Arbuscular mycorrhizas are present on Spitsbergen

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Abstract A previous study of 76 plant species on Spitsbergen in the High Arctic concluded that structures resembling arbuscular mycorrhizas were absent from roots. Here, we report a survey examining the roots of 13 grass and forb species collected from 12 sites on the island for arbuscular mycorrhizal (AM) colonisation. Of the 102 individuals collected, we recorded AM endophytes in the roots of 41 plants of 11 species (*Alopecurus ovatus, Deschampsia alpina, Festuca rubra* ssp. *richardsonii,* putative viviparous hybrids of *Poa arctica* and *P. pratensis*, *Poa arctica* ssp. *arctica*, *Trisetum spicatum, Coptidium spitsbergense*, *Ranunculus nivalis*, *R. pygmaeus*, *R. sulphureus* and *Taraxacum arcticum*) sampled from 10 sites. Both coarse AM endophyte, with hyphae of 5–10 µm width, vesicles and occasional arbuscules, and fine endophyte, consisting of hyphae of 1–3 µm width and sparse arbuscules, were recorded in roots. Coarse AM hyphae, vesicles, arbuscules and fine endophyte hyphae occupied 1.0–30.7%, 0.8–18.3%, 0.7–11.9% and 0.7–12.8% of the root lengths of colonised plants, respectively. Principal component analysis indicated no associations between the abundances of AM structures in roots and edaphic factors. We conclude that the AM symbiosis is present in grass and forb roots on Spitsbergen.

Keywords Arbuscular mycorrhizas • High Arctic • Spitsbergen • Svalbard

Introduction

The arbuscular mycorrhizal (AM) symbiosis, formed between roots and fungi in the Glomeromycotina and Mucoromycotina (Spatafora et al. 2016; Orchard et al. 2017), is central to the survival and reproduction of the majority of terrestrial plant species (Smith and Read 2008). The symbiosis enhances plant uptake of limiting nutrients, chiefly phosphorus (P), from soil (Smith and Read 2008), with the uptake of P and other elements being facilitated by the formation in root cortical cells of branched arbuscules. Intracellular and extracellular vesicles are also formed for the storage of fats, leading to the development of intraradical structures that are readily identifiable by microscopy.

The AM symbiosis is widespread in grass and forb roots in temperate grasslands, dry scrub and deserts, tropical savannahs and Mediterranean vegetation, and is also found in the roots of trees in tropical rainforests and tropical seasonal forests (Read 1991). Its abundance declines markedly in cold regions, probably owing to a reduction in suitable host plant taxa, or the effects on the fungal symbionts of abiotic factors associated with increasing latitude, such as lower temperature, water availability or growing season length (Upson et al. 2008; Newsham et al. 2009). The symbiosis has nevertheless been recorded in Arctic habitats. In the Canadian High Arctic, where mean annual air temperatures range from -18 °C to -14 °C and mean summer air temperatures from -2 °C to 1 °C (Olsson et al. 2004), abundant AM endophytes (21–94% root lengths colonised) have been recorded in the roots of six of seven Asteraceae species in the Geodetic Hills on Axel Heiberg Island at 80 ºN (Allen et al. 2006). Frequent AM colonisation (8–85% root lengths colonised) has been found in the roots of *Erigeron* and *Taraxacum* species from Ellesmere Island at 82 °N (Ormsby et al. 2007), and AM endophytes have also been found to be commonplace (37–85% root lengths colonised) in the roots of *Arnica*, *Erigeron* and *Potentilla* species sampled from Banks Island at 73 ºN (Olsson et al. 2004).

