Mycorrhizas and dark septate root endophytes in polar regions

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ABSTRACT

We review the distributions and functions of mycorrhizas and dark septate root endophytes in polar regions. Arbuscular mycorrhizas (AM) are present in the Arctic and Antarctic to 82 ºN and 63 ºS, respectively, with fine endophyte being the dominant form of AM in roots at higher latitudes. Ecto- (ECM) and ericoid (ERM) mycorrhizas both occur in the Arctic to 79 ºN, owing to the presence of species of *Salix*, *Dryas*, *Vaccinium* and *Cassiope* to this latitude. ECM and ERM are not present in Antarctic ecosystems, owing to an absence of suitable hosts. Arbutoid and orchid mycorrhizas are infrequent in the Arctic, whilst the latter is present at one location in the sub-Antarctic. Data from studies of AM, ECM and ERM colonisation along a latitudinal transect through the Arctic indicate that the frequency of plant species not colonised by mycorrhizas increases at higher latitudes, largely owing to an increase in non-mycorrhizal and a decrease in obligately mycorrhizal plant families at more northerly locations. A separate group of root- and rhizoid-associated fungi, the dark septate root endophytes (DSE), are widespread to 82 ºN and 77 ºS, and are apparently more frequent than mycorrhizal fungi in polar regions. The functions of DSE are largely unclear, but studies suggest beneficial effects on plant growth under defined conditions. We advocate further research into the effects of DSE on their host plants in polar regions.

Keywords: Antarctic, arbuscular mycorrhizas (AM), arbutoid mycorrhizas, Arctic, dark sterile (DS) fungi, ectomycorrhizas (ECM), ericoid mycorrhizas (ERM), orchid mycorrhizas

Introduction

Polar regions are cold, arid and windy. The mean air temperature of the warmest month in these regions is typically <10 ºC, usually coinciding with the limits of tree growth (Aleksandrova 1980), and their terrestrial habitats are often snow- and ice-covered for several months of the year, with consequently short growing seasons. They are exposed to continuous sunlight or darkness for periods in summer and winter within the Arctic and Antarctic Circles, parallels of latitude at 66º 33’ north and south, respectively. Freeze-thaw events are commonplace. These harsh conditions impose strong selection pressures on plants inhabiting such regions, leading to prostrate, cushion-forming life forms with aerodynamically smooth canopies, fewer woody species and reduced species richness at higher latitudes, both in Arctic and Antarctic ecosystems (Rannie 1986; Peat *et al*. 2007).

These changes in plant diversity are likely to exert a strong influence over the frequencies and forms of mycorrhizas in polar regions. Mycorrhizas, symbioses between plant roots and soil fungi, typically have roles in plant nutrition, facilitating the inflow, *via* hyphae, of limiting nutrients into plant tissues from beyond nutrient depletion zones around roots, and thus have pivotal roles in terrestrial ecosystem functioning (Smith & Read 2008). Several forms of the symbiosis are recognised, including the arbuscular, ecto-, ericoid, arbutoid and orchid mycorrhizal associations (Smith & Read 2008). The arbuscular mycorrhizal (AM) association typically forms in the roots of herbs and grasses, and is chiefly associated with the uptake of phosphorus from neutral temperate soils. The ectomycorrhizal (ECM) association develops in the roots of woody angiosperms and gymnosperms, whilst the ericoid mycorrhizal (ERM) and arbutoid mycorrhizal associations form in the roots of ericaceous species. These three forms of the symbiosis typically have roles in the uptake of nitrogen from acidic soils, and often organic forms of the element (Read 1991). Lastly, the orchid mycorrhizas, which develop in the roots of members of the Orchidales, have more specialised roles in the germination and early growth of orchid seedlings (Smith & Read 2008).

Despite the fact that changes in plant diversity in polar ecosystems are likely to influence mycorrhizal distribution, a synthesis of information on the occurrence of mycorrhizas in Arctic and Antarctic habitats is apparently absent from the literature. Below we review the literature on these associations in the roots or rhizoids of plants occurring in polar regions, including taiga, the sub-Arctic and sub-Antarctic, with the aim of consolidating information on their distributions in these regions. We also analyse changes in the frequencies of AM, ECM and ERM along a latitudinal gradient from taiga through to the High Arctic. Finally, information is reviewed on a separate group of root- and rhizoid-associated fungi, the dark septate endophytes (DSE), and their distribution and functional status are assessed. Firstly, however, in order to put this information into context, we describe the geobotanical regions of the Arctic and Antarctic.

Polar geobotanical regions

The sub-Arctic and Arctic regions can be divided into five geobotanical subzones (CAVM Team 2003). The first of these consists of southern sub-Arctic tundra, usually situated inland from the Arctic Ocean coast and typically composed of herbaceous plants and dwarf shrubs with a closed canopy, experiencing mean July temperatures (MJuT) of 9-12 ºC (subzone E; Fig 1). The second region, the northern sub-Arctic tundra, consists of herbaceous plants and dwarf shrubs but with an interrupted closed canopy. This region, usually located on the Arctic Ocean coast, experiences MJuT of 7-9 ºC (subzone D; Fig 1). Both of these subzones are frequently inhabited by dwarf woody shrubs such as *Dryas*, *Salix*, *Betula*, *Vaccinium*, *Cassiope* and *Empetrum*, along with sedges, such as *Carex* and *Eriophorum* (CAVM Team 2003). The third region, the southern Arctic tundra, is again formed by herbs and dwarf shrubs, but has a more open canopy than subzones D and E, and experiences MJuT of 5-7 ºC. This region covers large areas of Baffin and Victoria Islands and frequently forms a narrow coastal border in the Russian and North American Arctic regions and eastern Greenland (subzone C; Fig 1). The fourth region, the northern Arctic tundra, consists of an open canopy of herbs and dwarf shrubs, with up to 60% cover by cryptogams, and is exposed to MJuT of 3-5 ºC. It covers the offshore islands of the Russian Arctic, the northern Taimyr Peninsula, northern Greenland and the Queen Elizabeth Islands (subzone B; Fig 1). Although dwarf woody shrubs and sedges are still present in subzones B and C, grasses such as *Alopecurus*, *Deschampsia* and *Poa* tend to be more abundant (CAVM Team 2003). Lastly, the fifth region, the Arctic polar desert, consists of mostly barren ground, with lichens and mosses and very sparse vascular plant cover by grasses and cushion forbs such as *Papaver*, *Potentilla* and *Saxifraga*. The region experiences MJuT of 0-3 ºC and occurs on the offshore islands of the Russian Arctic and the northernmost of the Queen Elizabeth Islands (subzone A; Fig 1).

