

MiniReview

# Asymmetric symbiont adaptation to Arctic conditions could explain why high Arctic plants are non-mycorrhizal

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## Abstract

Mycorrhizal symbiosis generally improves nutrient and water acquisition of the host plant. Furthermore, mycorrhizal fungi affect plant herbivory and pathogen resistance. The symbiotic condition of land plants is evolutionarily ancient and the functions performed by the fungal symbiont are thought to be pivotal to successful plant life. Although most land plants are mycorrhizal, the extreme high Arctic habitats are dominated by plant species and genera characteristically free of mycorrhiza. In this paper, previous attempts to explain the lack of mycorrhizas in high Arctic are reviewed as well as a new idea of asymmetric symbiont adaptation is proposed as potential explanation why high Arctic plants are non-mycorrhizal.

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*Keywords:* Arctic; Mycorrhiza; Symbiosis; Evolution; Non-mycorrhizal

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## 1. Introduction

Mycorrhizal symbiosis is formed between plants and soil dwelling fungi. The relationship is evolutionarily ancient and considered important for plant performance in most if not all ecosystems. Treeless polar areas considered Arctic cover large areas of northern hemisphere. In these, plant and microbial life is constrained by low temperatures and short growing season, which results in resource fluxes that are different than in comparable temperate habitats and characteristic plant resource allocation strategies. The role of mycorrhizas in Arctic ecosystems remains relatively poorly studied, and especially there is scant information of symbiotic fungal adaptation to Arctic conditions. High Arctic flora is increasingly non-mycorrhizal, which is unpredicted in light of the important role of mycorrhizal symbiosis in

comparable nutrient poor stressful temperate habitats. In below, previous explanations are reviewed as well as a new idea of asymmetric symbiont adaptation is proposed as to why high Arctic plants are non-mycorrhizal.

## 2. Origin and evolution of the Arctic mycorrhizal symbionts

Arctic ecosystems have evolved relatively recently during the early Pleistocene [1,2] and many Arctic areas have been deglaciated only for the last 3000–8000 years. The Arctic flora is thus comparatively young and has evolved from plants initially adapted to cold steppe, alpine conditions and exposed and dry shoreline habitats [2]. Consequently, the circumpolar Arctic regions have repeatedly been colonised from various floristic elements of the nearby regions, and little adaptation seems to have taken place in the Arctic itself [2,3]. There are few genera of plants specific to Arctic, and even at spe-

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cies level Arctic examples are not numerous. Most of the land flora support mycorrhizal fungal associates in their roots as a rule, but the high Arctic flora is an exception. Mycorrhizal condition is thought to be evolutionarily ancient [4,5], and the symbiosis between early plants and fungi is thought to have facilitated the colonisation of terrestrial habitats by plants about 400 My ago [6,7]. The most ancient mycorrhizal symbiosis, the arbuscular mycorrhizal (AM) symbiosis, forms between about 150–200 species of fungi belonging to the Glomeromycota and about 80% of all plants [8]. Ectomycorrhizas (EM) are formed between some, mainly woody plant species and a large number of fungi (over 5000) belonging to the Basidiomycota and Ascomycota. Molecular data suggests that the EM symbiosis first appeared about 130 My ago [9]. Ericoid mycorrhizal (ERM) symbiosis is estimated to be about the same age, it probably evolved about 140 My ago [10]. ERM are formed with very limited number of plant hosts belonging to the Ericales and apparently less than 100 fungal partners of the phylum Ascomycota [11]. Similar to Arctic vegetation, the Arctic fungal component has migrated from more temperate regions and little evolution seems to have taken place in the Arctic itself [2]. For example, most Arctic fungi are psychrotrophic rather than psychrophilic, i.e. their optimum temperature for growth is over +15 °C [12], indicating limited adaptation to Arctic conditions.

