

Arbuscular mycorrhizae on Axel Heiberg Island (80°N) and at Saskatoon (52°N) Canada

Nathan Allen, Mattias Nordlander, Terence McGonigle, James Basinger, and Susan Kaminskyj

Abstract: Arbuscular mycorrhizae (AM) are seldom reported from high latitudes. We found that Asteraceae (*Arnica*, *Erigeron*, and *Taraxacum*) at a site on Axel Heiberg Island (approximately 80°N) have abundant AM and fine endophytes (FE). We used standard microscopic methods for examination and quantification, plus high-resolution confocal fluorescence imaging. AM in Arctic Asteraceae were compared with those in congeners from Saskatoon and with those in some other Arctic species. Arctic AM had 6 µm wide aseptate hyphae producing abundant arbuscules, vesicles, and inter- and intra-cellular hyphae. AM colonization exceeded 80% for Arctic Asteraceae, similar to 66%–90% for prairie *Taraxacum* and *Erigeron*, the first of this type of comparison. AM/FE abundance in Arctic *Ranunculus* was 68%. Within *Taraxacum* roots, hyphal coils predominated near the epidermis and arbuscules near the vascular cylinder. Arctic AM colonization did not vary with soil depth, although permafrost was approximately 15 cm below the surface. FE were abundant in our High Arctic samples, where they may have functional roles comparable with those of AM. Thus, low abundance of AM reported previously at the community level for high-latitude sites may reflect a combination of biotic and abiotic factors. The Axel Heiberg Island thermal oasis is ideal for functional fungal root endophyte studies in the High Arctic.

Key words: arbuscular mycorrhiza, Arctic, Asteraceae, confocal microscopy, fine endophyte, lactofuchsin.

Résumé : On mentionne rarement les mycorhizes arbusculaires (AM) des hautes latitudes. Les auteurs ont constaté que les Asteraceae (*Arnica*, *Erigeron* et *Taraxacum*), sur un site de l'île Axel Heiberg (ca. 80 °N), portent d'abondantes AM et de fins endophytes (FE). Ils ont utilisé des méthodes microscopiques standards pour l'examen et la quantification, des prires en plus de l'imagerie confocale en fluorescence à haute résolution. On compare les AM des Asteraceae de l'Arctique avec des congénères de la région de Saskatoon, et avec d'autres espèces de l'Arctique. Les AM de l'Arctique possèdent des hyphes aseptés de 6µm de large produisant d'abondants arbuscules, vésicules et hyphes intercellulaires et intracellulaires. La colonisation AM dépasse 80 % chez les Asteraceae de l'Arctique, similaire au 66 % – 90 % des *Taraxacum* et *Erigeron* des prairies, le premier de ce type de comparaison. L'abondance des AM chez les *Ranunculus* de l'Arctique est de 68 %. Dans les racines du *Taraxacum*, les pelotons d'hyphes prédominent près de l'épiderme, et les arbuscules près du cylindre vasculaire. La colonisation Arctique ne diffère pas selon la profondeur du sol, bien que le permafrost se retrouve à ca. 15 cm sous la surface. Les FE sont également abondants dans les échantillons de l'Arctique examinés, où ils pourraient jouer des rôles comparables à ceux des AM. Ainsi, la faible abondance en AM préalablement rapportée au niveau de la communauté pour des sites de haute latitude, peut refléter une combinaison de facteurs biotiques et abiotiques. L'oasis thermique de l'île d'Axel Heiberg constitue un endroit idéal pour étudier les endophytes racinaires fonctionnels du Haut Arctique.

Mots clés : AM, mycorhize arbusculaire, Asteraceae, microscopie confocale, endophyte fin, lactofuschine.

[Traduit par la Rédaction]

Introduction

Mycorrhizae are associated with most terrestrial plants, providing benefits including enhanced plant vigour and dis-

ease resistance (Read 1999). At high latitudes, plant growth is limited by low temperature, low soil nutrient levels, and short growing season, with up to several months of continual darkness. The advantage to the plant of hosting a mycorrhiz-

Received 18 April 2006. Published on the NRC Research Press Web site at <http://canjbot.nrc.ca> on 12 August 2006.

Abbreviations: AM, arbuscular mycorrhiza; CBE, chlorazole black E; DIC, differential interference contrast; DLAG, 1:1:1 distilled water – lactic acid – glycerol; FE, fine endophyte; LF, lactofuchsin.

N. Allen,¹ M. Nordlander,² and S. Kaminskyj.³ Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, SK S7N 5E2, Canada.

T. McGonigle. Department of Botany, Brandon University, Brandon, MB R7A 6A9, Canada.

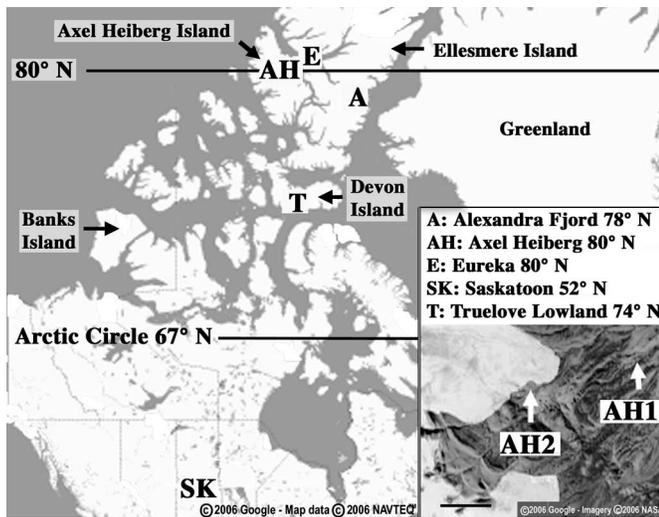
J. Basinger. Department of Geological Sciences, University of Saskatchewan, 114 Science Place, Saskatoon, SK S7N 5E2, Canada.