The Antarctic can be broadly divided into three geobotanical regions (Aleksandrova 1980). The first, the sub-Antarctic (Fig 1), consists of, amongst others, Macquarie, Marion, and Heard islands, South Georgia and Îles Kerguelen. These islands have cool oceanic climates, with mean annual temperatures >0 ºC and mean January temperatures (MJaT) of *c.* 5-7 ºC (Rosswall & Heal 1975; Walton 1984; Smith 1984). Their vegetation is broadly characterised by grasses, rushes, sedges, ferns and forbs, often tussock-forming species such as *Parodiochloa flabellata*, *Acaena magellanica* and *Azorella selago*, interspersed with numerous mosses, liverworts and lichens (Aleksandrova 1980; Smith 1984). Woody species and dwarf shrubs are absent. The second region, the maritime Antarctic (Fig 1), is characterised by cold moist maritime climates, with a mean monthly air temperature of >0 ºC for 3-4 months of the year and MJaT of ≤ 2 ºC (Aleksandrova 1980; Smith 1984). The areas of the maritime Antarctic pertinent to this review are the South Orkney and South Shetland Islands and the western Antarctic Peninsula and offshore islands to *c*. 68 ºS. The vegetation of the maritime Antarctic consists of herb-lichen-moss formations, with just two vascular plant species, the pearlwort *Colobanthus quitensis* and the grass *Deschampsia antarctica*, occurring with numerous cryptogams (Smith 1984). Finally, the third Antarctic geobotanical region, the continental Antarctic (Fig 1), consists of the western Antarctic Peninsula south of 68 ºS, the eastern side of the peninsula south of *c*. 63 ºS and Greater Antarctica. The region is characterised by a frigid and arid climate, with its northernmost limit formed by the 0 ºC isotherm for the warmest month (Aleksandrova 1980). Approximately 1% of the land is not covered with permanent glaciers. Vascular plants are absent from the region but bryophytes and lichens are present in ice-free oases and on nunataks (Smith 1984).

Distributions of mycorrhizas in polar ecosystems

Arbuscular mycorrhizas

The arbuscular mycorrhizal association is commonplace in taiga and sub-Arctic tundra (Fig 1), where it occurs frequently in the roots of members of the Poaceae, Ranunculaceae, Asteraceae, Saxifragaceae and Rosaceae. Greipsson *et al*. (2002) and Treu *et al*. (1996) recorded AM structures in roots from southern Iceland and at Denali National Park in central Alaska (both *c.* 63 ºN), whilst, in sub-Arctic tundra, the association has been recorded at Point Barrow (71 ºN) on the northern Alaskan coast (Miller & Laursen 1978), at Abisko (68 ºN) in northern Sweden (Michelsen *et al.* 1996) and in several studies in the Kilpisjärvi area (69 ºN) of north-western Finland (Väre *et al*. 1997; Ruotsalainen *et al*. 2004; Pietikäinen *et al*. 2007). In the Russian Arctic, the AM association has been recorded close to Vorkuta (67 ºN) in sub-Arctic tundra (Katenin 1964; Katenin 1972), at unspecified locations in Karelia (Sychuva 1952, cited in Katenin 1964) and on the Taimyr Peninsula (70-77 ºN; Tikhomirov & Strelkova 1954; Strelkova 1956).

The AM association apparently declines in abundance in Arctic tundra and polar deserts. Olsson *et al*. (2004) found that arbuscules and vesicles of AM fungi were frequent in the roots of *Arnica*, *Erigeron* and *Potentilla* species sampled from Banks Island (73 ºN), were infrequent in the roots of *Festuca*, *Trisetum* and *Potentilla* species sampled from Devon Island (74 ºN) and were absent from roots sampled from Ellesmere (76 ºN) and Ellef Ringnes Island, close to the magnetic North Pole (78 ºN), in which only fine endophyte without arbuscules was recorded in roots (Olsson *et al*. 2004). This form of the AM association, unlike coarse endophyte, lacks vesicles and possesses slender hyphae, usually $< 1.5\ \mu$m in diameter (Merryweather & Fitter 1998). AM structures were found to be absent from the roots of all 76 plant species examined from Spitsbergen (77 ºN) by Väre *et al*. (1992). Kohn & Stasovski (1990) also showed that of 23 plant species sampled, just one, the fern *Dryopteris fragrans*, was colonised by AM fungi at Alexandra Fjord on Ellesmere Island (79 ºN). In a study at the same location and at Truelove Lowland on the neighbouring Devon Island (75 ºN), Bledsoe *et al*. (1990) showed AM to be absent from the roots of 55 plant species. However, recent reports using differential interference contrast microscopy show that AM are present on Ellesmere and Axel Heiberg islands in the Queen Elizabeth Islands (Fig 1). Arbuscules, but not vesicles, are present in the roots of an *Erigeron* and a *Taraxacum* species to 82 ºN in the Lake Hazen area on the former island (Ormsby *et al*. 2007), possibly reflecting the fact that the area becomes a thermal oasis in the summer, owing to its favourable climate. Similarly, Dalpé & Aiken (1998) found hyphae and vesicles of AM fungi in the roots of *Festuca* spp. sampled from Ellesmere and Axel Heiberg islands, but only occasional arbuscules, whereas Allen *et al*. (2006) recorded abundant (11-36 % of root length colonised) arbuscules in the roots of six of seven Asteraceae species sampled from the Geodetic Hills area of Axel Heiberg Island (80 ºN), which, in common with the Lake Hazen area, becomes a thermal oasis during the summer.

The AM association is consistently present, and often abundant, in sub-Antarctic ecosystems (Fig 1). It has been recorded at all locations sampled in the sub-Antarctic, most frequently in the roots of the Poaceae and families typically regarded as facultatively mycorrhizal or non-mycorrhizal, such as the Juncaceae, Cyperaceae and Caryophyllaceae (Wang & Qui 2006). Frequent hosts in sub-Antarctic habitats are members of the genera *Deschampsia*, *Poa*, *Juncus*, *Ranunculus*, *Uncinia*, *Colobanthus* and *Acaena*. Christie & Nicolson (1983) examined roots sampled from South Georgia (55 ºS) for fungal colonisation and found AM to be abundant in the roots of nine vascular plant species, with 4 - 78% of root lengths occupied by these fungi. Subsequently, Smith & Newton (1986) recorded AM associations in the roots of all but one of 24 vascular plant species sampled from Marion Island (47 ºS), with between 0.2 and 25% of the root lengths of plants colonised by AM fungi. Strullu *et al*. (1999) found that six of the 17 vascular plant species sampled from Îles

Kergeulen (49 ºS) were colonised by AM structures. Of the 40 plant species examined by Laursen *et al*. (1997) on Macquarie Island (54 ºS), arbuscules and vesicles were recorded in the roots of three vascular plant species, and vesicles in fifteen other plant species. Frenot *et al*. (2005), who sampled nine plant species from a variety of habitats on Heard Island (53 ºS), found either vesicles, arbuscules or both structures in the roots of all species. Lastly, Upson *et al*. (2008) recorded coarse and fine AM endophytes to occupy 10% and 15% of the root lengths of *Deschampsia antarctica* and *Colobanthus quitensis* sampled from South Georgia, respectively.

