# Regeneration of trees in the treeline ecotone: northern Finnish Lapland

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The objective of our research was to find out if forest will invade the treeless areas in the present treeline ecotone in northern Finnish Lapland and which factors might impede forest advance. The field studies were carried out on Ailakkavaara near Kilpisjärvi, in the Pallastunturi area, and in northern Utsjoki (Rodjanoaivi, Koahppeloaivi-Staloskaidi, Jesnalvaara). In the Kilpisjärvi area and in northern Utsjoki only mountain birch is represented in the treeline ecotone, except for Jesnalvaara, where pine also occurs. In the Pallastunturi area, mountain birch, pine and spruce are represented in the treeline ecotone up to the treeline. In all study areas, a mosaic of widely scattered trees, tree groves and almost treeless subarctic dwarf shrub-lichen heath characterize the treeline ecotone. This mosaic is closely related to the locally varying topography and its influence on site conditions. In all the places, adverse physical and biological factors impede the forest from invading the present treeless areas within the treeline ecotone. Generally, seedlings are rare on top of wind-swept convex topography compared to better wind-protected snow-rich depressions such as little stream sides. Low or missing winter snow cover, ice particle abrasion, sand blast, and reindeer cause damage to seedlings and sparse young growth. Sandy till, typical of the ecotone on Rodjanoaivi, Koahppeloaivi and Staloskaidi (northern Utsjoki), is highly susceptible to wind erosion once the protecting plant cover has been destroyed. Thus, on the prevailing convex, wind-exposed topography, frequented by reindeer, the topsoil is eroded leaving the bare mineral soil exposed. Due to the sandy texture and lack of organic matter these sites drain rapidly. Drought and poor nutrient supply are most adverse to seedling establishment. In the other study areas (Ailakkavaara, Pallastunturi and also Jesnalvaara in northern Utsjoki) wind erosion is far less important. Seedlings are more frequent in wind-sheltered, snow-rich and moist shallow valleys and depressions. Altogether, our studies do not support the optimistic forecasts of a rapid advance of the forest to greater elevation. Even with warmer conditions the adverse effects of severe microclimate, drought and reindeer would override in spite of decades of slightly raised temperatures.

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## Introduction

In Finnish Lapland, the upper treeline occurs as an altitudinal limit declining from about 500–600 m on the southern fjells to about 300–350 m on the northernmost mountains. The forests have been influenced more or less by the Laplanders throughout history (fire wood, construction wood, reindeer husbandry). Thus, there are no longer real pristine forests, not even in the most remote areas (Holtmeier 1974; Haapasaari 1988).

Usually, treeline appears as a more or less wide transitional zone extending from the closed forest to the uppermost usually crippled trees. In the following, this transitional zone is called treeline ecotone (for terminology of treeline and related phenomena see Holtmeier 1993, 2000, 2003). We desist from considering the minimum height of two meters as criterion of a "tree", because even the most advanced stunted individuals of the tree species represented in the ecotone may grow taller and become a seed source in case of improving environment.

In the northern part of Finnish Lapland, mountain birch *(Betula pubescens* ssp. *czerepanovii)* forms the so-called Subarctic birch zone (Kallio et al. 1969) or upper oroboreal zone (Ahti et al. 1968; Haapasaari 1988). Birch is the only tree species represented in the treeline ecotone, while on the fells in the southern area of Lapland also Norway spruce *(Picea abies* L.) and Scots pine *(Pinus sylvestris* L.) occur at treeline. The treeline ecotone is characterized by a mosaic of widely scattered trees, tree groves and almost treeless areas covered by subarctic dwarf shrub heath and lichens or exposed mineral soil. This mosaic is closely related to the locally varying topography.

As it became obvious from our previous studies in northern Europe and also in the European Alps and in the Rocky Mountains, response of treeline (e.g., increasing number of trees, enhanced growth, distribution pattern of arborescent and other vegetation, changing physiognomy of the trees, etc.) to changing environment depends closely on the local conditions and thus may be different even in relatively small areas. Advance of tree growth to higher elevation is mediated by seed-produced regeneration. While production of viable seeds depends mainly on the regional thermal conditions (e.g., summer temperatures, number of growing degree days; e.g., Juntunen et al. 2002), germination, seedling establishment and survival, however, are primarily controlled by site conditions (microclimate, length of the winter snow cover, soil temperature, soil moisture, nutrient supply, mycorrhiza, etc.). Thus, local topography and highly varying site conditions above the present forest limit up to the potential upper tree species limit are key factors favouring or impeding the advance of tree vegetation to present treeless sites above and within the transition zone. Moreover, the situation in the treeline ecotone varies regionally (topography, soils) and in dependence from the tree species (pine, spruce, mountain birch) represented in the ecotone.

