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Mountain Birch Seedlings in the Treeline Ecotone, Subarctic Finland: Variation in Above- and Below-Ground Growth Depending on Microtopography

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Abstract

The treeline ecotone in northern Finnish Lapland is characterized by a mosaic of sites with highly varying environmental conditions. Density, age structure, growth, and root systems of mountain birch seedlings (*Betula pubescens* ssp. *czerepanovii* [Orlova] Hämet-Ahti) were studied in different microsite classes (deflation, lichen heath, dwarf shrub heath, hummock, willow shrub, sedge mire). On wind-exposed convex topography characterized by shortage of moisture and nutrients, seedling establishment is impeded, as is indicated by low seedling densities and lack of very young seedlings as well as by high rooting depths and root/shoot ratios of the few individuals. In sedge mires, birch seedlings occasionally occur in great numbers but die off at an early stage. Extremely shallow root systems point to anoxia as the main reason. Severe shoot damage is common to almost all saplings. This is likely due to grazing by reindeer (*Rangifer t. tarandus*). As a result, height growth is suppressed even on sites with otherwise relatively suitable conditions (e.g. willow shrub sites). Future effects of climate change which could locally improve conditions for germination and establishment of birch young growth might be overridden by the effects of high reindeer density.

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Introduction

In northern Finnish Lapland, treeline is formed by mountain birch (*Betula pubescens* ssp. *czerepanovii* [Orlova] Hämet-Ahti). The treeline is generally determined by thermal deficiency (e.g. Holtmeier, 1994; Wielgolaski, 1997; Körner, 1998). However, edaphic, topographic, anthropogenic, and biological factors have modifying effects (e.g. Oksanen et al., 1995; Sveinbjörnsson, 2000). Within the treeline ecotone, extending from the closed forest to the uppermost and usually crippled specimens of the tree species, site conditions vary strongly within a few meters distance (Holtmeier, 2003). The resulting microsite pattern (e.g. microclimate, soil conditions, duration of the winter snowpack) is a key factor for the regeneration of birch in the harsh treeline environment (Holtmeier, 1971; Kullman, 1984; Holtmeier et al., 2003; Holtmeier and Broll, 2005). Successful germination and establishment of tree seedlings rather than increasing growth of mature trees appear to be the most critical processes in treeline advance to higher altitude and more northern positions (Smith et al., 2003; Holtmeier and Broll, 2005, 2007; Karlsson et al., 2005). Thus, when assessing treeline response to climate change (cf. e.g. Seppä, 1996; Autio and Heikkinen, 2002; Kullman, 2002) tree regeneration and development of young growth in the treeline ecotone must particularly be considered.

Studies on mountain birch regeneration at Fennoscandian treelines are numerous (e.g. Sonesson and Hoogesteger, 1983; Holm, 1993; Kullman, 2002, 2003). Besides studies regarding stand structure and dynamics, investigations on root systems can substantially contribute to understanding the influence of the site pattern on birch performance (cf. e.g. Laitakari, 1935). However, although rooting zone conditions are particularly important for tree growth in the treeline ecotone, only a few studies concerning this matter exist for northern Fennoscandia (Sveinbjörnsson,

1987; cf. Sveinbjörnsson et al., 2002). Results from manipulative experiments with *Betula pubescens* ssp. *czerepanovii* seedlings (e.g. Karlsson and Nordell, 1996; Weih and Karlsson, 1997, 1999, 2002; Weih, 1998; Karlsson et al., 2000) are transferable to natural regeneration to a limited extent only. Thus, the objective of this study is to examine (1) how birch seedling occurrence is influenced by microtopography, (2) how birch root and shoot systems are influenced by environmental conditions depending on microtopography, and (3) how successful natural seed-based birch regeneration is in the study area.

Methods

STUDY AREA

The field studies (2002/2003) were carried out in northern Utsjoki in Finnish Lapland (Fig. 1). The climate of the area is subcontinental (Oksanen and Virtanen, 1995). Mean annual air temperature at the nearest meteorological station (Kevo, 107 m a.s.l.) is -1.7°C , mean monthly air temperature is -14.7°C in January and 9.7°C in June, and mean annual precipitation is 416 mm (data for 1962–2006). The acid bedrock of the study area (granulite and granodiorite) is covered by sandy till (2–3 m) (Geologinen Tutkimuslaitos, 1981).

The study area is situated in the Paistunturin cooperative herding district and is intensively grazed year-round by semi-domesticated reindeer (*Rangifer t. tarandus*), with additional winter feeding. Reindeer population has rapidly increased since the 1970s and peaked in the 1980s and early 1990s (Helle and Kojola, 2006). Recent summer stocking densities in the study area are 3.5–4.5 reindeer km^{-2} (Solberg et al., 2005).

All plots are located in the upper treeline ecotone near the uppermost mountain birch trees (≥ 2 m) between 260 and 380 m

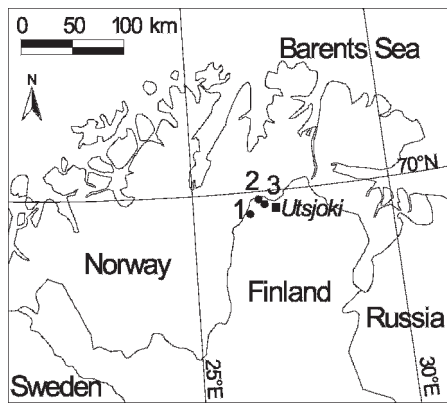


FIGURE 1. Location of the study sites. 1 = Rodjanoaivi, 2 = Koahppeloavi, 3 = Staloskaidi.

a.s.l. on the slopes of Rodjanoaivi (509 m a.s.l.), Koahppeloavi (419 m a.s.l.), and Staloskaidi (340 m a.s.l.) (Fig. 1).

MICROSITE CLASSIFICATION

Microtopography varies locally (basal till dissected by brooks; esker), and it strongly influences microclimate (wind exposure, snow distribution, soil moisture, soil temperature). As a result, very dry and wind-eroded ridges with hardly any vegetation alternate with more sheltered lichen heath and dwarf shrub heath areas. In valleys, where high water tables cause peat formation and waterlogging, willow coppice and sedge mires can be found, and hummock fields have been formed by cryoturbation (for a comprehensive description, cf. e.g. Haapasaari, 1988; Broll et al., 2007). Microsites were classified (Fig. 2) using local topography and vegetation as indicators (Holtmeier et al., 2003). Microsite classes are (1) deflation, (2) lichen heath, (3) dwarf shrub heath, (4) hummock, (5) willow shrub, and (6) sedge mire.

