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Mycorrhizae from Denali National Park and Preserve, Alaska

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Abstract Roots of 40 taxa of higher plants (Pteridophyta, Spermatophyta) from two alpine study sites in Denali National Park and Preserve in central Alaska were examined for their mycorrhizal colonization. We observed ectomycorrhizae on six species: *Betula nana*, *Salix reticulata*, *Salix polaris*, *Salix arctica*, *Polygonum viviparum*, and *Dryas octopetala*. Seven taxa, *Cassiope tetragona*, *Empetrum nigrum*, *Ledum palustre* subsp. *decumbens*, *Ledum palustre* subsp. *groenlandicum*, *Loiseleuria procumbens*, *Vaccinium uliginosum* and *Vaccinium vitis–idaea* (all Ericales), had ericoid mycorrhizae. One species, *Arctostaphylos alpina*, formed a typical arbutoid mycorrhiza. Two species (*Sibbaldia procumbens* and *Aconitum delphinifolium*) showed well-developed VA mycorrhizae, whereas three species of plants (*Lycopodium clavatum*, *Silene acaulis* and *Oxytropis scammaniana*) had vesicles, but no arbuscules. The roots of 11 other plants (*Lycopodium clavatum*, *Lycopodium selago*, *Silene acaulis*, *Gentiana algida*, *Lupinus arcticus*, *Oxytropis scammaniana*, *Pedicularis langsdorffii*, *Pedicularis capitata*, *Pedicularis verticillata*, *Artemisia* sp. and *Carex bigelowii*) had a variety of intracellular colonizations which are referred to as dark septate fungi. No mycorrhizae were found on 12 other plants: *Equisetum arvense*, *Equisetum variegatum*, *Lycopodium alpinum*, *Polygonum bistorta*, *Saxifraga hieracifolia*, *Saxifraga hirculus*, *Astragalus alpinus*, *Pedicularis kanei*, *Petasites frigidus*, *Carex podocarpa*, *Carex microchaeta* and *Poa arctica*. A possible ecological role of dark septate fungi is discussed.

Key words Mycorrhizae · Arctic-alpine · Dark septate fungi

Introduction

Although different classes of mycorrhizae may be encountered in most ecosystems (Brundrett 1991), these root-fungus associations play a particularly essential ecological role in some highly stressed environments such as areas of Arctic and alpine habitat (Haselwandter 1987). Arctic and alpine plant communities experience short growing periods, low temperatures, low nutrient status and low decomposition rates (Grime 1979). Mycorrhizal fungi aid their host in various ways to increase nutrient uptake from the soil (Harley and Smith 1983) and may therefore alleviate nutritional stress situations encountered by their host plants. Considering the benefits of mycorrhizae for the host plants, a high mycorrhizal colonization of Arctic-alpine plants might be expected.

Mycorrhizal colonization of Arctic and alpine plants has been studied to some extent in different parts of the northern hemisphere. A first and rather comprehensive study of Arctic plants from Spitsbergen was conducted by Hesselman (1900). Nespiak (1953) studied alpine plant roots in the Tatra Mountains. Katenin (1964) surveyed plants in the Siberian tundra. Miller and Laursen (1978), in the Alaskan Arctic at Barrow, and Miller (1982), on Eagle Summit, studied the mycorrhizal roots of a variety of plants. Haselwandter and Read (1980) as well as Read and Haselwandter (1981) reported a variety of mycorrhizal types on roots of alpine plants in the Austrian Alps. Lesica and Antibus (1986) studied VA

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mycorrhizae of plants from the Rocky Mountains of Montana and Wyoming. Allen et al. (1987) examined the status of VA plants at an alpine site in Montana. Kohn and Stasovski (1990) surveyed the mycorrhizae of higher plants on Ellesmere Island in the Canadian Arctic as did Bledsoe et al. (1990) for Truelove Lowland in the Northwest Territories of Canada. Arctic plants from Spitsbergen were recently examined by Väre et al. (1992). Plants from Antarctic areas were surveyed for mycorrhizae by Christie and Nicolson (1983) and by Smith and Newton (1986).

Although information on the mycorrhizal status of Arctic and alpine plants is now available for many species, the results of these studies are not consistent. Obviously, alpine plants are mycorrhizal to a high degree (Haselwandter 1987), and similar results are reported for Arctic plants from Siberia (Katenin 1964) and from alpine plants at Eagle Summit, Alaska by Miller (1982). On the other hand, Kohn and Stasovski (1990) and Väre et al. (1992) described a remarkable paucity at least in the case of VA colonizations in Arctic areas.

In the present study, an attempt was made to evaluate the mycorrhizal status of some vascular plants from two alpine study areas in Denali National Park and Preserve, Alaska.

Materials and methods

Site description

Five study sites from which vascular plant roots were collected are located in Central (Interior) Alaska and within Denali National Park and Preserve, latitude 63° 45′ N, 150° W. This region of Alaska is characterized by a continental montane climate with short, cool summers and long, severe winters. Mean monthly temperatures range from January lows of –17° C to July highs of 12° C. Annual snow fall averages 1090 mm and may persist from early October through early May. Vegetation is that typically found throughout Interior Alaska. Alpine tundra, as described by Viereck and Little (1972), occurs on the higher peaks and ridges, but gives way to low shrub communities on most slopes and to tall shrub communities along stream drainages. Upland forests dominated by white spruce [*Picea glauca* (Moench) Voss] occupy the lower slopes and river terraces.