Contrary to previous reports, recent data indicate that AM are sparse, but present, in maritime Antarctic habitats (Fig 1). In the survey of Christie & Nicolson (1983), plant roots were sampled not only from South Georgia but also from four locations in the South Orkney and South Shetland islands, and from six locations on the Antarctic Peninsula to 68 ºS. AM were found to be absent from the roots of *D. antarctica* and *C. quitensis*, leading Christie & Nicolson (1983) to propose that mycorrhizas might be absent from the region. Similarly, DeMars & Boerner (1995) found no AM structures in the roots of *D. antarctica* sampled from Anvers Island on the western Antarctic Peninsula (65 ºS). Other studies, however, have challenged the view that AM are absent from the maritime Antarctic: a recent study that sampled widely in the region has shown the presence of AM structures, including occasional arbuscules, in the roots of *D. antarctica* sampled from the South Shetland Islands to 63 ºS (Upson *et al*. 2008). As in the study of Olsson *et al*. (2004) in the Arctic, coarse endophyte with arbuscules was very rarely observed in roots sampled from the maritime Antarctic, with fine endophyte being the main form of AM recorded (Upson *et al*. 2008). Cabello *et al*. (1994) similarly showed the presence of AM propagules, and a new AM species, *Glomus antarcticum*, in the rhizosphere of *D. antarctica* on the Danco Coast of the western Antarctic Peninsula (64 ºS).

Ectomycorrhizas

Ectomycorrhizas are commonplace in Arctic ecosystems (Fig 1), where they frequently form on the roots of members of the Betulaceae, Salicaceae and Rosaceae. In taiga and sub-Arctic habitats in Alaska, northern Finland and Siberia, mantles have often been recorded on the roots of *Betula nana* and *Salix* species, often *S. arctica* (Miller 1982; Treu *et al*. 1996; Väre *et al*. 1997; Michelsen *et al*. 1998). *Dryas octopetala* is also colonised by ECM at Abisko in northern Sweden and Eagle Summit (65 ºN) in Alaska (Miller 1982; Michelsen *et al*. 1998). Other plant species colonised by ECM in taiga and the sub-Arctic include *Arctostaphylos* *rubra*, *Larix dahurica* and *Pinus pumila* (Miller 1982; Michelsen *et al*. 1998). Unusually for herbaceous species, *Polygonum viviparum* and *Kobresia myosuroides* also form ECM in these regions (Hesselman 1900; Treu *et al*. 1996; Väre *et al*. 1997; Michelsen *et al*. 1998).

ECM are often present in Arctic tundra but are less frequent in polar deserts (Fig 1), most probably reflecting a lack of suitable host species in the latter habitats. Studies on the eastern coast of Greenland and on Spitsbergen, Devon and Ellesmere islands indicate that *S. arctica* is a frequent host for the association, as are *Dryas integrifolia* and *D. octopetala* (Väre *et al*. 1992; Michelsen *et al*. 1998; Bledsoe *et al*. 1990). *P. viviparum* and *K. myosuroides* are also colonised by ECM at the former location (Michelsen *et al*. 1998), as are *K. myosuroides, Saxifraga oppositifolia* and *Pedicularis capitata* at Alexandra Fjord on Ellesmere Island (Kohn & Stasovski 1990). ECM have also been recorded at Disko Island (70 ºN), off the western Greenland coast, by Clemmensen & Hansen (1999).

Much information exists on the species of ectomycorrhizal fungi associated with the roots of Arctic plant species. A few of these records are *in planta*: mantles similar to those formed by *Cenococcum geophilum* have been recorded in central Alaska (Treu *et al*. 1996), the northern Alaskan coast (Linkins & Antibus 1982), north-western Finland (Väre *et al*. 1992) and Devon Island (Bledsoe *et al*. 1990). By contrast, there are many records of ectomycorrhizal fruiting bodies in Arctic tundra. Väre *et al*. (1992) summarise data from Arctic studies showing *S. polaris* and *D. octopetala* to be associated with approximately 50 ectomycorrhizal fungal species in the genera *Entoloma*, *Hebeloma*, *Helvella*, *Inocybe*, *Lactarius*, *Laccaria*, *Cortinarius* and *Russula*. Similar genera are present on the northern Alaskan coast (Linkins & Antibus 1982) and on the Taimyr Peninsula (Stepanova & Tomilin 1972), with the last three genera above present at Alexandra Fjord on Ellesmere Island (Kohn & Stasovski 1990). A thorough assessment of ectomycorrhizal fruiting bodies in Arctic ecosystems is beyond the scope of this review, but readers are directed to Laursen & Ammirati (1982) and Gulden *et al*. (1985), and subsequent editions of these volumes, for information on the occurrence of specific groups of ECM fruiting bodies in Arctic tundra.

Woody shrubs are absent from the Antarctic, and hence the ECM association is apparently not present on the continent or its surrounding islands (Fig 1). Horak (1982) similarly reports the absence of ectomycorrhizal agarics from the maritime and sub-Antarctic.

Ericoid mycorrhizas

Plant species in the Ericaceae are widespread in taiga and sub-Arctic tundra, and are routinely colonised by ERM in these regions (Fig 1). *Vaccinium* spp., often *V. uliginosum* and *V. vitis-*

idaea but also V. *myrtillus*, often host ERM in these habitats, as do *Cassiope tetragona* and *Empetrum nigrum* (Strelkova 1956; Katenin 1964; Katenin 1972; Miller 1982; Treu *et al.* 1996; Michelsen *et al.* 1996; 1998; Väre *et al.* 1997). *Ledum palustre* and *L. procumbens* also host ERM in central Alaska and in the Russian sub-Arctic, as does *Andromeda polifolia* in the latter region and at Abisko (Strelkova 1956; Katenin 1964; Katenin 1972; Miller 1982; Michelsen *et al.* 1996; 1998). *Phyllodoce caerulea* is similarly colonised by ERM at Kilpisjärvi in north-western Finland and at nearby Abisko, as is *Rhododendron lapponicum* at the latter location (Väre *et al.* 1997; Michelsen *et al.* 1996; 1998).