Across the three studied mountains, six investigation areas with highly variable microtopography were delimited (size of the areas: 1–4 ha; distance between areas: several hundred meters to several kilometers). Within an area, several individual plots per microsite class were examined. Individual and aggregated plot size for each microsite class varied between areas, depending on existence and spatial extent of the respective class. Emphasis was placed on heath sites which cover vast fell areas. Thus, deflation sites, lichen heath, and dwarf shrub heath were studied in all six areas. Hummock, willow shrub, and sedge mire sites were studied in three areas. Total square meters of studied plots varies between microsite classes because birch seedling availability is of different orders of magnitude (approximate sums: deflation 4500 m²; lichen heath 1200 m²; dwarf shrub heath 1200 m²; hummock 270 m²; willow shrub 120 m²; and sedge mire 120 m²).

Total vegetation cover and height (Table 1) were recorded in 20 representative plots per microsite class. Plot size was 4 m² (lichen heath, dwarf shrub heath, hummock) or 9 m² (deflation, willow shrub, sedge mire). Vegetation cover is very sparse at deflation sites and increases across heath sites to hummocks, willow shrub, and sedge mires. Vegetation height is about 20–40 cm on average, with lower vegetation at deflation sites and higher vegetation at willow shrub sites.

Soil profiles were described for all microsite classes following the German manual for soil mapping (AG Boden, 1994). Soil organic carbon and total nitrogen were measured by an elemental analyzer (EuroVector EA 3000). Soil conditions vary considerably between microsite classes (for representative soil profiles cf.

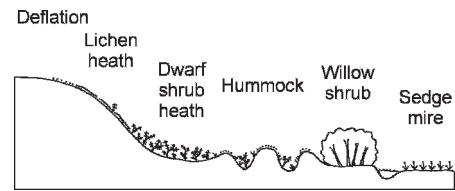


FIGURE 2. Topography-dependent microsite pattern (schematic).

Figs. 3a and 3b). Generally, topsoils at deflation sites were eroded and former Podzol subsoils became exposed. Consequently, organic carbon is frequently and total nitrogen is always below the detection limit at deflation sites (cf. Fig. 3a). At lichen heath and dwarf shrub heath sites, shallow Podzols occur, with soils under dwarf shrub heath being more developed. At these heath sites, detectable nitrogen is limited to the organic topsoils. Hummock sites are characterized by Podzols influenced by ground water, a relic peat cover, horizons partly mixed by cryoturbation, and normally wide C/N ratios (cf. Fig. 3b). Histosols of willow shrub sites and sedge mires show comparatively narrow C/N ratios. Usually, the ground water table is higher in sedge mires than in willow shrub sites.

Soil moisture of the topmost 6 cm was measured by TDR on five (deflation, lichen heath, dwarf shrub heath) or three (hummock, willow shrub, sedge mire) representative plots once a week (10 random measurements per date and plot; 24 June–28 August 2003). Soil moisture (Table 2) differs significantly with microsite class [$H(5) = 1742, p < 0.001$]. It is lowest at excessively drained deflation sites and increases across lichen and dwarf shrub heath and hummocks to poorly drained willow shrub sites and sedge mires.

Soil temperatures were recorded (Hotdog DT1, Elpro; September 2002–August 2003) in 2.5 cm depth in one representative deflation site, lichen heath site, and dwarf shrub heath site, respectively. Additionally, temperature was recorded on a brookside close to a willow shrub site and a sedge mire site; however, transferability to those site classes is restricted (ground water table, vegetation structure). Duration of snow cover was estimated from soil temperature data. Soil temperatures (Table 3) are most extreme at the studied deflation site (annual and daily amplitudes). There is little snow cover, and freeze-thaw cycles are frequent. Conditions are less extreme underneath lichen heath. Dwarf shrub heath is characterized by long-lasting snow and relatively few freeze-thaw cycles, but the soil is generally cold during the growing season. The brookside soil is generally rather warm, in spite of a long lasting winter snow cover. Freeze-thaw cycles underneath the snow cover are frequent.

TABLE 1

Mean cover and maximum height of the vegetation (\pm SE in parentheses) in the different microsite classes ($n = 20$ per microsite class).

	Mean vegetation cover (%)	Mean max. vegetation height (cm)
Deflation	6 (0.6)	5 (0.4)
Lichen heath	56 (2.7)	17 (1.4)
Dwarf shrub heath	90 (2.2)	43 (3.0)
Hummock	99 (0.4)	22 (1.5)
Willow shrub	99 (0.4)	72 (2.5)
Sedge mire	93 (1.4)	31 (2.1)

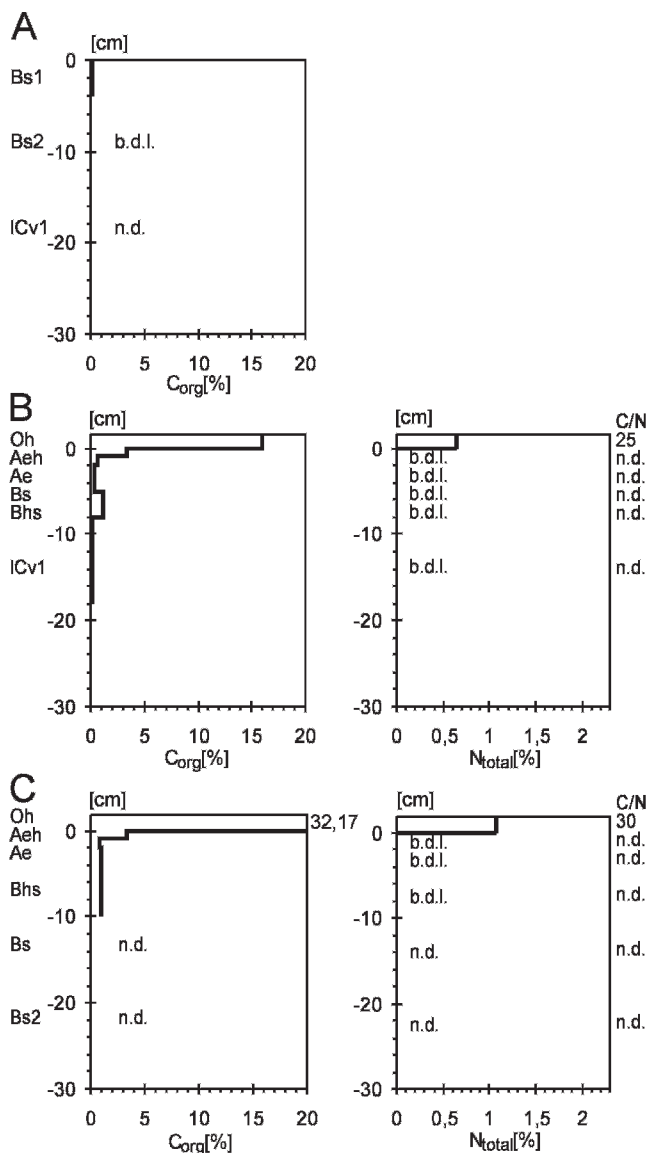


FIGURE 3A. Organic carbon and total nitrogen in representative soil profiles (b.d.l.: below detection limit, n.d.: not determined) A: deflation; B: lichen heath; C: dwarf shrub heath. No nitrogen could be detected in the deflation site profile. Nomenclature of soil horizons after the German soil classification (AG Boden, 1994).