¹Present address: College of Medicine, University of Saskatchewan, 107 Wiggins Road, Saskatoon, SK S7N 5E5, Canada.

²Present address: University of Umeå, Umeå, Sweden.

³Corresponding author (e-mail: Susan.Kaminskyj@usask.ca).

Fig. 1. Map and satellite image of the Canadian High Arctic downloaded from maps.google.com and annotated showing reference latitudes and field site positions. Inset: satellite image of the Axel Heiberg Island AH1 and AH2 collection sites. AH1 is just south of the fossil forest described in Kotyk et al. (2003).



zal interaction will depend on the value of minerals compared with the cost of supplying the fungus with carbohydrate (Fitter 1991).

Arbuscular mycorrhizae (AM) form between about 80% of plant species and seven genera of fungi in the Glomeromycota (Schüssler et al. 2001). AM fungi are obligate biotrophs that do not produce a macroscopic phenotype. AM hyphae are aseptate, approximately 6 μm wide, and form intracellular arbuscules, vesicles, and (or) hyphal coils. Fine endophytes (FE) have <1.5 μm wide aseptate hyphae, which produce intraradical networks that may have a mycorrhizal function (Gianinazzi-Pearson et al. 1981; Thippayarugs et al. 1999). Less is known about FE prevalence, in part because they are difficult to visualize with conventional microscopy. AM and FE propagules are produced in the soil (Peterson et al. 2004; Thippayarugs et al. 1999), so long distance transport is unlikely except by erosion. A plant's AM and FE status will depend in part on the soil in which it grows, and the abundance of viable AM and FE spores in the soil will depend in part on its recent history.

Canadian High Arctic research is limited by cost and logistics. Even in the few thermal oases (Fig. 1), the summer air temperature is typically below 10 $^{\circ}\text{C}$. Botanical fieldwork is typically conducted in July, after the melt and before substantial snowfall. Vegetation is sparse to semicontinuous. Permafrost is often within 15 cm of the surface, creating temperature and moisture gradients. Most High Arctic plants are perennial, as the growing season is brief at best. Many High Arctic soils are highly mineral, possibly approximating early terrestrial environments (Taylor et al. 1995; Malloch et al. 2000).

There are relatively few reports on any fungi (and fewer on AM and FE) from Arctic tundra, although tundra covers about 5% of the earth's land surface (Chapin and Körner 1995). Previous studies on plants hosting AM fungi in the high latitudes have mostly been conducted on islands ranging from 73 to 80 $^{\circ}\text{N}$ and from 53 to 69 $^{\circ}\text{S}$. Canadian local-

ities cited in the following reports are shown in Fig. 1. Bledsoe et al. (1990), who found no AM on 55 plant species at Truelove Lowland, Devon Island (74 $^{\circ}\text{N}$) over two seasons, suggested that AM-forming plants were infrequent in the High Arctic, although this would not have been predicted from the known biodiversity of the Canadian High Arctic flora (Porsild 1985). Kohn and Stasovski (1990) found that only *Dryopteris* had AM among 19 plant species from Alexandra Fjord, Ellesmere Island (78 $^{\circ}\text{N}$). Väre et al. (1992) reported a single AM spore in a soil sample from Svalbard (78 $^{\circ}\text{N}$). However, Dalpé and Aiken (1998) and Olsson et al. (2004) reported variable colonization by some AM, FE, and dark septate endophytes from several High Arctic sites ranging from 73 to 80 $^{\circ}\text{N}$, with the majority of AM being on Banks Island (73 $^{\circ}\text{N}$). Similarly, there are few AM reported from the Antarctic. Laursen et al. (1997) found arbuscules in only 3 of 40 taxa on Macquarie Island (54 $^{\circ}\text{S}$). *Deschampsia antarctica* at 69 $^{\circ}\text{S}$ has AM (Cabello et al. 1994), but AM were absent from *D. antarctica* at 64 $^{\circ}\text{S}$ (DeMars and Boerner 1995). Frenot et al. (2005) recorded variable AM colonization of nine species of forbs and grasses on Heard Island (53 $^{\circ}\text{S}$). To date, the AM status reported for high-latitude tundra is lower than for alpine tundra (Read and Haselwandter 1981; Cripps and Eddington 2005); furthermore, Ruotsalainen et al. (2004) did not find a decline in AM colonization with altitude. Clearly, additional studies from numerous sites are needed.

Low AM colonization at high latitudes is counterintuitive, especially as ectomycorrhizae are found on Arctic *Salix* and *Dryas* (Cripps and Eddington 2005), two common woody plants (Porsild 1985). Possibly, the AM inoculum in Arctic soils has become depauperate. Perhaps AM are less important to High Arctic plants, as sufficient mineral supply may be provided via their roots to meet the needs of their low growth rates. Regardless, it is premature to draw broad conclusions about AM function at high latitudes.

Given an opportunity in July 2004 to visit a thermal oasis, the Geodetic Hills on Axel Heiberg Island that had been studied for their paleobotany (e.g., Kotyk et al. 2003), and in an effort to extend our knowledge of High Arctic AM in an area that had not previously been sampled for this purpose, we collected roots and preserved them for light microscopy. In this report, we focus on the Asteraceae to compare this site with those of Olsson et al. (2004). We compared these Arctic samples with the same genera collected near Saskatoon in the Canadian Prairies. We also compared them with Arctic plants collected from similar and distinct soil types. Fortunately, the Geodetic Hills Asteraceae have similar AM abundance to those of Saskatoon, providing an opportunity in the future to assess their function in the High Arctic.