In the west and within the Kantishna Hills, two sites were established; Glen Creek revegetation plots on Glen Creek (GR) and the Glen Creek alpine meadow site (GA). Placer gold deposits occur in many of the stream drainages of the Kantishna Hills and have been mined since their discovery in 1903. Past mining activities have had a considerable impact on Glen, Spruce and Moose Creeks, those creeks forming the drainage within which the Glen Creek plots were established and which also drains site GA. The original Glen Creek stream channel was mildly to severely altered and most, if not virtually all, native riparian stream bank vegetation was lost. The most severely disturbed sections of the original stream consisted of channelized stream courses flanked by piles of placer mine tailings and barren areas. Natural vegetation recovery was very slow. In 1989, as part of an effort to reclaim the lower 3.6 km of Glen Creek, the National Park Service initiated a large-scale experiment in assisted revegetation. Along sections of the stream, debris was removed or contoured and with available fine material redistributed over the coarse cobble and rubble. This riparian zone of 12 large, permanently marked study plots representing different riparian restoration treatments contains feltleaf willow [*Salix alaxensis* (Andersson) Cov.] and green alder [*Alnus crispa* (Aiton) Pursh] established from the regraded Glen Creek cobble-rubble remains of placer gold mining operations. Study site GR lies within this area at an altitude of 640 m, lat. 63° 31′ 45′′ N, long. 150° 42′ 01′′ W. Precipitation is most often associated with that determined for Wonder Lake, ca. 469 mm (unpublished data), just a few miles WSW of the Glen Creek Field Camp and study site. Site GA, by contrast, is above the revegetation treatment plots at 975 m, lat. 63° 32′ 50′, long. 150° 44′ 33′′ and is composed of alpine tundra supported by 597 mm of precipitation. Higher plant components number approximately 20 species.

In contrast to the two western sites are the three eastern sites located within the Rock Creek drainage. The alpine site (RA) is located at 1346 m, lat. 63° 45′ 15′′ N, long. 149° 00′ 46′′ W. It maintains 630 mm of precipitation and is composed of an alpine tundra higher plant component once again numbering about 20 species. A treeline site (RT) was established at 980 m, lat. 63° 44′ 08′′, long. 149° 00′ 27′′. Here, a shrub dwarf Arctic birch (*Betula nana* L.) and resin birch (*Betula glandulosa* Michx.) community is supported by 457 mm of precipitation. A comparative riparian site (RR), but one which was not placer mined, was established along lower Rock Creek at 735 m, lat. 63° 43′ 54′′, long. 148° 58′ 59′′. This community consists primarily of closed, tall shrub green alder which is supported by 380 mm of precipitation, as measured at Park Headquarters (unpublished data) a few kilometers downstream.

The alpine tundra sites (GA and RA) were comparable. The GR riparian site was greatly disturbed and revegetated, whereas the Rock Creek sites (RA, RT and RR) were undisturbed.

Preparation of root material

In the summer (August) of 1992, plants with their roots were removed from organic soils with the aid of a large knife and stored in plastic bags. Roots were refrigerated as soon as possible. At least two root samples of each plant species were taken. Prior to examination under a dissecting microscope, the root samples were soaked in water for 12 h. For a closer examination of the rootlets, adhering soil particles were carefully removed with the aid of fine forceps. Due to the presence of an intertwined mass of many different roots in most of the samples, only those roots that could be traced back unambiguously to the plant under study were considered.

From ectomycorrhizal (and arbutoid) roots, a representative mycorrhizal type was chosen to make mantle scrapings with a fine insect needle following the methods described by Agerer (1987–1993). The same mycorrhiza was also used for cross sections. A CO_2-cooled hand cryotome was used to prepare sections from rootlets previously transferred into a watery solution of glycerol (2%) for at least 12 h. Cross sections were examined under a phase-contrast microscope for mantle, Hartig net, and possible intracellular colonizations. Rootlets that were not ectomycorrhizal were isolated, cleaned and transferred into formalin: ethanol 70%: acetic acid (5:90:5).

After fixation for at least one day the roots were stained in Chlorazol Black E solution after Brundrett et al. (1984) to evaluate VAM and other intracellular colonizations. The fine rootlets of members of the Ericales were also examined in lactic acid for the presence of intracellular hyphal coils.

A Leitz Dialux compound microscope was used and photographs were taken with an Orthomat W photo unit. A Zeiss dissection microscope with a Contox 35 mm camera was used for macrophotographs of external root architecture.

The nomenclature of plants follows Hultén (1968). Mycorrhizal classes are designated according to Harley and Smith (1983).