BIRCH SAMPLING

In the present paper, the term “seedlings” refers to birches up to 50 cm tall grown from seeds. Taller young growth, sprouts from old root stocks, and hybrids (*Betula pubescens* ssp. *czerepanovii* × *Betula nana*) were excluded from the study. Hybridization becomes apparent from leaf morphology (e.g. Jonsell, 2000). Shoot length was mapped in the field for all seedlings in the study plots (total $n = 736$). Seedling density was calculated for the combined plots of each microsite class.

A subsample of seedlings was randomly chosen (5 seedlings per area for deflation, hummock, willow shrub, and sedge mire; 12 seedlings per area for lichen heath and dwarf shrub heath; plus a total of 6 seedlings from preliminary tests). All visible shoot lesions per seedling were counted and later related to the seedling’s age (to account for differences of seedling age distribution between microsite classes). Plants were excavated (total $n = 225$), and depth of the rooting systems was determined. For calculation of root/shoot ratios, leafless seedlings were dried (75 °C, 48 h) and

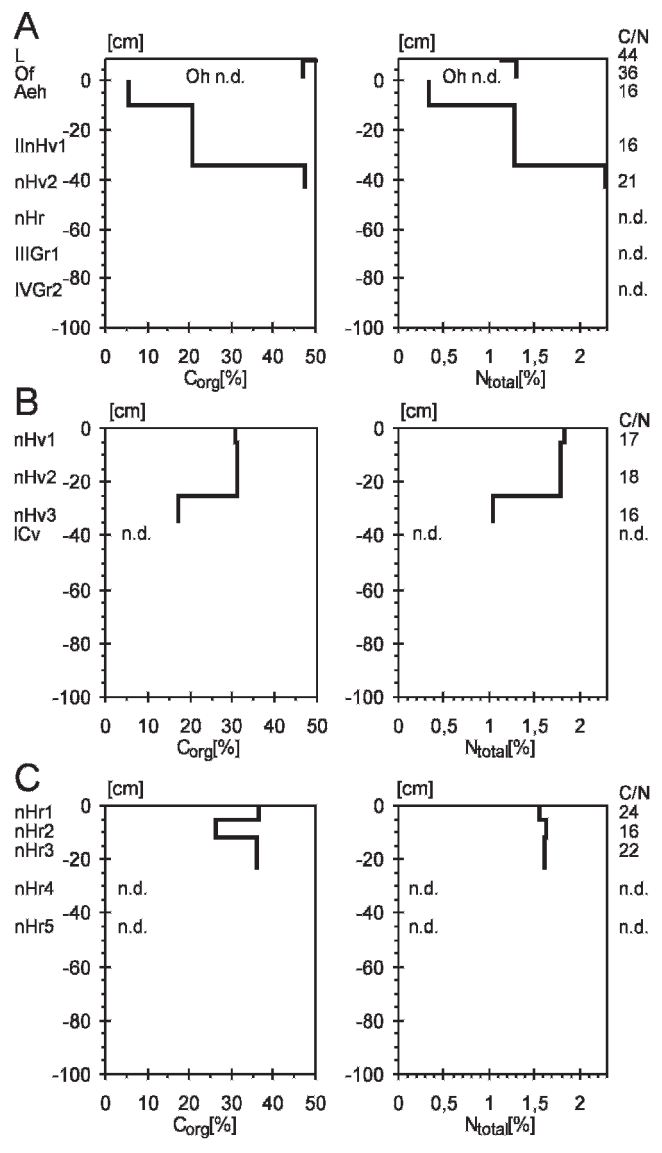


FIGURE 3B. Organic carbon and total nitrogen in representative soil profiles (b.d.l.: below detection limit, n.d.: not determined). A: hummock; B: willow shrub; C: sedge mire. Nomenclature of soil horizons after the German soil classification (AG Boden, 1994).

separated into above- and below-ground compartments (in case of adventitious root formation at the level of the uppermost root). Age of excavated plants was determined from stem discs under the stereomicroscope after staining with safranin solution and chalk (Iseli and Schweingruber, 1989). Age values are approximate due to narrow and obscure rings, frequent fungal damage, and possibly false and missing rings. Thus, correlation with climatic data is not possible.

STATISTICAL ANALYSIS

Data were compared between microsite classes with one-way ANOVA and Student-Newman-Keuls test or with Kruskal-Wallis test and Nemenyi test for unequal sample sizes when parametric assumptions were not met (Lozán and Kausch, 1998). The significance level is 0.05. Since the root/shoot ratio does not differ significantly with plant age, the complete data set is used for analysis. As seedling age influences maximum rooting depth, only data from age class 5–12 years are presented here.

TABLE 2

Soil moisture (topmost 6 cm) at the different microsite classes (total number of measurements in the respective class: ¹*n* = 500, ²*n* = 300) (b.d.l. = below detection limit).

	Soil moisture (vol.%)		
	Mean (\pm SE)	Min.	Max.
Deflation ¹	8.7 ^a (0.2)	0.5	23.6
Lichen heath ¹	12.2 ^b (0.3)	b.d.l.	66.0
Dwarf shrub heath ¹	22.1 ^c (0.5)	1.5	57.3
Hummock ²	25.2 ^c (0.7)	5.9	80.0
Willow shrub ²	65.6 ^d (0.9)	22.7	96.2
Sedge mire ²	77.4 ^d (0.6)	32.4	87.6

Results

Mean densities of birch young growth (Fig. 4) are lowest at deflation sites where seedlings grow mainly close to the surrounding heath. On lichen heath sites, young growth often occurs at disturbed patches with exposed mineral soil, which are common because of steep slopes. Quite low densities are recorded in dwarf shrub heath where seedlings occasionally grow clustered in places with comparatively sparse vegetation. In hummock fields, birches usually grow at the sides of the hummocks, while they do not occur on dry hummock tops or in the wet troughs between the hummocks. Willow shrub sites are characterized by fairly high numbers of birch seedlings and also constant occurrence over the various field plots. Very high densities can be found in sedge mires.

