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Root Fungus Colonization along an Altitudinal Gradient in North Norway

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Abstract

Mycorrhizal symbiosis is generally advantageous for plants in nutrient-poor soils, but this advantage may be low in arcto-alpine conditions. While the relative coverage of nonmycorrhizal plant species has been found to increase along an altitudinal gradient, the within-species patterns of mycorrhizal colonization in arctic and alpine plants are not well known, and different results have been obtained in relation to altitude. We investigated arbuscular mycorrhizal (AM) and dark-septate endophytic (DSE) root colonization in six subarctic herbaceous plants *Ranunculus glacialis* L., *Saxifraga aizoides* L., *Sibbaldia procumbens* L., *Solidago virgaurea* L., *Trientalis europaea* L., and *Viola biflora* L. along an altitudinal gradient (0–1400 m a.s.l.) at Mt. Paras, North Norway. We did not find any consistent decline in the different types of fungus colonization along the entire gradient. There was no statistically significant shift in coarse AM or DSE colonization with altitude. However, fine endophyte type AM colonization showed a statistically significant, positive relationship with altitude. These results suggest that root colonization of any particular mycorrhizal species may yield different gradient patterns with altitude than the relative coverages of mycorrhizal and nonmycorrhizal plant taxa. Because of its positive association with altitude, fine endophyte colonization may have a specific role in the nutrition of arctic and alpine plants.

Introduction

Mycorrhizal symbiosis is a generally mutualistic relationship between plants and fungi in which carbon and nutrients are translocated between the symbionts (Smith and Read, 1997). Mycorrhizas impose a considerable carbon cost on the host plant (Jones et al., 1991), but generally are beneficial to plants, especially at low soil nutrient levels (Koide, 1991). Opposing this generalization, mycorrhizal symbiosis has been found to be quite rare under arctic and alpine conditions (e.g., Haselwandter, 1979; Read and Haselwandter, 1981; Bledsoe et al., 1990; Kohn and Stasovski, 1990; Väre et al., 1992) even though arctic and alpine soils are poor in phosphorus and nitrogen available to plants (Rehder and Schäfer, 1978). The relative coverage of mycorrhizal plants has been found to decrease with increased altitude, mainly because of an increased proportion of nonmycorrhizal plant taxa, such as Cyperaceae and Juncaceae (Väre et al., 1997). It has been proposed that the relative advantage of mycorrhizal symbiosis for the host plant declines in arctic and alpine conditions, possibly because of the constraints of carbon economy for the maintenance of symbiosis in cold (Haselwandter, 1979; Väre et al., 1997; Tuomi et al., 2001; Ruotsalainen et al., 2002a). Thus, it could be advantageous for mycorrhizal plants to maintain different amounts of fungus colonization in their roots at different altitudes.

Different mycorrhizal types could yield variable colonization patterns along with altitude because the dependency of the host plant from the symbiosis is different (Trappe, 1987). Ericoid and ectomycorrhizas are considered obligatory for their host plants, but arbuscular mycorrhizas (AM) can be more facultative (Trappe, 1987). The colonization intensity of ericoid mycorrhizas has been found to decrease (Haselwandter, 1979; Haselwandter and Read, 1980; *Vaccinium myrtillus* L., *Vaccinium vitis-idaea* L.) or increase (Väre et al., 1997; *Cassiope hypnoides* (L.) D. Don, *V. vitis-idaea*) relative to altitude. Väre et al. (1997) found ectomycorrhizal colonization in *Salix herbacea* L. to be more or less constant at different altitudes. The comparison of AM plants (graminoids, herbs) growing at different altitudes has shown that the average mycorrhizal colonization of these plant groups decreases with increasing altitude (Read and Haselwandter, 1981; Väre et al., 1997), but species-level information about AM colonization patterns along altitudinal gradients is generally lacking (but see Väre et al., 1997). Additionally, another root-associated fungus group, dark-septate endophytes (DSE) with unknown function (Jumpponen and Trappe, 1998), is commonly found in the roots of arcto-alpine plants. It is possible that it is more common at high than at low altitudes (Haselwandter and Read, 1980; Read and Haselwandter, 1981; Schadt et al., 2001).