The ERM association is also widespread in Arctic tundra, but is apparently absent from the northernmost of the Queen Elizabeth Islands (Fig 1), most probably reflecting an absence of suitable ericaceous dwarf shrubs from Arctic polar deserts. It has been recorded in the roots of *C. tetragona* on the eastern coast of Greenland, at Spitsbergen, and on Devon and Ellesmere islands, and in the roots of *Empetrum hermaphroditum* at the former two locations (Bledsoe *et al.* 1990; Kohn & Stasovski 1990; Väre *et al.* 1992; Michelsen *et al.* 1998). *V. uliginosum* is also colonised by ERM on Devon and Ellesmere islands and on the eastern coast of Greenland (Bledsoe *et al.* 1990; Kohn & Stasovski 1990; Michelsen *et al.* 1998), as are *R. lapponicum* and *A. polifolia* at the latter location (Michelsen *et al.* 1998). Clemmensen & Hansen (1999) also recorded ERM in dwarf shrub heaths at Disko Island off the western coast of Greenland.

Ericoid mycorrhizas are apparently not present in Antarctic ecosystems (Fig 1), owing to an absence of suitable ericaceous plant hosts. However, studies indicate that the typical fungal associate of ERM, *Rhizoscyphus ericae*, is present in the leafy liverwort *Cephaloziella varians* at Bird Island in the sub-Antarctic, throughout the maritime Antarctic and at one location in the continental Antarctic (Chambers *et al.* 1999; Upson *et al.* 2007).

Arbutoid mycorrhizas

Arbutoid mycorrhizas have been recorded at five locations in taiga and Arctic tundra (Fig 1). The association is present on the roots of *Anemone parviflora* and *Arctostaphylos rubra* at Eagle Summit in Alaska (Miller 1982), and on those of *Arctostaphylos alpina* in central Alaska, Abisko, the eastern coast of Greenland and Disko Island (Treu *et al.* 1996; Michelsen *et al.* 1998; Clemmensen & Hansen 1999). At Alexandra Fjord on Ellesmere Island in the High Arctic, Kohn & Stasovski (1990) found the roots of *Pyrola grandiflora* to be colonised by arbutoid mycorrhizal fungi. Ericaceous plant species that host arbutoid mycorrhizas do not occur in the southern hemisphere, and hence this form of mycorrhiza is absent from Antarctic habitats (Fig 1).

Orchid mycorrhizas

Orchid mycorrhizas are infrequent in taiga and sub-Arctic plant communities (Fig 1). Hesselman (1900) recorded the formation of these mycorrhizas on *Habenaria obtusata* and *Chamaeorchis alpina* in sub-Arctic Norway, as did Sychuva (1952, cited in Katenin 1964) in two unspecified orchid species in Karelia. Hitherto, only one record of the orchid mycorrhizal association exists in Antarctica: Laursen *et al*. (1997) recorded pelotons in the root cells of the orchid *Corybas dienemus* on Macquarie Island in the sub-Antarctic (Fig 1).

Patterns of mycorrhizal colonisation along a latitudinal transect

In order to determine how mycorrhizal colonisation might alter along a latitudinal transect, we analysed data from studies that recorded mycorrhizal structures in plant roots sampled from taiga and the Arctic. Studies that examined less than nine plant species or five families in a given plant community, or examined just one form of mycorrhizal association, were disregarded. A total of 13 studies, examining AM, ECM and ERM colonisation at 11 locations, from Sibik in Siberia (62 ºN) to Alexandra Fjord on Ellesmere Island (79 ºN), met these criteria. Typically these studies reported either the presence or absence of mycorrhiza in a given plant species, and not the root length or frequency of root tips colonised by mycorrhizal fungi, precluding more detailed analyses. Records of arbutoid and orchid mycorrhizas, which were infrequently recorded, were not included in the analyses.

Several patterns emerged from the analyses. Pearson's correlations indicated that the percentage of plant species in each community not colonised by any form of mycorrhiza increased at higher latitudes ($r = 0.711$, $P = 0.001$; Fig 2a). This increase in the percentage of plant species not colonised by mycorrhiza at more northerly locations might be explained by a decrease in the number of suitable hosts in colder habitats, as suggested by Väre *et al*. (1997), who found an increase in non-mycorrhizal plant species at higher points along an altitudinal transect in northern Scandinavia. We therefore calculated the number of obligately, facultatively and non-mycorrhizal plant families in each plant community along the latitudinal transect. A family was deemed to be obligately, facultatively or non-mycorrhizal if the majority of its species were reported to be so by Wang & Qui (2006). A total of 30, 3 and 13 families of gymnosperm and angiosperm trees and shrubs, ferns, horsetails, spike- and clubmosses, forbs and grasses from the 13 studies fell into each of these categories, respectively. The commonest five obligately mycorrhizal families from which plants were sampled were the Poaceae, Ericaceae, Asteraceae, Salicaceae and Scrophulariaceae, and the three facultatively mycorrhizal families were the Equisetaceae, Juncaceae and Saxifragaceae. The commonest five non-mycorrhizal families from which plants were sampled were the Caryophyllaceae, Brassicaceae, Cyperaceae, Polygonaceae and Lycopodiaceae.

We expressed the number of plant families in each of the three categories as a percentage of the total number of families in each community sampled along the latitudinal transect. These analyses showed there to be a significant increase in the percentage of non-mycorrhizal plant families at higher latitudes ($r = 0.752$, $P = 0.001$; Fig 2b). Conversely, analyses of the percentage of obligately mycorrhizal families in each plant community showed a significant decrease at more northerly locations ($r = -0.772$, $P < 0.001$; Fig 2c). Thus, it appears that the increase in the frequency of species not colonised by mycorrhizas at higher latitudes (Fig 2a) is caused largely by a lack of suitable host plant families and species in more northerly habitats. However, Smith & Read (2008) point out that a lack of suitable host plant taxa in colder habitats does not fully explain reductions in mycorrhizal frequency (Väre *et al.* 1997), since many species that are suitable hosts are either lightly, or not, colonised by mycorrhizal fungi in such environments. This view was supported by our analyses: there was a marginally significant, negative association between the percentage of plant species in obligately mycorrhizal families that were colonised by mycorrhizas and latitude ($r = -0.473$, $P = 0.055$; Fig 2d), indicating that, in plant species from families capable of forming mycorrhizas, the associations are less frequent at higher latitudes. Because mean July air temperature (MJuT) was strongly correlated with latitude ($r = -0.832$, $P < 0.001$), MJuT was also significantly associated with the percentage of plant species in a community not colonised by mycorrhizas ($r = -0.611$, $P = 0.012$), and the percentage of non-mycorrhizal ($r = -0.768$, $P = 0.001$) and obligately mycorrhizal plant families ($r = 0.776$, $P < 0.001$) in each plant community (Fig 2a-c, *insets*).