The objective of our studies in Finnish Lapland was to find out why many areas within the ecotone are treeless or almost devoid of arboreous vegetation and which factors have prevented and are impeding the establishment of trees in these open patches. The study areas were selected to look for differences in regeneration and spatial dynamics in the treeline ecotone, caused, for example, by different microtopography and substrate. Substrate is glacial till of different thickness. The study sites, in particular the microsite patterns, are considered to be representative of the treeline ecotone in northern Finnish Lapland. The study areas are easily accessible, and the areas in northern Utsjoki and Pallastunturi were familiar to us from previous studies.

## Location and general characteristics of the study areas

The field studies (1996–2002) were carried out in northern Utsjoki (Jesnalvaara, Koahppeloaivi, Staloskaidi and Rodjanoaivi), in the Pallastunturi area, and on Ailakkavaara about eight kilometers southeast of Kilpisjärvi (Fig. 1). The location of the transects and main sampling sites is shown by maps of the different study areas in the Results

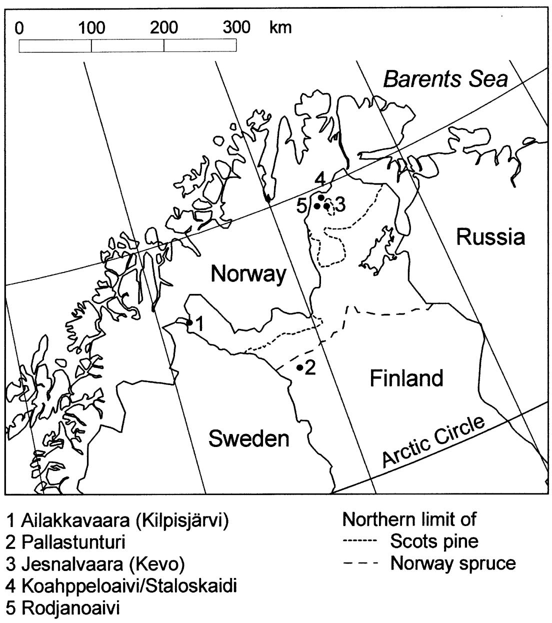



Fig. 1. Location of the study sites and position of the northern limits of Scots pine and Norway spruce (according to Juntunen et al. 2002).

chapter. Along with the photos the maps also illustrate the topographical situation.

Jesnalvaara (330 m), a north-south oriented mountain, is located about two kilometers northwest of the Kevo Subarctic Research Institute. Koahppeloaivi (420 m) is the northernmost top of a north-south oriented fell massif located between the Koahppela-Šavdšejohka (West), a tributary of the Tenojoki, and the Tenojoki itself (East). Staloskaidi is an approximately southwest-northeast oriented spur (about 240–280 m) located about 2.5 kilometers southeast of Koahppeloaivi on the east slope of the fell massif. Field work was conducted on the northeast-facing slope of the mountain. Rodjanoaivi, about 30 kilometers southwest of Koahppeloaivi rises up to 500 m. Our studies were focused on the northwest-exposed slope.

Pallastunturi is the southern part of a 50 km long mountain range running from north to south through the Pallas-Ounastunturi National Park. The fell tops rise over 500 m above the surrounding area (Palkaskero 712 m, Taivaskero 807 m, Laukukero 750 m). In contrast to the northern study areas, Pallastunturi is located within the boreal coniferous forest. Our studies were conducted in the southern part of the Pallastunturi area south of the northern limit of Norway spruce (cf. Fig. 1).

Ailakkavaara (910 m) is a southeast-northwest oriented mountain. The study area is located in the western part of Ailakkavaara on a west-facing slope. The slope is dissected by two shallow east-west trending valleys alternating with gently sculptured convex slope topography. The valley sides are comparatively steep and rocky.

The study sites on Rodjanoaivi, Koahppeloaivi and Staloskaidi are covered by two to three meters thick sandy till. Locally, mainly on Rodjanoaivi and Koahppeloaivi, small bedrock outcrops project through the till. At Jesnalvaara, till is eroded for the most part, and crystalline bedrock (granodiorite) is exposed. At Pallastunturi and Ailakkavaara, soils developed on the weathered bedrock (granodiorite on Ailakkavaara, amphibolite on Pallastunturi) or on very thin remains of basal till. In contrast to the Utsjoki area, the bedrock around Kilpisjärvi is mostly rich in base cations and weathers easily (Mikkola & Sepponen 1986).

