W	1	NM	3NI
C. lachenalii	W	1	NM	15KI
C. subspathecea	R	1	NM	14NI
Poaceae		54		
Hierocloë alpina	R	1	NM	14CI
Alopecurus alpinus	C	2	NM	1BI, 1NII
Phippsia concinna	C	1	NM	15KI
P. algida	C	3	NM	3NI–II, 3JIII
Deschampsia alpina	C	3	NM	1NI, 4NI–II
Trisetum spicatum	C	4	NM	1BI, 1CII, 1NIII–IV
Poa alpigena	C	7	NM	1NI–II, 3NI–II, 3CIII, 4BFKI, 4DII
P. arctica	W	5	NM	1KI, 2CI, 2NII–III, 2KIV
P. alpina	C	5	NM	1NI–IV, 15KI
P. abbreviata	W	1	NM	14NI
Dupontia pelligera	C	2	NM	10NI–II
Puccinellia angustata	C	5	NM	7NI–V
P. phryganodes	W	4	NM	7NI–IV
Festuca rubra var. mutica	C	4	NM	1FI–II, 1DIII, 1NIV
F. vivipara	C	6	NM	1BI, 1EII, 1HIII, 1NIV–VI
F. brachyphylla	W	1	NM	15KI
F. hyperborea	R	2	NM	2NI, 7CI, 7DII

[a] Explanations for arabic numerals in this column are given in Fig. 1 and for capital letters in Table 4; roman numerals following the capital letters indicate the number of individual samples at each site

Table 2. Localities of soil samples analysed for VAM spores

Locality	n[a]	Substrate
Reindalen, Stormyra	1	Peat
Midterhuken	1	Humus from a bird cliff meadow
Midterhuken	1	Soil from a wind-exposed heath
Sveagruva	4	Humus from a *Dryas* heath
Sveagruva	1	Soil from a polygon
Sveagruva	1	Till
Camp Morton	1	Humus from a *Salix polaris* moss heath
Camp Morton	1	Humus from a bird cliff meadow

[a] n, Number of samples analysed

Table 3. Ectomycorrhizal fungi of Spitsbergen, including synonyms or misapplied names and ectotrophic symbionts around the Arctic

Fungus taxa[a,m]	References	Ectotrophic symbiont	References
Cortinarius cinereoviolaceus[b] (*simulatus*)	Kobayasi et al. 1968; Ohenoja 1971; Watling 1983	*Betula nana, Salix polaris*	Kobayasi et al. 1968; Ammirati and Laursen 1982; Watling 1983
C. favrei[c] (*alpinus*)	Kobayasi et al. 1968; Ohenoja 1971	*S. polaris*	Kobayasi et al. 1968; Ohenoja 1971; Gulden et al. 1985
C. mucosus	Kobayasi et al. 1968	*B. nana, Dryas octopetala, Salix rotundifolia*	Miller 1982; Linkins and Antibus 1982
C. glandicolor var. *exilis*	Dobbs 1942; Kobayasi et al. 1968; Watling 1983	*S. polaris*	Watling 1983
C. alboviolaceus	Dobbs 1942; Kankainen et al. 1967		
C. polaris	Gulden et al. 1985	*D. octopetala, S. herbacea, S. polaris, S. reticulata*	Gulden et al. 1985
C. subtorvus	Gulden et al. 1985	*D. octopatala, S. herbacea, S. polaris, S. reticulata, S. retusa*	Gulden et al. 1985
C. pauperculus	Gulden and Jenssen 1988	*D. octopetala, S. polaris, S. herbacea, S. retusa, S. serpyllifolia*	Gulden and Jenssen 1988
C. phaeopygmaeus	Gulden and Jensen 1988	*S. polaris, S. herbacea, S. reticulata, S. retusa*	Gulden and Jensen 1988
C. cinnamomeolutea[d]	Ohenoja 1971	*S. polaris*	Ohenoja 1971
Entoloma sericeum	Kobayasi et al. 1968; Ohenoja 1971	*S. polaris, S. rotundifolia*	Ohenoja 1971; Linkins and Antibus 1982; Senn-Irlet et al. 1990
E. junceum[d]	Kobayasi et al. 1968		
E. alpicola	Noordeloos 1984; Gulden et al. 1985	*S. herbacea*	Gulden et al. 1985
E. fuscotomentosum	Noordeloos 1984	*S. arctophila, S. glauca, S. herbacea*	Noordeloos 1984
Hebeloma mesophaeum	Lange 1955; Kobayasi et al. 1968; Ohenoja 1971	*D. octopetala, S. polaris*	Watling 1983
H. fastible[d]	Lindblom 1841; Karsten 1872		
H. firmum[d]	Karsten 1872		
H. cf. *crustuliniforme*	Ohenoja 1971		
H. pusillum	Kobayasi et al. 1968; Ohenoja 1971	*S. rotundifolia*	Linkins and Antibus 1982
H. marginatulum	Watling 1983	*D. octopetala, S. herbacea*	Debaud 1987; Watling 1987
H. versipelle	Watling 1983	*S. herbacea*	Watling 1983
H. alpinum	Senn-Irlet et al. 1990	*D. octopetala, S. reticulata, S. serpyllifolia*	Senn-Irlet et al. 1990
Helvella corium[e]	Karsten 1872; Kobayasi et al. 1968; Ohenoja 1971; Reid 1979	*Salix* ssp.	Laursen and Chmielewski 1982
Inocybe dulcamara	Lange 1955; Kobayasi et al. 1968; Reid 1979	*D. octopetala, S. herbacea*	Miller 1987; Watling 1987
I. fastigiata (*rimosa*)	Kobayasi et al. 1968; Ohenoja 1971	*S. herbacea*	Watling 1987
I. geophylla	Ohenoja 1971		
I. leucoblema	Huhtinen 1987	*S. polaris*	Huhtinen 1987
I. praetervisa	Ohenoja 1971; Huhtinen 1987	*S. polaris*	Huhtinen 1987
I. rufo-alba	Ohenoja 1971; Huhtinen 1987	*Salix* spp.	Miller 1987
I. cf. *fuscomarginata*	Watling 1983	*D. octopetala, S. polaris*	Watling 1983
I. cf. *maleconii*[f]	Reid 1979		
I. giacomi	Senn-Irlet et al. 1990	*S. polaris, S. herbacea*	Senn-Irlet et al. 1990

Table 3 (continued)