Dark septate endophytes

Surveys of plant roots from many cold-stressed habitats, including alpine regions (e.g. Read & Haselwandter 1981), indicate the prevalence in roots of fungi with dematiaceous septate hyphae, the so-called dark septate endophytes (DSE). These fungi, which are not regarded as true mycorrhizal symbionts (Smith & Read 2008), colonise a wide range of plant taxa (Jumpponen & Trappe 1998). They are usually sterile in culture and often form clusters of spherical or ovoid cells, termed microsclerotia, in roots. Although these fungi are recognised in roots by their formation of dematiaceous hyphae and microsclerotia, several studies indicate that these dark walled structures are continuous with hyaline septate hyphae in roots (e.g. Haselwandter & Read 1982; Newsham 1999), and hence it is likely that their abundance has been underestimated in previous studies (Smith & Read 2008). Despite this, existing data suggest that DSE are more frequent in the roots of plants in polar regions than mycorrhizas: studies in taiga, Arctic tundra and the sub-Antarctic that have each recorded the occurrence of mycorrhizas and DSE in the roots of nine or more plant species show that DSE are commonplace, with only one study (Strullu *et al*. 1999) showing that they are less abundant than mycorrhizas (Table 1). In the four studies that have examined the fungi present in the roots of > 20 plant species (Kohn & Stasovski 1990; Väre *et al*. 1992; Treu *et al*. 1996; Laursen *et al*. 1997), DSE have been found to be consistently more frequent than any form of mycorrhiza (Table 1). This conclusion is further supported by a recent study indicating that, in contrast to mycorrhizas, the frequency of DSE in roots does not decrease at higher latitudes (Upson *et al*. 2008). Currently little is known of the taxonomic affinities of these fungi. They belong to a wide range of taxa, but are often ascomycetes in the order Helotiales such as *Leptodontidium orchidicola, Cryptosporiopsis rhizophila* or the widely-studied *Phialocephala fortinii* (Jumpponen & Trappe 1998; Addy *et al*. 2005).

DSE are commonly recorded in the roots of Arctic plant species (Fig 1), where they often occur in the roots of members of the Asteraceae, Poaceae, Ranunculaceae and Rosaceae. In central Alaska, Treu *et al*. (1996) found microsclerotia of DSE to be present in the roots of 11 of 40 plant species. In the Tromsø district of northern Norway, Ruotsalainen *et al*. (2004) also recorded DSE in the roots of all six of the plant species studied, with between 2% (*Ranunculus glacialis*) and 89% (*Solidago virgaurea*) of root length occupied by hyphae of these fungi. In the nearby Kilpisjärvi area, Ruotsalainen *et al*. (2002) similarly found that the roots of all four plant species studied (*Alchemilla glomerulans*, *Carex vaginata*, *Ranunculus acris* and *Trollius europaeus*) were each colonised by DSE.

DSE have been recorded at seven locations in Arctic tundra and polar deserts (Fig 1). At Spitsbergen, Väre *et al*. (1992) found DSE to be the commonest fungi in roots, with 30 of the 76 plant species sampled being colonised by hyphae of these fungi. At Truelove Lowland on Devon Island, Bledsoe *et al*. (1990) similarly found that 33 of the 55 plant species sampled were extensively colonised by intraradical hyphae, of which an unspecified number were similar to DSE. From the 24 plant species studied at Alexandra Fjord, Kohn & Stasovski (1990) frequently recorded septate endophytes in the roots of *Festuca brachyphylla*, *Carex nardina*, *Kobresia myosuroides* and *Silene acaulis*, and less frequently in the roots of 12 other plant species. In their study of root-associated fungi in the High Arctic, Olsson *et al*. (2004) similarly recorded DSE in the roots of seven of 20 plant species sampled from Banks, Devon, Ellesmere and Ellef Ringnes islands. Septate endophytes were also commonly recorded in the roots of *Arnica*, *Erigeron* and *Taraxacum* spp. sampled from Ellesmere and Axel Heiberg Islands by Ormsby *et al*. (2007). Hyphae of these fungi occupied between 27% (*A. alpina*) and 51% (*E. eriocephalus*) of root length. At the most northerly site from which DSE have been recorded, Lake Hazen on Ellesmere Island, 45% of the root length of *E. eriocephalus* was found to be occupied by septate hyphae (Ormsby *et al*. 2007).

DSE are also frequent associates of vascular plant roots in sub-Antarctic ecosystems (Fig 1), where they are widespread in the Poaceae, but also present in the Caryophyllaceae, Juncaceae, Apiaceae and Asteraceae. Christie & Nicolson (1983) found DSE to be present at frequencies of between 1% and 19% in the roots of eight of 16 plant species sampled from South Georgia. Of the four grasses examined, the roots of three were found to be colonised by DSE (Christie & Nicolson 1983). At the same location, Upson *et al*. (2008) also found *c*. 20% of the root lengths of *C. quitensis* and *D. antarctica* to be colonised by DSE hyphae. On Macquarie Island, Laursen *et al*. (1997) found that the roots of 21 of the 40 species sampled, including six of the nine grasses, were colonised by intracellular dark septate hyphae. At sub-Antarctic Heard Island, Frenot *et al*. (2005) also found that the roots of seven of the nine vascular plant species sampled were colonised by DSE, with the roots of three of the four grasses colonised by these fungi. In contrast, Strullu *et al*. (1999) found that of the 17 vascular plant species sampled from Îles Kergeulen (49 ºS), just three, none of which were grasses, were colonised by DSE.

DSE are also present in the maritime and continental Antarctic (Fig 1). Christie & Nicolson (1983) found these fungi to be present in the roots of *D. antarctica* and *C. quitensis* sampled from the South Orkney Islands (60 ºS), and in the roots of the former species from Livingston Island (62 ºS) and Cuverville Island (64 ºS). Upson *et al*. (2008) recently reported DSE to be present in the roots of both species at all 14 points sampled on the South Orkney Islands, the South Shetland Islands (62 ºS) and the Léonie Islands (67 ºS), with dark septate hyphae occupying between 3% and 75% of root length. DSE are also present in the rhizoids of *Cephaloziella varians* from the Windmill Islands (66 ºS) and Botany Bay (77 ºS) in the continental Antarctic (Williams *et al*. 1994).

Functions of mycorrhizas and DSE in polar regions

It is probable that mycorrhizal associations in polar regions have similar nutritional roles, outlined in the Introduction, to those that they have in other ecosystems. For example, Kytöviita & Ruotsalainen (2007) found AM to enhance the phosphorus uptake of the Arctic plant species *Potentilla crantzii* and *Ranunculus acris* under controlled conditions. Phosphorus uptake is most probably enhanced by fine endophyte, the main form of the AM symbiosis at high latitudes, since studies indicate that it has a similar role to coarse endophyte in enhancing plant phosphorus acquisition (Crush 1973; Smith & Read 2008). Arctic ECM also appear to have similar functions to those of ECM at lower latitudes: Tibbett *et al*. (1998) found that Arctic *Hebeloma* isolates utilised a range of organic nitrogen sources, whilst Hobbie & Hobbie (2006) estimated that 61-86% of nitrogen present in the tissues of Arctic plants is provided by mycorrhizal fungi.