Materials and methods

Sample collection

Samples were collected from sites shown in Fig. 1. *Arnica*, *Erigeron*, *Taraxacum*, and *Epilobium* were collected at AH2 (79 $^{\circ}53'\text{N}$, 89 $^{\circ}33'\text{W}$) and *Ranunculus* was collected at AH1 (79 $^{\circ}53'\text{N}$, 89 $^{\circ}11'\text{W}$), both part of the Geodetic Hills area on Axel Heiberg Island. *Taraxacum* and *Erigeron* were collected at SK (52 $^{\circ}06'\text{N}$, 106 $^{\circ}24'\text{W}$), Saskatoon, Saskatchewan.

Fig. 2. Representative root systems of *Taraxacum officinale* (a), *Taraxacum phymatocarpum* (b), and *Taraxacum hyparcticum* (c) prior to analysis.

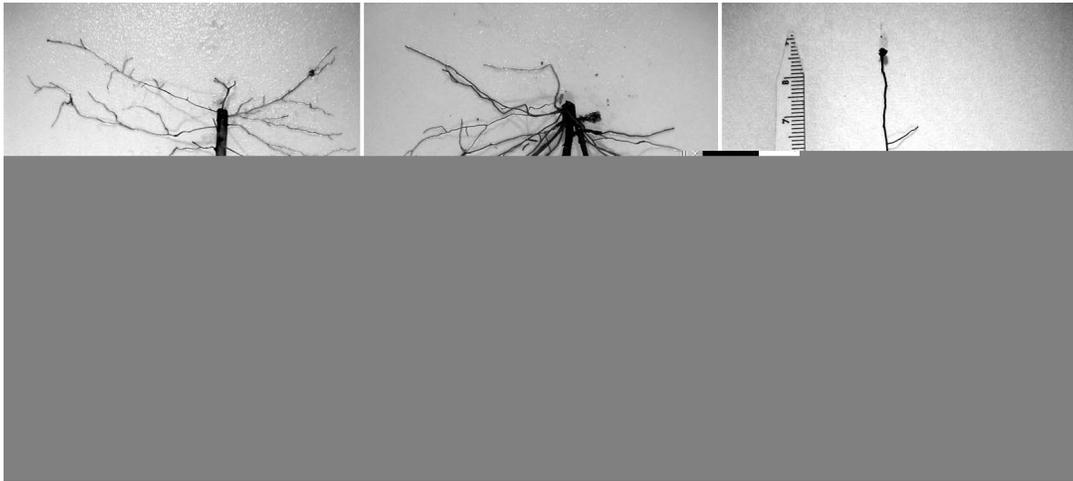
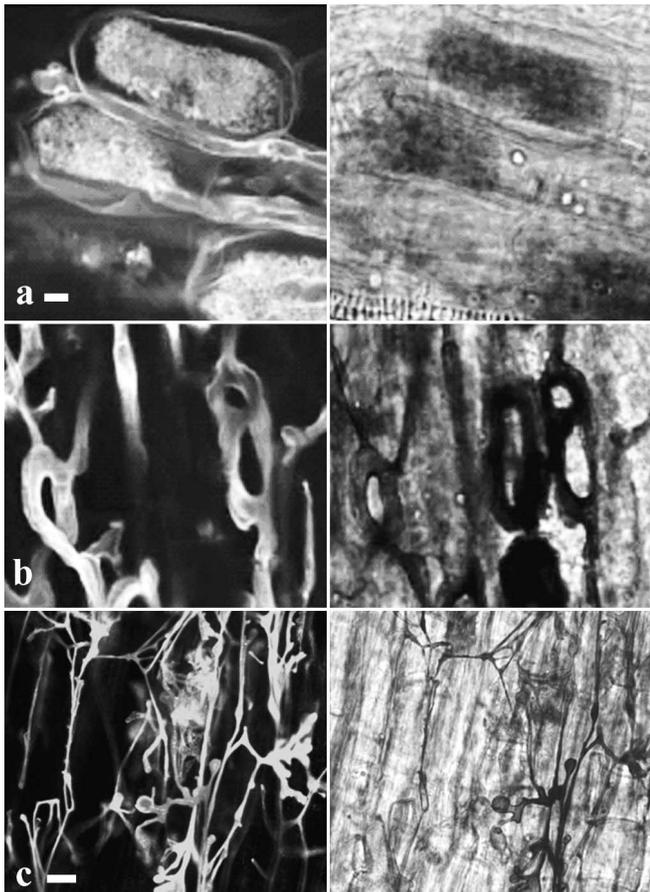


Fig. 3. Paired confocal epifluorescence (left) and differential interference contrast (right) micrographs of lactofuchsin-stained arbuscular mycorrhizae in Arctic *Taraxacum phymatocarpum* showing arbuscules (a), hyphal coils (b), and fine endophyte hyphae (c). Differential interference contrast images were collected simultaneously with fluorescence using a 63× N.A.1.2 objective. Scale bars = 10 μm (scale bar shown in Fig. 3a applies for Figs. 3a and 3b).



Arctic plants were identified using Porsild (1985) and Aiken et al. (1999 onwards). These included Asteraceae (*Arnica alpina* L., *Erigeron compositus* Pursh., *Erigeron eriocephalus* J. Vahl, *Taraxacum phymatocarpum* J. Vahl., and *Taraxacum hyparcticum* Dahlst.), Ongraceae (*Epilobium latifolium* L.), and Ranunculaceae (*Ranunculus nivalis* L.). Saskatoon samples were from the Asteraceae (*Taraxacum officinale* Weber ex Wigg., *Erigeron asper* Nutt., and *Erigeron caespitosus* Nutt.). Saskatoon samples were collected from the University of Saskatchewan campus: *Taraxacum* specimens from sandy-loam soil at the Department of Biology garden and *Erigeron* specimens from dry gravelly soil at the Kernan's Prairie site.

