The Mycorrhizal Status in Mountainous Vegetation in the Faroe Islands

Sopparót í Føroyskum Fjallavøkstri

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Úrtak
Ein plantufrøðilig kanning á fimm fjallasíðum í Føroyum, har m.a. hugt varð eftir vøkstrinum í ymsum hæddum, er nýtt sum grundarlag undir eini meting av, hvussu nær tengdar planturnar eru at teim gagnligu moldsoppunum (sopparót), sum m.a. kunnu veita teimum fleiri føðsluevni og verja tær móti sjúkuelvandi moldsoppum. Afturfyri fáa hesir gagnligu sopparnir sukurevni frá plantunum. Tað vísir seg, at hóast nógvar plantur finnast, sum ikki krevja sopparót, so er títtleikin hjá teimum upp á seg væl minni enn hjá teimum plantum, sum helst skulu hava sopparót. Fleiri sløg av soppum eru, sum kunnu gera sopparót, men tað vísir seg sum um summir teirra ikki trívast saman, t.d. er tað slagið av sopparót, sum ger hundalond, ikki vanligt á heiðalendi. Tað mest vanliga slagið, arbuskul sopparót, tykist at vera saman við øðrum sløgum av sopparót uttan stórvegis trupulleikar. Nøkur plantusløg eru, sum kunnu hava fleiri sløg av sopparót, m.a. sera vanligar plantur so sum reyðvingul.

Abstract
A vegetation survey on five mountainslopes in the Faroes, recording the vegetation at different altitudes, is the basis for an estimate of how dependent the plants are on the beneficial soil fungi (mycorrhiza), which are able to provide the plants with nutrients and protect them against pathogenic soil fungi. In return these beneficial soil fungi require carbohydrates from the plants. Although several plants are not able to or less dependent upon mycorrhiza, they seem to be less frequent than the plant species, which normally are mycorrhizal. There are different types of mycorrhiza, and some of them do not coexist. For example mushroom-forming mycorrhiza is rare on heathland. The most common type, arbuscular mycorrhiza, seems to coexist with other types of mycorrhiza. The data presented in this paper indicate that dual infection, where a plant is colonised by different types of mycorrhiza could be of importance in the Faroese mountainous vegetation.

Introduction
An ancient relationship exists between plant roots and some soil fungi. It is believed to have evolved together with the land plants approx. 400 mill. years ago (Smith and Read, 1997). This symbiosis is called mycorrhiza, which means fungus root, and is beneficial for both species. The plant achieves nutrients from the fungus, which is much better adapted to explore the soil due to its fine hyphae. In return the fungus gets carbohydrates.

There exist several types of mycorrhizas, involving different fungi. Some are living in symbiosis mainly with trees, and are visible because of the big mushrooms they create for spore dispersal.

Mycorrhiza is known to have several benefits for the plant. Apart from providing nutrients, it is also thought to protect the root against drought and pathogens (Newsham *et al.*, 1995).

Mineralisation is slow in cold environments, and organic materials accumulate in the soil, including organically bound phosphorus and nitrogen, which are unavailable for the plants. Arbuscular mycorrhizal fungi explore the soil better than the plant roots do simply because the hyphae are crossing the depletion zone and explore soils for nutrients, which physically are inaccessible to the plant roots (Fitter and Hay, 2002). It is increasingly evident that ericoid and some ecto-mycorrhizal fungi produce extra-cellular enzymes that break down organic compounds, thereby exposing new sources of organic nitrogen and phosphorus to attack (Smith and Read, 1997). Until recently it was assumed that arbuscular mycorrhizal fungi do not utilise the organic sources of nitrogen and phosphorus. However, Hodge *et al.* (2001) showed that the arbuscular mycorrhizal symbiosis can both enhance decomposition of and increase nitrogen capture from complex organic material in soil. Further there is also evidence that some of the carbon cost of mycorrhizal infections may be met by heterotrophic carbon assimilation from organic sources (Finlay *et al.*, 1992).

The Faroes and the vegetation in general

The Faroese vegetation is mostly perennial and is influenced by several factors. The two most obvious are the oceanic climate and the ubiquitous sheep. The landscape is mostly dominated by steep mountains.

The temperature is relatively constant in both winter and summer, with an average of 4°C in the coldest month (January) and 11°C in the warmest month (July). The climate is oceanic with much precipitation, clouds and wind.

The sheep consist of 70,000 ewes, grazing the mountains both summer and winter. The number of animals is assumed to be held just below the overgrazing limit.