### 3. Role of mycorrhizal symbiosis in the Arctic

The distribution of mycorrhizal types in general is partially determined by soil conditions [13] and partially by phylogenetic constraints [14]. Arctic heaths form in areas with cool soil where plant production is higher than microbial degradation and consequently organic matter accumulates in soil and most nutrients are bound in acid raw humus. The dominant heath plants are Ericaceous and form symbiosis with ERM fungi with exoenzymatic capacities to degrade chitin and proteins and thus liberate and acquire nutrients bound in organic matter [15]. Trees occur only in the low arctic and they all form EM symbiosis. Also EM symbionts degrade organic matter and mycorrhiza-mediated nutrient acquisition from the organically bound soil reserve is thought to be main nutrient source for EM plants in low arctic woodlands. The AM is mainly formed by herbaceous vegetation and is consequently dominant in Arctic meadows. Arctic flora is not diverse and even so, a few genera such as *Empetrum*, *Eriophorum*, *Carex*, *Betula* and *Salix* dominate large areas [16]. None of these dominants are AM, and *Eriophorum* and *Carex* that grow in water logged soils are actually non-mycorrhizal. AM fungi improve plant's nutrient and water acquisition [17]. In the main, AM fungi do not possess saproph-

ytic capacities and the whole phylum Glomeromycota is biotrophic [18]. Thus AM does not alter the nature of resources available to the plant, but simply scavenge and compete for soil resources effectively. Furthermore, AM fungi may improve plant resistance to root herbivores and root pathogens and consequently have compound functions in plant ecology [19]. AM symbioses are most common in warm climates and as AM symbioses enhance plant P acquisition, their prevalence in temperate ecosystems is thought to correlate with P limitation of plant production in these ecosystems [13]. Although N limits plant production in Arctic ecosystems, co-limitation by P also occurs [20]. It has been shown that like plant P demand, plant N demand is important in controlling the colonisation of plant roots by AM [21] and that AM are important in plant N acquisition [22]. In addition to AM, EM and ERM, a phylogenetically diverse fungal group belonging to Ascomycota grow as dark septate (DS) hyphae in roots [23] and frequently colonise plant roots. DS fungi are particularly common in the roots of Arctic plants, and may be the most common fungal type in plant roots, especially in roots of *Carex* [24]. Unfortunately, nearly nothing is known of the ecological role of these root inhabiting fungi.

In conclusion, mycorrhizal symbiosis seems warranted in Arctic ecosystems where low soil moisture and nutrient availability, low soil and air temperatures and short growing season limit plant growth and productivity. The rates of organic matter mineralization are low in arctic tundra and most of the soil nutrients are organically bound. Therefore, like in comparable temperate ecosystems, the mycorrhizal symbioses with degradative abilities such as ERM and EM would seem indispensable in organic soils, as well as AM in more mineral soils in high latitude habitats.

### 4. High Arctic plants are increasingly non-mycorrhizal

Although mycorrhizal condition is the rule in the present land flora, it is generally observed that high Arctic floras are dominated by non-mycorrhizal plants or by plants that host very limited mycorrhizal colonisation [25–28]. All land plants are thought to have mycorrhizal ancestors, but secondarily some species have evolved to be free of mycorrhizal fungus [29]. The evolution of non-mycorrhizal condition seems to correlate with reduction in host size and shortening of the host life-cycle as well as evolution of vegetative propagation, extensive root systems and large storage organs [29], all of which coincide with plant adaptation to Arctic conditions [2]. The paucity of mycorrhizas in the high Arctic ecosystems has been previously related to:

- (i) soil moisture remains too high for too long a period after the snow-melt [27];
- (ii) soil moisture is too low for too long a period later in the growth season [27];
- (iii) the saprobic activity is too low and consequently the nutrient availability is too low [30];
- (iv) too short growing season [26,31];
- (v) photosynthetically active radiation is too low and the plants are carbon limited and thus cannot afford to spend carbon on mycorrhizas [32].

These factors are inadequate to fully explain the abundance of non-mycorrhizal taxa in high Arctic. (i) In temperate systems, non-mycorrhizal condition is most common in wet habitats [33,31], but in the high Arctic, also non-mycorrhizal species belonging to the genera *Luzula*, *Cerastium*, *Festuca*, *Poa*, *Saxifraga*, *Astragalus*, *Draba*, *Potentilla*, *Arnica*, *Taraxacum*, *Campanula* and *Papaver* thrive in habitats that are not water-logged [27,28,34]. (ii) Mycorrhizal symbiosis is important in plant water acquisition in dry habitats, and, e.g. plants growing in sand dunes are commonly mycorrhizal [35]. Furthermore, nutrient acquisition becomes increasingly difficult in dry soil and mycorrhizal fungal hyphal network should be advantageous in nutrient uptake from dry soil. Therefore, periodical drought should increase, not decrease the importance of mycorrhizal symbiosis [36]. (iii) Mycorrhizal symbiosis is generally thought to be important in nutrient acquisition when the availability is low, however, extremely low nutrient levels have been shown to reduce mycorrhizal colonisation in pot experiments [37]. It is uncertain whether such extreme low nutrient levels ever occur in natural ecosystems. Furthermore, ERM and EM symbioses with their degradative abilities should be a benefit in respect to the low activity of competing saprophytes. (iv) Short growing season and lower levels of photosynthetically active radiation could both limit plant carbon acquisition and thus could affect carbon allocation to symbionts in Arctic habitats. However, Arctic plants show no signs of being carbon limited. For instance, the non-structural carbohydrate levels of leaves show no latitudinal trends [38]. In temperate ecosystems, shade habitats have very low light levels, but non-mycorrhizal plants are not particularly common in these.