In a survey of 76 plant species sampled from the shores of Van Mijenfjorden on Spitsbergen in the Svalbard archipelago, Väre et al. (1992) recorded no AM hyphae, vesicles or arbuscules in roots. The only evidence for the presence of AM fungi was a single spore, derived from a meadow below bird cliffs. This observation is counterintuitive: although situated in the High Arctic at *c*. 77–80 °N, Spitsbergen has a mild climate for its latitude, with the West Spitsbergen Current bringing warm water to the island's western shores all year round, and with approximate mean annual and summer air temperatures (2001–2015) of -3.3 °C and 4.8 °C, respectively (Isaksen et al. 2016). Given that the abundance of AM fungal structures in roots in polar ecosystems is positively associated with seasonal air temperatures (Upson et al. 2008) and that AM endophytes colonise roots in the colder Canadian High Arctic (Olsson et al. 2004; Allen et al. 2006; Ormsby et al. 2007), it seems plausible that the AM symbiosis is present on Spitsbergen. In support of this, a recent study used the polymerase chain reaction (PCR) to amplify AM fungal DNA from the roots of one *Saxifraga oppositifolia* and three *Ranunculus sulphureus* plants sampled from two locations in Longyearbyen on the island (Öpik et al. 2013). However, it is not presently known if the structural features of the symbiosis form in roots on Spitsbergen. We hence report a morphological study that examined the roots of likely host plant species sampled from 12 locations on Spitsbergen for arbuscular mycorrhizas to determine if structures indicative of the symbiosis are present, and to determine if edaphic factors explain the abundance of the symbiosis on the island.

Materials and methods

One hundred and two individuals of 13 plant species were collected in summer (late July–early September) 2014, 2015 and 2016 from 12 sites on Spitsbergen in the Svalbard archipelago (Table 1). The 12 sites were located on the shores of Isfjorden and Kongsfjorden, 40 km and 150 km north of Van Mijenfjorden, respectively (Online Resource 1). Where possible, plants were collected from closed, undisturbed swards of vegetation, in which AM inoculum is more likely to develop and persist (Evans and Miller 1988). The plant species chosen were members of the Poaceae, Ranunculaceae and Compositae, and thus likely hosts for AM fungi. In order to facilitate identifications, which were performed using the flora of Lid and Lid (2005) and descriptions of vascular plants on Svalbard (www.svalbardflora.no), flowering individuals of the majority of plants, and of all grasses, were collected. Mean summer air temperatures in 2001–2015 at three locations situated 1–18 km from the sampling sites ranged between 4.5 °C and 5.9 °C (Isaksen et al. 2016).

Individuals of each plant species were excavated with roots and attached soil and were placed into clean plastic bags, which were brought to the laboratory and kept at *c*. 4 °C. Within three days of sampling, the roots of each plant were removed from soil after tracing them back to the aboveground plant parts. The roots were initially cleaned in running water, were cleared in 10% KOH at 70 °C for 30 min and were then washed three times in water. Hydrogen peroxide (4%) was applied for 1–2 min. to roots that had not cleared sufficiently and was subsequently removed by washing several times in water. The roots were then acidified in 5% lactic acid at 70 °C for 30 min and were stained with aniline blue (0.01%) in lactic acid, again at 70 °C for 30 min. The roots were then removed from the aniline blue solution, were blotted on tissue to remove excess stain, and were stored in 80% lactic acid. All of the roots obtained from each plant (200–530 mm) were mounted on glass slides in 80% lactic acid and were examined under UV fluorescence at 200–400 × magnification using an Olympus BX51 microscope equipped with UPlanApo 20 × and 40 × objective lenses, a 100 W mercury short arc lamp and a UV fluorescence filter cube (U-MWU2, consisting of a BP 330–385 excitation filter, a DM 400 dichromatic mirror and an LP 420 emission filter; Olympus Life Science, Tokyo, Japan). The magnified intersections method of McGonigle et al. (1990) was used to determine the abundances of AM structures in roots. These were defined as either coarse AM endophyte with aseptate hyphae (5–10 μm diameter) and branched arbuscules with or without the presence of vesicles, or fine AM endophyte, with arbuscules and thin (1–3 μm diameter) hyphae, occasionally branching into fan-like patterns (Orchard et al. 2017). Between 100 and 150 evenly-spaced intersections were scored per individual root system (McGonigle et al. 1990).