Table 1 Plants examined and their type of mycorrhizal colonization. Sites: *GA* Glen Creek alpine site, *GR* Glen Creek riparian site, *RA* Rock Creek alpine site, *RR* Rock Creek riparian site, *RT* Rock Creek, treeline. Mycorrhizas: *AR* arbutoid mycorrhiza, *EM* ectomycorrhiza, *ER* ericoid mycorrhiza, *MS* microsclerotia, *NM* nonmycorrhizal without intracellular colonization, *VA* vesicular-arbuscular mycorrhiza

Plant species	Site	Mycorrhiza
Equisetaceae		
Equisetum arvense L.	RR	NM
E. variegatum Schleich.	GR	NM
Lycopodiaceae		
Lycopodium alpinum L.	GA	NM
L. clavatum L.	GA	MS
L. selago L.	GA	MS
Ranunculaceae		
Aconitum delphinifolium DC.	GA	VA
Salicaceae		
Salix arctica Pall.	RA	EM
S. polaris Wahlenb.	RA	EM
S. reticulata L.	RA	EM
Polygonaceae		
Polygonum bistorta L.	GA	NM
P. viviparum L.	RA	EM
P. viviparum L.	GA	EM
Betulaceae		
Betula nana L.	RT	EM
Caryophyllaceae		
Silene acaulis L.	RA	MS
Empetraceae		
Empetrum nigrum L.	RA	ER
Ericaceae		
Arctostaphylos alpina (L.) Spreng.	RT	AR
Cassiope tetragona (L.) D. Don	GA	ER
Ledum palustre L. subsp. *decumbens* (Aiton) Hult.	RA	ER
L. palustre L. subsp. *groenlandicum* (Oeder) Hult.	RR	ER
L. palustre L. subsp. *groenlandicum* (Oeder) Hult.	GA	ER
Loiseleuria procumbens (L.) Desv.	GA	ER
Vaccinium uliginosum L.	RR	ER
V. uliginosum L.	GA	ER
V. vitis-idaea L.	RT	ER
V. vitis-idaea L.	GA	ER
Gentianaceae		
Gentiana algida Pall.	GA	MS
Saxifragaceae		
Saxifraga hieracifolia Waldst. & Kit.	RA	NM
S. hirculus L.	GA	NM
Rosaceae		
Dryas octopetala L.	RA	EM
Sibbaldia procumbens L.	RA	VA
Fabaceae		
Astragalus alpinus L.	RA	NM
Lupinus arcticus S. Watson	RT	MS
Oxytropis scammaniana Hult.	RA	MS
Scrophulariaceae		
Pedicularis capitata Adams	RA	MS
P. kanei Durand	GA	NM
P. langsdorffii Fisch.	RA	MS
P. verticillata L.	RA	MS
Asteraceae		
Artemisia spec.	GA	MS
Petasites frigidus (L.) Franch.	RA	NM
Cyperaceae		
Carex bigelowii Torr.	GA	MS
C. microchaeta Holm	RA	NM
C. podocarpa C. B. Clarke	GA	NM
Poaceae		
Poa arctica R. Br.	RA	NM

Results and discussion

Table 1 shows the occurrence of mycorrhizae in the species examined.