Although mycorrhizas in Arctic ecosystems are likely to have similar roles to those at lower latitudes, a significant gap in knowledge exists about the functions of DSE in polar ecosystems. Over a decade ago, Gardes & Dahlberg (1996) stated that '*because of the abundance and widespread distribution [of DSE] in all Arctic and alpine environments, the elucidation of their ecological and physiological role is of primary interest*', yet little progress has been made since then of understanding the functional roles of DSE in cold-stressed habitats. Owing to the apparent health of plants from which DSE are isolated, and the paucity of AM associations in High Arctic ecosystems, some authors suggest that DSE may act as surrogate mycorrhizas in these habitats (e.g. Bledsoe *et al*. 1990). The evidence for this is at best fragmentary: whilst DSE are typically isolated from apparently healthy host plants, they do not form highly-branched or convoluted structures in roots to facilitate the efficient transfer of nutrients to their hosts, such as the arbuscules formed by AM or coils formed by ERM associations. It is therefore precipitous to assume uniformly positive benefits of these fungi on their hosts, particularly since some are almost certainly weak pathogens, possibly with asymptomatic but detrimental effects on their host plants (e.g. Newsham *et al*. 1994).

Few studies have performed Koch's Postulates (Koch 1882) on DSE, in which the fungi are isolated from roots and then inoculated back onto axenically-grown host plants to determine their effects on plant growth. This is surprising, given the simplicity of such experiments. This approach was adopted by Haselwandter & Read (1982), who isolated two DSE from alpine *Carex* species and re-inoculated them onto the roots of *C. firma* and *C. sempervirens*. They found that both isolates enhanced the biomass and phosphorus concentration of *C. firma* plants. Similarly, Jumpponen *et al*. (1998) found that plants of *Pinus contorta* grown in glacier forefront soil with the DSE *Phialocephala fortinii* absorbed more phosphorus from the soil than those grown without the DSE. When nitrogen was added to the soil, *P. fortinii* also increased plant biomass and nitrogen uptake. In a similar study, Jumpponen & Trappe (1997) found that *P. fortinii* increased the root and shoot biomass of *P. contorta*, but that the DSE decreased nitrogen and phosphorus concentrations in plant tissues.

Recent data suggest that DSE may have active roles in plant nitrogen acquisition. In a study on the alpine snow buttercup *Ranunculus adoneus*, Mullen *et al*. (1998) showed that phosphorus uptake by the plant occurs late in the growing season and is associated with the development of arbuscules in roots. Early in the growing season, *R. adoneus* takes up large amounts of nitrogen from the soil, when the frequency of arbuscules in roots is low, but that by DSE hyphae is an order of magnitude higher, leading to the suggestion that DSE may have a role in nitrogen acquisition by roots (Mullen *et al*. 1998). In a laboratory study, Upson *et al*. (unpublished) similarly showed that, in comparison with uninoculated controls, the growth of *D. antarctica* inoculated with seven DSE isolated from the roots of the species was typically inhibited in the presence of an inorganic nitrogen source, but was increased by as much as 2.5-fold, typically by members of the Helotiales, when seedlings were supplied with an organic nitrogen source. This observation suggests that DSE may mineralise organic nitrogen in the rhizosphere, making nitrogen more freely available to roots (Upson *et al*. unpublished), and corroborates previous data showing DSE, including *P. fortinii* and *Phialophora finlandia*, to utilise proteins as sole nitrogen sources (Caldwell *et al*. 2000). Given the abundance of organic forms of nitrogen in polar soils compared with inorganic sources (Kielland 1994), DSE might thus play significant roles in the growth and survival of their host plants in the natural environment.

Conclusions and future research directions

Our review reveals consistent trends in the occurrence of mycorrhizas in polar ecosystems. The plant species present in such ecosystems have an overriding influence on the presence of the different mycorrhizal types: ECM, ERM and arbutoid mycorrhizas are apparently absent from Antarctic habitats, owing to a paucity of suitable host plant species, whereas the former two mycorrhizal types occur throughout Arctic and sub-Arctic tundra, owing to the widespread presence of *Salix*, *Dryas*, *Betula*, *Vaccinium*, *Cassiope* and *Empetrum* spp. in these regions. In contrast, the AM association is present in both the Arctic and Antarctic, owing to the presence of herbaceous plant species in both regions. This association is, however, only sparsely distributed in Arctic polar deserts and the maritime Antarctic, with fine endophyte being the dominant form of the AM association in roots at high latitudes. Arbutoid and orchid mycorrhizas are less frequent than other forms of the symbiosis in Arctic ecosystems. The latter association is present at only one location in the sub-Antarctic. An increase at high latitudes in the frequency of non-mycorrhizal plant families, and a decrease in that of obligately mycorrhizal families, explains a marked rise in the occurrence of Arctic plant species not colonised by mycorrhizas at more northerly locations. We suggest that further work on mycorrhizas in polar regions should utilise PCR-based methods, which are likely to improve the detection of mycorrhizal fungi, and particularly fine AM endophyte, in roots and soils from High Arctic tundra and the maritime Antarctic. The reasons for the frequent occurrence in polar regions of AM in the Cyperaceae, Polygonaceae and Caryophyllaceae, plant families normally regarded as being non-mycorrhizal, are also worthy of further investigation.

DSE are probably the most widespread of any root-fungal association in polar regions, and yet their roles in plant nutrition and survival are at present poorly defined. The apparent health of plants with which they are associated suggest the majority do not act as pathogens, and recent data indicate that they may have beneficial effects on plant growth and nutrient uptake when amino acids, peptides and proteins are the dominant forms of nitrogen available to roots. Although there are many different questions about the interactions between DSE and plants that are yet to be answered (Mandyam & Jumpponen 2005), we suggest that Koch's Postulate experiments under realistic conditions, coupled with a thorough understanding of the mechanisms responsible for any positive effects on host plant growth, would most effectively advance knowledge of these associations. In particular, further work is needed to determine whether or not organic forms of nitrogen can be mineralised in the rhizosphere by DSE and thus made more freely available to roots, or if elements are transported directly from soil to roots *via* DSE hyphae. Such experiments would resolve the question of whether or not DSE have similar functional roles to mycorrhizas in polar regions.