Soil chemistry

Between four and 11 replicate soil samples from each site were analysed for pH and organic matter, soil moisture, and total carbon (C), nitrogen (N) and P concentrations. Soil pH was measured by adding double the volume of distilled water to each soil sample and recording pH using a glass electrode (Hanna Instruments, Leighton Buzzard, U.K.). Soil moisture was measured by heating 1–3 g of fresh soil to 105 °C for >3 h, prior to weighing, and organic matter concentrations were measured by heating the dried soil to 550 °C for 2 h, also prior to weighing (Allen 1989). Following grinding and sieving (2 mm), dried soil samples (2–9 mg) were placed into tin capsules and analysed for total C and N using a Costech ECS 4010 elemental analyser (Costech Analytical Technologies Inc., Valencia, USA). Total P was analysed for by digesting a sub-sample (0.36 g) of dried soil in 4.4 ml of a sulphuric acid and hydrogen peroxide mixture with lithium sulphate and selenium powder, followed

by heating for 2 h, dilution and then colorimetric determination using molybdenum blue chemistry on a SEAL AQ2 discrete analyser (SEAL Analytical Ltd., Southampton, UK).

Statistical analyses

Associations between edaphic factors and the abundances of AM structures in roots were tested with principal component analysis (PCA), using the mean values of the measured response and predictor variables at each sampling site. All edaphic variables were zero-skew transformed and scaled from -1 to 1. In order to circumvent multiple testing and covariation between edaphic variables, a site-based PCA was conducted on the edaphic variables using the vegan package in R (Oksanen et al. 2017). Associations between the PCA axes and the individual edaphic variables were estimated using Kendall's Tau correlations, and those between the first two PCA axis scores and the abundance of each AM structure were tested using Pearson's product moment correlations. Air temperature measurements were not available at sufficient resolution to include them in the PCA.

Results

AM colonisation was recorded in the roots of 41 of the 102 plants sampled (Table 1). Eleven species of plant were found to be colonised by AM endophytes at 10 of the 12 sites (Table 1). Colonisation was particularly frequent in roots sampled from dense grass swards in Colesdalen and Adventdalen and at Ossian Sars, and was absent from roots sampled from one site at Kapp Linné and one in Longyearbyen (Table 1). The structures observed in roots were typical of AM colonisation, with characteristic infection units being formed consisting of vesicles, coarse AM hyphae with angular projections, entry points in root hairs and occasional arbuscules (Online Resource 2). Coarse AM hyphae and vesicles were recorded in the roots of 31 and 29 plants, in which they colonised 1.0–30.7% and 0.8–18.3% of root length, respectively (Table 1). Arbuscules occupied 0.7–11.9% of root length in 15 plants, all but two of which were grasses (Table 1). The hyphae of fine endophytes were also recorded in the roots of 28 plants, in which they colonised 0.7–12.8% of root length (Table 1).

In the PCA on the associations between AM abundances and edaphic factors (Table 2), the first two axes summarized 79% of the total variation in edaphic variables (PC1=61%, PC2=18%). Soil moisture and C, N, P and total organic matter concentrations were correlated with the first ordination axis ($P<0.01$), while soil pH and C:N ratio were associated with the second axis ($P<0.005$). The abundance of each individual AM structure, and of total AM colonisation, was not significantly correlated with the edaphic PCA axis scores (all $P>0.07$, data not shown).

Discussion

The observations reported here show that structures indicative of the AM symbiosis occur in the roots of grasses and forbs at several locations on the west coast of Spitsbergen. Whilst molecular analyses have PCR-amplified the DNA of *Glomus*, *Archaeospora* and *Claroideoglomus* spp. from the roots of plants in Longyearbyen (Öpik et al. 2013), our observations indicate that the symbiosis occurs more widely on the island, and that significant lengths of root can be occupied by AM structures in colonised plants. In common with observations at other locations in the High Arctic (Olsson et al. 2004; Allen et al. 2006; Ormsby et al. 2007), the occurrence in roots of arbuscules, the point at which P and other elements are transferred from the fungal symbiont to plant tissues

(Smith and Read 2008), suggests that AM symbioses have the capacity to influence plant nutrient acquisition on Spitsbergen.