Fungus taxa[a,m]	References	Ectotrophic symbiont	References
Laccaria laccata (tetraspora)	Dobbs 1942; Ohenoja 1971; Gulden 1988	*B. nana, D. octopetala, S. herbacea, S. rotundifolia*	Linkins and Antibus 1982; Miller 1982; Watling 1987; Gulden 1988
L. montana	Gulden 1988	*S. polaris, Saxifraga oppositifolia*	Gulden 1988
L. pumila (*torilis, striatula, altaica*)	Kobayasi et al. 1968; Ohenoja 1971; Reid 1979; Gulden 1988; Gulden and Jenssen 1988	*D. octopetala, S. polaris*	Gulden 1988; Gulden and Jenssen 1988
Lactarius nanus[e]	Ohenoja 1971; Gulden et al. 1985; Gulden 1988	*B. nana, S. herbacea, S. reticulata, S. polaris*	Gulden 1988; Gulden et al. 1988
L. groenlandicus (*dryadophilus*)	Gulden 1988	*D. octopetala, S. polaris*	Gulden 1988
L. pseudouvidus (*uvidus*)	Gulden 1988	*S. polaris*	Gulden 1988
L. robertianus[h] (*uvidus*)	Gulden 1988	*S. polaris, S. reticulata*	Ohenoja 1971; Gulden 1988
L. subdulcis[d,i]	Karsten 1872; Hagen 1950		
L. lanceolatus[j] (*thejogalus*)	Kobayasi et al. 1968; Ohenoja 1971; Watling 1983	*Betula glandulosa, D. octopetala, S. polaris, S. rotundifolia*	Knudsen and Borgen 1982; Linkins and Antibus 1982; Gulden 1988; Gulden and Jenssen 1988
L. glyciosmus	Ohenoja 1971	*S. polaris, S. reticulata*	Ohenoja 1971
Leccinum rotundifoliae	Hesselmann 1900; Gulden et al. 1985; Gulden 1988	*B. glandulosa, B. nana*	Gulden et al. 1985; Gulden 1988
Russula integra[d]	Karsten 1872		
R. ochroleuca[d]	Dobbs 1942		
R. altaica	Kobayasi et al. 1968	*S. herbacea, S. polaris*	Kobayasi et al. 1968; Knudsen and Borgen 1982
R. delica	Kobayasi et al. 1968; Ohenoja 1971	*Salix* spp.	Knudsen and Borgen 1982
R. oreina[k,l] (*xerampelina, pascua*)	Ohenoja 1971	*B. nana, D. octopetala, S. herbacea, S. rotundifolia*	Knudsen and Borgen 1982; Linkins and Antibus 1982
R. nana[n] (*emetica* var. *alpestris, alpina*)	Kobayasi et al. 1968; Ohenoja 1971	*Alchemilla alpina, B. nana, D. octopetala, Polygonum viviparum, S. polaris, S. reticulata, S. retusa, S. rotundifolia*	Hallgrimson 1963; Ohenoja 1971; Knudsen and Borgen 1982; Linkins and Antibus 1982
R. nitida	Reid 1979		

[a] Synonyms and misapplied names are given in parentheses

[b] Correct name for this taxa is probably *C. subtorvus* (Ammirati and Laursen 1982)

[c] Ohenoja (1971) and Ammirati and Laursen (1982) stated that *C. alpinus* is synonymous to *C. favrei*

[d] These names needs taxonomic re-evaluation

[e] Mycorrhizal status of this taxa needs verification

[f] Belongs to *I. fastigiata* complex

[g] Odourless form of *L. glyciosmus* by Ohenoja (1971) represents this taxa

[h] *L. uvidus* by Ohenoja (1971) represents this taxa

[i] *L. subdulcis* not recognized by Gulden (1988)

[j] *L. cf. thejogalus* by Watling 1983 represents perhaps *L. lapponicus* (Gulden 1988)

[k] *R. oreina* correct name according to Knudsen and Borgen (1982)

[l] *Russula chamiteae* is probably pro parte involved in this group (Gulden et al. 1985)

[m] Genus *Hygrophorus* probably includes mycorrhizal species which are not included and genus *Entoloma* is inadequately known

[n] *R. nana* correct name according to Gulden et al. (1985)

croscope slides, involving 10–20 cm of root from each plant. The roots studied for VA mycorrhiza were also examined for the presence of ectomycorrhiza.

Roots of potentially ectomycorrhizal species (*Salix, Dryas, Empetrum, Vaccinum, Polygonum, Pedicularis, Saxifraga*) were embedded in plastic for light microscopy. Five root segments from each sample were stained on one slide with Pianese III-B (Wilcox and Marsh 1964).

Extraction of VAM spores

A total of 11 soil samples stored dry for 21 years (collection sites in Table 2) were rehydrated for 2 weeks and then centrifuged to extract VAM spores. A 100-ml soil sample was first stirred thoroughly in a bucket containing 5 l water and then allowed to settle for 15 s. The contents of the bucket were then decanted through a 0.5-mm sieve into a second bucket, in which the suspension was swirled vigorously and again allowed to settle for 15 s. The super-

natant was poured through a 0.036-mm sieve and the trapped material was washed into a beaker. After stirring, the material was transferred to 100-ml centrifuge tubes and centrifuged in a horizontal Hettich Universal centrifuge at 895 g for 3 min. The supernatant was replaced with a 50% sucrose solution, the tubes were stirred and then centrifuged for 15 s at 395 g. The resulting supernatant was poured through a 0.036-mm sieve and the residue on the sieve washed with water to remove the sucrose solution. Finally, the residue was washed into a Petri dish and examined under a stereomicroscope.

Nomenclature

The nomenclature of the vascular plants follows Svalbards Flora (Rønning 1979) and that of the fungi is according to the literature cited in Table 3.

Results

Ecto- and ericoid mycorrhiza

Ectomycorrhizae (Table 1) were found in S. polaris, D. octopetala, and P. dasyantha, of which the first two were always mycorrhizal. These former two species form important plant communities in Spitsbergen (Eurola 1968; Hadac 1989). The mycorrhiza of S. polaris formed only in the upper soil layers, between 0 and 5 cm, below which only non-mycorrhizal roots occurred. The average mantle thickness was 10 μm in S. polaris and 25 μm in D. octopetala. P. dasyantha showed only weak infection on the tips of one root. Both C. tetragona and E. hermaphroditum possessed ericoid mycorrhiza in the present material.

VA mycorrhiza

No structures resembling VA mycorrhiza were found in 205 samples of stained roots but the centrifugation of 11 soil samples did yield one mycorrhizal spore of the genus Glomus (Fig. 2) in a sample collected in a bird cliff meadow in Midterhuken. The spore was yellowish brown, globular and 164 μm in size. Its wall was stiff, finely laminated, and consisted of one broad 23-μm layer with the remains of a very thin, outermost unit wall. The hyphal attachment was 15 μm wide and the hyphae were slightly broader at the place of attachment than elsewhere. One spore is not enough to allow identiciation of the species. The samples collected in bird cliff meadows at Camp Morton and Midterhuken and on a Dryas heath at Sveagruva also contained structures resembling VAM spores (Scutellospora sp.). However, these had very thin walls and were consequently so badly wrinkled that they could not be identified as mycorrhizal spores. The soil of bird cliff meadows is much richer in many minerals, such as N, P, K, Ca and Mg, than many other Spitsbergen soil types but the pH is much lower due to a high urea content (Eurola and Hakala 1977).

Other endophytic fungi

Fungi with spores and conidia. Endophytic fungi were commonly found in Spitsbergen. Since all the observations of fungal structures in plant roots were made from stained samples on microscope slides, assignment of the structures to fungal species is hazardous. It was possible, however, to place the fungal structures into 14 groups (Table 4). Only O. brassicae, Pleospora herbarum, Papulaspora sp. and M. bolleyi and R. solani could be identified with reasonable certainty. More than one type of endophytic fungus was found in 14% of the samples (Table 4).