Plants were harvested along with adhering soil, which was carefully removed by washing prior to fixation. Roots were fixed in 3.7% formaldehyde containing 0.5% ethanol, buffered to pH 7.0 in sodium–potassium phosphate at 50 mmol/L. All chemicals were purchased from VWR (<http://www.vwrcanlab.com>) or Sigma (<http://www.sigmaaldrich.com>). Fixative stock solution (5×) was diluted to working strength with glacial meltwater (Arctic samples) or reverse osmosis water (Saskatoon samples). Arctic samples were stored in fixative at 4 °C for 10+ months and Saskatoon samples overnight at 4 °C.

Microscopy

Roots were cleared by autoclaving in 10% KOH for 20 min and then rinsed twice in 70% ethanol. Twenty to 30 root segments were randomly sampled for staining with chlorazole black E (Brundrett et al. 1996) or lactofuchsin (LF). For AM colonization, roots were stained for 3 h at 68 °C in 0.05% chlorazole black E (CBE) in 1:1:1 distilled water – 85% lactic acid – glycerol (DLAG). For destaining, roots were rinsed twice in DLAG and incubated at 47 °C first for 20 min and then overnight in two changes of fresh DLAG. Roots were mounted on slides in DLAG and the cover slips sealed with nail polish. Roots were examined with a Zeiss Axioplan upright microscope using a Plan Aplanachromat 63× N.A.1.4 objective equipped with differential interference contrast (DIC) optics. Images were captured with a Sensys CCD (<http://www.roper.com>) driven by MetaVue

Fig. 4. Arbuscular mycorrhizae in Arctic *Taraxacum phymatocarpum* and *Erigeron compositus*. (a–c) Optical sections of a *Taraxacum* root stained with lactofuchsin and imaged with confocal epifluorescence microscopy. The vascular cylinder is in the lower left-hand corner, unstained. Sections a–c were 1 μm in optical thickness and 3 μm apart. Paris-type intercellular hyphal coils in Fig. 4a were continuous with the intercellular hyphae forming arbuscules in Figs. 4b and 4c. (d) Arctic *Erigeron compositus* arbuscular mycorrhiza visualized with chlorazole black E staining and differential interference contrast microscopy showing hyphal coils and arbuscules formed by the same mycorrhizal interaction. Scale bars = 20 μm (scale bar in Fig. 4c applies for Figs. 4a–4c).

software (<http://www.image1.com>). Other root samples were stained in LF (0.1% acid fuchsin in 85% lactic acid) for 3 h at 68 °C and then rinsed and destained in DLAG as for CBE-stained samples. LF-stained roots were examined using a Zeiss META 510 confocal laser scanning microscope (<http://www.zeiss.com>) with 514 nm excitation and LP585 emission filters. Images were collected using a Plan-Neofluar 25 \times N.A.0.8 DIC multiimmersion objective or a C-Apochromat 63 \times N.A.1.2 phase-contrast water immersion objective. Fluorescence and transmitted images were collected simultaneously.

Mycorrhizal abundance

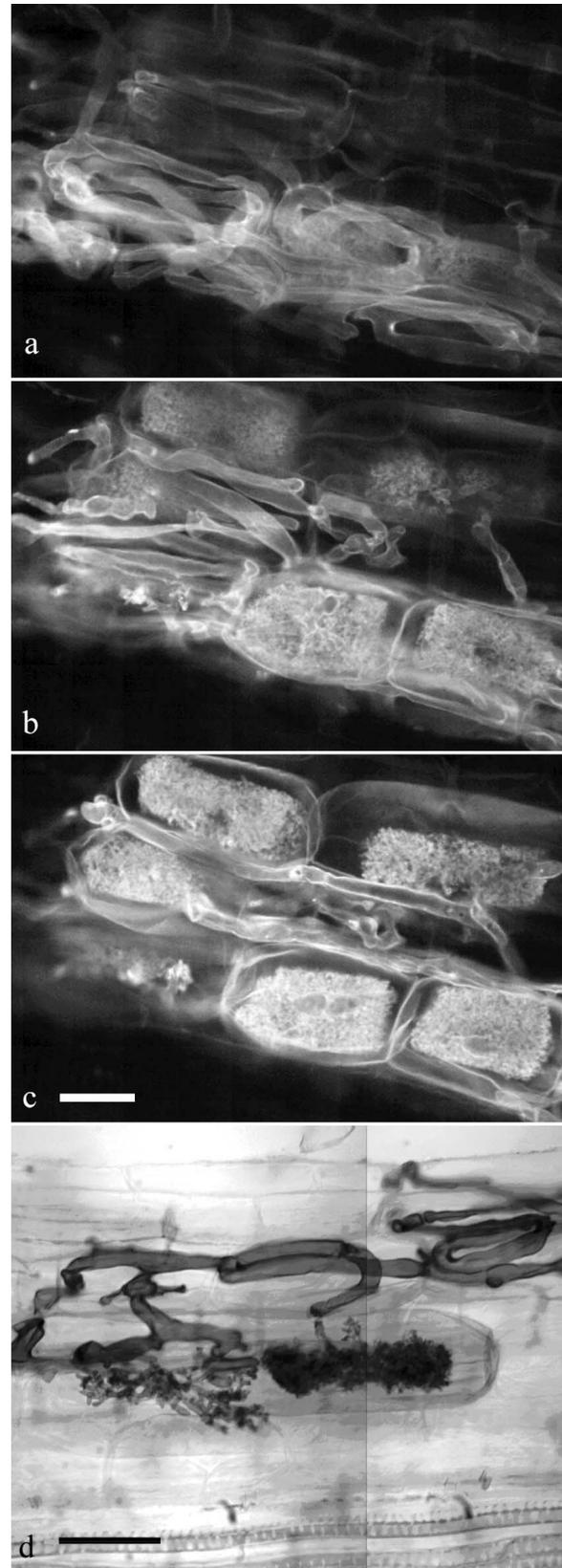
AM colonization of root systems was estimated by the microintersect method of McGonigle et al. (1990) using CBE-stained roots. Large *Taraxacum* root systems were cut into two to four segments along the taproot axis and analyzed separately so that colonization could be compared at positions roughly corresponding to different soil depths. Comparison used ANOVA with post hoc pairwise analysis by Fisher PLSD (Statview SE plus Graphics 1.02). If root segments were scored separately, whole-root system colonization used the sum of the total and colonized lengths for individual segments. Data were available from six plants (two *T. officinale*, three *T. phymatocarpum*, and one *T. hyarcticum*) to compare AM colonization of the most proximal and most distal segments.