Several of the plant species that were found to be colonised by AM endophytes in the present study (*Deschampsia alpina, Trisetum spicatum, Ranunculus sulphureus*, *R. pygmaeus*, *R. nivalis* and *Taraxacum arcticum*) were reported to be non-mycorrhizal by Väre et al. (1992). What might explain the previously reported absence of the AM symbiosis from the roots of these plant species on Spitsbergen? One possibility is that the sampling employed by Väre et al. (1992) was not extensive enough to have detected AM symbionts in roots. This is unlikely, since a total of 205 root samples – twice the number of samples gathered here – collected from 17 sites distributed over a distance of >100 km on the shores of Van Mijenfjorden were examined for AM structures by Väre et al. (1992). Although many of these samples were of plant species belonging to typically non-mycorrhizal families, which increase in abundance at high latitudes (Newsham et al. 2009), AM colonisation was found to be absent from the roots of 54 members of the Poaceae and 15 members of the Ranunculaceae (Väre et al. 1992), families that were found to be colonised by AM endophytes in the present study.

Contrary to previous reports (e.g. Liu et al. 2017), edaphic factors had no apparent influence on the abundances of AM structures in the present study. It thus seems unlikely that differences in soil chemistry between the sites sampled by Väre et al. (1992) and those studied here explain the discrepancies between the two studies. Differences in the plant community types sampled might also explain these discrepancies, but the communities from which plants were sampled by Väre et al. (1992) included dwarf shrub heaths, meadows and grass swards, and were thus similar to those studied here. The previously reported absence of AM structures from plant roots on Spitsbergen may have been owing to Väre et al. (1992) gathering some roots at the start of the growing season on the island (early June), when the abundances of AM structures in roots may have been low (Mullen and Schmidt 1993). However, Väre et al. (1992) also sampled roots up to the middle of the growing season (mid August), by which time suitable conditions for AM colonisation of roots should have occurred, and so this explanation can most probably also be discounted.

It is possible that increasing surface air temperatures on Spitsbergen since 1969 may have led to more abundant AM colonisation of roots in recent decades, explaining the difference between the results of Väre et al. (1992) and those reported here. Assuming a rise in mean annual air temperature on the island of *c*. 2.0 °C since the early 1970s (Isaksen et al. 2016), and 0.6–3.0% increases in the percentage of root length occupied by AM structures per degree Celsius increase in air temperature along transects through polar habitats (Upson et al. 2008), then up to 6% increases in the abundances of AM endophytes in roots might be anticipated over this period. Modest increases in root lengths occupied by AM structures owing to climate warming since the late 1960s are, however, unlikely to explain the differences between the findings of the two studies. A more plausible explanation is that some of the sites sampled here had more favourable microclimates than those on the shores of Van Mijenfjorden: although ambient air temperatures around this fjord are only *c*. 1 °C lower than those around Isfjorden and Kongsfjorden (Pryzbylak 1992), it is notable that AM colonisation was particularly abundant in the present study at Colesdalen, which has a high concentration of thermophilous plant species (Alsos et al. 2004), and at Ossian Sars, which short-term meteorological data indicate is one of the warmest locations in Kongsfjorden (Joly et al. 2010). Microclimatic data at sufficient resolution to make meaningful predictions of soil biological activity at the sites studied here are unavailable, and we were hence unable to include air or soil

temperatures as predictors in our statistical analyses. However, we propose that by sampling from locations with favourable microclimates, and particularly from dense swards of vegetation, in which AM inoculum is more likely to persist (Evans and Miller 1988), we would have increased the likelihood of recording AM symbionts in roots, perhaps explaining the disparity between the results of the present study and those of Väre et al. (1992).