In addition to the above, high levels of soil disturbance may reduce the possibilities for fungal growth and non-mycorrhizal plants are common in disturbed temperate habitats [33]. Soil disturbance by frost upheaval increases towards higher latitudes, and high Arctic sites are characterised by frequent freeze–thaw cycles. AM extraradical hyphae have been shown to survive winter freezing of soil [39] indicating that natural soil disturbance associated with freezing may not eliminate AM fungal hyphae. However, the importance of freeze–thaw induced mechanical disturbance during

growth season on AM performance may be more critical. Annuals are typically non-mycorrhizal in temperate ecosystems, however, annuals are rare in Arctic flora and their presence does not explain the increasingly non-mycorrhizal flora of the high latitude areas.

## 5. Limitations for mycorrhizal fungal performance in the Arctic

Previous explanations for prevalence of non-mycorrhizal taxa in the high Arctic have mainly focussed on the plant performance. As an alternative explanation, the possibility that it is the fungal performance that limits the occurrence of mycorrhizal symbioses in the high latitude habitats is explored below.

Temperature is thought to be the single most important factor to limit root-inhabiting fungal occurrence in general [40]. Temperature effects on symbiotic fungi may be either direct or indirect via effects on the host plant. The direct effects that may limit fungal performance in Arctic soils are soil temperatures during winter that are low enough to kill hyphae and spores and soil temperatures during growth season that are low enough to prevent or seriously limit physiological activities of fungal hyphae. Even in the Arctic, soils under snow cover do not experience very low temperatures and remain around 0 °C most of the winter, but in exposed wind-swept habitats with shallow snow cover soil may freeze down to –30 °C [41]. Low temperature and freezing tolerance are connected with tolerance of drying because of the dehydration associated with freezing. Extraradical AM mycelium is well adapted to tolerate prolonged periods of drought [42], and AM are common in habitats with frequent prolonged dry spells such as sand dunes [35] and deserts [43]. AM and EM mycelium tolerate short-term freezing at least to –10 °C [44,45] and prolonged freezing at –1 to –2 °C [39]. Fungal spores tolerate environmental stresses and are very resistant to cold, for instance AM spores remain viable after exposure to –80 °C [46]. The large AM spores with thick walls and abundant nutrient and carbon reserves seem ideal for long-term persistence in Arctic soil conditions and it seems unlikely that the soil temperatures limit fungal survival during winter in the Arctic.

During the growth season, the average monthly soil temperatures in Arctic habitats may range between +1 and +12 °C [47,48]. Low temperature may directly affect germination of spores, growth of hyphae, excretion of extracellular enzymes, nutrient uptake, nutrient transfer to the host and host carbon assimilation by mycorrhizal fungi. Although EM fungi have been shown to grow in pure culture at +2 °C, the optimum temperature for EM fungal growth is generally over +20 °C [49–51] with no apparent difference between Arctic and temperate strains [51]. Growth of the obligatorily biotrophic AM

independent of the host has only been assessed with germinating spores. Germination of AM spores is generally reported to be low or absent in soil temperatures under +10 °C and optimum germination near or above +20 °C [52–55]. However, at least *Glomus caledonium* germinates at 5 °C [54]. AM mycelium has been shown to be incapable of P absorption at 0 °C [56], whereas EM mycelium remain active at 0 °C [57] and at +1 °C [58]. This very limited available data suggest that low growing season temperatures seriously constrain AM performance, but to lesser extent EM fungi. There are no reports of effects of cold soil temperature on ERM fungal performance.