Along altitudinal gradients, plant growth conditions have fundamental shifts because of changes in temperature, precipitation, and soil conditions (Körner, 1999). Globally, a temperature decline of 0.6°C per every 100 m of elevation is consistent when altitudinal gradients are compared (Lamb, 1972). Changes in temperature conditions, nutrient availability, and vegetation coverage are known to affect mycorrhizal colonization (Hayman, 1974; Koide, 1991; Genney et al., 2001). Thus, if any species-level mycorrhizal colonization patterns along with altitude can be found, they will help to understand the conditions where mycorrhizas are favored.

In order to determine if there are species-level altitudinal shifts in mycorrhizal colonization, we investigated the roots of alpine herbs at Mt. Paras in northern Norway, and used altitude to explain variation in arbuscular mycorrhizal (AM) and dark-septate endophytic (DSE) colonization. We expected that AM colonization would decrease with increasing altitude.

Material and Methods

Samples were collected from Mt. Paras, Signaldalen, Tromsø district, in northern Norway (69°05′–69°22′ N, 20°00′–20°13′ E) on 3–5 August 1999. The sampled altitudes (Table 1) ranged from the sea level to the mountain top (1419 m a.s.l.), representing a transition from the middle boreal zone to the high-alpine belt (Hedberg, 1952; Ahti et al.,

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TABLE 1

The altitudes and species studied at Mt. Paras in 1999. From each sampling site, three to five replicates were collected. Ra = Ranunculus galcialis, *Sax* = Saxifraga aizoides, *Sib* = Sibbaldia procumbens, *Sol* = Solidago virgauera, *Tri* = Trientalis europaea, *and Vi* = Viola biflora. Saxifraga aizoides *was only analyzed for its DSE colonization because it was found not to have unambiguous AM structures. The number of sites/altitude = the number of n/altitude in the statistical analysis. Alpine zonation as proposed by Hedberg (1952).*

Altitude (m)	Species (number of sites)	Zone/site description
0	Sax (3), Sol (1), Tri (3)	Sandy sea-and roadside, Sax in stony brooks
200	Tri (3), Vi (2)	Mixed forest (*Picea abies*, *Betula* spp.)
400	Tri (3)	Herb-rich birch forest
600	Sib (1), Vi (3)	Low-alpine meadow
700	Sol (1), Tri (3)	Low-alpine meadow
800	Vi (1)	Low-to middle-alpine
900	Ra (1), Sax (3)	Low-to middle-alpine
1000	Vi (2)	Middle-alpine
1100	Sib (1)	Middle-alpine
1400	Ra (1)	High-alpine

1968). The length of the growing season is about 2 mo in the low-alpine belt in this area (Hedberg, 1952), and the treeline formed by mountain birch (*Betula pubescens* ssp. *czerepanovii*) is at 600 m a.s.l. The mean annual temperature is –2.5°C (1961–1985), the mean temperature in July +10.5°C and annual precipitation, measured at the nearest climatological station at Kilpisjärvi, Finland (about 40 km west of Mt. Paras at about 500 m a.s.l.), is 422 mm (Järvinen, 1987).

The following species were investigated mainly on the basis of their wide altitudinal distribution: *Ranunculus glacialis* L. (Ranunculaceae), *Saxifraga aizoides* L. (Saxifragaceae), *Sibbaldia procumbens* L. (Rosaceae), *Solidago virgaurea* L. (Asteraceae), *Trientalis europaea* L. (Primulaceae), and *Viola biflora* L. (Violaceae). At every sampling site, three to five replicate root samples with 1 L of soil were collected near each other, and the samples were pooled for statistical analysis (Table 1). In the case of *R. glacialis, S. aizoides, S. procumbens*, and *S. virgaurea* only the highest and lowest altitudes were sampled. At each altitude, sites were used only for blocking purposes and they had relatively similar kind of vegetation (Table 1). In the laboratory, the roots were cleaned and preserved in 50% alcohol. The roots were stained using the method described by Phillips and Hayman (1970), with slight modifications described in Ruotsalainen et al. (2002b). Root fungus colonization was assessed under a compound microscope by using the magnified intersection method (McGonigle et al., 1990) with 50 intersects at 150× magnification.