Microsclerotia resembling those of M. bolleyi or Phialocephala fortinii (Fig. 3) were found inside the root cells of Polemonium boreale and Poa alpigena.

Resting sporangia of Olpidium (Fig. 4) were found in 4 samples of Saxifraga flagellaris and S. cespitosa, and structures resembling zoosporangia of Olpidium occurred in 1 sample each of Papaver dahlianum, Draba fladnizensis, Saxifraga hyperborea, S. cespitosa, Alopecurus alpinus, Trisetum spicatum, P. alpigena and Festuca vivipara.

Hyphae resembling those of R. solani (Fig. 5) were found in 7 (3.5%) samples (Table 1) studied. Papulaspora-like spores were found on Saxifraga nivalis and F. vivipara.

Dark-septate fungi. The most common fungal structures detected were DSF (Fig. 6), found in 30 (39.5%) of the species studied. Based on morphological differences, these were grouped into four categories (Table 1). There remains the possibility, however, that some of these groups overlap. The production of fungal microsclerotia is also a common feature in the roots of several plant species on Spitsbergen (Table 1). Hyaline septate hyphae (Fig. 7) were found in 7 species. Ascostromata resembling P. herbarum, the hyphae of which belong to the DSF group, were found in 1 sample each of Draba alpina, D. nivalis, S. hyperborea and S. cespitosa. Ascospores were observed inside the stroma.

Literature review and discussion

Ectomycorrhiza

We detected ectomycorrhiza on S. polaris, D. octopetala and P. dasyantha. Other ectomycorrhizal plants on Spitsbergen are Salix reticulata, which is widespread but rare on the west coast, S. glauca, S. herbacea and B. nana, which are all very rare (Rønning 1979). Salix sp. are always ectomycorrhizal in the Arctic (for references, see Table 3).

The occurrence of mycorrhiza in S. polaris and D. octopetala agrees with earlier investigations (for references, see Table 3), but in contrast to most investigations we did not detect any ectomycorrhiza in Polygonum viviparum (Hesselman 1900; Katenin 1964, 1972; Fontana 1977; Read and Haselwandter 1981; Lesica and Antibus 1986). Since Hesselman (1900) also examined
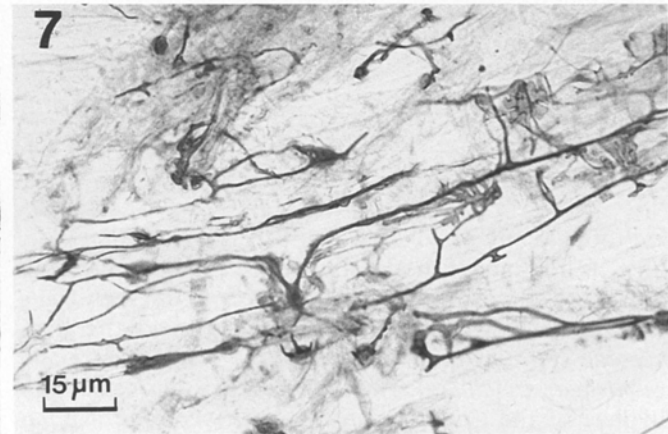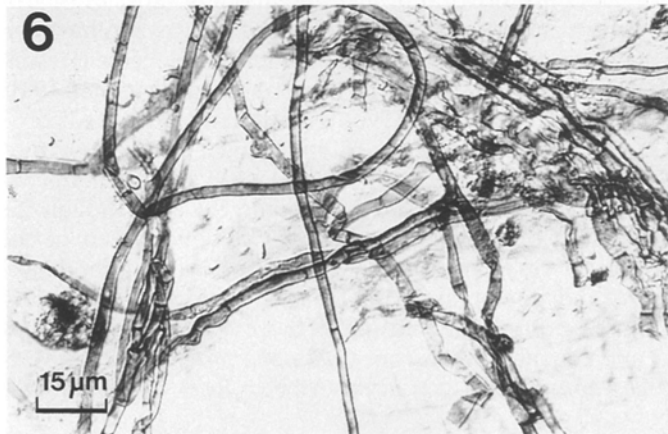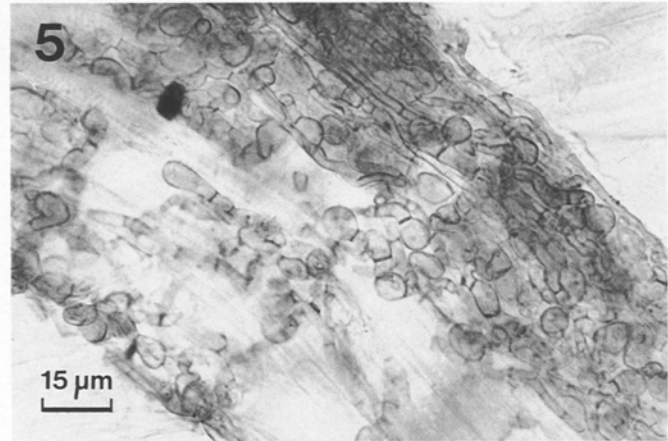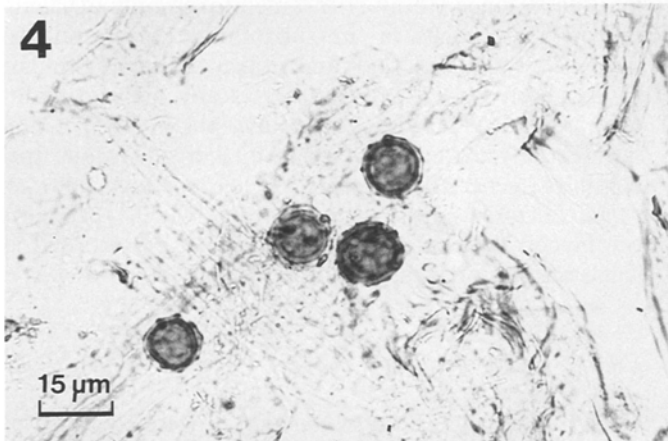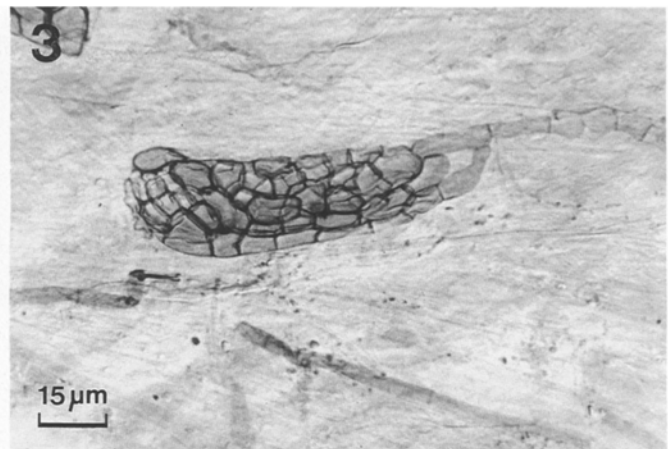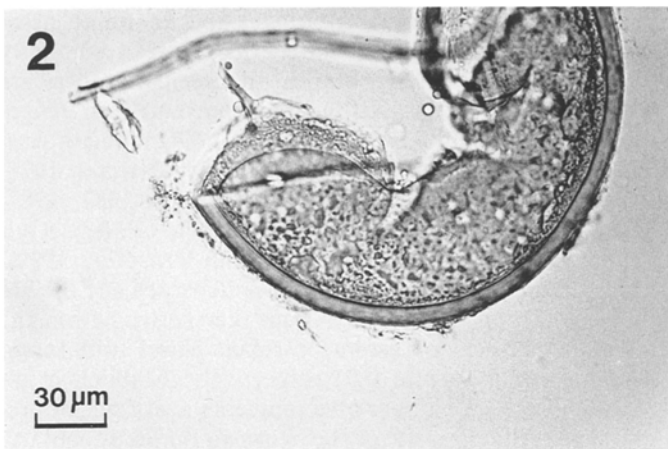
Fig. 2. Spore of *Glomus* sp. detected by centrifugation of soil from Spitsbergen; ×310