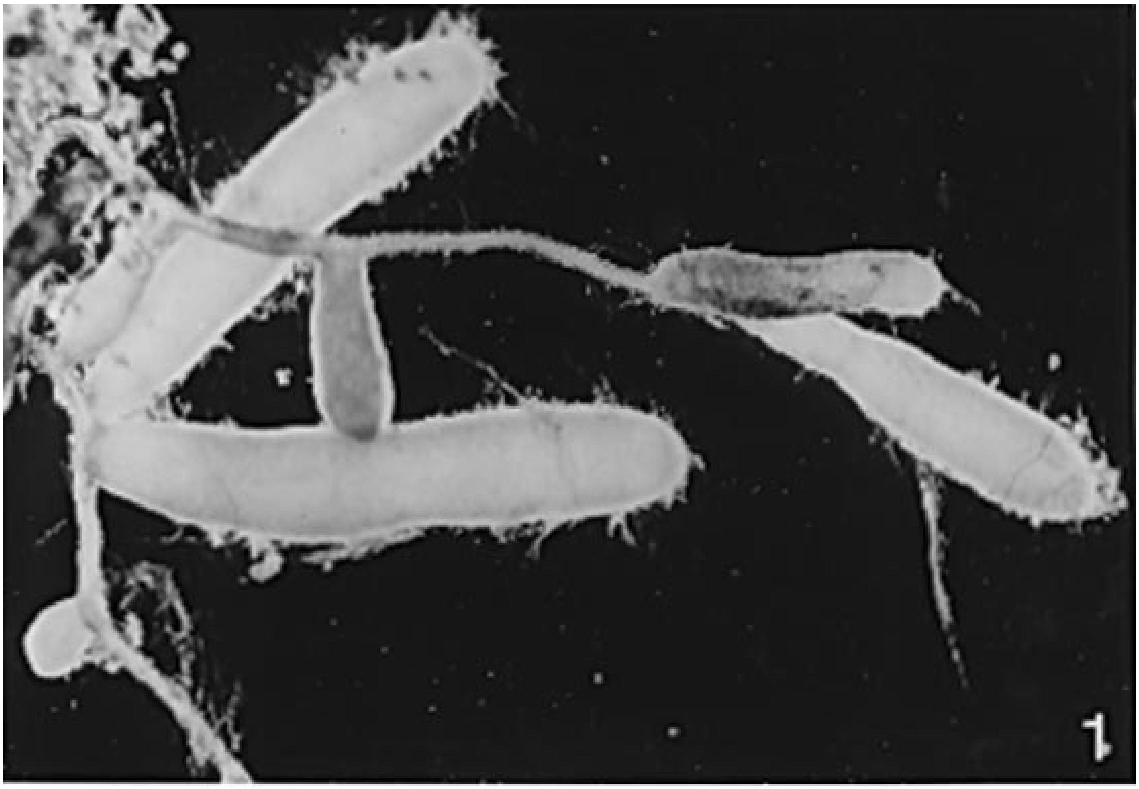
Ectomycorrhizae

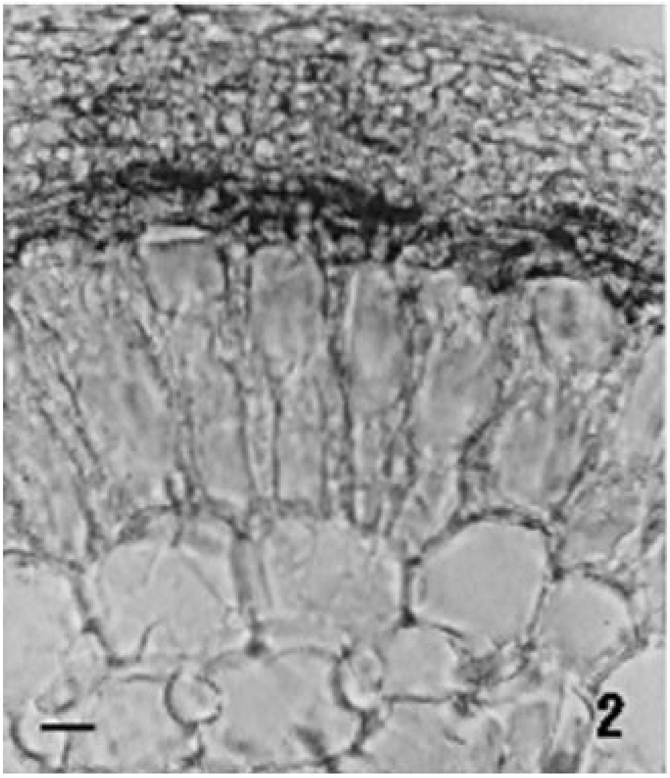
Ectomycorrhizae were consistently present on *Betula nana* (Fig. 2), on all *Salix* species and on *Dryas octopetala*. All ectomycorrhizae formed a mantle and a well-developed Hartig net. All these species have been reported to be ectomycorrhizal by numerous workers (e.g. Trappe 1962; Miller 1982; Harley and Harley 1987). *Polygonum viviparum* was also ectomycorrhizal (Fig. 1) with unramified, club-like mycorrhizae. The reports about the mycorrhizal status of this plant are incongruous considering both alpine and Arctic habitats. In the Arctic neither Bledsoe et al. (1990) nor Väre et al. (1992) found *Polygonum viviparum* to be ectomycorrhizal; however, both Hesselman (1900) and Katenin (1964) indicated ectomycorrhizae from this plant. In alpine habitats, Nespiak (1953) did not find ectomycorrhizae on roots of *Polygonum viviparum* in the Tatra mountains, but they were reported by Fontana (1977) from the Italian Alps, by Haselwandter and Read (1980) from the Austrian Alps, by Blaschke (1991) from the Bavarian Alps, and by Lesica and Antibus (1986) from the Rocky Mountains. In summary, these various reports suggest that ecological conditions determine whether or not ectomycorrhizae are formed by this species.

Mycorrhizae of *Cenococcum geophilum* are easy to recognize (Trappe 1964; Gronbach 1988) and were found on *Salix arctica*, *Salix reticulata*, *Dryas octopetala* and *Polygonum viviparum*. Although this mycorrhiza is especially adaptable to dry conditions (Mexal and Reid 1973), it has also been found in Arctic-alpine areas numerous times (Trappe 1964).

Arbutoid mycorrhizae

One plant, *Arctostaphylos alpina*, showed arbutoid mycorrhizae with all the characters defining that structure,





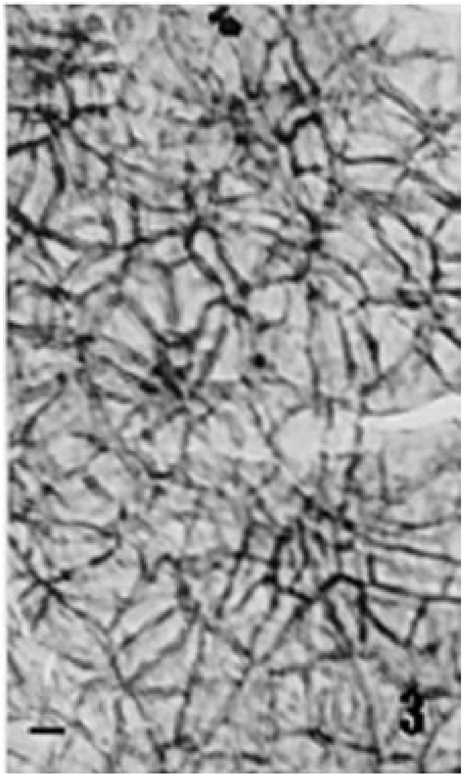


Fig. 1 *Polygonum viviparum*. Ectomycorrhizae. ×50

Fig. 2 *Betula nana*. Ectomycorrhiza in cross section showing mantle and Hartig net. *Bar* (Figs. 2–9) 10 μm