## 6. Asymmetric symbiont adaptation to Arctic

In contrast to AM fungi which seem not well adapted to nutrient uptake from cold soil, Arctic plants have been shown to effectively absorb phosphate [59] and nitrogen [60] from soils as cold as +1 °C. Consequently, in habitats where soil temperature is low, AM symbiosis is unlikely to be a cost effective mode of nutrient acquisition. This seems to be the case in reported studies. The cost or benefit of the symbiosis to the host may be defined as plant performance in symbiosis in relation to without symbionts; e.g. mass ratio of mycorrhizal to non-mycorrhizal plants. When there is no benefit, but no cost either of the symbiosis to the host, this ratio is 1. It has been shown that in AM symbioses the host benefit decreases with decreasing temperature in temperate host plants such as in *Gossypium* [61,62] and *Allium* [63,64] and also in an Arctic host plant *Gnaphalium* [65]. In cold soil, AM may still be consuming plant carbon, but incapable of nutrient uptake and/or transfer to the host [56]. It has been shown that at 8 °C in case of *Gnaphalium* [65] and at 11/16 °C in case of *Allium* [63], the fungi acted parasitically and plant performance was decreased by mycorrhizas.

If the main benefit of AM is improved nutrient acquisition and if the limited data summarised above is generally true in that nutrient uptake by AM is not effective in cold soil, then herbaceous plants should limit mycorrhizal colonisation in Arctic habitats. Although the high Arctic plants are generally non-mycorrhizal, herbaceous plants that form AM in the low Arctic seem to host relatively high and seasonally stable colonisation levels [24]. However, presence of fungi in plant roots is not evidence of mutualistic relationship and the plants may not be capable of avoiding fungal colonisation. Despite the relatively low average soil temperatures, a few warm spells could facilitate colonisation of roots without associated nutritional benefits to the host. Also, there may be other benefits than nutrient acquisition in hosting AM. Nevertheless, as plant root growth is less

affected by cold than growth of fungi, low soil temperatures generally reduce the relative abundance of AM in plant roots in pot experiments [65–67] and may be the reason for low occurrence of AM colonisation in high Arctic *Festuca* in field [25].

ERM and EM plants retain high mycorrhizal colonisation rates in their Arctic habitats [32], which agrees favourably with the notion above that EM remain active at low soil temperatures. A few plants such as *Salix* species are capable of forming both AM and EM symbioses. In boreal and temperate climates, species of *Salix* form mycorrhizas both with EM and AM fungi [68], but in Arctic regions only with EM [28], which may be taken as one further evidence of AM being poorly adapted to Arctic conditions. If EM and ERM fungi are adapted to Arctic conditions, why is not Arctic vegetation increasingly ERM and EM? Dispersal of EM should not be the limiting factor as spores of Ascomycetes and Basidiomycetes easily migrate vast distances. Dispersal of AM spores must be more limited, because the large AM spores are mainly born within soil, and sometimes even within plant roots. Furthermore, evolution of novel characteristics and thus adaptations into Arctic conditions are likely to take place in the sexually reproducing EM fungi rather than AM fungi that do not reproduce sexually.

It may be that although EM and perhaps also ERM fungi are preadapted for Arctic conditions, the evolutionarily young floral component is mainly capable of forming AM symbiosis or of non-mycorrhizal life, but not evolved to form EM symbiosis. Consequently, the occurrence of mycorrhizal plants in the Arctic may be limited because of the asymmetric adaptation to Arctic conditions by the symbionts: EM fungal range may be limited by host constraints, whereas AM host range may be limited due to inability of AM fungi to grow in cold Arctic soils. However, although herbaceous plants are mainly AM in temperate regions, some herbaceous species do form EM in the Arctic; for example *Kobresia myosuroides*, *Saxifraga oppositifolia*, *Pedicularis capitata* [27] and *Potentilla hyparctica* [26] are reported to be EM. These may evidence adaptation to Arctic conditions in terms of shift of fungal symbiont type from AM to EM. If adaptation to cold climate includes mycorrhizal symbiont shift from AM to EM in herbaceous vegetation, this shift should be more pronounced in alpine habitats because the old age of alpine environments in comparison to Arctic.

Finally, it must be noted that very few cold climate mycorrhizal strains have been studied, and therefore future work on characterising the performance and temperature dependence of fungal symbionts from Arctic habitats is necessary prior accepting the above presented idea of asymmetric symbiont adaptation as a hypothesis.

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