Fig. 3. Microsclerotium of a *Microdochium bolleyi*-like fungus on a root of *Poa alpigena* stained in acid fuchsin; ×625

Fig. 4. Resting sporangia of *Olpidium brassicae* on a root of *Saxifraga cespitosa* stained in acid fuchsin; ×625

Fig. 5. Hyphal swellings resembling *Rhizoctonia* sp. on roots of *Cerastium arcticum* stained in acid fuchsin; ×625

Fig. 6. Broad dark septate fungi on a root of *Silene aculis* stained in acid fuchsin; ×625

Fig. 7. Thin hyaline mycelium with sclerotia stained in acid fuchsin on a root of *Taraxacum arcticum*; ×625

mycorrhiza in Spitsbergen, *P. viviparum* is obviously ectomycorrhizal in some circumstances, e.g. when growing in the vicinity of other ectomycorrhizal plants. In accordance with our findings, Nespiak (1953) found *P. viviparum* to be non-mycorrhizal in the High Tatra Mountains (1900–2050 m).

Silene aculis and *Festuca rubra* were found to be ectomycorrhizal in the Alps (Read and Haselwandter

1981), and *Saxifraga oppositifolia* in the high Arctic of Canada (Kohn and Stasovski 1990), although these were non-mycorrhizal in the present material. *S. oppositifolia* is VAM in the High Tatra Mountains (Nespiak 1953). The occurrence of ectomycorrhiza in these species is also perhaps explained by their close co-existence with other ectomycorrhizal plants. Read and Haselwandter (1981) state that *D. octopetala* possessed typical ectomycorrhi-

Table 4. Occurrence of endophytic fungal structures on plant roots collected on Spitsbergen

Fungal structure	No. of samples	Total samples (%)
A. Resting sporangia of *Olpidium brassicae*	4	2.0
B. Zoosporangium of *O. brassicae* or others phycomycetous fungi	8	4.0
C. Broad, brown septate hyphae	14	7.0
D. Brown septate hyphae (diameter <3 μm)	25	12.5
E. Brown septate hyphae resembling *Rhizoctonia solani*	7	3.5
F. Brown septate hyphae forming sclerotia	9	4.5
G. Ascomycetous fungus resembling *Pleospora herbarum*	4	2.0
H. *Papulaspora*-like spore	2	1.0
I. *Microdochium bolleyi*-like sclerotia in cells	2	1.0
J. Hyaline hyphae turning red in acid fuchsin	7	3.5
K. Small, globose to subglobose or irregular, single spores	13	6.5
L. Coiled hyphae inside root cells	2	1.0
M. Miscellaneous structures (*Silene acaulis*; tight, hyaline hyphal clamps, *Draba fladnizensis*; oospore 13 μm, *Luzula confusa*; tightly arranged hyaline hyphae in cells, *Salix polaris*; 1 diffuse spore resembling VAM, *Draba alpina* light sclerotia in cells)	5	2.5
N. No structures	130	63.5
Total		114.5

zal roots, many of which were of the *Cenococcum* type, and the dominance of mycelium of this kind in the vicinity of *Dryas* was reflected in the presence of such fungi on a number of herbaceous species, e.g. *Kobresia myosuroides*, *P. viviparum*, *Campanula scheuchezeri* and *Saxifraga paniculata*, which were heavily infected with hyphae of the *Cenococcum* type. *Cenococcum geophilum* was not found in the present material. *Pedicularis* has been reported to be ectomycorrhizal in the high Arctic of Canada (Kohn and Stasovski 1990), in accordance with the present observations.

We did not examine *K. myosuroides*, which has been reported to be ectomycorrhizal both in alpine and arctic sites (Read and Haselwandter 1981; Kohn and Stasovski 1990). Also *K. belliardi* have been reported to be ectomycorrhizal (Fontana 1963).

The two common species, *S. polaris* and *D. octopetala*, are symbiotic with approximately 50 fungal species (Table 3), but not with *Leccinum rotundifoliae*, which is associated with *B. nana* (Hesselman 1900; Gulden 1988). *Salix* sp. have at least 38 associated fungal species in Spitsbergen, *S. polaris* 25 and *D. octopetala* 15 (for references, see Table 3). Stepanova and Tomilin (1972) re-

ported 26 ectomycorrhizal fungal species to be associated with *D. octopetala* in a *Dryas* – sedge community in the low arctic Taimyr tundra. In Greenland, there are 10 plant species involved in the ectomycorrhizal genera *Betula*, *Dryas* and *Salix* (Böcher et al. 1966), and at least 137 ectomycorrhizal fungi (Lange 1955; Petersen 1977; Watling 1977, 1983; Knudsen and Borgen 1982, 1987; Lamoure et al. 1982; Noordeloos 1984; Gulden et al. 1985; Gulden and Jenssen 1988; Senn-Irlet et al. 1990). These plant : fungi ratios, 0.04 in Spitsbergen and 0.07 in Greenland, are much lower than that derived from the overall numbers of ectomycorrhizal plants and fungi, 3500 and 5000 (ratio 0.7) respectively (Malloch et al. 1980). The high number of ectomycorrhizal fungi at arctic sites is the opposite of the situation on the subantarctic islands, since Horak (1982) mentioned only one ectomycorrhizal fungus in the subantarctic Macquarie Islands, New Zealand, and none in the Antarctic. Similarly, it is stated elsewhere that no ectomycorrhizal plants grow in the Antarctic (Komárková et al. 1985). Common ectomycorrhizal fungi on Spitsbergen include species in the genera *Cortinarius*, *Hebeloma*, *Inocybe*, *Laccaria*, *Lactarius* and *Russula*, and it is likely that more ectomycorrhizal fungi will be described or recorded as some ectomycorrhizal genera become better known.

Ericoid mycorrhiza

C. tetragona and *E. hermaphroditum* were found to be ericoid mycorrhizal in the present study. Species of *Ericaceae* and *Empetraceae* are reported always to have ericoid mycorrhiza in both alpine and arctic sites (Hesselman 1900; Katenin 1972; Read and Haselwandter 1981; Kohn and Stasovski 1990). Hesselman (1900) studied *C. (Andromeda) tetragona* in Spitsbergen, and it may thus be assumed that species of *Ericaceae* and *Empetraceae* are ericoid mycorrhizal in Spitsbergen, even though the number of individuals of *C. tetragona* studied in the present research was low in relation to its abundance. We did not obtain DSF from *C. tetragona* or *E. hermaphroditum*, in contrast to those obtained by Stoykey and Currah (1991) from *Cassiope mertensiana* and *Arctostaphylos uva-ursi* in the Alberta Rocky Mountains.