Fig. 3 *Arctostaphylos alpina*. Mantle surface view of arbutoid mycorrhiza

i.e. a mantle (Fig. 3), a Hartig net and distinct intracellular haustoria in the first row of cortical cells (Fig. 4), the latter being the only character distinguishing them from true ectomycorrhizae. *Arctostaphylos uva–ursi* (L.)Spreng. has been reported in the literature to be arbutoid mycorrhizal (Zak 1976; Molina and Trappe

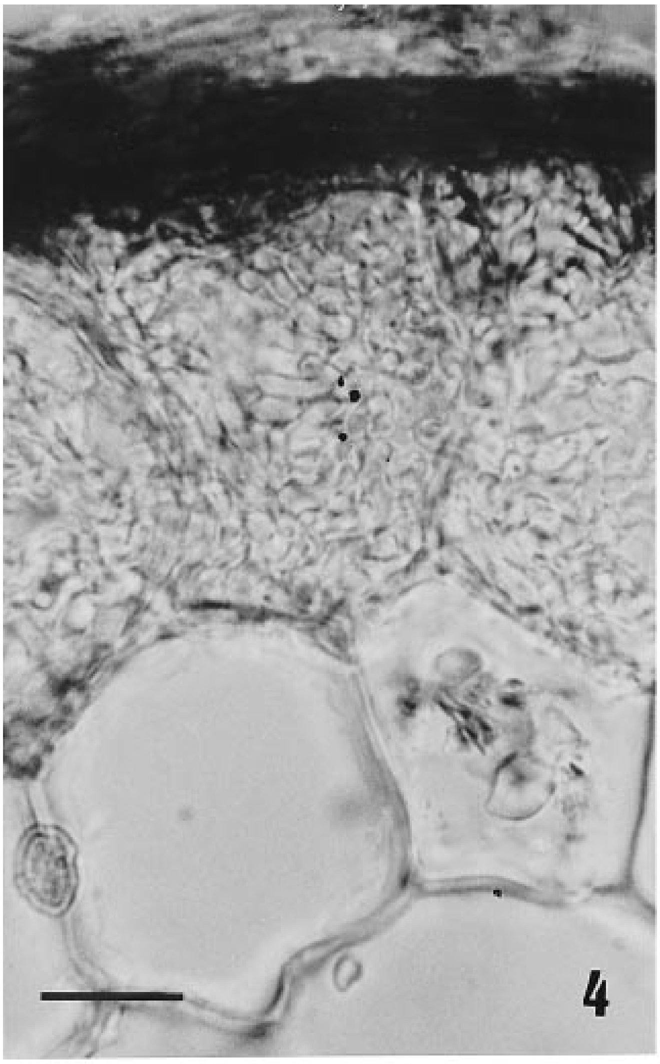


Fig. 4 *Arctostaphylos alpina*. Cross section of arbutoid mycorrhiza with intracellular hyphae

Fig. 5 *Ledum palustre* subsp. *decumbens*. Ericoid mycorrhiza. Dark hypha with extension penetrating root cortical cell to form intracellular coiling

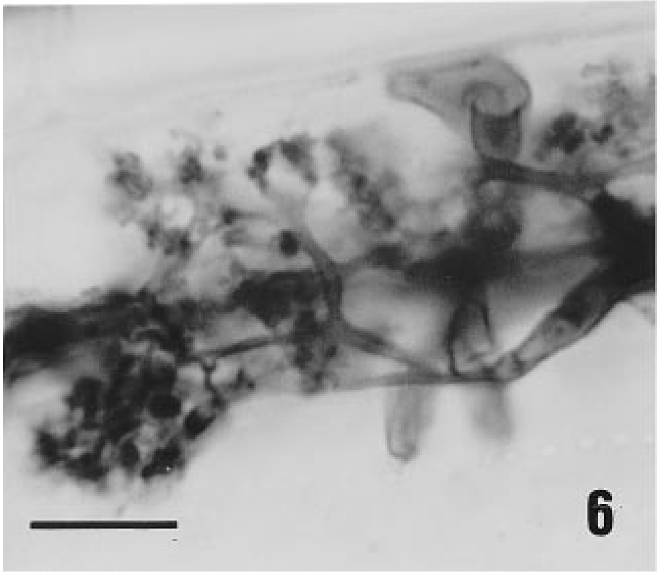


Fig. 6 *Sibbaldia procumbens* VA mycorrhiza arbuscles

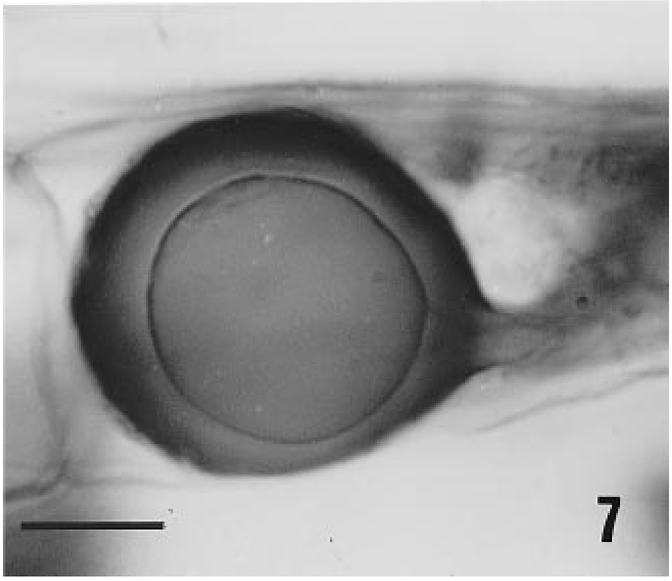


Fig. 7 *Sibbaldia procumbens* VA mycorrhiza vesicle

1982) but the intracellular hyphae may sometimes be absent, which would define such a structure as a true ectomycorrhiza (Mejstřík and Hadač 1975). Miller (1982) found *Arctostaphylos rubra* (Rehd. & Wils.) Fern. to have arbutoid mycorrhizae or ectomycorrhizae.