We conclude that structures formed by AM fungi are indeed present in the roots of plants on Spitsbergen, expanding the known range of the symbiosis in the High Arctic (*c.f.* Olsson et al. 2004; Allen et al. 2006; Ormsby et al. 2007; Newsham et al. 2009). Further studies should examine whether microclimate does influence the abundances of AM structures in roots on Spitsbergen, as it appears to at other locations in the High Arctic (Allen et al. 2006), and whether the AM symbiosis affects plant performance on the island, for example if it enhances drought tolerance or nutrient acquisition from cold soils (Tibbett and Cairney 2007; Helgason and Fitter 2009). Further research should also determine whether the roots of other plant species on Spitsbergen are colonised by AM fungi, focusing on the remaining members of the families studied here and members of speciose families present on the island that are usually AM at lower latitudes, such as the Saxifragaceae and Rosaceae (Wang and Qui 2006).

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Table 1 Details of the 12 sampling sites and the frequencies of AM colonisation in roots

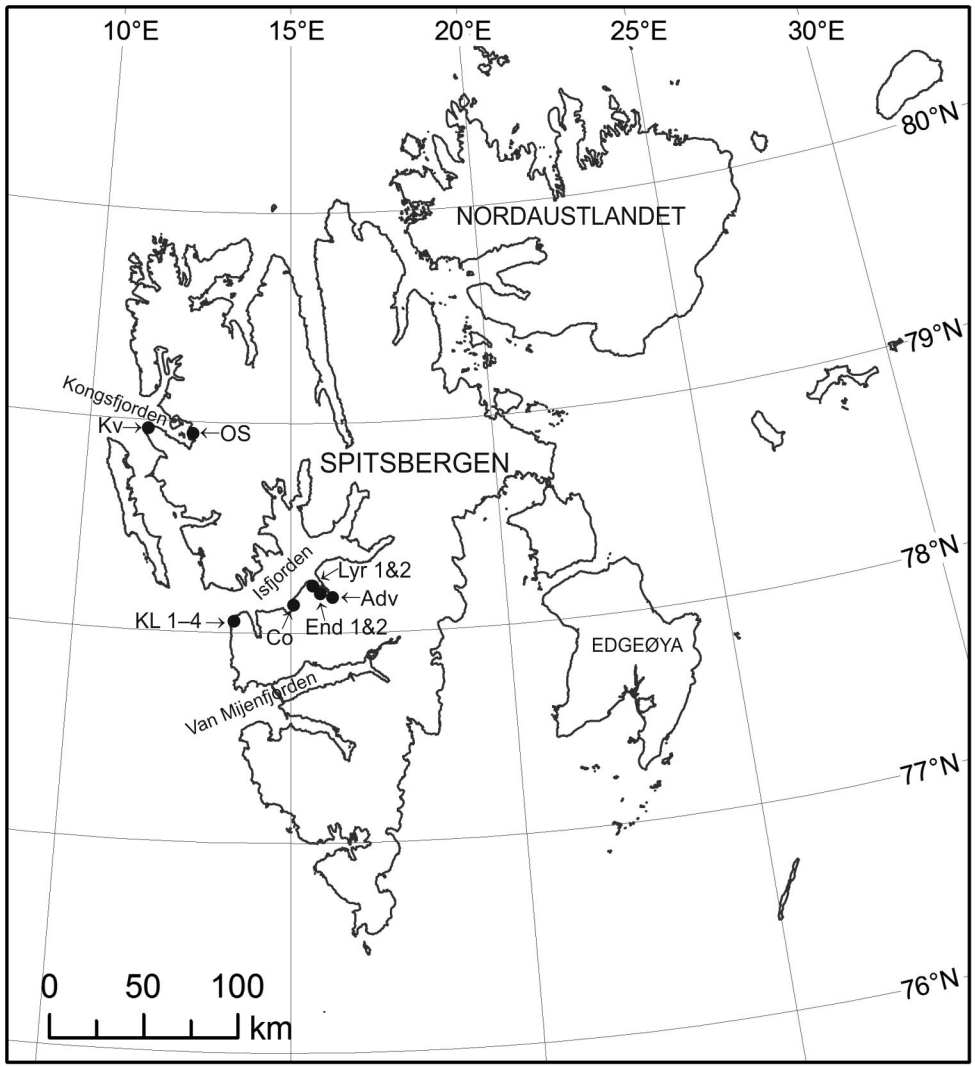
Sampling site [a]	Latitude and longitude	Plant community	Plant species	Plants sampled (*n*)	Coarse AM hyphae [b]	Vesicles [b]	Arbuscules [b]	Fine endophyte hyphae [b]
Adventdalen	78°10.271'N, 16°00.668'E	Dense grass swards interspersed with forbs	*Alopecurus ovatus* Knapp	7	2 (22.9, 6.6)	2 (18.3, 6.2)	1 (11.9)	1 (0.9)
			Calamagrostis neglecta (Ehrh.) P. Gaertn., B. Mey. & Scherb.	1	0	0	0	0
			Festuca rubra L. ssp. *richardsonii* (Hook.) Hultén	5	1 (14.7)	1 (6.2)	1 (2.3)	1 (3.8)
			Poa arctica R. Br. / *P. pratensis* L. [c]	2	0	0	0	0
			Poa arctica ssp. *arctica* R. Br.	1	0	0	0	0
			Poa pratensis L.	2	0	0	0	0
			Ranunculus sulphureus Sol.	4	3 (21.8, 10.0, 3.4)	3 (11.9, 8.2, 3.4)	0	1 (11.9)
Colesdalen	78°06.468'N, 15°04.729'E	Dense grass swards interspersed with forbs	*Alopecurus ovatus*	2	0	0	0	0
			Festuca rubra ssp. *richardsonii*	1	1 (8.6)	1 (2.9)	1 (3.8)	0
			Ranunculus pygmaeus L.	1	1 (22.5)	1 (12.5)	0	1 (1.7)
			Ranunculus sulphureus	4	3 (4.2, 3.3, 1.7)	3 (2.5, 2.4, 0.8)	1 (0.8)	2 (4.2, 2.5)