Median age of birch seedlings at deflation sites (17 yrs.), lichen heath (15 yrs.), and dwarf shrub heath (15 yrs.) is significantly greater than at willow shrub sites (7 yrs.) and in sedge mires (9 yrs.), with intermediate values at the hummock sites (13 yrs.) [H (5) = 40.05; *p* < 0.001]. Seedling establishment after the onset of the 1990s is especially low at the deflation sites; by contrast, none of the examined specimens from the willow shrub and sedge mire sites became established earlier than approximately 1990 (Fig. 5). At the willow shrub sites, however, birches taller than 0.5 m and presumably accordingly older than the examined seedlings could occasionally be found.

At deflation sites, root/shoot ratio of birch seedlings (Fig. 6A) is significantly higher than at all other sites (median: 2.90 g g⁻¹). Relative investment into root systems is also high at lichen heath sites (median: 1.66 g g⁻¹). There are no significant differences between the root/shoot ratios of the remaining site

classes (medians from 0.88 to 1.28 g g⁻¹), but birch seedlings at willow shrub sites show the tendency towards a very low relative root mass.

Maximum rooting depth of birch seedlings (5–12 yrs.; Fig. 6B) is on average greatest at the deflation sites, but significantly differs only from the dwarf shrub sites and sedge mires. No shallow root systems occur at the deflation sites and the willow shrub sites. By contrast, root systems in sedge mires are uniformly shallow (with frequent formation of adventitious roots). At lichen heath and especially at dwarf shrub heath sites, both shallow root systems (restricted to the topsoil rich in organic carbon) and deep reaching root systems occur. Older seedlings (data not shown) reach rooting depths of up to 50 cm at deflation sites, 43 cm in lichen heath, and 35 cm in dwarf shrub heath. Seedlings at deflation sites and also at lichen heath sites often show intense root ramification underneath boulders or along channels of old, decaying roots.

Shoot length of the birch seedlings is on average 6 cm (Fig. 6C). Only at the willow shrub sites, birch seedlings show a higher average shoot length. Some young growth larger than 0.5 m growing at the willow shrub sites was not included in this study. However, none of those birches grew higher than the canopy of the surrounding willows that obviously had been browsed.

The overall number of visible shoot lesions relative to plant age (Fig. 6D) is highest at the deflation sites, though not differing very much from numbers in lichen heath and dwarf shrub heath. Damage is low in sedge mires and also in hummock fields. At deflation sites, birches often show partly exposed roots systems with up to 30 cm of the main root laying bare. Depending on grain size at the individual deflation patches, 15% (sandy-skeletal substrate) to more than 50% (sandy substrate) of birch seedlings show this particular trait.

Discussion

Germination of birch is extremely poor at deflation sites under current conditions, as may be concluded from seedling density and age structure. One reason might be the lack of birch seeds. As these are dispersed by the wind, they may accumulate in more sheltered places (Sveinbjörnsson et al., 2002; Seppälä, 2004). Also, dryness of deflation sites enforced by the highly permeable substrate as well as frost damage and frost heave because of sparse snow cover and frequent freeze-thaw cycles are especially

TABLE 3

Soil temperatures (2.5 cm depth) at representative plots (brookside data are transferable to willow shrub and sedge mire to a limited extent).

	Deflation	Lichen heath	Dwarf shrub heath	Brookside
22.09.2002–25.08.2003				
Min. temperature (°C)	−30.1	−18.6	−4.8	−3.3
Max. temperature (°C)	30.2	19.2	19.5	21.8
Mean temperature (°C)	−0.4	−0.4	1.9	2.8
Days with mean temp. < 0 °C (n)	190	194	202	179
Days with mean temp. > 5 °C (n)	107	89	67	83
Freeze-thaw cycles (n)	66	44	30	196
Days with snow cover (n)	19	44	248	236
Snow-free from	22.02.2003	10.05.2003	12.06.2003	26.05.2003
01.06.2003–25.08.2003				
Min. temperature (°C)	2.1	1.5	0.1	0.4
Mean temperature (°C)	14.9	10.8	9.4	12.3
Mean daily temp. amplitude (°C)	8.1	4.7	4.0	6.5

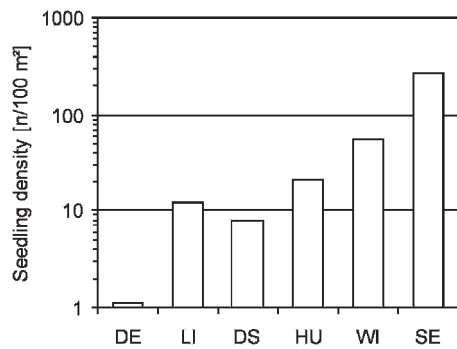


FIGURE 4. Mean seedling density in the different microsite classes across all study plots. DE = deflation, LI = lichen heath, DS = dwarf shrub heath, HU = hummock, WI = willow shrub, SE = sedge mire.

detrimental to very young seedlings with weakly developed root systems (Holtmeier et al., 2003; Forbes et al., 2005; Holtmeier and Broll, 2005; Karlsson et al., 2005).

Soil profiles clearly show that the deflation sites were formerly covered by Podzols (Holtmeier et al., 2003). The frequent occurrence of birch young growth near the edges of deflation patches as well as partly exposed roots suggest that many of the seedlings may have become established before the deflation areas reached their current extent. Hardly any birch seedlings date from after the beginning of the 1990s, which is also the time when reindeer population peaked in the study area (Helle and Kojola, 2006). The rapid increase since the mid 1970s was due to the use of off-road vehicles for herding, additional winter feeding, veterinarian care, decrease of the number of predators, and restricted slaughtering because of the Chernobyl nuclear disaster (Kashulina et al., 1997; Colpaert et al., 2003). It is possible that the deflation areas reached their present extent at the time of the population peak, since high reindeer numbers are often considered to be responsible for soil erosion on exposed topography (e.g. Kashulina et al., 1997; Broll, 2000; Löffler, 2000; Uhlig and Zink, 2006). On the other hand, a dense plant cover also hampers germination (e.g. Forbes et al., 2005). This can be seen from the occasional clustering of seedlings in small patches with sparser vegetation in heath sites. In this respect, reindeer grazing creating gaps in the field layer can be beneficial for germination, because competition is reduced, soil temperature increases, and N mineralization is enhanced (Broll, 2000; Cairns and Moen, 2004; Karlsson et al., 2005).

Occasionally extremely high birch germination in sedge mires is not followed by successful long-term establishment, although damage to shoot systems is negligible. The reason for this could be high water tables and thus a lack of oxygen in the soil, as indicated by shallow root systems of seedlings and frequently high soil moisture recordings (cf. Fitter, 1991; Jackson and Ricard, 2003).