Ericoid mycorrhizae

All species of the Ericales (*Cassiope tetragona*, *Empetrum nigrum*, *Ledum palustre* subsp. *decumbens* (Fig. 5), *Ledum palustre* subsp. *groenlandicum*, *Loiseleuria procumbens*, *Vaccinium uliginosum*, *Vaccinium vitis–idaea*) with the exception of *Arctostaphylos alpina* (with arbutoid mycorrhizae) were ericoid mycorrhizal with dark brown hyphae and typical intracellular coils, a condition that has consistently been reported in the literature (Miller 1982; Read 1983; Brundrett 1991; Stoyke and Currah 1991).

Mycorrhizal diversity

Ectomycorrhizae and arbutoid mycorrhizae show enough morphological and anatomical differentiation to recognize different species of mycorrhiza-forming fungi. Roots of individual ectomycorrhizal plants (*Dryas octopetala*, *Polygonum viviparum*, *Salix arctica*, *Salix polaris*, *Salix reticulata*) always had at least three different ectomycorrhizae associated with their root systems, formed by an equal number of different fungi. *Betula nana* was an exception with almost exclusively one type of ectomycorrhiza. At least four different arbutoid mycorrhizae could be distinguished on the roots of *Arctostaphylos alpina*. The mycorrhizae of *Cenococcum geophilum* Fr. were found on *Dryas octopetala*, *Salix arctica*, *Salix reticulata* and *Polygonum viviparum*.

Mycorrhizae from different sites

Three species of plants were collected from two different sites: *Polygonum viviparum* from the RA and GA sites, *Ledum palustre* subsp. *groenlandicum* from RR and GA and *Vaccinium vitis–idaea* from RT and GA. In each case the plant species had the same classes of mycorrhizae from both sites: ectomycorrhizae on roots of *Polygonum viviparum* and ericoid mycorrhizae on *Ledum palustre* and *Vaccinium vitis–idaea*.

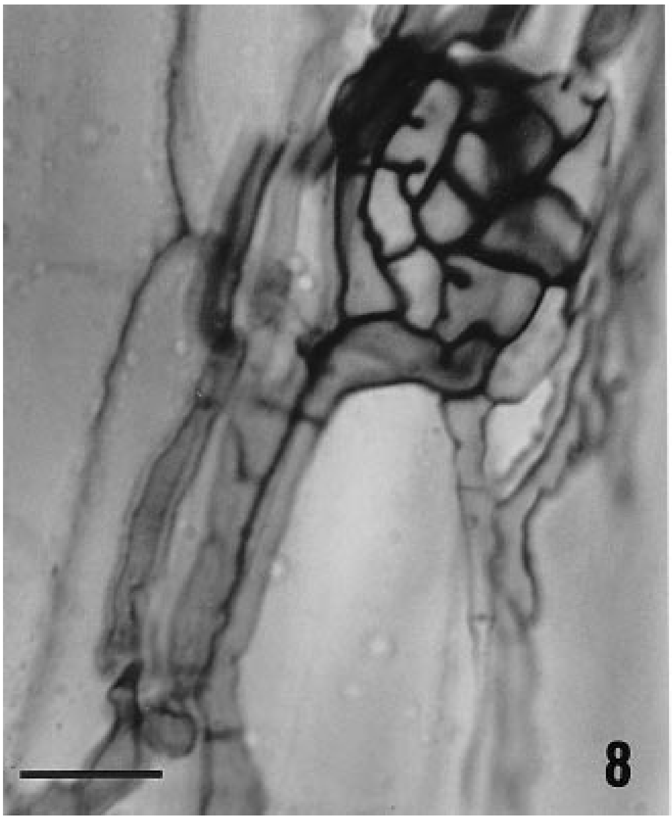
Dark septate fungi

A few plants, *Artemisia* sp., *Carex bigelowii*, *Gentiana algida*, *Lupinus arcticus*, *Lycopodium clavatum*, *Lycopodium selago*, *Oxytropis scammaniana*, *Pedicularis capitata*, *Pedicularis langsdorffii*, *Pedicularis verticillata*, and *Silene acaulis*, all had a variety of intracellular colonizations which were not VA but instead were characterized by the formation of intracellular microsclerotia (Figs. 8, 9). These are termed dark septate (DS) fungi in accordance with similar structures described by Read and Haselwandter (1981), who found DS fungi in roots of a variety of higher plant species from the Austrian Alps, especially Cyperaceae. Without doubt the term "dark septate fungi" in itself is not sufficient to describe what appears to be a whole assemblage of different species or strains of fungi, and in the literature it is not always specified whether dark septate fungi actually implies the occurrence of microsclerotia. However, it is important to stress some common features of these fungi, because there is evidence that they share some important ecological features. We use the term in the sense of Haselwandter and Read (1982) for those hyphae connected with so-called microsclerotia formed within the root cortical cells. Haselwandter (1987) assigned the DS fungi in part to the genus *Rhizoctonia* DC. and in part to the genus *Phialophora* Medlar.