			Ranunculus nivalis L.	2	2 (19.2, 17.7)	2 (15.4, 9.7)	0	0
			Taraxacum arcticum (Trautv.) Dahlst.	1	1 (7.7)	1 (4.3)	0	1 (1.7)
Endalen 1	78°11.035'N, 15°45.557'E	Dwarf-shrub heath tundra	*Alopecurus ovatus*	4	1 (3.0)	1 (3.0)	0	0
			Festuca rubra ssp. *richardsonii*	2	0	0	0	1 (3.0)
			Poa arctica / *P. pratensis* [c]	3	2 (16.5, 12.4)	2 (9.5, 3.1)	2 (0.8, 0.7)	1 (1.6)
			Poa arctica ssp. *arctica*	1	0	0	0	0
			Ranunculus sulphureus	11	3 (12.0, 5.7, 5.1)	3 (5.2, 4.4)	0	4 (4.4, 4.1, 3.0, 2.0)
Endalen 2	78°11.180'N, 15°45.557'E	Dwarf-shrub heath tundra	*Alopecurus ovatus*	2	0	0	0	0
			Ranunculus sulphureus	4	1 (7.6)	1 (5.9)	0	1 (4.0)
Kapp Linné 1	78°03.614'N, 13°38.293'E	Dwarf-shrub heath tundra	*Deschampsia alpina* (L.) Roem. & Schult.	1	0	0	0	0
			Poa arctica / *P. pratensis* [c]	3	0	0	0	1 (0.7)
Kapp Linné 2	78°03.569'N, 13°38.554'E	Dwarf-shrub heath tundra	*Poa arctica* / *P. pratensis* [c]	1	0	0	0	0
			Poa arctica ssp. *arctica*	2	0	0	0	1 (1.0)
Kapp Linné 3	78°03.532'N, 13°39.075'E	Dwarf-shrub heath tundra	*Deschampsia alpina*	1	0	0	0	0
			Poa arctica / *P. pratensis* [c]	1	0	0	0	0
			Poa arctica ssp. *arctica*	1	0	0	0	0
Kapp Linné 4	78°04.484'N, 13°45.508'E	Dwarf-shrub heath tundra	*Deschampsia alpina*	2	1 (2.0)	1 (1.0)	0	1 (1.0)
			Festuca rubra ssp. *richardsonii*	1	0	0	0	0
			Poa arctica / *P. pratensis* [c]	3	0	0	0	0
Kvadehuken	78°58.243'N, 11°28.521'E	Sparse grass sward	*Festuca rubra* ssp. *richardsonii*	4	0	0	1 (5.2)	1 (5.2)
Longyearbyen 1	78°13.148'N, 15°38.825'E	Moss wetland	*Coptidium spitsbergense* (Hadač) Luferov & Prob.	4	1 (3.0)	0	0	0
Longyearbyen 2	78°13.033'N, 15°39.114'E	Dwarf-shrub heath tundra	*Alopecurus ovatus*	5	0	0	0	0
			Coptidium spitsbergense	1	0	0	0	0
			Ranunculus sulphureus	1	0	0	0	0
Ossian Sars	78°55.795'N, 12°26.680'E	Dense grass swards interspersed with forbs	*Festuca rubra* ssp. *richardsonii*	5	4 (16.8, 14.2, 13.4, 8.4)	4 (10.4, 9.8, 6.7, 6.5)	4 (5.9, 2.5, 1.1, 0.7)	4 (9.2, 5.8, 1.1, 0.7)
			Poa arctica / *P. pratensis* [c]	1	1 (1.0)	1 (1.0)	1 (2.5)	1 (10.0)
			Poa arctica ssp. *arctica*	2	1 (1.1)	1 (1.1)	1 (2.4)	2 (6.4, 1.1)
			Ranunculus sulphureus	2	1 (12.0)	1 (7.7)	1 (0.7)	2 (12.8, 5.9)
			Trisetum spicatum (L.) K. Richt.	1	1 (30.7)	1 (17.3)	1 (2.7)	1 (1.7)