In general the area is eroded, and according to farmers the situation has become worse during the last century. Probably both weather conditions and overgrazing are to blame for the erosion.

The vegetation consist mainly of herbs, although some dwarf shrubs occur. Trees are only present as single trees planted in gardens or in plantations at some very sheltered locations.

Material and methods

In July-August 1999 and 2000 the vegetation on five mountains in the Faroe Islands was investigated along five transects with north and south aspects, from the top (between 750-850 m a.s.l.) down to 150 m a.s.l. The dominant vegetation on these mountains is open grassland vegetation, *Racomitrium* vegetation and moist dwarf shrub vegetation (Fosaa, 2002).

A total of 532 plots were sampled. Within 50 m altitudinal intervals along the transects, 10x10 m quadrats (macro-plots) were placed. In each macro-plot, 8 smaller (0.5x0.5 m) quadrates (sub-plots) were placed. These subplots were again divided into 25 quadrate (micro-plots) and the frequencies of the plant species were measured based on presence/absence in each microplot, from 1 to 25. Soil samples were taken at each macroplot (0-10 cm depth) and the pH, humus (% loss of ignition),

Alchemilla filicaulis
Alchemilla faroensis
Deschampsia alpina
Epilobium lactiflorum
Gnaphalium supina
Juncus triglumis
Luzula arcuata
Luzula multiflora ssp. multiflora
Poa glauca
Thalictrum alpinum

Table 1. *Species probably arbuscular mycorrhizal.*

Cardaminopsis petraea
Cerastium nigrescens
Cochlearia officinalis
Euphrasia arctica
Euphrasia frigida
Euphrasia micrantha
Euphrasia scottica
Koenigia islandica
Rhinanthus minor

Table 2. *Species probably non-mycorrhizal.*

Ranunculus glacialis
Rhodiola rosea
Saxifraga hyperborea
Saxifraga hypnoides
Saxifraga rosacea
Sedum villosum

Table 3. *Species with no mycorrhizal record.*

phosphorus and nitrogen content were measured (Fig. 1).

This mycorrhizal study has combined the field results with the checklist from Harley and Harley (1987) and the Ecoflora-database from the University of York (Fitter and Peat, 1994) as the main source to determine whether a plant species is mycorrhizal or not, and if it is mycorrhizal, what type of mycorrhiza the plant is likely to associate with.

The sum of frequencies of angiosperms was 24,516. Ferns, lycopods, equisetum and bryophytes are omitted from the dataset.

Results

Of a total of 102 species the mycorrhizal status was unknown for 25 species. However, by looking at relatives, some of these species are estimated as probably arbuscular (Table 1) or probably non-mycorrhizal (Table 2). The group with no mycorrhizal record (Table 3) now consist of 6 species, and accounts for 0.3% of the total plant frequency.

In this study the number of plant species which form ericoid mycorrhiza is higher than the number of plant species which are likely to form ecto-mycorrhiza. However, when considering the frequency, the ecto-mycorrhizal plant species occur twice as frequently in the survey (Table 4). In contrast 17% of the species are non-mycorrhizal, but non-mycorrhizal plants account for less than 7% of the total sum of frequencies.

	% of total plant species	% of total plant frequency
Ericoid	2.9	6.8
Ecto	2.0	12.9
Orchid	2.0	0.3
Arbuscular	69.6	73.0
Non-mycorrhizal	16.7	6.7

Table 4. *The distribution of plant species grouped after their mycorrhizal status. First column shows how the mycorrhizal types are distributed based on the number of plant species involved. The second column shows how the mycorrhizal types are distributed based upon the sum of frequencies.*