In the microscopic examination, AM colonization was calculated as arbuscules, coils, hyphae (which may possibly also include nonsymbiotic hyphae) and vesicles. Fungus coils and arbuscules were pooled in the statistical analysis because they were often impossible to separate confidently. Fine endophyte type AM colonization could in most cases be separated from the coarse AM type. The fine endophyte was identified based on the following characteristics: thin (1–2 μm), usually nonseptate, deep blue staining hyphae which contained vesicles and/or swellings and sometimes fan-like structures (Hall, 1977; Abbott, 1982). Superficial thin, deep blue hyphae also were classified as the fine endophyte (see also Hall, 1977; Read and Haselwandter, 1981; Abbott, 1982; Bledsoe et al., 1990). All kinds of arbuscules (fine and coarse) were classified as one variable, because they cannot be reliably separated. The fine endophyte colonization parameter thus includes hyphae and vesicles. DSE hyphae and microsclerotia were calculated separately, but because sclerotia were occasional, the data were pooled.

STATISTICS

Statistical analysis was performed with the R-program, version 1.1.1 (Ihaka and Gentleman, 1996). A generalized linear model was fitted to the data using altitude and species as the explanatory variables and the presence of fungus colonization as the response variable (see also Alvarez-Santiago et al., 1996). The model used had the expression:

$$g(B_{ij}) = \ln[p_{ij}/(1 - p_{ij})] = B_0 + A_i + S_j + AS_{ij} + E_{ij}$$

where $g(B_{ij})$ was the link function (logit) for the probability of colonization (p_{ij} = colonized intersects, $1 - p_{ij}$ = noncolonized intersects for the ith altitude and the jth species), B_0 was the overall mean, A_i was the altitude effect, S_j was the species effect, AS_{ij} was the interaction effect, and E_{ij} was the error term with binomial distribution. For evaluation of the overall coefficients for altitude, a model without an interaction term was also fitted. All the studied parameters were overdispersed, which means that the probability of colonization at each "treatment level" was not constant (Aitkin et al., 1989; Crawley, 1993). This was taken into account in the analysis by using a quasibinomial instead of binomial error distribution and by using F-statistics instead of χ^2 (Crawley, 1993). We used the sum of successes/failures at each site ($p_{ij}/1–p_{ij}$) as a sample unit because the intersects of individual samples and samples at sites were not independent (Table 1).

Results

Obvious AM structures (= arbuscules, vesicles, and typical nonseptate hyphae) were detected in *Ranunculus glacialis*, *Sibbaldia procumbens*, *Solidago virgaurea*, *Trientalis europaea* and *Viola biflora* (Table 2). AM fungi in *T. europaea* and *V. biflora* formed intracellular coils, and intercellular hyphae were lacking, which both suggest that these species form *Paris*-type mycorrhizas (Smith and Read, 1997). The mycorrhizal morphology in the other plant species was of the *Arum* type with intercellular hyphae and without coil structures. We pooled arbuscules and coils in the analysis, however, because they cannot always be reliably separated from each other. *Saxifraga aizoides* had colonization by hyaline hyphae, which resembled AM hyphae, and vesicles were also occasionally found. These colonizations were rare, however, and because arbuscules were not found, these were not considered as AM (Table 2). Fine endophyte (FE) type colonization was found in all AM species (Table 2). As the difference between coarse and fine AM hyphae was not always clear, it is possible that a minor amount of fine hyphae were included in coarse AM. DSE colonization was common in all species studied (Table 2).

FE colonization was found to have a statistically significant positive relationship with altitude, but the other colonization parameters (coarse AM arbuscules, vesicles, hyphae and DSE) showed no differences (Tables 3 and 4). Average colonization differed between species in all cases (Table 3). The species by altitude interaction was not significant for any of the parameters studied (Table 3).

Discussion

Contrary to our expectation, we did not find any statistically significant decline in coarse AM colonization with altitude. In contrast, fine endophyte type AM was positively related to altitude. Species-level shifts in colonization with altitude have not been detected in AM plants, and the hypothesis concerning decreasing colonization is based on comparisons of congeneric plants at different altitudes (Haselwandter and Read, 1980; Väre et al., 1997). In the case of ericoid mycorrhizal plant species, both increasing and decreasing colonization patterns with altitude have been found (Haselwandter, 1979;

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TABLE 2

Root fungus colonization percentages ± SD in the plants at Mt. Paras. FE = Fine endophyte, DSE = Dark-septate endophyte. In Saxifraga aizoides*, only DSE colonization was quantified. The numbers of specimens studied per altitude are given in parentheses*