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Table 1 Percentages of plant species colonised by different mycorrhizal associations and DSE in studies in taiga, Arctic tundra and the sub-Antarctic

reference	region	mycorrhiza					
		arbuscular	ecto-	ericoid	arbutoid	orchid	DSE
Treu *et al*. (1996)	taiga	5	15	18	3	0	28
Kohn & Stasovski (1990)	Arctic tundra	4	25	17	4	0	67
Väre *et al*. (1992)	Arctic tundra	0	4	3	0	0	40
Olsson *et al*. (2004)	Arctic tundra	35	0	0	0	0	35
Laursen *et al*. (1997)	sub-Antarctic	45	0	0	0	3	53
Strullu *et al*. (1999)	sub-Antarctic	35	0	0	0	0	18
Frenot *et al*. (2005)	sub-Antarctic	78	0	0	0	0	78

Figure legends

Fig 1 Locations at which mycorrhizas and dark septate root endophytes have been recorded in taiga and polar regions. The five sub-zones of sub-Arctic and Arctic vegetation (CAVM Team 2003) are described in the text. The presence of mycorrhizas outside of the sub-Antarctic are not shown. Numbers in circles indicate approximate locations at which studies have been made, as follow: 1, Denali National Park (Treu *et al.* 1996); 2, Eagle Summit (Miller 1982); 3, Sibik, E Siberia (Michelsen *et al.* 1998); 4, Karelia (Sychuva 1952, cited in Katenin 1964); 5, Kilpisjärvi, NW Finland (Ruotsalainen *et al.* 2002; 2004; Pietikainen *et al.* 2007); 6, Kilpisjärvi (Väre *et al.* 1997); 7, Abisko, N Sweden (Michelsen *et al.* 1996); 8, Abisko (Michelsen *et al.* 1998); 9, Cape Simpson (Linkins & Antibus 1982); 10, Point Barrow (Miller & Laursen 1978); 11, Taimyr Peninsula (Tikhomirov & Strelkova 1954); 12, NW Taimyr Peninsula (Strelkova 1956); 13, Vorkuta (Katenin 1964; 1972); 14, Novaya Zemlya (Hesselman 1900); 15, Spitsbergen (Väre *et al.* 1992); 16, N Spitsbergen (Hesselman 1900); 17, NE Greenland (Michelsen *et al.* 1998); 18, Disko Island, Greenland (Hesselman 1900; Clemmensen & Hansen 1999); 19, Lake Hazen, Ellesmere Island (Ormsby *et al.* 2007); 20, Alexandra Fjord, Ellesmere Island (Kohn & Stasovski 1990); 21, Alexandra Fjord (Bledsoe *et al.* 1990); 22, S Ellesmere Island (Olsson *et al.* 2004; Ormsby *et al.* 2007); 23, Eureka, Ellesmere Island (Dalpé & Aiken 1998); 24, Axel Heiberg Island (Dalpé & Aiken 1998; Allen *et al.* 2006; Ormsby *et al.* 2007); 25, Bathurst Island (Dalpé & Aiken 1998); 26, Truelove Lowland, Devon Island (Stutz 1972); 27, Truelove Lowland (Bledsoe *et al.* 1990); 28, S Devon Island (Olsson *et al.* 2004); 29, Ellef Ringnes Island (Olsson *et al.* 2004); 30, Banks Island (Olsson *et al.* 2004); 31, South Georgia (Christie & Nicolson 1983; Upson *et al.* 2008); 32, Marion Island (Smith & Newton 1986); 33, Îles Kergeulen (Strullu *et al.* 1999); 34, Heard Island (Frenot *et al.* 2005); 35, Macquarie Island (Laursen *et al.* 1997); 36, Signy Island (Christie & Nicolson 1983; Upson *et al.* 2008); 37, King George and Livingston Islands (Christie & Nicolson 1983; Upson *et al.* 2008); 38, Danco Coast (Cabello *et al.* 1994); 39, Cuverville Island (Christie & Nicolson 1983); 40, Léonie Islands (Upson *et al.* 2008); 41, Botany Bay (Williams *et al.* 1994); 42, Windmill Islands (Williams *et al.* 1994). Letters adjacent to circles indicate the form of mycorrhiza recorded at each location, as follow: AM, arbuscular mycorrhiza; ECM, ectomycorrhiza; ERM, ericoid mycorrhiza; AR, arbutoid mycorrhiza; OM, orchid mycorrhiza; DS, dark septate endophyte.

Fig 2 Percentages of (a) plant species not colonised by mycorrhizas, (b) non-mycorrhizal plant families, (c) obligately mycorrhizal plant families and (d) species in obligately mycorrhizal families that are colonised by mycorrhizas, as a function of latitude along a latitudinal transect from Siberia through to Ellesmere Island. Data are from studies 1-3, 6-8, 11-13, 15, 17, 20, 21, 26 and 27, listed in the legend to Fig 1. *Insets* are data on *y*-axes in main Figures as a function of mean July air temperature (MJuT). Air temperature data are from the original papers or from Rosswall & Heal (1975), Courtin & Labine (1977), Labine (1994) and Havström *et al*. (1993) for Vorkuta and locations on the Taimyr Peninsula, Truelove Lowland, Alexandra Fjord and Abisko, respectively.