Christie and Nicolson (1983) reported about DS fungi from Antarctic and sub-Antarctic sites. In the Canadian Arctic, Bledsoe et al. (1990) found some plant roots colonized by what they thought were DS fungi. From north-eastern China, microsclerotia in roots of nitrogen-fixing plants were described by Herrmann (1990). Similar structures were found by Blaschke (1991) from the Bavarian Alps. Stoyke and Currah (1991) assume a close relationship or even identity of DS fungi with *Phialocephala fortinii* C. J. K. Wang & H. E. Wilcox. Väre et al. (1992), in their extensive survey of Arctic sites in Spitsbergen, likewise observed a high frequency of these fungi and assigned microsclerotia of their survey to the genus *Microdochium* H. Sydow.

It is important to note that *Phialophora finlandia* C. J. K. Wang & H. E. Wilcox and *Phialocephala fortinii* have been shown to be part of the *mycelium radicis atrovirens* complex (Wang and Wilcox 1985), which was first mentioned by Melin (1921) and is known from many different soils (Gams 1963). *Mycelium radicis atrovirens* consists of a number of different strains and species (Melin 1923; Gams 1963; Kowalski 1973; Wang and Wilcox 1985), and there is evidence now that some of these fungi are mutualistic rather than parasitic. *Phialophora finlandia* has been shown to form ectendomycorrhizae with a variety of host trees (Wilcox and Wang 1987), and *Phialocephala fortinii* has been isolated from mycorrhizal orchid roots (Currah et al. 1987). Haselwandter and Read (1982) inoculated two *Carex* species with DS fungi and observed a significant increase of shoot phosphorus content, and for one species a distinct growth response. Deacon (1973) reported the occurrence of *Phialophora radicicola* Cain in grasses and cereals as a "parasite" which caused no visible damage to its host.

The high abundance of DS fungi in highly stressed environments such as the alpine and Arctic habitats, al-



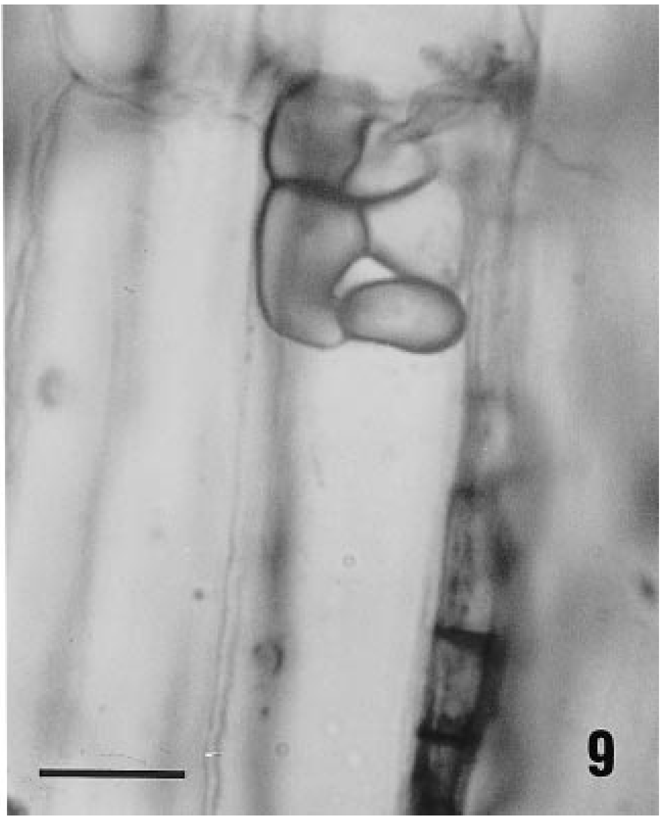


Fig. 8 *Pedicularis verticillata*. Microsclerotium

Fig. 9 *Carex bigelowii*. Microsclerotium, younger stage

though constituting no proof, strongly suggests a more mutualistic role for these fungi. Deacon (1973) reported a competitive effect on grass roots colonized by *Phialophora* which prevented the roots from becoming infected by the parasite *Gaeumannomyces graminis* (Sacc.) Arx & D. L. Olivier. Similar interactions were also proposed by Haselwandter (1987) for the DS fungi. It is likely that DS fungi assume the role of VA fungi in some alpine environments where VA fungi can no longer persist due to ecological factors (Haselwandter and Read 1980). Currah and Van Dyk (1986) observed that DS fungi occur in soils low in organic matter. Following Herrmann (1990), we therefore suggest the term "mycorrhizae" for these structures. However, they can not be accommodated in the present system of mycorrhizae by Harley and Smith (1983) and require the addition of a new category within the current system of mycorrhizal classes.

It seems essential to test more isolates of DS fungi from different regions for their effects on alpine host plants, similar to the studies of Haselwandter and Read (1982). In addition, more emphasis should be placed on identifying DS fungi from Arctic-alpine sites, possibly by studying cultural characters.