	Arbuscules	Vesicles	Hyphae	FE	DSE
Ranunculus glacialis					
900 m (5)	8.4 ± 11.5	0.8 ± 1.8	25.4 ± 37.6	2.0 ± 3.5	2.4 ± 2.6
1400 m (5)	0.4 ± 0.9	0	2.4 ± 3.3	1.4 ± 3.1	0
Saxifraga aizoides					
0 m (15)	—	—	—	—	4.0 ± 6.8
900 m (15)	—	—	—	—	9.3 ± 11.1
Sibbaldia procumbens					
600 m (5)	54.8 ± 18.2	12.0 ± 8.0	84.0 ± 19.0	6.8 ± 11.7	18.4 ± 14.2
1100 m (5)	44.8 ± 6.4	3.0 ± 2.4	87.2 ± 17.6	17.2 ± 7.9	26.0 ± 19.5
Solidago virgaurea					
0 m (5)	9.2 ± 14.0	0.4 ± 0.9	57.2 ± 18.7	1.6 ± 1.7	86.8 ± 7.0
700 m (5)	18.6 ± 16.6	4.8 ± 3.3	70.4 ± 15.1	26.4 ± 21.2	47.6 ± 7.4
Trientalis europaea					
0 m (15)	52.2 ± 18.2	0.4 ± 1.1	49.2 ± 23.3	1.6 ± 2.5	21.6 ± 20.4
200 m (12)	29.8 ± 24.5	0	29.8 ± 21.0	0	27.0 ± 23.4
400 m (13)	49.1 ± 18.8	0.3 ± 0.8	46.9 ± 21.8	2.6 ± 4.3	38 ± 25.9
700 m (12)	58.7 ± 18.7	0.2 ± 0.6	51.4 ± 24.0	0.9 ± 1.3	10.5 ± 10.8
Viola biflora					
200 m (15)	23.5 ± 10.8	0.8 ± 1.5	52.1 ± 19.3	2.7 ± 3.3	19.3 ± 20.6
600 m (15)	21.1 ± 13.9	7.7 ± 5.2	62.7 ± 13.7	3.6 ± 3.4	24.4 ± 17.1
800 m (5)	15.6 ± 14.4	1.6 ± 1.7	30.0 ± 19.4	13.6 ± 11.8	7.2 ± 9.0
1000 m (9)	23.1 ± 13.6	2.0 ± 2.5	51.9 ± 17.4	3.7 ± 3.6	24.9 ± 20.1

Haselwandter and Read, 1980; Väre et al., 1997). Our results agree with previous observations that coarse AM are not common in high-alpine conditions (see also Haselwandter and Read, 1980; Read and Haselwandter, 1981). This could be because of climatic constraints on the advantage of mycorrhizal symbiosis (Tuomi et al., 2001; Ruotsalainen et al., 2002a), but there may also be other factors to be considered. In our study, the high-alpine zone was characterized by bare ground and open vegetation. In contrast, in continuous vegetation patches in high-alpine conditions, coarse AM and FE have been found to be relatively common (Haselwandter and Read, 1980; Read and Haselwandter, 1981). Mycorrhizal colonization percentage has been found to be positively related to host plant density (Hartnett et al., 1993; Genney et al., 2001) and thus, vegetation coverage probably affects the mycorrhizal colonization patterns along altitudinal gradients.

Fine endophyte (FE) was found to correlate positively with altitude. Similar results have been obtained by Crush (1973a) and Haselwandter and Read (1980), who found FE to be more common at high than at low altitudes. FE has been proposed to be beneficial for host plants in phosphate-deficient conditions (Crush, 1973b, Rabatin, 1979). The presence of FE colonization may be related to soil phosphorus levels because plant-available phosphorus probably decreases with altitude (Widden, 1987; Kyllönen, 1988; Väre et al., 1997; Körner, 1999). Even though FE showed an increasing trend along the altitudinal gradient, FE colonization in high-alpine *Ranunculus glacialis* was low (but still relatively high compared to other colonization types). This agrees with Haselwandter and Read (1980), who found FE to be rare in open and isolated vegetation in the high-alpine zone, but relatively common in densely vegetated patches at the same altitude.