The examined root systems show a strong response to microtopographic gradients in water and nutrient availability. Because of the excessively drained sandy substrate and the lack of organic topsoil at deflation sites, water and nutrient supply are very poor. This also holds true for plant available phosphorus, potassium, and cation exchange capacity (Holtmeier et al., 2003). Drought stress and nutrient shortage are commonly reported to cause deep reaching root systems and high root/shoot ratios (Cairns et al., 1997; Davies and Bacon, 2003; Ovaska et al., 2005), just as they are displayed by birch seedlings at the deflation sites and, to a lesser extent, at the lichen heath sites. Also, intense root branching that frequently occurs along former root channels and

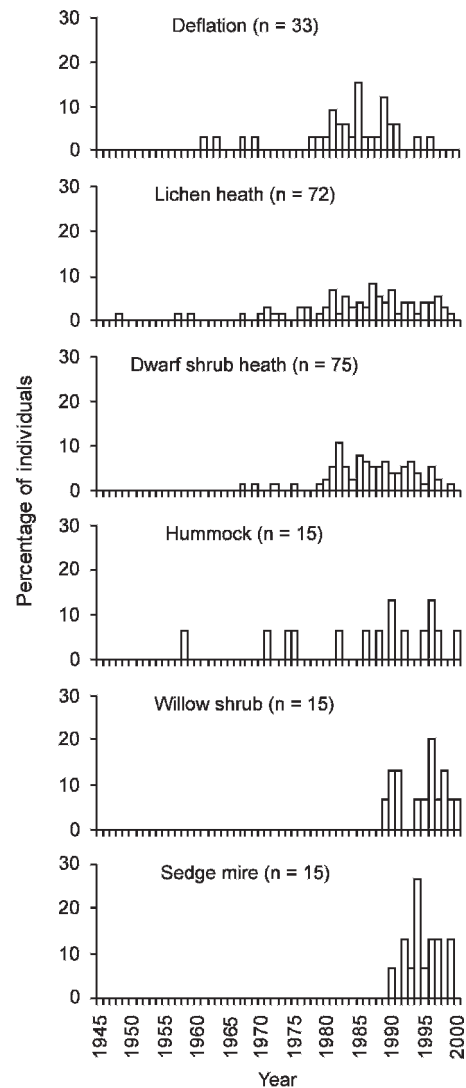


FIGURE 5. Years of birch establishment in dependence of microsite class.

underneath boulders can be explained by enhanced nutrient supply and water percolation in such places (cf. Broll, 1994). The fact that the root systems of some seedlings at the lichen heath and dwarf shrub heath sites grow exclusively in organic topsoils clearly reflects the importance of humus content for water and nutrient availability at these sites.

Reindeer grazing may enhance or slow down nutrient cycling in tundra, depending on timing and intensity of the grazing (Olofsson et al., 2004). For soils comparable to the heath site soils in this study (poor and dry sites), a reduction of carbon and nitrogen content has been shown (Broll et al., 1999) which further diminishes nutrient and water supply to seedlings. This is also how herbivory can indirectly influence root/shoot ratios in the long term. By contrast, direct grazing impacts on the root/shoot ratio soon get counterbalanced by tissue growth in order to readjust to resource availability (e.g. water, nutrients, light) (Farrar and Jones, 2003).

Seedlings at sites with good resource availability usually show small investments into the root systems (Karlsson et al., 2000; Hutchings and John, 2003). For example, lowest root/shoot ratios occur at the willow shrub sites, which generally are comparatively productive sites (Hobbie and Chapin, 1998). This can be attributed to lateral nutrient input with (melt-)water and to

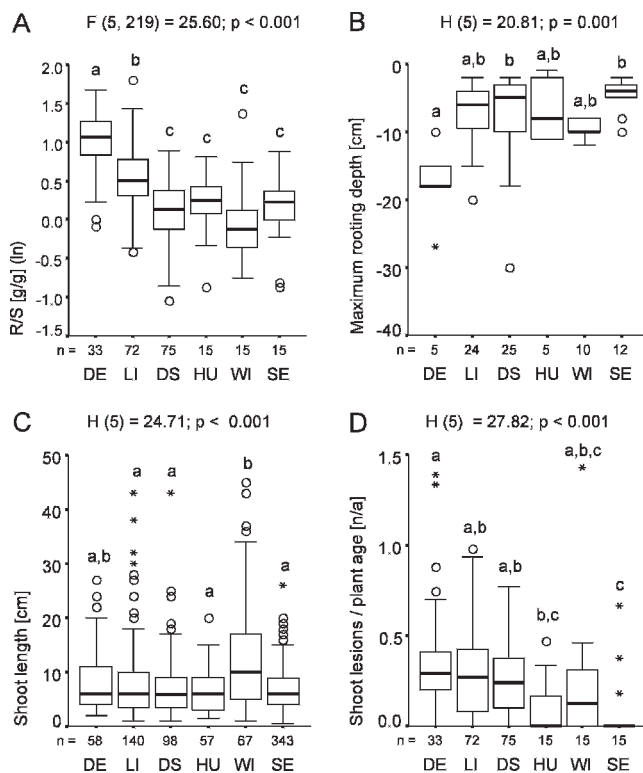


FIGURE 6. Root/shoot ratio (R/S) (A); maximum rooting depth in age class 5–12 years (B); shoot length (C); and number of shoot lesions in relation to plant age (D) in dependence of microsite class. Circles = outliers, asterisks = extreme cases. DE = deflation, LI = lichen heath, DS = dwarf shrub heath, HU = hummock, WI = willow shrub, SE = sedge mire.

relatively high soil temperatures under a thick snow cover and thus ongoing N mineralization during winter (Karlsson et al., 2005).

In contrast to the root system characteristics, average shoot size does not correspond to any gradient in microclimate or resource availability. The only microsite class displaying relatively larger birch seedlings (willow shrub) mainly differs from all the other microsite classes regarding vegetation structure (comparatively dense and high). A possible explanation for the enhanced shoot size might be more effective shelter from herbivory (cf. Cairns and Moen, 2004). A connection between intensive reindeer grazing and trampling on the one hand and low birch seedling densities and growth rates on the other hand has been documented by several studies (e.g. Eilertsen et al., 2002; den Herder and Niemelä, 2003; Lempa et al., 2005). A comparable shelter effect of willow coppice on birch seedlings at the treeline is reported from Norwegian sheep pastures (Löffler et al., 2004). Another reason for larger shoot systems at the willow shrub sites might be stronger competition for light, which usually triggers higher shoot growth (Farrar and Jones, 2003).