VA mycorrhiza

VA mycorrhiza was not found on roots in the present study and the extraction of spores from soil yielded only one VAM spore. The lack of VAM fungi in the roots agrees with findings in the high Arctic of Canada (Kohn and Stasovski 1990) and in maritime Antarctic (Christie and Nicolson 1983). Kohn and Stasovski (1990) detected VA mycorrhiza only in *Dryopteris fragrans*, all of their other herbaceous taxa being non-mycorrhizal or ericoid and ectomycorrhizal.

VA mycorrhiza are present in the low arctic of Siberia and Alaska (Katenin 1972; Laursen and Chmielewski 1982) and are ubiquitous in Alpine areas, where they colonize roots to varying degrees (Nespiak 1953; Crush

1973; Haselwandter and Read 1980; Read and Haselwandter 1981; Fitter 1986; Lesica and Antibus 1986; Blaschke 1991). *Deschampsia antarctica* and *Colobanthus quitensis* were VA mycorrhizal in the subantarctic islands of South Georgia and in the Falkland Islands, but non-mycorrhizal in the maritime Antarctic (Christie and Nicolson 1983).

The number of VAM spores, especially of the *Glomus* type, was low in all soils studied by Read and Haselwandter (1981) in the Austrian Alps. VAM spores (*Acaulospora scrobiculata*) were detected in the subantarctic islands of South Georgia (54°17'S), but soil samples from *D. antarctica* stands revealed no spores on Signy Island (60°43'S) (Christie and Nicolson 1983). Our results further support the notion that mycorrhizal colonization at alpine and arctic sites spreads largely by root or mycelial contact. Spores of mycorrhiza-forming *Endogonaceae* (and *Glomaceae*) are probably too large for dispersal in the upper atmosphere (Mosse 1973).

Many authors found the same herbaceous groups to be either VA mycorrhizal or non-mycorrhizal at alpine or arctic sites. For example, *Trisetum spicatum* is reported to be VA mycorrhizal by Lesica and Antibus (1986) but non-mycorrhizal by Katenin (1964), in common with the present findings. A general feature of these descriptions is the relative decrease in the number of plants colonized by VAM fungi and in the infection percentage towards polar sites and higher altitudes.

Fitter (1986) hypothesized that VAM fungi are only beneficial to plants under particular environmental conditions or at specific times in the year in alpine environments, where numerous stresses and/or external constraints limit the productivity of plant communities, e.g. a short growing season, low temperatures, mineral nutrient stress and water stress. The carbon sink from the plants to VAM fungi may be too costly under the harsh conditions prevailing at arctic sites, since the period of net photosynthesis is very short. However, the abundance of ecto- and encoid mycorrhizal associations is at variance with this, since perennial woody plants are able to allocate sugars to their ectomycorrhizal fungi at least in favourable years.

Other endophytic fungi

Microsclerotia of *M. bolleyi* (Fig. 3) were found inside the root cells of *Polemonium boreale* and *Poa alpigena*. *M. bolleyi* is a common, non-pathogenic soil fungus mainly inhabiting gramineous species but also found on potato, sugar beet and alfalfa (Domsch et al. 1980). Fitt and Hornby (1975) found that infection by this species reduced the dry weight of wheat.

The identification of *Olpidium* zoosporangia remains doubtful, however, because the root staining caused shrinking and wrinkling of these thin-walled structures. *Olpidium* is a ubiquitous soil fungus which infects the roots of various plant species in a harmless manner or acts as a fungal vector for some plant viruses such as tobacco necrosis, tobacco stunt or lettuce big vein virus (Barr and Slykhuis 1969). *Olpidium pendulum* has been

reported in Greenland, but no other species of this genus was isolated from soil samples in Alaska, Greenland or Spitsbergen (Kobayasi 1982).

Hyphae resembling those of *R. solani* were found in 7 samples. *Rhizoctonia* is widely distributed in native soils (Domsch et al. 1980). This heterogeneous genus is commonly reported to be mycorrhizal with orchids (Warcup 1981) and to have teleomorphs in several micromycetous genera, e.g. *Ceratobasidium*, *Sebacina*, *Thanatephorus* and *Tulasnella*. *R. repens* has been shown to be an anamorph of *Tulasnella calospora* (Warcup and Talbot 1967). Mature sclerotia of many rhizoctonian genera show great diversity, although the mycelium is very similar (Tu and Kimbrough 1975). *Rhizoctonia* forming mycorrhiza with orchids has been isolated from the roots of legumes and grasses (Williams 1985). In pure culture, pale or yellow-brown, irregularly septate hyphae were formed which developed monilioid hyphae and terminal or intercalary, spherical chlamydospores (12 μm) in older mycelia (Williams 1985). When inoculated onto non-orchidaceous flowering plants, growth was increased, decreased or there was no effect, depending on the strain of *Rhizoctonia* used (Williams 1985). *Rhizoctonia* isolated in a subterranean Australian orchid formed ectomycorrhiza with a myrtaceous shrub *Melaleuca uncinata* (Warcup 1985). This indicates that some rhizoctonias are also mutualistic rather than saprophytic in non-orchidaceous flowering plants.

Dark septate fungi

DSF occurred commonly in the present study. Root colonization by DSF and microsclerotia has been found above 3000 m in the nival zone of the Austrian Alps, where endomycorrhizal colonization is light (Read and Haselwandter 1981), and in the subantarctic islands (Christie and Nicolson 1983). Many plants throughout the altitude range of the Alps are infected with DSF, and it appears that the DSF become more important than the VAM fungi in increasingly stressed environments (Read and Haselwandter 1981; Haselwandter and Read 1982). DSF is the dominant infection in the *Cyperaceae*, with *Uncinia meridensis* in the Subantarctic being reported as having abundant DSF colonization in addition to heavy colonization by VAM fungi (Christie and Nicolson 1983). The *Cyperaceae* were not colonized by DSF in our material, but the number of studied species was low. In contrast, DSF was highly abundant in the *Brassicaceae*, *Caryophyllaceae*, *Saxifragaceae* and *Poaceae*, of which the former two are traditionally considered non-mycorrhizal, with minor exceptions (Tester et al. 1987), and the latter two are usually VAM. DSF are very rare in arctic Canada, where the roots are colonized instead by hyaline, translucent septate or non-septate fungal hyphae (Kohn and Stasovski 1990). Seventeen (47%) of the species investigated in subantarctic South Georgia and the Falkland Islands were colonized by DSF, including different plant families. Plate counts in the Signy Island in the Subantarctic showed that sterile dark mycelia dominated the soil fungi of *D. antarctica*

stands (Heal et al. 1967). Recently, Stoyke and Currah (1991) obtained DSF from *C. mertensiana, A. uva-ursi* and *Luetkea pectinata*. The endophyte was identified as *Phialophora fortinii*. In addition they obtained sterile DSF in *Poaceae, Caryophyllaceae, Saxifragaceae (S. oppositifolia), Rosaceae, Ericaceae (C. tetragona), Primulaceae* and *Asteraceae. Phialophora* was identified also on certain herbaceous plants in the Alps between 1910 and 1990 m above sea level (Blaschke 1991).