Results

Most Arctic Asteraceae plants were growing in undisturbed, highly mineral soil associated with *Salix arctica*, forbs, and grasses. *Erigeron compositus*, *Arnica*, and *Epilobium* were in similar soil but not close to other plants. The soil from which the Asteraceae and *Epilobium* were collected was well drained, dry on the surface, and damp beneath from melting permafrost. *Ranunculus nivalis* was growing in saturated soil by a stream associated with other forbs and grasses. Root systems of *T. officinale* and *T. phymatocarpum* were fourfold larger than those of *T. hyarcticum* (Fig. 2 and data not shown), but the plants had similar aboveground size.

Mycorrhizal morphology

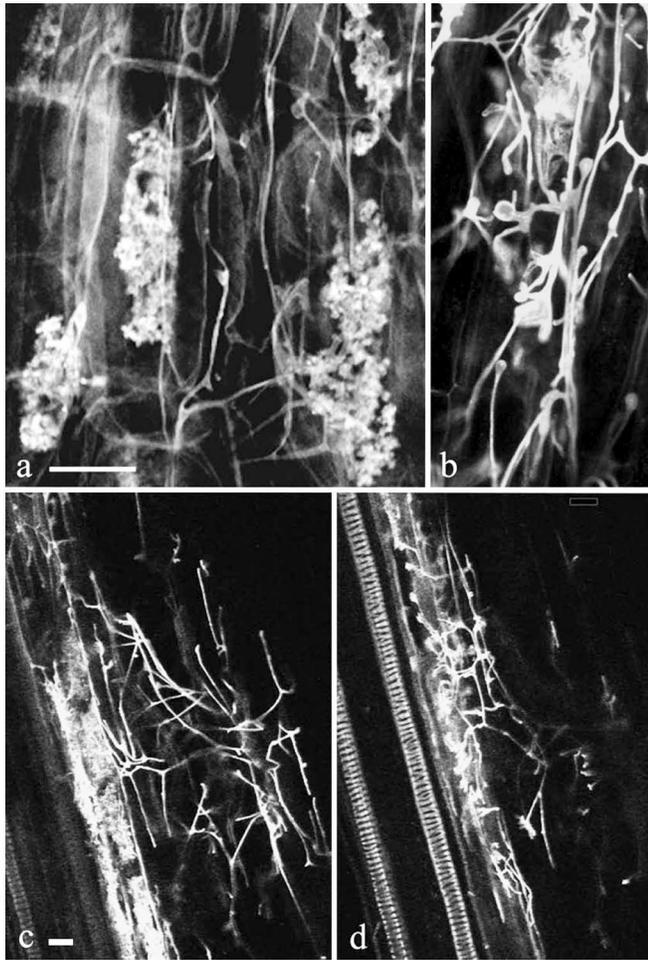
Members of the Asteraceae, as well as *Ranunculus nivalis*, had AM that formed arbuscules, vesicles, coils, and intercellular hyphae (Figs. 3 and 4) as well as FE (Figs. 3c and 5). In contrast, hyphae associated with *Epilobium* roots



were mostly on the surface and did not produce AM structures.

LF fluorescence staining for AM was described by Merryweather and Fitter (1991) but not widely adopted (Dickson

Fig. 5. Fine endophyte hyphae in Arctic specimens of *Taraxacum phymatocarpum* (a), and *Ranunculus nivalis* (b, c) visualized with lactofuchsin and confocal epifluorescence microscopy. (a) Fine endophyte hyphae and putative fine endophyte arbuscules; no coarse arbuscular mycorrhizae hyphae were found in this series of 43 optical sections 1 μm apart in depth. (b and c) Optical sections of *Ranunculus* 11 μm apart in depth showing fine endophyte hyphae closely associated with arbuscules. Scale bars = 20 μm (scale bar in Fig. 5a applies for Figs. 5a and 5b; scale bar in Fig. 5c applies for Figs. 5c and 5d).



et al. 2003; Geil et al. 2001; Vierheilig et al. 2005) and was rediscovered independently in the course of this work. LF has a wide excitation range, spanning the 514 nm (Ar) and 543 nm (HeNe) laser lines. BP560-615 or comparable long-pass emission filters gave excellent images. CBE produced unacceptable background fluorescence. We obtained considerably more morphological detail with LF confocal fluorescence than with CBE-DIC, particularly for fine structures (Fig. 3). Analysis was facilitated by using serial confocal sections at multiple depths (Figs. 4 and 5).

In *Taraxacum*, AM fungi produced intracellular hyphal coils in the root periphery (Fig. 4a) that were continuous with intercellular hyphae that produced arbuscules (Figs. 4b and 4c). Similar results were found for *Erigeron* (Fig. 4d) and *Arnica* (not shown). Most arbuscules in these samples were relatively close to the root vascular cylinder. Arbuscules (Figs. 3a and 4) were finely ramified around a central

core and filled most of the root cell. Arctic Asteraceae and *Ranunculus* roots also had fine endophytes, networks of 1–1.5 μm wide aseptate hyphae with at least three distinct morphologies (cf. Figs. 3c and 5a–5c). Some of these were closely associated with arbuscules.