VA mycorrhizae and nonmycorrhizal plants

Only two species, *Sibbaldia procumbens* (Figs. 6, 7) and *Aconitum delphinifolium*, were undoubtedly VA mycorrhizal, showing both vesicles and arbuscles in their roots. *Sibbaldia procumbens* was described as being VA mycorrhizal both by Katenin (1964) and by Allen et al. (1987), whereas Currah and Van Dyk (1986) reported VA mycorrhizae in roots of *Aconitum delphinifolium*. In three other species, *Lycopodium clavatum*, *Oxytropis scammaniana* and *Silene acaulis*, vesicles but no arbuscules were observed, and it is thus doubtful whether these plants can be designated as VA mycorrhizal. It is possible, however, that the presence of arbuscules in some plants is restricted to a short time period during the growing season (Brundrett 1991).

Many of the plants examined did not have any mycorrhizae (*Equisetum arvense*, *Equisetum variegatum*, *Lycopodium alpinum*, *Polygonum bistorta*, *Saxifraga hieracifolia*, *Saxifraga hirculus*, *Astragalus alpinus*, *Pedicularis kanei*, *Petasites frigidus*, *Carex podocarpa*, *Carex microchaeta*, and *Poa arctica*). All of the nonmycorrhizal species belong to families which are considered either nonmycorrhizal or VA mycorrhizal.

Both species of *Equisetum* collected in the Park were nonmycorrhizal, which seems to be the common state for sporophytes of Equisetaceae (Harley 1969). The nonmycorrhizal condition has also been confirmed for Arctic specimens of several *Equisetum* species (Katenin 1964; Väre et al. 1992). Recent reports, however, indicate that this group may have a considerable amount of VA colonization under certain ecological conditions (Koske et al. 1985). Roots of *Lycopodium clavatum* showed a few vesicles but no arbuscules, and a VAM condition is thus not proven. The other two species examined (*Lycopodium alpinum* and *Lycopodium selago*) had neither vesicles nor arbuscules and *Lycopodium alpinum* was completely without any fungal colonization. This seems to confirm a report by Katenin (1964) about this species from the Arctic. Nespiak (1953) likewise reported the absence of VAM in roots of *Lycopodium selago* from the Tatra mountains.

Polygonum bistorta was found to be nonmycorrhizal in this study as well as in plants from the Siberian Arctic (Katenin 1964). Nespiak (1953), however, reported VAM in roots of this species collected from the Tatra mountains. A VA colonization was also absent in two species of *Saxifraga*, confirming reports about this genus from Spitsbergen (Väre et al. 1992), from the Canadian Arctic (Bledsoe et al. 1990) and from the Siberian Arctic (Katenin 1964). *Astragalus alpinus* roots were nonmycorrhizal, a result also reported by Katenin (1964) and by Currah and Van Dyk (1986). None of the four species of *Pedicularis* from Denali National Park had VAM, and *Pedicularis kanei* was completely without fungal colonization. Absence of VAM in Arctic-alpine *Pedicularis* species has been confirmed repeatedly (Katenin 1964; Bledsoe et al. 1990; Kohn and Stasovski 1990; Väre et al. 1992). *Petasites frigidus* was found to be nonmycorrhizal in our study, confirming the reports of Miller (1982) and Väre et al. (1992). *Poa arctica* roots were devoid of VAM, in agreement with Bledsoe et al. (1990), Kohn and Stasovski (1990), and Väre et al. (1992).

The Cyperaceae are reported to have no or very sporadic VA colonization (Harley and Smith 1983) and accordingly none of the *Carex* species examined in this study were found to be VA-mycorrhizal. These results are in agreement with reports from the Arctic (Katenin 1964; Bledsoe et al. 1990; Kohn and Stasovski 1990; Väre et al. 1992) and from alpine habitats (Nespiak 1953; Miller 1982). However, Lesica and Antibus (1986) and Allen et al. (1987) found VAM in *Carex* species from the Rocky Mountains, and Haselwandter and Read (1982) reported their occasional occurrence in *Carex* species from the Alps. The frequent absence of VAM in this family might be compensated in alpine areas by the presence of DS fungi (Haselwandter and Read 1980).

Reports in the literature about the mycorrhizal status of many plants from Arctic-alpine areas are not consistent. Although the great majority of higher land plants usually form VAM (Harley and Smith 1983), a small number of plant families appear to be predominantly non-mycorrhizal (Brundrett 1991). A closer look at the groups concerned, however, often reveals that even in those families VAM may be present under certain conditions. Both Equisetaceae and Cyperaceae are regarded as non-mycorrhizal families (Harley and Smith 1983; Brundrett 1991), but recent reports indicate that plants of both families may be colonized by VA fungi under some circumstances (Koske et al. 1985; Harley and Harley 1987). A recent comprehensive review by Harley and Harley (1987) on British plant species shows that there is virtually no family of higher plants without an occasional report on the occurrence of VA mycorrhizae (with the exception of Ericales, Orchidaceae and ectomycorrhizal families). One possible explanation for this phenomenon is that the formation of VAM is dependent on a variety of ecological factors (Mejstřík 1965; Harley 1969). Currah and Van Dyk (1986) reported the occurrence of VAM on soils with sufficient organic matter, whereas roots in soils low in organic matter were colonized by DS fungi. The failure to detect VAM in most of the plant roots examined in this study may also be the result of seasonal variations in the colonization of roots which have been observed in studies extending over a whole vegetation season (Puppi et al. 1986; López-Sánchez and Honrubia 1992). Finally, it cannot be excluded that DS fungi often assume the role of VAM in Arctic-alpine habitats.

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