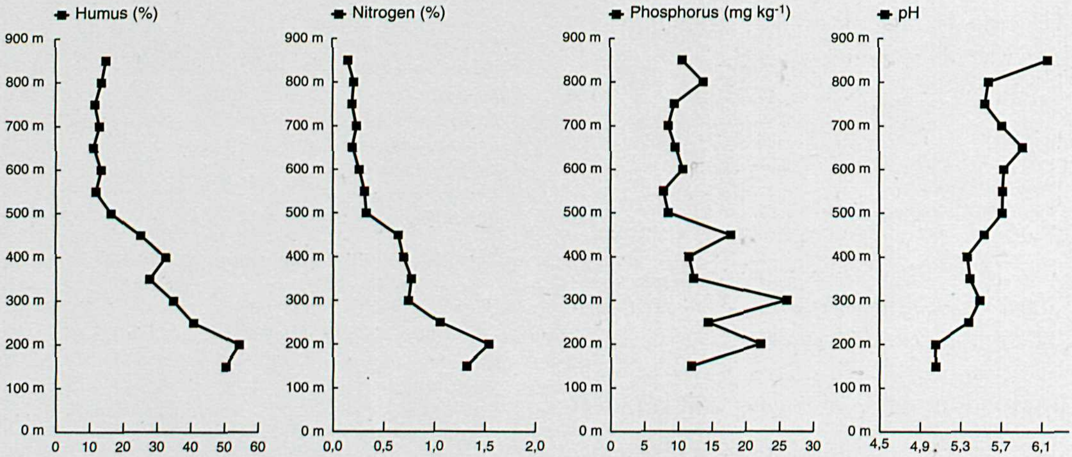

Fig. 1. Humus, nitrogen and phosphorus decrease with increasing altitude, while pH values increase with increasing altitude.

Apart from an increase of the non-mycorrhizal plant species in the summit region – due to the annual *Koenigia islandica* – the mycorrhizal rates are strikingly stable (Table 5).

Soil pH and nutrients (Fig. 1).

Soil samples were analysed for Mg, Ca, Na, K, H^+, P, N, pH and humus according to the Danish Plantdirectorat's manual (Sørensen and Bülow-Olsen, 1994)

The soil pH in the Faroes is relatively

Altitude (m)	Non-myc.	Arbuscular	Ecto	Ericoid	Orchid	Max. myc. frequency	Min. myc. frequency
	%	%	%	%	%	%	%
≥ 800	15.0	65.8	15.5	2.2	0.5	84.2	68.9
≥ 750	9.5	69.3	15.5	5.3	0.1	90.3	76.8
≥ 700	5.2	78.4	9.2	7.0	0.1	94.7	74.6
≥ 650	9.8	75.2	10.5	4.2	0.0	89.9	73.3
≥ 550	6.9	74.4	9.3	8.3	1.1	93.1	76.1
≥ 500	6.7	72.1	11.4	9.3	0.3	93.1	73.4
≥ 450	6.1	72.5	13.1	8.1	0.0	93.8	70.3
≥ 400	9.1	68.9	18.3	2.5	0.3	90.0	74.2
≥ 350	3.9	75.7	13.5	6.3	0.3	95.8	71.8
≥ 300	4.9	72.6	18.6	3.6	0.0	94.8	76.9
≥ 250	3.5	73.0	12.2	10.7	0.2	96.1	73.4
≥ 150	5.7	73.0	11.6	9.1	0.5	94.2	76.4

***Table 5.** The distribution of the different mycorrhizal categories with altitude.The estimated maximum mycorrhizal frequency is based upon that all plants, that have the ability to form mycorrhiza, actually do so. Minimum mycorrhizal frequency is based upon, that the plant species that rarely or occasionally form arbuscular mycorrhiza, in this case do not.*

low, decreasing from the mountain-tops downward. Average pH is 5.5.

The methods used to measure soil phosphorus concentrations are based on the work of Olsen *et al.* (1954) and Banderis *et al.* (1976). It is a spectrophotometric estimate of extractable phosphorus in soils. The phosphorus levels are low, approximately 10 mg kg^{-1} at high altitude, but are increasing downslope (Fig. 1).

The level of soil total nitrogen is on average 0.6% and is a measure of both inorganic and organic nitrogen (Fig. 1).

The humus content is relative high. The loss of ignition was on average 25% (Fig. 1).

Thus the Faroese soils are phosphorus-limited, while it is not known whether the nitrogen sources are directly available for the plants.

Arbuscular mycorrhiza

Arbuscular mycorrhiza is considered as the most ancient form of mycorrhiza, and is more or less invisible, except microscopically. This symbiosis occurs mainly with herbs. The fungal partner in this mycorrhiza belongs to the zygomycetes, and provides the plant with mainly phosphorus (Fitter, 1985), by exploring the soil better than the plant roots are able to do.

One striking thing with this symbiosis is, that while perhaps 200,000 plant species worldwide are involved, less than 200 fungal species have been described.

Sixty-one plant species were found in this vegetation survey which are known able to form arbuscular mycorrhiza. In addition to these there are 10 plant species,

	% of total AM plant species	% of total AM plant frequency
Rarely AM	21.1	11.2
Occasionally AM	19.7	9.3
Normally AM	45.1	74.3
Probably AM	14.1	5.2

Table 6. *The distribution of arbuscular mycorrhizal (AM) plant species. First column shows how the AM categories are distributed based on the number of AM plant species involved. The second column shows how the different groups of AM plants are distributed based upon the sum of frequencies.*

which probably form arbuscular mycorrhiza, estimated from their relatives (Table 1).