Mycorrhizal abundance

We assessed the AM colonization rate using the microintersect method (Table 1), scoring intercellular *Arum*-type hyphae and intracellular *Paris*-type hyphal coils as a single group (Fig. 4). FEs could not be counted reliably in CBE-stained roots. AM colonization was similar for *Taraxacum* lateral roots proximal and distal to the crown, which for Arctic specimens correlated with changes in soil temperature and moisture related to soil depth. AM colonization was similar for *Arnica*, *Erigeron*, and *Taraxacum* collected at AH2: 80%–95% of the root length contained fungal structures (Table 1). Vesicles were less abundant than arbuscules in these samples, perhaps because plants were harvested early in the growing season (Peterson et al. 2004). AM colonization was similar in *Taraxacum* and *Erigeron* species from the Arctic (>80%) and from Saskatoon (66%–90%) (Table 1). *Ranunculus nivalis*, collected from saturated soil, also had abundant AM and FEs (Table 1). In contrast, *Epilobium* collected from dry soil near the Asteraceae samples had few hyphae and no AM structures.

Discussion

This is the first report describing AM in Arctic Asteraceae and *Ranunculus* from the Geodetic Hills on Axel Heiberg Island and the first to compare AM colonization among congenics from high- and midlatitude sites. AM colonization was abundant in six species collected from dry (Asteraceae) to saturated (*Ranunculus*) Arctic soils. AM abundance among the Arctic Asteraceae was similar to that of congenics collected at Saskatoon, Saskatchewan. Logistics permitting, better understanding of Arctic AM will require multiyear sampling from these and additional habitats and a broad analytical strategy encompassing identification of the endophytic species and soil analyses.

The High Arctic is relatively unexplored regarding the presence of AM fungi and less so for their function. Thermal oases are few, and their characteristics do not correlate with latitude. Consequently, finding abundant AM at the Geodetic Hills was propitious. Truelove Lowland (74°N) is a large plain, snow free in summer, whereas site AH2 (80°N) from where most of our samples were collected is adjacent to a glacier, similar to the Alexandra Fjord site. However, AM were lacking at Truelove Lowland (Bledsoe et al. 1990) and were found only in a *Dryopteris* sample at Alexandra Fjord (Kohn and Stasovski 1990). AM fungi are obligate biotrophs without efficient means for long-range dispersal, so their occurrence at a given place and time depends to a great extent on previous local conditions. AM colonization of *Erigeron eriocephalus* at the Axel Heiberg Island Geodetic Hills was similar to that reported by Olsson et al. (2004) for Banks Island, as were their results for an *Arnica* species. As yet, we know little about AM abundance in roots of High Arctic plants, except that it is not simply related to AM spore persistence in Arctic soils (Olsson et

Table 1. Mycorrhizal colonization of entire *Taraxacum* and *Erigeron* root systems and representative samples of *Arnica*, *Epilobium*, and *Ranunculus* root systems shown as arbuscular, vesicular, and hyphal colonization.

Species ^a	No. of plants	Arbuscules	Vesicles	Hyphae
<i>Arnica alpina</i>	2	21.0±7.0	2.5±1.0	60.0±6.0
<i>Erigeron asper</i>	8	51.6±5.8b	19.1±3.1b	90.8±8.3b
<i>E. caespitosus</i>	5	22.1±7.7a	2.0±1.1a	83.7±8.2b
<i>E. compositus</i>	8	21.8±4.7a	1.3±1.3a	94.0±3.6b
<i>E. eriocephalus</i>	8	18.8±5.9a	2.7±1.2a	89.3±3.0b
<i>Epilobium latifolium</i>	8	0±0	0±0	21.4±5.2
<i>Ranunculus nivalis</i>	2	10.5±7.1	4.0±0	54.0±8.0
<i>Taraxacum hyparcticum</i>	12	29.6±3.9a	2.0±0.7a	91.7±1.6b
<i>T. officinale</i>	6	27.4±4.8a	2.6±1.0a	66.0±9.2a
<i>T. phymatocarpum</i>	3	35.8±2.7a	12.2±3.4a	91.2±1.9b

Note: The entire root cross section was examined microscopically (63× objective) using the magnified intersection method (see Materials and methods). Some cross sections had more than one type of colonization, so totals for all types may exceed 100%. Data are expressed as a percentage of root length ± SE of the mean. Means (*Erigeron* and *Taraxacum* species only) in a column followed by a different letter are significantly different ($P = 0.05$; ANOVA followed by Fisher PLSD). Hyphal coils, intercellular hyphae, and fine endophyte hyphae were scored as a group.

^aArctic species are in bold.

al. 2004). Clearly, Arctic tundra soils are heterogeneous regarding AM inoculum potential and plant AM receptivity. Similarly, results for AM in alpine tundra sites vary widely between species and individual sites and between sites for individual species (Read and Haselwandter 1981; Cripps and Eddington 2005).

This is also the first study to examine LF-stained FEs with high-resolution confocal epifluorescence microscopy. Visualization of AM and FE structures using LF fluorescence has been known since Merryweather and Fitter (1991) but has not been widely adopted (e.g., Dickson et al. 2003; Geil et al. 2001; Vierheilig et al. 2005). We found that confocal fluorescence visualization of LF-stained samples provided an unparalleled method for studying fungal mycelium in plant tissues, particularly for FEs, consistent with but more extensive than that seen with conventional techniques.

Unexpectedly, AM in Asteraceae produced both *Paris*- and *Arum*-type intracellular structures depending on their position within the root. This was more readily detected with confocal examination owing to the ease of optical sectioning but was also found with transmitted microscopy. The position of AM coils and arbuscules was consistent with variation in root cell packing, at least in *Taraxacum officinale*, which are tightly packed near the epidermis but loosely packed near the endodermis (Y. Li and S. Kaminskyj, unpublished data).