The slight decrease of shoot lesions in relation to plant age from deflation sites across lichen heath to dwarf shrub heath might be at least partly attributed to the microclimatic gradient (e.g. less abrasion by sand and ice particles, Holtmeier, 2003, 2005; Holtmeier et al., 2004). However, microclimatic differences cannot explain the large discrepancy in the amount of damage between those sites that are all similarly sheltered by a thick snow cover in winter (dwarf shrub heath, hummock fields, willow shrub sites, and sedge mires). Accessibility to herbivores is likely to be at least one reason (cf. Cairns and Moen, 2004). During the summer, reindeer usually avoid areas in wind-sheltered depressions because

of molestation by insects (Helle, 2001). On the other hand, willow shrub foliage is an attractive food source for reindeer in low-productivity dwarf shrub heath (den Herder et al., 2004). In willow shrub sites, birch seedlings are therefore more exposed to browsing than in sedge mires or hummock fields, while they are still more protected from browsing than in dwarf shrub heath, for example, because of the denser vegetation structure. Also, other herbivores such as snow hare (*Lepus timidus*) and willow grouse (*Lagopus lagopus*) might affect birch seedlings.

Climate warming is generally supposed to be very pronounced in Northern Europe (IPCC, 2007). In principle, this is expected to cause a treeline rise (e.g. Callaghan et al., 2002; Holtmeier, 2003; Holtmeier and Broll, 2005). However, the influence of local site conditions will have a modifying effect on establishment and survival of birch seedlings as it is also evident in the present study. For Northern Europe, an increase of both precipitation and evapotranspiration is expected in the future, and snow depth and duration of the snow season might be reduced due to higher temperatures (IPCC, 2007). The resulting changes in soil moisture and snow distribution will determine the suitability of microsites for treeline advance. For example, in case of drier conditions, birch treeline advance is most likely in concave topography providing sufficient soil moisture and winter snowpack (cf. Kullman, 2004, 2005; Holtmeier and Broll, 2005). However, in case of higher soil moisture, conditions for birch regeneration might deteriorate at these sites due to waterlogging. At the same time, moister conditions (e.g. because of more frequent rainfall events) might improve regeneration on permeable substrates covered by only thin organic topsoils, i.e. at sites suboptimally supplied with water for seedling establishment at present (cf. Holtmeier and Broll, 2005). Nevertheless, increased precipitation cannot compensate for the loss of nutrients and water storage capacity caused by removal of the topsoil on convex topography. Thus, birch will invade such sites with great delay.

Another important factor regarding treeline development is a possible future increase in mass outbreaks of the autumnal moth *Epirrita autumnata*. In warmer winters, more eggs will survive (Virtanen et al., 1998; Neuvonen et al., 1999). Additionally, the winter moth *Operophtera brumata* has recently defoliated birch forests in northern Utsjoki for the first time. Mass outbreaks destroying forest stands in junction with high reindeer grazing pressure preventing birch regeneration have caused a treeline decline before (Kallio and Lehtonen, 1975; Lehtonen and Heikkinen, 1995). This is witnessed in the actual study area by numerous old remains of birch root stocks above the present treeline (Holtmeier and Broll, 2006). The same could easily happen again in the future. So, even though climatic change might improve the conditions for regeneration at some of the microsites in the treeline ecotone, successful seed-based regeneration of birch in this study area is likely to depend on future reindeer pasture management.

Conclusions

Locally varying environmental conditions strongly affect below-ground characteristics of birch young growth. Root systems clearly reflect differences in soil moisture and nutrient supply along a microtopographical gradient. Shoot system characteristics, however, though partly showing an influence of microclimate, seem to be strongly affected by herbivory. Consequently, a positive effect of rising temperatures on the future treeline position in the study area might be overridden by the impact of intensive reindeer grazing. This has to be taken into account if the treeline is considered as an indicator for climate change.