[a] See Online Resource 1 for a map showing the locations of the sampling sites; [b] values shown are the numbers of colonised plants, followed in parentheses by the mean percentage root length occupied by each AM structure in the roots of each colonised plant; [c] viviparous plants. The viviparous plants of the *Poa arctica*–*P. pratensis* complex (except for *P. pratensis* ssp. *colpodea*) span the range of morphological variation between *P. arctica* ssp. *arctica* and *P. pratensis* ssp. *alpigena*, possibly arising from hybridization between the two species, and are thus morphologically indistinguishable (R. Elven, pers. comm.).

Table 2 Edaphic factors at the 12 sampling sites

Site [a]	Edaphic factor [a]						
	pH	Carbon (%)	Nitrogen (%)	Carbon : nitrogen ratio	Phosphorus (%)	Organic matter (%)	Moisture (g water per 100 g oven-dried soil)
Adventdalen	6.0 ± 0.3	25.1 ± 5.5	1.0 ± 0.1	25.4 ± 1.9	0.10 ± 0.03	26.7 ± 16.7	44.4 ± 11.6
Colesdalen	5.3 ± 0.2	6.5 ± 6.1	0.5 ± 0.4	12.3 ± 3.3	0.09 ± 0.01	9.3 ± 2.1	29.2 ± 13.2
Endalen 1	5.4 ± 0.5	11.5 ± 5.7	0.5 ± 0.2	23.9 ± 5.7	0.04 ± 0.02	10.0 ± 4.6	34.4 ± 9.1
Endalen 2	6.5 ± 0.4	32.4 ± 13.2	2.4 ± 3.2	13.3 ± 6.8	0.08 ± 0.01	27.2 ± 12.7	56.8 ± 17.9
Kapp Linné 1	6.9 ± 0.2	6.6 ± 1.6	0.3 ± 0.2	20.6 ± 1.9	0.03 ± 0.01	4.0 ± 0.2	30.6 ± 17.8
Kapp Linné 2	7.3 ± 0.4	6.8 ± 2.2	0.4 ± 0.2	16.5 ± 0.12	0.06 ± 0.01	10.8 ± 4.6	25.4 ± 15.7
Kapp Linné 3	6.8 ± 0.3	12.1 ± 7.3	1.0 ± 0.4	12.5 ± 1.2	0.09 ± 0.06	11.3 ± 12.4	60.4 ± 6.9
Kapp Linné 4	6.6	8.1	1.3	6.2	m.d.	m.d.	m.d.
Kvadehuken	6.7 ± 0.3	28.7 ± 7.7	1.7 ± 0.4	16.8 ± 2.4	0.24 ± 0.14	46.5 ± 17.2	63.6 ± 10.1
Longyearbyen 1	4.7 ± 0.3	27.7 ± 2.4	1.0 ± 0.2	27.5 ± 6.8	0.13 ± 0.02	58.1 ± 5.1	80.4 ± 4.4
Longyearbyen 2	6.4 ± 0.2	17.0 ± 3.5	0.8 ± 0.1	22.6 ± 2.5	0.03 ± 0.01	15.6 ± 4.3	53.8 ± 9.1
Ossian Sars	6.2 ± 0.4	32.1 ± 15.9	1.9 ± 0.8	16.9 ± 8.2	0.13 ± 0.03	65.5 ± 28.6	59.8 ± 13.3