Attempts have been made to clarify how likely a species is to form mycorrhiza (Harley and Harley, 1987; Fitter and Peat, 1994). In the Ecological Flora database from the University of York, Fitter and Peat (1994) used the coding:

never mycorrhizal
rarely mycorrhizal
occasionally mycorrhizal
normally mycorrhizal

Using this coding, the group »Normally arbuscular mycorrhizal« is the most dominating (Table 6). 45% of the arbuscular mycorrhizal species (31% of the total plant species in this survey) are normally arbuscular mycorrhizal. In addition, they account for 74.3% of the arbuscular mycorrhizal frequency (54% of the total sum of frequencies). From this follows, that it seems to be beneficial for the plants to be normally arbuscular mycorrhizal.

Ectomycorrhiza
Most of the fungal partners in this mycorrhiza belong to the basidiomycetes. Compared with the few fungal species forming arbuscular mycorrhiza, the ecto-mycorrhizal fungal species are numerous, approx. 5,000. Ectomycorrhiza provides the plant mainly with nitrogen, from both inorganic and, dependent on the fungal species, organic nitrogen sources (Smith and Read, 1997).

The ectomycorrhizal plant species in this vegetation study were *Salix herbacea* and *Polygonum viviparum.*

Ericoid mycorrhiza
Calluna vulgaris, *Empetrum nigrum* and *Vaccinium myrtillus* were the only plant species likely to form ericoid mycorrhiza found in this vegetation survey. Ericoid mycorrhiza dominates in the heath community. The fungal partner in this mycorrhiza belongs to the ascomycetes. This type of mycorrhiza usually occurs in environments where nutrients are extremely unavailable.

In addition to organic sources such as proteins the ericoid mycorrhizal fungi are able to use chitin as a sole nitrogen source (Finlay *et al.*, 1992).

Orchid mycorrhiza
Orchid mycorrhiza provides the plant with carbohydrates, nitrogen and phosphorus, and the fungus apparently gets nothing in return. Most of the basidiomycetes which form orchid symbiosis, are relatively fast-growing saprophytes, while other are known as parasites (Smith and Read, 1997).

In addition to saprophytic sources there is mounting evidence of mycelial links between orchids and ectomycorrhizal plant species (Smith and Read, 1997). With such a link it is possible for both orchid and fungus to acieve carbohydrates, produced by a ectomycorrhizal plant.

Dactylorhiza maculata and *Listera cordata* were the only plant species found in this study which form orchid mycorrhiza. *Listera cordata* was only represented by a single specimen.

There could be objections that orchid mycorrhiza is not a mutualistic symbiosis, but rather that the plant is a parasite on the fungus. However, when the plant dies, the fungus is ready to utilise the plant in a saprophytic way. Further it is known that if the host plant is unable to restrict the fungal colonisation, then the plant is killed by the fungus (Smith and Read, 1997).

Non-mycorrhizal species and species with no mycorrhizal record
Eight plant species known to be non-mycorrhizal were found in the survey described here. In addition nine plant species are estimated to be non-mycorrhizal (Table 2). Of these *Koenigia islandica* is the most frequent.

In this vegetation survey the mycorrhizal status is unknown for six plant species, accounting for 0.3 per cent of the total sum of plant frequencies (Table 3). In addition, 10 species are considered as arbuscular mycorrhizal plant species, by looking at their relatives (Table 1).

Statistic

The statistic is based upon a correlation matrix, where all 102 plant species in all 532 plots are correlated using Microsoft Exel. A Spearman's rank-order corelation is then performed on the factors, that seems to have the best correlations. For the Spearman test, the SPSS package was used.

The plants are divided into groups after what type of mycorrhiza they form, and then the different types of mycorrhiza are correlated to each other (Table 7). The most significant results of correlations performed directly on plants with a sum of frequencies of at least 100, are presented in Table 8.

Finally the different types of mycorrhiza are correlated to nutrients (Table 10).

Discussion

The overall results suggests that the Faroese vegetation is heavily dependent on mycorrhiza.

The statistical results indicate that some common arbuscular mycorrhizal plant species are connected to ectomycorrhizal plant species. For example are *Festuca rubra* and *F. vivipara* both positively correlated with *Polygonum viviparum*, while *Agrostis canina* is positively correlated to both *Polygonum viviparum* and *Salix herbacea* (Table 8).