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References Cited

- AG Boden, 1994: *Bodenkundliche Kartieranleitung*. Hannover: Schweizerbart'sche Verlagsbuchhandlung, 392 pp.
- Autio, J., and Heikkinen, O., 2002: The climate of northern Finland. *Fennia*, 180: 61–66.
- Broll, G., 1994: Influence of the soil mosaic on biodiversity at heath sites in the European subarctic. In International Society of Soil Science. (ed.), *15th World Congress of Soil Science, Acapulco, Mexico, July 1994. Transactions Vol. 4a: Commission III: Symposia*, 220–231.
- Broll, G., 2000: Influence of overgrazing by reindeer on soil organic matter and soil microclimate of well-drained soils in the Finnish subarctic. In Lal, R. (ed.), *Global climate change and cold regions ecosystems. Advances in soil science*. Boca Raton: CRC/Lewis Publishers, 163–172.
- Broll, G., Ohtonen, R., and Stark, S., 1999: Effects of reindeer grazing on soil properties in Finnish Lapland. In Turunen, M., Hukkinen, J., Heal, O. W., Saelthun, N. R., and Holten, J. I. (eds.), *A terrestrial transect for Scandinavian/northern Europe: proceedings of the international SCANTRAN Conference, 19–23.3.1998, Rovaniemi, Finland. Ecosystems Research Report 31*. Brussels: European Commission, 56.
- Broll, G., Holtmeier, F.-K., Anschlag, K., Brauckmann, H.-J., Wald, S., and Drees, B., 2007: Landscape mosaic in the treeline ecotone on Mt Rodjanoaivi, subarctic Finland. *Fennia*, 185: 89–105.
- Cairns, D. M., and Moen, J., 2004: Herbivory influences tree lines. *Journal of Ecology*, 92: 1019–1024.
- Cairns, M. A., Brown, S., Helmer, E. H., and Baumgardner, G. A., 1997: Root biomass allocation in the world's upland forests. *Oecologia*, 111: 1–11.
- Callaghan, T. V., Werkman, B. R., and Crawford, R. M. M., 2002: The tundra-taiga interface and its dynamics: concepts and applications. *Ambio Special Report*, 12: 6–14.
- Colpaert, A., Kumpula, J., and Nieminen, M., 2003: Reindeer pasture biomass assessment using satellite remote sensing. *Arctic*, 56: 147–158.
- Davies, W. J., and Bacon, M. A., 2003: Adaptation of roots to drought. In de Kroon, H., and Visser, J. W. (eds.), *Root ecology*. Berlin: Springer, 173–192.
- den Herder, M., and Niemelä, P., 2003: Effects of reindeer on the re-establishment of *Betula pubescens* subsp. *czerepanovii* and *Salix phylicifolia* in a subarctic meadow. *Rangifer*, 23: 3–12.
- den Herder, M., Virtanen, R., and Roininen, H., 2004: Effects of reindeer browsing on tundra willow and its associated insect herbivores. *Journal of Applied Ecology*, 41: 870–879.
- Eilertsen, S. M., Schjelderup, U., and Mathiesen, S. D., 2002: Early season grazing effects on birch, grass, herbs and plant litter in coastal meadows used by reindeer: a short-term case study. *Rangifer*, 22: 123–131.
- Farrar, J. F., and Jones, D. L., 2003: The control of carbon acquisition by and growth of roots. In de Kroon, H., and Visser, J. W. (eds.), *Root ecology*. Berlin: Springer, 91–124.
- Fitter, A. H., 1991: The ecological significance of root system architecture: an economic approach. In Atkinson, D. (ed.), *Plant root growth: an ecological perspective*. London: Blackwell, 229–243.
- Forbes, B. C., Tolvanen, A., Wielgolaski, F. E., and Laine, K., 2005: Rates and processes of natural regeneration in disturbed habitats. In Wielgolaski, F. E. (ed.), *Plant ecology, herbivory, and human impact in Nordic mountain birch forests*. Berlin: Springer, 193–202.
- Geologinen Tutkimuslaitos, 1981: *General geological map of Finland. Quaternary deposits*. Helsinki, Geologinen Tutkimuslaitos (Geological Survey of Finland), 1:400.000, No. 39 + 49 Utsjoki.
- Haapasaari, M., 1988: The oligotrophic heath vegetation of northern Fennoscandia and its zonation. *Acta Botanica Fennica*, 135: 1–219.
- Helle, T., 2001: Mountain birch forests and reindeer husbandry. In Wielgolaski, F. E. (ed.), *Nordic mountain birch ecosystems*. New York: UNESCO and The Parthenon Publishing Group, 279–291.
- Helle, T., and Kojola, I., 2006: Population trends of semi-domesticated reindeer in Fennoscandia—Evaluation of explanations. In Forbes, B. C., Bølter, M., Müller-Wille, L., Hukkinen, J., Müller, F., Gunsley, N., and Konstantinov, Y. (eds.), *Reindeer management in northernmost Europe: linking practical and scientific knowledge in social-ecological systems*. Berlin: Springer, 319–339.
- Hobbie, S. E., and Chapin, F. S. III, 1998: An experimental test of limits to tree establishment in arctic tundra. *Journal of Ecology*, 86: 449–461.
- Holm, S. O., 1993: Regeneration of *Betula pendula* and *B. pubescens* coll. above and below the natural altitudinal distribution limit of *B. pendula* in south-east Norway. *Oecologia Montana*, 2: 1–6.
- Holtmeier, F.-K., 1971: Waldgrenzstudien im nördlichen Finnisch-Lappland und angrenzenden Nordnorwegen. *Reports from the Kevo Subarctic Research Station*, 8: 53–62.
- Holtmeier, F.-K., 1994: Ecological aspects of climatically-caused timberline fluctuations. Review and outlook. In Beniston, M. (ed.), *Mountain environments in changing climates*. London: Routledge, 220–233.
- Holtmeier, F.-K., 2003: *Mountain timberlines. Ecology, patchiness, and dynamics*. Dordrecht: Kluwer, 369 pp.
- Holtmeier, F.-K., 2005: Change in the timberline ecotone in northern Finnish Lapland during the last thirty years. *Reports from the Kevo Subarctic Research Station*, 23: 97–113.
- Holtmeier, F.-K., and Broll, G., 2005: Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecology and Biogeography*, 14: 395–410.
- Holtmeier, F.-K., and Broll, G., 2006: Radiocarbon-dated peat and wood remains from the Finnish subarctic: evidence of treeline and landscape history. *The Holocene*, 16: 743–751.
- Holtmeier, F.-K., and Broll, G., 2007: Treeline advance—Driving processes and adverse factors. *Landscape Online*, 1: 1–33.
- Holtmeier, F.-K., Broll, G., Müterthies, A., and Anschlag, K., 2003: Regeneration of trees in the treeline ecotone: northern Finnish Lapland. *Fennia*, 181: 103–128.
- Holtmeier, F.-K., Broll, G., and Anschlag, K., 2004: Winderosion und ihre Folgen im Waldgrenzbereich und in der alpinen Stufe einiger nordfinnischer Fjelle. *Geoöko*, 25: 203–224.
- Hutchings, M. J., and John, E. A., 2003: Distribution of roots in soil, and root foraging activity. In de Kroon, H., and Visser, J. W. (eds.), *Root ecology*. Berlin: Springer, 33–60.
- IPCC, 2007: *Climate Change 2007: the physical basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press, 996 pp.
- Iseli, M., and Schweingruber, F. H., 1989: Sichtbarmachen von Jahrringen für dendrochronologische Untersuchungen. *Dendrochronologia*, 7: 145–157.
- Jackson, M. B., and Ricard, B., 2003: Physiology, biochemistry and molecular biology of plant root systems subjected to flooding of the soil. In de Kroon, H., and Visser, J. W. (eds.), *Root ecology*. Berlin: Springer, 193–213.