This is the first light micrography report to show that at least some Arctic FEs produce arbuscules. Such has been documented for raspberry roots using freeze-substitution transmission electron microscopy (Gianinazzi-Pearson et al. 1981) with ultrastructural evidence to suggest that those arbuscules function as sites of nutrient exchange. FE arbuscules were shown with light microscopy in clover from western Australia pot cultures (Thippayarugs et al. 1999). FEs are reported to be more abundant than AM at high latitudes (Olsson et al. 2004), and FE occurrence was correlated with acidic soil pH in pot cultures (Thippayarugs et al. 1999). Rabatin (1979) suggested that FE fungi may be pio-

neer endophytes because in the midlatitudes, they are found with primary colonizing plant species. Thus, the role of FEs in tundra environments may be significant. The relative paucity of reports to date may be partly attributable to the difficulty in resolving them with conventional techniques.

At our Arctic Asteraceae sites, the soil surface was dry, but the soil was wet within a few centimetres of depth owing to shallow permafrost; we did not find a difference between Arctic *Taraxacum* AM colonization at different taproot depths. AM were present in *Ranunculus nivalis* collected from saturated soil. Cooke and Lefor (1998) found that >90% of 89 plant species collected from Connecticut wetlands supported AM, although their single collection from the Ranunculaceae, *Calthia palustris* L., had low AM abundance. Søndergaard and Laegaard (1977) suggested that root hair abundance is negatively correlated with AM abundance, particularly for plants growing in saturated soils. None of our samples had abundant root hairs except for *Erigeron caespitosus* (approximately 14/mm). *Erigeron caespitosus* AM colonization did not vary systematically compared with other *Erigeron* species that lacked abundant root hairs. Root hairs are unlikely to have been lost during processing because comparable techniques have been used by us to examine taxa with hairy roots.

We have shown that Asteraceae and *Ranunculus* collected at the Geodetic Hills on Axel Heiberg Island have extensive development of AM and also contain FEs. The latter may be functionally analogous. AM abundance was similar between Arctic and temperate species of *Taraxacum* and *Erigeron*, suggesting that AM inoculum levels and (or) plant receptivity are sufficient in some Arctic sites. More generally, these results suggest that low abundance of AM reported previously at the community level for high-latitude sites may reflect a combination of biotic and abiotic factors. The Geodetic Hills region of Axel Heiberg Island has a wide variety of habitats and floral communities ranging from bare mineral soil to sparse vegetation to hummocks, meadows, and marshy areas, each with characteristic forbs, grasses,

and woody plants. The Geodetic Hills site is clearly well suited to research that extends studies of Arctic AM identification towards function and ecology.

Acknowledgements

This work was supported by the Natural Sciences and Engineering Research Council of Canada (J.B. and S.K.) and the Polar Continental Shelf Project of Natural Resources Canada (project 619-04, Government of Nunavut Scientific permit 04-03P, PCSP/EPCP publication No. 008-06). N.A. was supported by the University of Saskatchewan USTEP program. M.N. was an undergraduate exchange student. Funding for the Zeiss META 510 laser scanning confocal microscope was from the Canadian Foundation for Innovation.