The climate in northern Utsjoki, and also in the Pallastunturi area, is continental compared to Ailakkavaara (Seppälä & Rastas 1980; Oksanen & Virtanen 1995). Since long-term recordings of climatic parameters are not available from the very study areas, the data of the nearest meteorological stations are presented (Fig. 2). Snow cover, which is of great importance to site conditions and seedling establishment, varies widely in dependence on local topography. Commonly, wind-exposed topography may temporarily be snow-free in winter, while big snow masses pile up at wind-sheltered sites (Holtmeier 1971; 1974; Clark et al. 1985; Seppälä 1993). Rapidly changing weather conditions are typical of northern Lapland (Holtmeier 1974). Cold spells (sudden drop of the mean temperature below 5 °C) are very common, particularly in May/June and August/September, while they do not occur in July. Also, freeze-thaw cycles frequently occur in spring and fall.

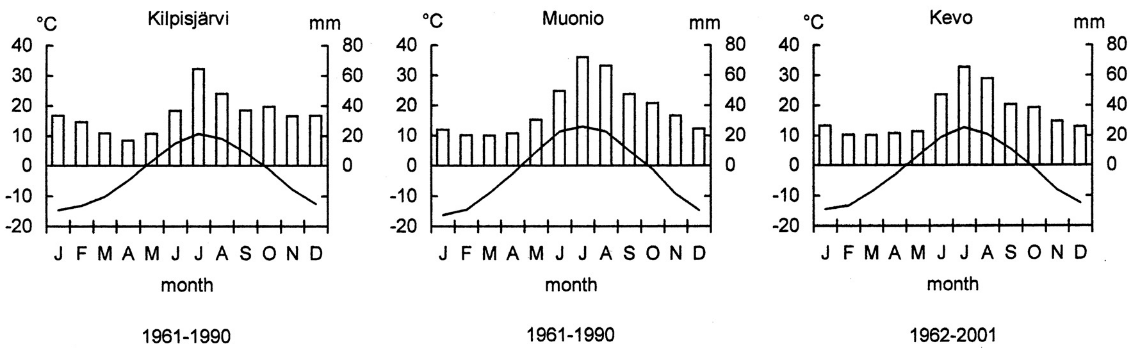



Fig. 2. Mean monthly temperature and precipitation for Kilpisjärvi, Muonio and Kevo. Kilpisjärvi represents Ailakkavaara, Muonio stands for Pallastunturi and Kevo for the northern Utsjoki area (Jesnalvaara, Koahppeloaivi/Staloskaidi and Rodjanoaivi). Data: Finnish Meteorological Institute.

The thermal trend in northern Finland has been negative since the middle of the previous century (Koutaniemi 1990). The annual mean temperature decreased by about 1 °C (up to 2 °C in winter). Springtime temperatures, however, rose by 0.5 °C over the same period (Heino 1994). The annual and monthly mean temperatures during the last decade at Kevo do not reflect any continuous positive trend. The early 1990s were a little warmer than the 1980s (annual mean temperature and monthly mean temperature of the growing season, May–September). However, the positive deviation from the long-term (1962–2001) annual and monthly means of temperature are of the same magnitude as in the early 1970s. Since about 1999, June and July show slight positive deviations from the long-term average. However, this should not be considered a trend, particularly in view of the high variability of the climate in this area, which is caused by alternating influence of maritime (Barents Sea, North Atlantic) and continental air masses (from the east and south-east; cf. Blüthgen 1952; Holtmeier, 1974).

On Rodjanoaivi, Koahppeloaivi and Staloskaidi, forest and treeline are formed by mountain birch, as is also the case on Ailakkavaara. On Jesnalvaara, which is located within an outlier of the boreal pine forest, scattered pines occur on the mountain top. Although Jesnalvaara does not rise above the climatic treeline, the stunted growth forms indicate that tree growth is close to its upper climatic limit there. On Pallastunturi, south of the northern spruce limit (cf. Fig. 1), mountain birch, pine and spruce are represented in the treeline ecotone. Thus, Pallastunturi was the only area where we could study regeneration and distribution pattern of seedlings and young growth of spruce. In this area, and also on Ailakkavaara, the forest limit is located at 500–600 m, while solitary, stunted trees are growing even at higher elevation. On the northern fells in Utsjoki, closed forests end at 250–300 m, while the uppermost, crippled trees and tree clumps occur at about 350–380 m. All study areas are more or less intensively grazed by reindeer.