It is known from the literature that some plant species are able to associate with different types of mycorrhiza. In the checklist of mycorrhiza (Harley and Harley, 1987) *Polygonum viviparum* has a single arbuscular record, but several ectomycorrhizal records. Also *Silene acaulis* is able to support more than one form of mycorrhiza; it is able to form both arbuscular and ectomycorrhiza. According to Harley and Harley (1987) *S. acaulis* is more likely to be arbuscular, and has therefore been considered as only arbuscular mycorrhizal in this dataset.

Arbuscular mycorrhizal plant species can be divided into two groups, coexisting with either ericoid mycorrhiza or ectomycorrhiza. Arbuscular mycorrhizal plants which typically coexist with ericoid mycorrhizal plants are *Nardus stricta* and *Potentilla erecta* (Table 8).

Arbuscular mycorrhizal plant species together with ectomycorrhizal species are such as *Deschampsia flexuosa* and *Festuca rubra* (Table 8).

One atypical plant species in this context seems to be *Thymus praecox*, which manages to coexist with both the ectomycorrhizal *Polygonum viviparum* ($r = 0.14$, $p = 0.001$) and the two ericoid mycorrhizal plants *Vaccinium myrtillus* ($r = 0.25$, $p = 0.000$) and *Empetrum nigrum* ($r = 0.24$, $p = 0.000$). There is a negative correlation with

Type of mycorrhiza	Type of mycorrhiza	correlation	P (r_S)
Arbuscular	Ecto	-0.005	0.905
Arbuscular	Ericoid	0.358	0.000
Arbuscular	Orchid	0.200	0.000
Arbuscular	Non-mycorrhizal	-0.143	0.001
Ecto	Ericoid	-0.373	0.000
Ecto	Orchid	-0.229	0.000
Ecto	Non-mycorrhizal	0.096	0.027
Ericoid	Orchid	0.240	0.000
Ericoid	Non-mycorrhizal	-0.148	0.001
Orchid	Non-mycorrhizal	-0.028	0.525

Table 7. *The different mycorrhizas correlated. Negative correlations could indicate that these mycorrhizal associations do not coexist.*

Plant	Mycorrhizal status	Plant	Mycorrhizal status	cor-lation
Thymus praecox	Normally AM	*Viola riviniana*	Normally AM	0.58
Calluna vulgaris	Ericoid	*Potentilla erecta*	Normally AM	0.55
Empetrum nigrum	Ericoid	*Vaccinium myrtillus*	Ericoid	0.54
Potentilla erecta	Normally AM	*Nardus stricta*	Normally AM	0.53
Galium saxatile	Normally AM	*Agrostis capillaris*	Normally AM	0.53
Empetrum nigrum	Ericoid	*Calluna vulgaris*	Ericoid	0.51
Viola palustris	Normally AM	*Agrostis capillaris*	Normally AM	0.50
Sibbaldia procumbens	Non-mycorrhizal	*Alchemilla alpina*	Occasionally AM	0.49
Narthecium ossifragum	AM	*Nardus stricta*	Normally AM	0.49
Empetrum nigrum	Ericoid	*Nardus stricta*	Normaly AM	0.46
Narthecium ossifragum	AM	*Calluna vulgaris*	Ericoid	0.39
Silene acaulis	Occasionally AM	*Polygonum viviparum*	Ecto	0.39
Deschampsia flexuosa	Normally AM	*Salix herbacea*	Ecto	0.38
Juncus squarrosus	Occasionally AM	*Nardus stricta*	Normally AM	0.37
Juncus squarrosus	Occasionally AM	*Calluna vulgaris*	Ericoid	0.32
Festuca vivipara	Normally AM	*Polygonum viviparum*	Ecto	0.30
Polygonum viviparum	Ecto	*Salix herbacea*	Ecto	0.27
Agrostis canina	Normally AM	*Salis herbacea*	Ecto	0.24
Agrostis canina	Normally AM	*Polygonum viviparum*	Ecto	0.21
Festuca rubra	Normally AM	*Polygonum viviparum*	Ecto	0.21

Table 8. *The most significant results of correlations performed directly on plants with a frequency of at least 100. All the results are significant. AM= Arbuscular Mycorrhizal. Ericoid plant species have a strong correlation with some species, for example* Potentilla erecta, Nardus stricta, Narthecium ossifragum *and* Juncus squarrosus, *while ectomycorrhizal plant species have strong correlations to other plant species, such as* Silene acaulis, Deschampsia flexuosa, Festuca vivipara *and* Festuca rubra.