P. herbarum is a cosmopolitan fungal species found in a wide diversity of ecosystems, especially in the temperate and subtropical regions (Domsch et al. 1980); it has also been reported in Spitsbergen (Lind 1928; Zabawski 1976; Kobayasi et al. 1982) and has a wide arctic, circumpolar distribution (Lind 1934). The brown septate hyphae forming sclerotia-like structures in our material were presumably young hyphae of *P. herbarum* or another ascomycete, suggesting that the former is quite common in root samples from Spitsbergen. *P. herbarum* was found on the stems and leaves of 20 plant species on Spitsbergen (Lind 1928), but not in the soil (Kobayasi 1982).

Haselwandter (1987) suggested that DSF may belong either to the *Rhizoctonia* or *Phialophora*, according to descriptions published by Peyronel (1924), Cain (1952), Saksena and Vaartaja (1960) and Deacon (1973). The DSF in Spitsbergen are very similar in morphology to these genera (group D in Table 4 particularly resembles *Phialospora*) and to those described in many other articles about these or closely related fungal genera (e.g. McKeen 1952; Warcup and Talbot 1967; Cole and Kendrick 1973; Richard and Fortin 1973; Tu and Kimbrough 1975; Yang and Wilcox 1984; Iwatsu and Udagawa 1985; Wang and Wilcox 1985; Williams 1985; Yang and Korf 1985a, b). *Rhizoctonia, Phialophora* and related genera (Kendrick 1961; Yang and Wilcox 1984; Wang and Wilcox 1985; Yang and Korf 1985a, b) inhabit different substrata. Many invade rotten wood (Cain 1952; Cole and Kendrick 1973; Iwatsu and Udagawa 1985; Yang and Korf 1985b), some are pathogenic in grass roots (McKeen 1952) and some are known only as soil fungi (Yang and Korf 1985b).

Most interestingly, some DSF are reported to be mycorrhizal with various conifers. Richard and Fortin (1973) decribed *Phialocephala dimorphospora*, known earlier as *Mycelium radicis atrovirens*, a well-known E-strain, i.e. a ectendomycorrhizal fungus (Laiho 1965; Mikola 1965). Later Yang and Wilcox (1984) described a new species, *Tricharina mikolae*, forming mycorrhiza of this kind, and Wang and Wilcox (1985) three new species, *Phialophora finlandia, Chloridium paucisporum* and *P. fortinii*. The first of these was subsequently transferred to a new genus, *Wilcoxina*, and one new mycorrhizal species, *W. rehmii*, and one new variety, *W. mikolae* var. *tetraspora*, were described (Yang and Korf 1985b). A third species in the *Wilcoxina* was reported to grow on decaying mossy logs (Yang and Korf 1985b). The *Tricharina* have anamorphs in *Ascorhizoctonia* and the *Wilcoxina* in *Complexipes* (Yang and Korf 1985a, b). All these species are reported to be mycorrhizal with different conifers. The *Tricharina* includes few species

in the low Arctic sites of Alaska and Greenland (Yang and Korf 1985b) and the *Phialophora* three or four species on Spitsbergen (Kobayasi et al. 1968; Zabawski 1976; Kobayasi 1982). The *M. bolley* like sclerotia in Fig. 3 of the present paper greatly resembles Figs. 4 and 8 in the paper by Stoyke and Currah (1991), which they suggest depicts a sclerotia formed by *P. fortinii. P. fortinii* was reported in the roots of *C. mertensiana, A. uva-ursi* and *L. pectinata* (Stoyke and Currah 1991).

Healthy lateral roots of alpine *Carex* species are frequently infected by fungi which have dark septate surface hyphae and produce weakly staining, hyaline hyphal extensions in the tissues (Davies et al. 1973). Haselwandter and Read (1982) isolated two DSF strains and re-inoculated them onto aseptically germinated seedlings of two host species. The dry weight of both the roots and shoots of *Carex firma* seedlings increased significantly as a result of inoculation with DSF, whereas inoculation of *C. sempervirens* did not lead to any significant differences compared to uninoculated controls. The shoot phosphorus content increased significantly in both cases when the seedlings were inoculated with DSF (Haselwandter and Read 1982). In another study McKeen (1952) found that *Phialophora radicicola* infected corn roots aggressively but was not very pathogenic, while Peyronel (1924) reported that sterile, septate fungi were regularly associated with VAM fungi in over 100 species of flowering plants, sometimes in the same cell. Thus the functional relationship between DSF and plants may be comparable to those between ectendomycorrhizal fungi or VAM fungi and their hosts and infection with DSF seems to be mutualistic rather than parasitic, as suggested by Haselwandter (1987). The results of Peyronel (1923, 1924), Christie and Nicolson (1983) and Williams (1985) indicate that these sterile septate fungi occur together with VAM fungi at temperate and subantarctic sites, whereas they occur alone at antarctic, arctic and alpine sites.

These observations based on the literature are given as indirect evidence that at least some septate fungi (dark-septate or hyaline) colonizing various groups of plant roots operate as mutualistic entities on *Chloridium, Phialphora, Phialocephala, Rhizoctonia* s. lat., *Tricharina* and *Wilcoxina*. They may also be facultative mycorrhizal fungi, depending on a number of abiotic and biotic factors. More laboratory experiments with isolated strains such as that of Haselwandter and Read (1982) are needed to clarify the real situation. The common occurrence of DSF or hyaline septate fungi at arctic and alpine sites indicates at least that these fungi are not pathogenic for flowering plants.

References

Ammirati JF, Laursen GA (1982) Cortinarii in Alaskan arctic tundra. In: Laursen GA, Ammirati JF (eds) Arctic and alpine mycology. (The First International Symposium on Arcto-Alpine Mycology) University of Washington Press, Seattle London, pp 282–309

Barr DJS, Slykhuis JT (1969) Zoosporic fungi associated with wheat spindle streak mosaic in Ontario. Can Plant Dis Surv 49:112–113

Blaschke H (1991) Multiple mycorrhizal associations of individual calcicole host plants in the alpine grass-heath zone. Mycorrhiza 1:31–34

Böcher TW, Holmen K, Jakobsen K (1966) Grønlands flora. Haase, Copenhagen

Cain RF (1952) Studies of fungi imperfecti I. *Phialophora.* Can J Bot 30:338–343

Christie P, Nicolson TH (1983) Are mycorrhizas absent from the Antarctic? Trans Br Mycol Soc 80:557–560

Cole GT, Kendrick B (1973) Taxonomic studies of *Phialophora.* Mycologia 65:661–688

Crush JR (1973) Significance of endomycorrhizas in Tussock grassland in Otago, New Zealand. NZ J Bot 11:645–660

Davies J, Briarty LG, Rieley JO (1973) Observations on the swollen lateral roots of the *Cyparaceae.* New Phytol 72:167–174