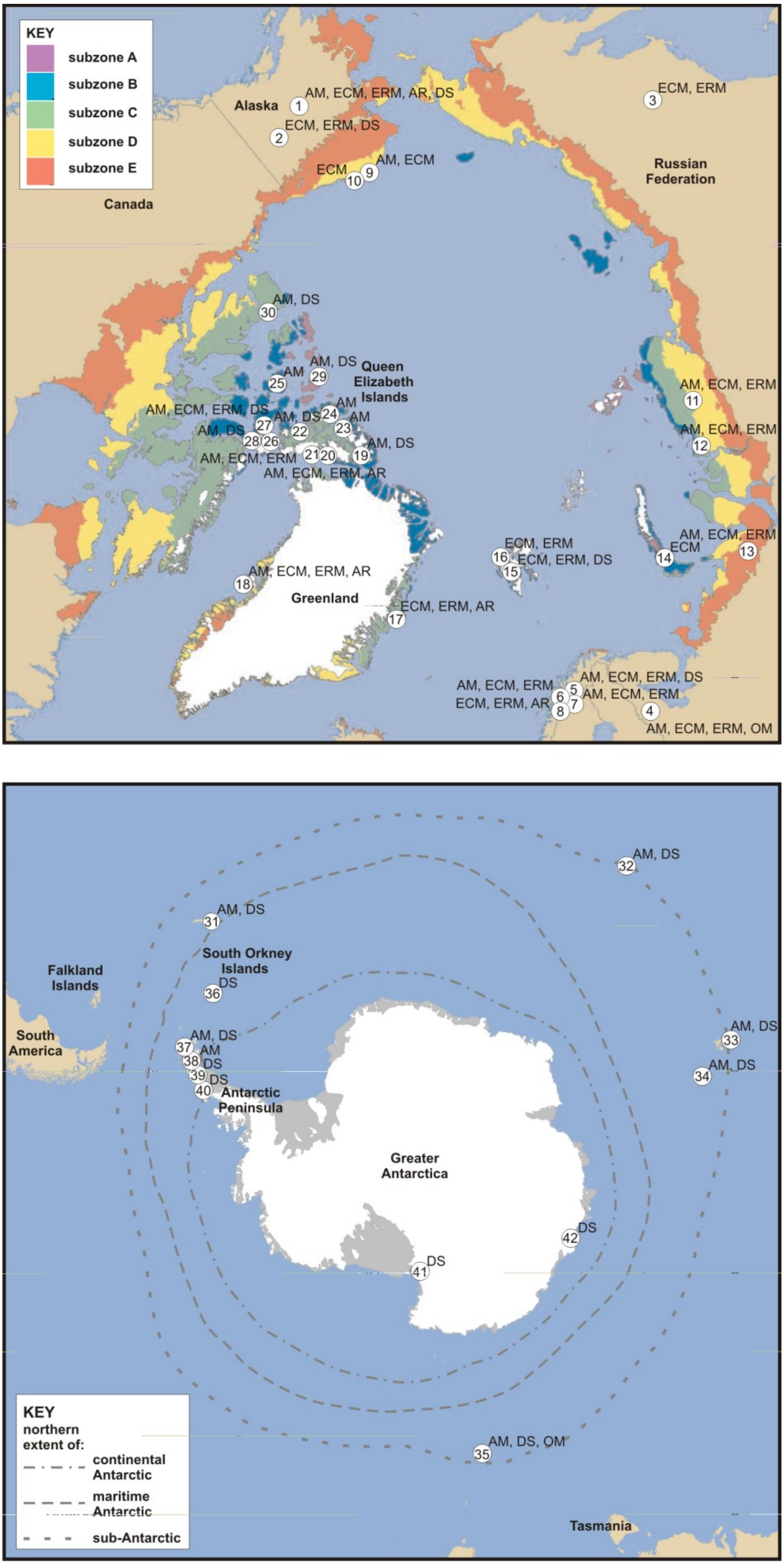
KEY
subzone A
subzone B
subzone C
subzone D
subzone E
Alaska
Canada
Russian Federation
Queen Elizabeth Islands
Greenland
AM, ECM, ERM, AR, DS ①
② ECM, ERM, DS
③ ECM, ERM
ECM ⑩ ⑨ AM, ECM
AM, DS ㉚
AM ㉕
AM, DS ㉙
AM, ECM, ERM, DS ㉗
AM, DS ㉘ ㉖
AM, DS ㉒ ㉔ AM
㉓ AM
AM, ECM, ERM ㉑ ⑳
⑲ AM, DS
AM, ECM, ERM, AR
AM, ECM, ERM ⑪
AM, ECM, ERM ⑫
AM, ECM, ERM ⑬
ECM ⑭
ECM, ERM ⑯
ECM, ERM, DS ⑮
AM, ECM, ERM, AR ⑱
ECM, ERM, AR ⑰
AM, ECM, ERM ⑥
ECM, ERM, AR ⑧
AM, ECM, ERM, DS ⑤
AM, ECM, ERM ⑦
④ AM, ECM, ERM, OM
AM, DS ㉜
AM, DS ㉛
South Orkney Islands
Falkland Islands
South America
DS ㊱
AM, DS ㊲
AM ㊳
DS ㊴
DS ㊵
Antarctic Peninsula
Greater Antarctica
AM, DS ㉝
AM, DS ㉞
DS ㊷
DS ㊶
AM, DS, OM ㉟
Tasmania
KEY
northern extent of:
continental Antarctic
maritime Antarctic
sub-Antarctic

Fig. 1

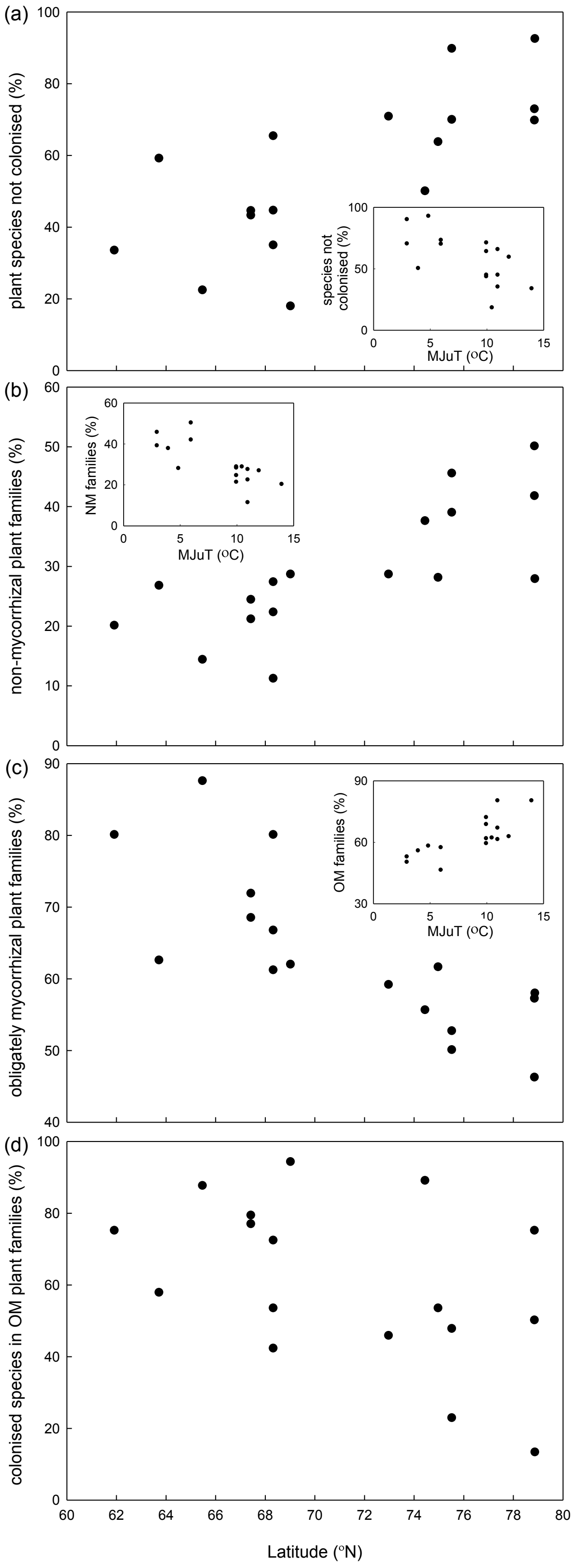
(a)
plant species not colonised (%)
0
20
40
60
80
100
species not colonised (%)
MJuT (oC)
0
5
10
15
0
50
100
(b)
non-mycorrhizal plant families (%)
0
10
20
30
40
50
60
NM families (%)
MJuT (oC)
0
20
40
60
0
5
10
15
(c)
obligately mycorrhizal plant families (%)
40
50
60
70
80
90
OM families (%)
MJuT (oC)
30
60
90
0
5
10
15
(d)
colonised species in OM plant families (%)
0
20
40
60
80
100
60
62
64
66
68
70
72
74
76
78
80
Latitude (oN)

Fig. 2