- Jonsell, B., 2000: *Flora Nordica Vol. 1*. Stockholm: The Bergius Foundation, 368 pp.
- Kallio, P., and Lehtonen, J., 1975: On the ecocatastrophy of birch forests caused by *Oporinia autumnata* (Bkh.) and the problem of reforestation. In Wielgolaski, F. E. (ed.), *Fennoscandian tundra ecosystems. Part 2: animals and system analysis*. Berlin: Springer, 174–180.
- Karlsson, P. S., and Nordell, K. O., 1996: Effects of soil temperature on the nitrogen economy and growth of mountain birch seedlings near its presumed low temperature distribution limit. *Ecoscience*, 3: 183–189.
- Karlsson, P. S., Schleicher, L. F., and Weih, M., 2000: Seedling growth characteristics in three birches originating from different environments. *Ecoscience*, 7: 80–85.
- Karlsson, P. S., Weih, M., and Borg, C., 2005: Mountain birch growth in relation to climate and herbivores. In Wielgolaski, F. E. (ed.), *Plant ecology, herbivory, and human impact in Nordic mountain birch forests*. Berlin: Springer, 71–86.
- Kashulina, G., Reimann, C., Finne, T. E., Halleraker, J. H., Åyräs, M., and Chekushin, V. A., 1997: The state of the ecosystems in the central Barents region: scale, factors and mechanism of disturbance. *The Science of the Total Environment*, 205: 203–225.
- Körner, C., 1998: Worldwide positions of alpine treelines and their causes. In Beniston, M., and Innes, J. L. (eds.), *The impacts of climate variability on forests*. Berlin: Springer, 221–229.
- Kullman, L., 1984: Transplantation experiments with saplings of *Betula pubescens* ssp. *tortuosa* near the tree-limit in central Sweden. *Holarctic Ecology*, 7: 289–293.
- Kullman, L., 2002: Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology*, 90: 68–77.
- Kullman, L., 2003: Recent reversal of neoglacial climate cooling trend in the Swedish Scandes as evidenced by mountain birch tree-limit rise. *Global and Planetary Change*, 36: 77–88.
- Kullman, L., 2004: Tree-limit landscape evolution at the southern fringe of the Swedish Scandes (Dalarna province)—Holocene and 20th century. *Fennia*, 182: 73–94.
- Kullman, L., 2005: Wind-conditioned 20th century decline of birch treeline vegetation in the Swedish Scandes. *Arctic*, 58: 286–294.
- Laitakari, E., 1935: The root system of birch (*Betula verrucosa* and *odorata*). *Acta Forestalia Fennica*, 41: 1–216.
- Lehtonen, J., and Heikkinen, R. K., 1995: On the recovery of mountain birch after *Epirrita* damage in Finnish Lapland, with a particular emphasis on reindeer grazing. *Ecoscience*, 2: 349–356.
- Lempa, K., Neuvonen, S., and Tømmervik, H., 2005: Effects of reindeer grazing on pastures in a mountain birch ecosystem. In Wielgolaski, F. E. (ed.), *Plant ecology, herbivory, and human impact in Nordic mountain birch forests*. Berlin: Springer, 157–164.
- Löffler, J., 2000: High mountain ecosystems and landscape degradation in northern Norway. *Mountain Research and Development*, 20: 356–363.
- Löffler, J., Lundberg, A., Rössler, O., Bräuning, A., Jung, G., Pape, R., and Wundram, D., 2004: The alpine treeline under changing land use and changing climate: approach and preliminary results from continental Norway. *Norsk Geografisk Tidsskrift*, 58: 183–193.
- Lozán, J. L., and Kausch, H., 1998: *Angewandte Statistik für Naturwissenschaftler*. Berlin: Parey, 287 pp.
- Neuvonen, S., Niemelä, P., and Virtanen, T., 1999: Climatic change and insect outbreaks in boreal forests: the role of winter temperatures. *Ecological Bulletins*, 47: 63–67.
- Oksanen, L., and Virtanen, R., 1995: Topographic, altitudinal and regional patterns in continental and suboceanic heath vegetation of northern Fennoscandia. *Acta Botanica Fennica*, 153: 1–80.
- Oksanen, L., Moen, J., and Helle, T., 1995: Timberline patterns in northernmost Fennoscandia. Relative importance of climate and grazing. *Acta Botanica Fennica*, 153: 93–105.
- Olofsson, J., Stark, S., and Oksanen, L., 2004: Reindeer influence on ecosystem processes in the tundra. *Oikos*, 105: 386–396.
- Ovaska, J., Nilsen, J., Wielgolaski, F. E., Kauhanen, H., Partanen, R., Neuvonen, S., Kapari, L., Skre, O., and Laine, K., 2005: Phenology and performance of mountain birch provenances in transplant gardens: latitudinal, altitudinal and oceanicity-continentiality gradients. In Wielgolaski, F. E. (ed.), *Plant ecology, herbivory, and human impact in Nordic mountain birch forests*. Berlin: Springer, 99–115.
- Seppä, H., 1996: Post-glacial dynamics of vegetation and tree-lines in the far north of Fennoscandia. *Fennia*, 174: 1–96.
- Seppälä, M., 2004: *Wind as a geomorphic agent in cold climates*. Cambridge: Cambridge University Press, 358 pp.
- Smith, W. K., Germino, M. J., Hancock, T. E., and Johnson, D. M., 2003: Another perspective on altitudinal limits of alpine timberlines. *Tree Physiology*, 23: 1101–1112.
- Solberg, B., Tømmervik, H., Thannheiser, D., and Neuvonen, S., 2005: Economic limits and possibilities for sustainable utilization of northern birch forests. In Wielgolaski, F. E. (ed.), *Plant ecology, herbivory, and human impact in Nordic mountain birch forests*. Berlin: Springer, 219–233.
- Sonesson, M., and Hoogesteger, J., 1983: Recent tree-line dynamics (*Betula pubescens* Ehrh. ssp. *tortuosa* [Ledeb.] Nyman) in northern Sweden. *Collection Nordicana*, 47: 47–54.
- Sveinbjörnsson, B., 1987: Biomass proportioning as related to plant size in juvenile mountain birch near Abisko, Swedish Lapland. *Reports from the Kevo Subarctic Research Station*, 20: 1–8.
- Sveinbjörnsson, B., 2000: North American and European tree-lines: external forces and internal processes controlling position. *Ambio*, 29: 388–395.
- Sveinbjörnsson, B., Hofgaard, A., and Lloyd, A., 2002: Natural causes of the tundra-taiga boundary. *Ambio Special Report*, 12: 23–29.
- Uhlig, C., and Zink, A., 2006: Changes in organic horizon soil properties due to reindeer herding and changing management. In Forbes, B. C., Bølter, M., Müller-Wille, L., Hukkinen, J., Müller, F., Gunsley, N., and Konstantinov, Y. (eds.), *Reindeer management in northernmost Europe: linking practical and scientific knowledge in social-ecological systems*. Berlin: Springer, 245–264.
- Virtanen, T., Neuvonen, S., and Nikula, A., 1998: Modelling topoclimatic patterns of egg mortality of *Epirrita autumnata* (Lepidoptera: Geometridae) with a geographical information system: predictions for current climate and warmer climate scenarios. *Journal of Applied Ecology*, 35: 311–322.
- Weih, M., 1998: Seasonality of nutrient availability in soils of subarctic mountain birch woodlands, Swedish Lapland. *Arctic and Alpine Research*, 30: 19–25.
- Weih, M., and Karlsson, P. S., 1997: Growth and nitrogen utilization in seedlings of mountain birch (*Betula pubescens* ssp. *tortuosa*) as related to plant nitrogen status and temperature: a two-year study. *Ecoscience*, 4: 365–373.
- Weih, M., and Karlsson, P. S., 1999: The nitrogen economy of mountain birch seedlings: implications for winter survival. *Journal of Ecology*, 87: 211–219.
- Weih, M., and Karlsson, P. S., 2002: Low winter soil temperature affects summertime nutrient uptake capacity and growth rate of mountain birch seedlings in the subarctic, Swedish Lapland. *Arctic, Antarctic, and Alpine Research*, 34: 434–439.
- Wielgolaski, F. E., 1997: Fennoscandian tundra. In Wielgolaski, F. E. (ed.), *Polar and alpine tundra*. Amsterdam: Elsevier, 27–83.

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