[a] all values except those for Kapp Linné 4 (which are single measurements) are means (n = 4–11) ± standard deviation; m.d.; missing data.



Online Resource 1 Map of the Svalbard archipelago showing the locations of the 12 sampling sites on Spitsbergen. Abbreviations: Kv, Kvadehuken; OS, Ossian Sars; KL, Kapp Linné; Co, Colesdalen; Lyr, Longyearbyen; End, Endalen; Adv, Adventdalen.

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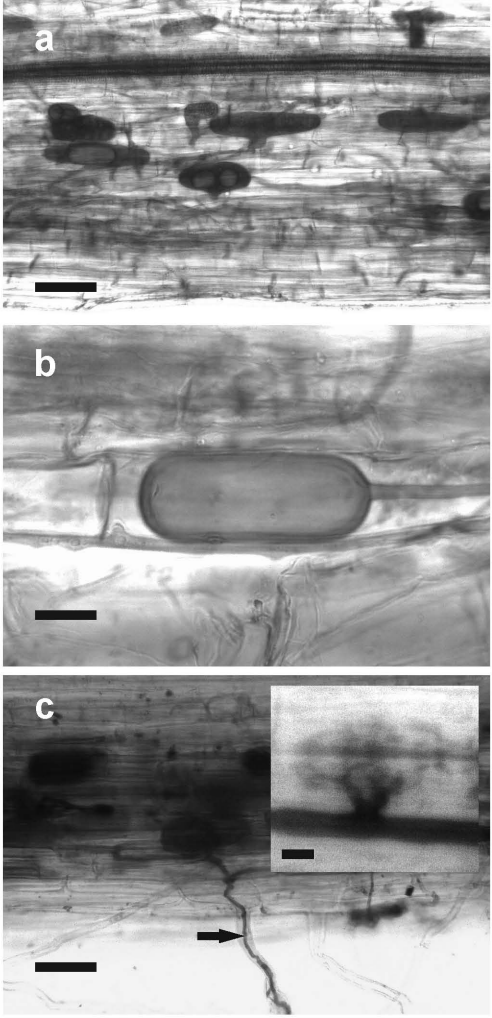

Online Resource 2 Light micrographs of AM structures in plant roots from Spitsbergen. **a** Vesicles in a *Ranunculus sulphureus* root. **b** An intracellular vesicle in a root epidermal cell of *Alopecurus ovatus*. **c** An entry point of coarse AM hyphae (arrowed) in a root hair of *A. ovatus*. Insert in **c** shows an arbuscule formed in a root cortical cell of *A. ovatus*. The image is a composite of five successive images stacked using Helicon Focus v. 6.7.1 with automatic contrast optimization. Scale bars in **a**–**c** are 100, 30 and 60 µm respectively and that in the insert in c is 5 µm.

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