Deacon JW (1973) *Phialophora radicicola* and *Gaeumannomyces graminis* on roots of grasses and cereals. Trans Br Mycol Soc 61:471–485

Debaud JC (1987) Ecophysiological studies on alpine macromycetes: saprophytic *Clitocybe* and mycorrhizal *Hebeloma* associated with *Dryas octopetala.* In: Laursen GA, Ammirati JF, Redhead SA (eds) Arctic and alpine mycology II. Plenum Press, New York London, pp 47–60

Dobbs CG (1942) Note on the larger fungi of Spitsbergen. J Bot 80:94–101

Domsch KH, Gams W, Anderson T-H (1980) Compendium of soil fungi. Academic Press, London New York Toronto

Eurola S (1968) Über die Fjeldheidevegetation in den Gebieten von Isfjorden und Hornsund in Westspitzbergen. Aquilo Ser Bot 7:1–56

Eurola S, Hakala A (1977) The bird cliff vegetation of Svalbard. Aquilo Ser Bot 15:1–18

Fitt BDL, Hornby D (1975) Effects of root-infecting fungi on transport of materials by young wheat plants. Rothamsted Exp Stn Rep part 1, pp 248–249

Fitter AH (1986) Effect of benomyl on leaf phosphorus concentration in alpine grasslands: a test of mycorrhizal benefit. New Phytol 103:767–776

Fontana A (1963) Micorrize ectrofiche in una Ciperacea: *Kobresia belliardi* Dgl. Giorn Bot Ital 70:639–641

Fontana A (1977) Ectomycorrhizae in *Polygonum viviparum* L. Abstracts of the 3rd North American Conference on Mycorrhizae, Athens, Georgia, 1977, p 53

Gulden G (1988) Contributions to an agaric flora of Svalbard. Botanical Museum, University of Oslo

Gulden G, Jenssen KM (1988) Arctic and alpine fungi 2. Soppkonsulenten, Oslo

Gulden G, Jenssen KM, Stordal J (1985) Arctic and alpine fungi 1. Soppkonsulenten, Oslo

Hadac E (1989) Notes on plant communities of Spitsbergen. Folia Geobot Phytotaxon 24:131–169

Hagen A (1950) Notes on the arctic fungi 1. Fungi from Jan Mayen 2. Fungi collected by Scholander on the Swedish-Norwegian arctic expedition 1931. Nor Polarinst Skr 93:1–25

Hallgrimson H (1963) Notes on *Russula alpina* (Blytt) Möll. & Schaeff. Nátturufraedingurinn 33:22–29

Haselwandter K (1987) Mycorrhizal infection and its possible ecological significance in climatically and nutritionally stressed alpine plant communities. Angew Bot 61:107–114

Haselwandter K, Read DJ (1982) The significance of root-fungus association in two *Carex* species of high-alpine plant communities. Oecologia 53:352–354

Heal OW, Bailey AD, Latter PM (1967) Bacteria, fungi and protozoa in Signy Island soils compared with those from a temperate moorland. Phil Trans R Soc Ser B 252:191–197

Hesselman H (1900) Mycorrhizal formation in arctic plants (in Swedish). Bihang Till K Svensk Vetens-Akad Handlinger 26:1–46

Horak E (1982) Agaricales in Antarctica and Subantarctica: distribution, ecology, and taxonomy. In: Laursen GA, Ammirati JF (eds) Arctic and alpine mycology. (The First International Symposium on Arcto-Alpine Mycology) University of Washington Press, Seattle London, pp 82–118

Huhtinen S (1987) New Svalbard fungi. In: Laursen GA, Ammirati JF, Redhead SA (eds) Arctic and alpine mycology II. Plenum Press, New York London, pp 123–151

Iwatsu T, Udagawa S-I (1985) A new species of *Phialophora* from Japan. Mycotaxon 24:387–393

Kankainen E, Karlström P, Heikkilä H (1967) Expedition to Spitsbergen by Kevo biological station researchers in 1966 (in Finnish). Luonnon Tutkija 71:118–123

Karsten PA (1872) Fungi of Spitsbergen and Bear Island (in Latin). Övers Kongl Vet-Akad Förhandl 2:91–108

Katenin AE (1964) Mycorrhiza of arctic plants (in Russian). Probl Severa 8:148–154

Katenin AE (1972) Mycorrhiza in tundra plants of the northeastern European part of the USSR (in Russian with English summary). In: Tikhomirov BA (ed) The vegetation of the north of the USSR and its utilization. Bot Inst Ameni BL Komarova, Leningrad, pp 1–140

Kendrick WB (1961) The *Leptographium* complex. *Phialocephala* gen. nov. Can J Bot 39:1079–1085

Knudsen H, Borgen B (1982) *Russulaceae* in Greenland. In: Laursen GA, Ammirati JF (eds) Arctic and alpine mycology. (The First International Symposium on Arcto-Alpine Mycology) University of Washington Press, Seattle London, pp 216–239

Knudsen H, Borgen B (1987) *Agaricaceae, Amanitaceae, Boletaceae, Gomphidiaceae* and *Pluteaceae* in Greenland. In: Laursen GA, Ammirati JF, Redhead SA (eds) Arctic and alpine mycology II. Plenum Press, New York London, pp 235–253

Kobayasi Y (1982) Ecology and distribution of Arctic lower fungi. In: Laursen GA, Ammirati JF (eds) Arctic and alpine mycology. (The first International Symposium on Arcto-Alpine Mycology) University of Washington Press, Seattle London, pp 16–23

Kobayasi Y, Tubaki K, Soneda M (1968) Enumeration of the higher fungi, moulds and yeasts of Spitsbergen. Bull Nat Sci Mus 11:76

Kohn LM, Stasovski E (1990) The mycorrhizal status of plants at Alexandra Fiord, Ellesmere Island, Canada, a high arctic site. Mycologia 82:23–35

Komárková V, Ponchet S, Ponchet J (1985) Two native Antarctic vascular plants, *Dechampsia antarctica* and *Colobanthus quitensis*: a new southernmost locality and other localities in the Antarctic Peninsula area. Arct Alp Res 17:401–416

Kormanik PP, Bryan WC, Schultz RC (1980) Procedures and equipment for staining large numbers of plant roots for endomycorrhizal assay. Can J Microbiol 26:536–538

Krzywy T, Szerszen L, Wieczorek J (1961) Occurrence of Actinomycetes in Spitsbergen in relation to ecologic factors. Arch Immunol Ter Dosw 9:253–260

Laiho O (1965) Further studies on the ectendotrophic mycorrhiza. Acta For Fenn 79:1–35

Lamoure D, Lange M, Petersen PM (1982) Agaricales found in the Godhavn area, W. Greenland. Nord J Bot 2:85–90

Lange M (1955) Macromycetes, part II. Greenland Agaricales. Medd Grøn 147:1–69

Laursen GA, Chmielewski MA (1982) The ecological significance of soil fungi in arctic tundra. In: Laursen GA, Ammirati JF (eds) Arctic and alpine mycology. (The First International Symposium on Arcto-Alpine Mycology) University of Washington Press, Seattle London, pp 432–488