Salix herbacea (r = -0.1, p = 0.03) while *Thymus praecox* seems not to be dependent upon *Calluna vulgaris* (r = 0.04, p = 0.39).

In a study from 1981 Read and Haselwandter found that *Festuca rubra* was ectomycorrhizal as well as arbuscular mycorrhizal. This single record from 1981 is mentioned in the mycorrhiza check-list from Harley and Harley (1987), but is not supported from any additional record in the additional checklist from 1990 (Harley and Harley, 1990).

Distribution

Some of the different types of mycorrhiza co-occur in the same ecosystem, while other types seems to avoid each other.

One of the general findings is that ectomycorrhizal plants does not coexist with ericoid or orchid mycorrhizal plants.

Ectomycorrhizal plant species were never found in the same plots as orchids. This is in contrast to findings suggesting a mycelial link between orchids and ectomycorrhizal plant species, as proposed by Smith and Read (1997). Instead orchids and ericoid species do coexist (Table 7). This could indicate that it is the fungus' saprophytic abilities that are required.

Type of mycorrhiza	Correlation		Probability (r_s)	
	Phos.	Nitr.	Phos.	Nitr.
Arbuscular	0.102	0.236	0.000	0.000
Ecto	0.152	0.143	0.000	0.001
Ericoid	-0.076	0.052	0.078	0.232

***Table 10**. The different mycorrhizas correlated with phosphorus and nitrogen. While both arbuscular and ecto mycorrhizal plants as a group seem to be correlated to the nutrients at a significiant level, ericoid mycorrhizal plants are not.*

The fact that ecto- and ericoid mycorrhizal plants do not grow together, has been noticed before. Robinson (1972) describes how the endophyte in *Calluna vulgaris* is eradicated by applying fertilisers, and after the endophyte is eradicated, the plant is vulnerable for fungal pathogenic infections. Further Robinson concludes from experiments that it is likely that the ericoid fungal symbiont is responsible for this by excreting fungicides into the soil. Apart from preventing pathogenic infections, it also seems to be a growth inhibitor for ectomycorrhizal fungi.

Robinson conducted only experiments with *Calluna* heath. However, it is likely that the same is valid for *Empetrum nigrum*, but not for *Vaccinium myrtillus*. Only once does *Calluna vulgaris* get a score in a plot where ecto-mycorrhizal plant species are identified. This occurs twice for *Empetrum*, but *Vaccinium* achieves 88 scores together with ecto-mycorrhizal species.

The only nutrients with good correlations to the vegetation were phosphorus and nitrogen. The correlations with some of the mycorrhizal groups are presented in Table 9.

Conclusion

Arbuscular mycorrhiza is the most widespread type of mycorrhiza. However, despite of few species forming ericoid and ectomycorrhiza, they are much more widespread than would be expected, if only the number of species was to account for their distribution. Both ecto- and ericoid mycorrhizal fungi are able to degrade organic compounds and thus provide the plants with nutrients from organic sources. The Faroese soils are poor in available phosphorus, and probably also in inorganic nitrogen (humus and total nitrogen in soil samples are extremely well correlated, r = 0.95). Further the temperature is low, so mineralisation of organic material is slow.

At such conditions ectomycorrhizas can be more competitive than arbuscular mycorrhizas (Moyersoen *et al.*, 1998). However, other findings indicate, that ectomycorrhizal species impose a greater carbon drain on their host than do arbuscular mycorrhizas, owing to the greater biomass of associated fungi (Moyersoen *et al.*, 1998).

Ericoid mycorrhizal fungi can be more efficient than ectomycorrhizal as decomposers. On the other hand there seems to be a limited number of plant species capable to coexist with ericoid mycorrhizal fungi.

Arbuscular mycorrhiza is the most widespread. This is probably because it is the type which is "cheapest" for the system. However, it is not as efficient as decomposer as the other types of mycorrhiza, and that could be why other types of mycorrhiza, despite their association with very few plant species, are so successful.

The connection between some arbuscular mycorrhizal plant species and ecto- or ericoid plant species could be due to dual infection, but that can not be concluded from this study.

The fact that the type which requires least photosynthetic products from the plant, and is least efficient in degrading organic compunds is the most widespread could indicate that there are other factors than phosphorus and nitrogen which are limiting. These could be, for example, temperature and/or light.

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