Haselwandter and Read (1980) and Read and Haselwandter (1981) found more abundant DSE colonization at high altitudes than at low altitudes. DSE probably overlaps the soil fungal groups "sterile mycelia" or "sterile-dark fungi" mentioned by Bissett and Parkinson (1979a, 1979b) and Widden (1987), who, by contrast, did not find an increase with altitude. In high-alpine *R. glacialis*, we did not find DSE at all, but our full data set suggests that there are no remarkable shifts in DSE with altitude (Table 4). DSE showed high intraspecific variation (Table 2) (see also Ruotsalainen et al., 2002b), a possible reason being that it is a functionally nonuniform group that probably includes

TABLE 3

The F-values of the impacts of species, altitude and their interaction on the AM and DSE colonization parameters in the Mt. Paras data on the basis of a generalized linear model (Analysis of deviance). Residual df = 17

Source of variation	df	F	*P*
Arbuscules			
Species	4	18.44	**<0.001**
Altitude	1	0.93	0.347
Species * altitude	4	1.21	0.344
Vesicles			
Species	4	7.49	**0.001**
Altitude	1	0.183	0.673
Species * altitude	4	1.539	0.236
Hyphae			
Species	4	7.84	**<0.001**
Altitude	1	0.14	0.717
Species * altitude	4	1.21	0.343
Fine endophyte			
Species	4	9.50	**<0.001**
Altitude	1	12.12	**0.003**
Species * altitude	4	2.20	0.113
DSE			
Species	4	7.23	**<0.001**
Altitude	1	0.01	0.947
Species * altitude	4	0.97	0.459

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TABLE 4

*Coefficients of the linear predictor in the generalized linear model for altitude in the Mt. Paras-data. The coefficients are given for every species studied and for the whole data set. The sign of the coefficient indicates the relationship of the colonization parameter with the altitude (positive or negative) and the value (=logarithm of an odds ratio) gives an estimate for the probability of change per 100 meters. * = statistically significant. See Table 3 for F and* P *values*

	Arbuscules	Vesicles	Hyphae	FE*	DSE
Ranunculus glacialis	−0.595	−1.459	−0.642	−0.304	−1.282
Saxifraga aizoides	—	—	—	—	0.102
Sibbaldia procumbens	0.067	−0.268	0.790	0.245	0.148
Solidago virgaurea	0.099	0.377	0.088	0.462	−0.279
Trientalis europaea	0.082	−0.096	0.049	0.017	0.002
Viola biflora	−0.012	0.067	−0.013	0.091	0.020
Overall	0.033	0.029	0.015	0.171	−0.003

saprophytic, pathogenic, and mutualistic species or strains (Jumpponen and Trappe, 1998). In our data, DSE colonization was especially high in low-altitude *Solidago virgaurea*. The site of collection was a sandy, sparsely vegetated roadside seashore with *Empetrum nigrum* L. patches. Vrålstad (2001) used molecular methods to show that ericoid mycorrhizal and DSE colonizations could be formed by same taxa. We speculate that such association also might have been possible in our study plot, and, may partly explain the high DSE colonization at this particular site. Another possibility is that the studied roots were old and had high colonization by saprotrophic DSE (Jumpponen and Trappe, 1998; Mullen et al., 1998).

The different numbers of samples collected from different species may have affected our data. Additionally, more samples were collected from low altitudes than from high altitudes, and only one site per altitude was studied above 1000 m a.s.l. This is justified by the decrease of species diversity and vegetation coverage (at 1400 m a.s.l. only two vascular plant species existed). *Sibbaldia procumbens* had especially high AM colonization at high altitude. This species may be highly mycotrophic, as previously observed (Väre et al., 1997). If *Sibbaldia* had been excluded from the data, the average colonization patterns would, in most cases, have decreased markedly with altitude, and the increase of FE with altitude would have been less considerable than with *S. procumbens* included. It is possible that the study plants from different altitudes were in different phenological stages when they were harvested, and this also may have affected our results (Mullen and Schmidt, 1993; Mullen et al., 1998). Our previous study, however, indicated that seasonal variation in colonization is not so great in alpine conditions (Ruotsalainen et al., 2002b).

Our results indicate that (1) coarse AM and DSE colonization do not have a consistent relationship with altitude, and (2) fine endophyte colonization may have a specific role at high altitudes. Our results agree with previous studies in which AM colonization was found to be rare in the high-alpine zone, but do not support the view that DSE are especially common there. It also is likely that site-specific variation below the high-alpine zone may lead to variable within-species colonization patterns with altitude.

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