References

- Aiken, S.G., Dallwitz, M.J., Consaul, L.L., McJannet, C.J., Gillespie, L.J., Boles, R.L., Argus, G.W., Gillett, J.M., Scott, P.J., Elven, R., LeBlanc, M.C., Brysting, A.K., and Solstad, H. 1999 onwards. Flora of the Canadian Arctic Archipelago: descriptions, illustrations, identification, and information retrieval. Version: 29 April 2003. Available from <http://www.mun.ca/biology/delta/arctic/>.
- Bledsoe, C., Klein, P., and Bliss, L.C. 1990. A survey of mycorrhizal plants on Truelove Lowland, Devon Island, N.W.T., Canada. *Can. J. Bot.* **68**: 1848–1856.
- Brundrett, M., Bougher, N., Dell, B., Grove, T., and Malajczuk, N. 1996. Working with mycorrhizas in forestry and agriculture. ACIAR Monogr. 32. ACIAR, Canberra, Australia.
- Cabello, M., Gaspar, L., and Pollero, R. 1994. *Glomus antarcticum* sp. nov., a vesicular–arbuscular mycorrhizal fungus from Antarctica. *Mycotaxon*, **51**: 123–128.
- Chapin, F.S., III, and Körner, C.H. 1995. Patterns, causes, changes, and consequences of biodiversity in Arctic and Alpine ecosystems. In *Arctic and Alpine biodiversity: patterns, causes, and ecosystem consequences*. Edited by F.S. Chapman III and C. Körner. Springer-Verlag, Berlin. pp. 313–320.
- Cooke, J.C., and Lefor, M.W. 1998. The mycorrhizal status of selected plant species from Connecticut wetlands and transition zones. *Restor. Ecol.* **6**: 214–222. doi:10.1111/j.1526-100X.1998.00628.x.
- Cripps, C.L., and Eddington, L.H. 2005. Distribution of mycorrhizal types among alpine vascular plants families on the Beartooth Plateau, Rocky Mountains, U.S.A., in reference to large-scale patterns in Arctic–Alpine habitats. *Arct. Antarct. Alp. Res.* **37**: 177–188.
- Dalpé, Y., and Aiken, S.G. 1998. Arbuscular mycorrhizal fungi associated with *Festuca* species in the Canadian High Arctic. *Can. J. Bot.* **76**: 1930–1938.
- DeMars, B.G., and Boerner, R.E.J. 1995. Mycorrhizal status of *Deschampsia antarctica* in the Palmer Station area, Antarctica. *Mycologia*, **87**: 451–453.
- Dickson, S., Schweiger, P., Smith, F.A., Söderström, B., and Smith, S. 2003. Paired arbuscules in the *Arum*-type arbuscular mycorrhizal symbiosis with *Linum usitatissimum*. *Can. J. Bot.* **81**: 457–463. doi:10.1139/b03-037.
- Fitter, A.H. 1991. Costs and benefits of mycorrhizas: implications for functioning under natural conditions. *Experientia*, **47**: 350–355. doi:10.1007/BF01972076.
- Frenot, Y., Bergstrom, D.M., Gloaguen, J.C., Tavenard, R., and Strullu, D.G. 2005. The first record of mycorrhizae on sub-Antarctic Heard Island: a preliminary examination. *Antarct. Sci.* **17**: 205–210. doi:10.1017/S0954102005002609.
- Geil, R.D., Peterson, R.L., and Guinel, F.C. 2001. Morphological alterations of pea (*Pisum sativum* cv. Sparkle) arbuscular mycorrhizas as a result of exogenous ethylene treatment. *Mycorrhiza*, **11**: 137–143. doi:10.1007/s005720100120.
- Gianinazzi-Pearson, V., Morandi, D., Dexheimer, J., and Gianinazzi, S. 1981. Ultrastructural and ultracytochemical features of a *Glomus tenuis* mycorrhiza. *New Phytol.* **88**: 633–639.
- Kohn, L.M., and Stasovski, E. 1990. The mycorrhizal status of plants at Alexandra Fiord, Ellesmere Island, Canada, a high arctic site. *Mycologia*, **82**: 23–35.
- Kotyk, M.E.A., Basinger, J.F., and McIver, E.E. 2003. Early tertiary *Chamaecyparis* Spach from Axel Heiberg Island, Canadian High Arctic. *Can. J. Bot.* **81**: 113–130. doi:10.1139/b03-007.
- Laursen, G.A., Treu, R., Seppelt, R.D., and Stephenson, S.L. 1997. Mycorrhizal assessment of vascular plants from Subantarctic Macquarie Island. *Arct. Alp. Res.* **29**: 483–491.
- Malloch, D.W., Pirozynski, K.A., and Raven, P.H. 2000. Ecological and evolutionary significance of mycorrhizal symbioses in vascular plants (a review). *Proc. Natl. Acad. Sci. U.S.A.* **77**: 2113–2118.
- McGonigle, T.P., Miller, M.H., Evans, D.G., Fairchild, G.L., and Swan, J.A. 1990. A new method which gives an objective measure of colonization of roots by vesicular–arbuscular mycorrhizal fungi. *New Phytol.* **115**: 495–501. doi:10.1111/j.1469-8137.1990.tb00476.x.
- Merryweather, J.W., and Fitter, A.H. 1991. A modified method for elucidating the structure of the fungal partner in a vesicular–arbuscular mycorrhiza. *Mycol. Res.* **95**: 1435–1437.
- Olsson, P.A., Eriksen, B., and Dahlberg, A. 2004. Colonization by arbuscular mycorrhizal and fine endophytic fungi in herbaceous vegetation in the Canadian High Arctic. *Can. J. Bot.* **82**: 1547–1556. doi:10.1139/b04-111.
- Peterson, R.L., Massicote, H.B., and Melville, L.H. 2004. Mycorrhizas: anatomy and cell biology. CABI, Wallingford, U.K.
- Porsild, A.E. 1985. Illustrated flora of the Canadian Arctic Archipelago. National Museum of Canada, Ottawa, Ont.
- Rabatin, S.C. 1979. Seasonal and edaphic variation in vesicular–arbuscular mycorrhizal infection of grasses by *Glomus tenuis*. *New Phytol.* **83**: 95–102. doi:10.1111/j.1469-8137.1979.tb00730.x.
- Read, D.J. 1999. The ecophysiology of mycorrhizal symbioses with special reference to impacts upon plant fitness. In *Physiological plant ecology*. Edited by M.C. Press, J.D. Scholes, and M.G. Barker. Blackwell Science, Oxford, U.K. pp. 133–152.
- Read, D.J., and Haselwandter, K. 1981. Observations on the mycorrhizal status of some alpine plant communities. *New Phytol.* **88**: 341–352. doi:10.1111/j.1469-8137.1981.tb01729.x.
- Ruotsalainen, A.L., Väre, H., Oksanen, J., and Tuomi, J. 2004. Root colonization along an altitudinal gradient in North Norway. *Arct. Antarct. Alp. Res.* **36**: 239–243.
- Schüssler, A., Schwarzott, D., and Walker, C. 2001. A new fungal phylum, the Glomeromycota: phylogeny and evolution. *Mycol. Res.* **105**: 1413–1421.
- Søndergaard, M., and Laegaard, S. 1977. Vesicular–arbuscular mycorrhiza in some aquatic vascular plants. *Nature (Lond.)*, **268**: 332–333. PMID:887160.
- Taylor, T.N., Remy, W., Haas, H., and Kerp, H. 1995. Fossil arbuscular mycorrhizae from the early Devonian. *Mycologia*, **87**: 560–573.
- Thippayarugs, S., Bansal, M., and Abbott, K.L. 1999. Morphology and infectivity of a fine endophyte in a Mediterranean environment. *Mycol. Res.* **103**: 1369–1379. doi:10.1017/S0953756299001094.
- Väre, H., Vesterberg, M., and Euroala, S. 1992. Mycorrhiza and root-associated fungi in Spitsbergen. *Mycorrhiza*, **1**: 93–104.
- Vierheilig, H., Schweiger, P., and Brundrett, M. 2005. An overview of methods for the detection and observation of arbuscular mycorrhizal fungi in roots. *Physiol. Plant.* **125**: 393–404.