Lesica P, Antibus RK (1986) Mycorrhizae of alpine fell-field communities on soils derived from crystalline and calcareous parent materials. Can J Bot 64:1691–1697

Lind J (1928) The micromycetes of Svalbard. Skr Svalbard Ishavet 13:1–61

Lind J (1934) Studies on the geographical distribution of arctic circumpolar micromycetes. Dan Vidensk Selsk Biol Medd 11:1–152

Lindblom AF (1841) Notes on plants in Spitsbergen and Bear Island (in Swedish). Bot Not 1839–1840:153–158

Linkins AE, Antibus RK (1982) Mycorrhizae of *Salix rotundifolia* in coastal arctic tundra. In: Laursen GA, Ammirati JF (eds) Arctic and alpine mycology. (The First International Symposium on Arcto-Alpine Mycology) University of Washington Press, Seattle London, pp 509–526

Malloch DW, Pirozynski KA, Raven PH (1980) Ecological and evolutionary significance of mycorrhizal symbiosis in vascular plants (a review). Proc Natl Acad Sci USA 77:2113–2118

McKeen WE (1952) *Phialophora radicicola* Cain, a corn root-rot pathogen. Can J Bot 30:344–347

Mikola P (1965) Studies on the ectendotrophic mycorrhiza of pine. Acta For Fenn 79:1–56

Miller OK Jr (1982) Higher fungi in Alaskan subarctic tundra and taiga plant communities. In: Laursen GA, Ammirati JF (eds) Arctic and alpine mycology. (The First International Symposium on Arcto-Alpine Mycology) University of Washington Press, Seattle London, pp 123–144

Miller OK Jr (1987) Higher fungi in tundra and subalpine tundra from the Yukon territory and Alaska. In: Laursen GA, Ammirati JF, Redhead SA (eds) Arctic and alpine mycology II. Plenum Press, New York London, pp 287–297

Mosse B (1973) Advances in the study of vesicular-arbuscular mycorrhiza. Annu Rev Phytopathol 11:171–196

Nespiak A (1953) Mycotrophy of the alpine vegetation of the Tatra Mountains (in Polish with English summary). Acta Soc Bot Pol 22:97–125

Noordeloos ME (1984) *Entolomataceae* (Agaricales, Basidiomycetes) in Greenland. I. The genus *Entoloma*. Persoonia 12:263–305

Ohenoja E (1971) The larger fungi of Svalbard and their ecology. Rep Kevo Subarct Res Stn 8:122–147

Petersen PM (1977) Investigations on the ecology and phenology of the macromycetes in the arctic. Medd Grønl 199:1–72

Peyronel B (1923) Fructifications de l'endophyte á vésicles des mycorrhizes endotrophes. Bull Trimest Soc Mycol Fr 39:119–126

Peyronel B (1924) Prime ricerche sulle micorrize endotrofiche e sulla microflora radicicola normale delle fanerogame. Riv Biol 6:17–53

Read DJ, Haselwandter K (1981) Observations on the mycorrhizal status of some alpine plant communities. New Phytol 88:341–352

Reid DA (1979) Some fungi from Spitsbergen. Rep Kevo Subarct Res Stn 15:41–47

Richard C, Fortin J-A (1973) The identification of *Mycelium radicis atrovirens* (*Phialocephala dimorphospora*). Can J Bot 51:2247–2248

Rønning OI (1979) Flora of Spitsbergen (in Norwegian). Polarhåndbok Nr. 1. Norsk Polarinstitutt, Oslo

Saksena HK, Vaartaja O (1960) Descriptions of new species of *Rhizoctonia*. Can J Bot 38:930–943

Senn-Irlet B, Jenssen KM, Gulden G (1990) Arctic and alpine fungi 3. Soppkonsulenten, Oslo

Smith VR, Newton IP (1986) Vesicular-arbuscular mycorrhizas at a sub-antarctic island. Soil Biol Biochem 18:547–549

Stepanova IV, Tomilin B (1972) Fungi of basic plant communities in Taimyr tundras. In: Wielgolaski FE, Rosswall T (eds) International Biological Programme Tundra Biome Proceedings II. Berlinska Boktryckeriet, Lund, pp 193–198

Stoyke G, Currah RS (1991) Endophytic fungi from the mycorrhizae of alpine ericoid plants. Can J Bot 69:347–352

Stutz RC (1972) Survey of mycorrhizal plants. In: Bliss LC (ed) Devon Island I.B.P. project. High arctic ecosystem project report 1970 and 1971. Department of Botany, University of Alberta, pp 214–216

Tester M, Smith SE, Smith FA (1987) The phenomenon of "nonmycorrhizal" plants. Can J Bot 65:419–431

Tu CC, Kimbrough JW (1975) Morphology, development, and cytochemistry of the hyphae and sclerotia of species in the *Rhizoctonia* complex. Can J Bot 53:2282–2296

Wang CJK, Wilcox HE (1985) New species of ectendomycorrhizal and pseudomycorrhizal fungi: *Phialophora finlandia, Chloridium paucisporum*, and *Phialacephala fortinii*. Mycologia 77:951–958

Warcup JH (1981) The mycorrhizal relationships of Australian orchids. New Phytol 87:371–381

Warcup JH (1985) *Rhizanthella gardneri* (*Orchidaceae*), its *Rhizoctonia* endophyte in close association with *Melaleuca uncinata* (*Myrtaceae*) in western Australia. New Phytol 99:273–280

Warcup JH, Talbot PHB (1967) Perfect states of rhizoctonias associated with orchids. New Phytol 66:631–641

Watling R (1977) Larger fungi from Greenland. Astarte 10:61–71

Watling R (1983) Larger cold-climate fungi. Sydowia 36:308–325

Watling R (1987) Larger arctic-alpine fungi in Scotland. In: Laursen GA, Ammirati JF, Redhead SA (eds) Arctic and alpine mycology II. Plenum Press, New York London, pp 17–45

Wieczorek J, Szerszen L, Krzywy T, Baranowski S (1964) The occurrence of Actinomycetes in the region of the Werenskiold glacier (SW Spitsbergen) in relation to ecologic factors. Arch Immunol Ther Exp 12:14–24

Wilcox HE, Marsh LG (1964) Staining plant tissues with chlorazol black E and Pianese III-B. Stain Technol 39:81–86

Williams PG (1985) Orchidaceous rhizoctonias pot cultures of vesicular-arbuscular mycorrhizal fungi. Can J Bot 63:1329–1333

Yang CS, Korf RP (1985a) *Ascorhizoctonia* gen. nov. and *Complexipes* emend., two genera for anamorphs of species assigned to *Tricharina* (Discomycetes). Mycotaxon 23:457–481

Yang CS, Korf RP (1985b) A monograph of the genus *Tricharina* and of a new, segregate genus, *Wilcoxina* (Pezizales). Mycotaxon 24:467–551

Yang CS, Wildcox HE (1984) An E-strain ectendomycorrhiza formed by a new species, *Tricharina mikolae*. Mycologia 76:675–684

Zabawski J (1976) Soil fungi isolated from peat bogs in Hornsund region (West Spitsbergen). In: New recognitions of peatlands and peat II. Proceedings of the 5th International Peat Congress, Poznań, Poland, pp 158–170