## Methods

On all study sites we studied the distribution pattern of seedlings in relation to topography, mapping microsite characteristics and seedling density. The results are presented by means of small schematic transects. Moreover, seedlings were mapped along six to ten meters wide altitudinal transects (Pallastunturi, Rodjanoaivi). Visible damage was noted. In the present paper, the term "seedling" includes small trees up to forty years old and not higher than 50 cm. Seedlings of mountain birch were mapped and sampled when in leaf, because they can hardly be identified after having lost their foliage in fall and then may easily be confused with dwarf birch. Germinants were not included in our studies as search would have consumed too much time. Also "pseudo-seedlings", i.e. "seedlings", which did not originate from seeds but from root stocks and basal burls below the surface, were disregarded.

On convex, wind-eroded sites (Koahppeloaivi, Staloskaidi) seedlings were sampled for age determination. The age of seedlings and trees was determined by tree ring analysis using LINTAB (Linear measuring table) and TSAP (Time series analysis program) software package (Frank Rinn, Heidelberg, Germany). Tree ring width was measured to the nearest 0.01 mm. Indexation and age trend elimination were done by standard procedures (Cook & Kairiukstis 1992) using the exponential regression of TSAP indexation routine E (Rinn 1996). All tree ring analyses were done in the Institute of Landscape Ecology (University of Münster). A few samples of buried dead wood from Rodjanoaivi were radiocarbon-dated by the *Niedersächsisches Amt für Bodenforschung* (Hannover, Germany).

Soil profiles were described at all study sites to characterize the soil type. At the study sites on Koahppeloaivi in northern Utsjoki, soil temperatures were continuously recorded by DT3-data logger at 2.5 cm depth in the topsoil, and soil moisture (Vol. %) was measured gravimetrically (0–4 cm depth) and by TDR (Time domain reflectometry). Soil was sampled randomly (0–4 cm depth) on wind-eroded and non-eroded sites. At the same sites, soil acidity was measured in 0.01 M $CaCl_2$ using a glass electrode (Page et al. 1982). Plant-available phosphorus was determined by extraction with calciumacetatelactate (Schüller 1969) and photometric determination using the Mo blue method (Perkin Elmer 550 SE). Organic carbon and total nitrogen were measured by an elemental analyzer (Carlo Erba NA 1500) and cation exchange capacity (CEC) by extraction with unbuffered $BaCl_2$ (DIN ISO 11260). All soil analyses were done in the Institute of Landscape Ecology at Münster.

## Results

### Ailakkavaara

On Ailakkavaara (Fig. 3), the treeline ecotone ranges from about 600–700 m a.s.l. In the valleys, closed birch forest (tree height 5–6 m, mainly single stems) climbs to an elevation of about 600–640 m (Fig. 4). Solitary birches (3–4 m), however, can be found up to an altitude of 675 m. The uppermost birches (> 3 m) are growing at 700 m, close to the upper rim of the valley sides (back slopes), at block-rich sites, where fine mineral and organic matter accumulated between the blocks.

The wind-exposed slope area between the valleys is covered by low dwarf shrub heath (mainly *Empetrum hermaphroditum, Vaccinium uliginosum, Loiseleuria procumbens*, mat-like *Betula nana)*, grasses, sedges and heavily grazed lichens alternating with patches of exposed mineral soil. The uppermost birches (600–700 m) are to be found here in a few meters high step-like rocky scarps (Fig. 5), within shallow depressions and on small block fields at the bottom of the scarps, where the blocks and snow cover provide some protection from strong western winds. These birches display more or less stunted growth forms, ranging from flagged table growth (usually not higher than 1–1.5 m) to table growth and mat growth at the most wind-exposed sites. Between small blocks, where less wind-protection is given, mat growth prevails.

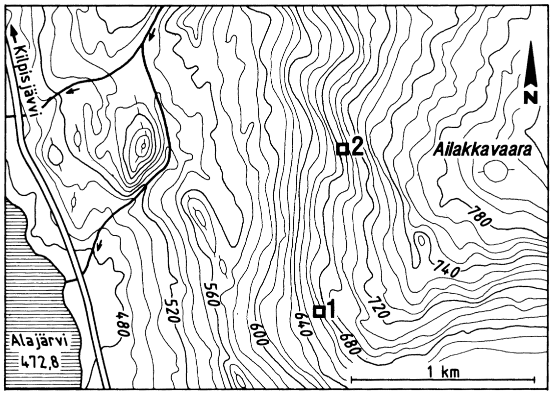



Fig. 3. Ailakkavaara study area. The open squares show the location of the figures 5 (□1) and 6 (□2). Map redrawn from Topographic Map of Finland 1:20 000, sheet Kilpisjärvi, no. 182311

The bottom of the shallow valleys is partly waterlogged. Fine mineral and organic material has accumulated, partly covering frost-shattered block debris. Humus-rich Gleysols partly with a peaty phase are common. These sites are covered by dense thickets of willows *(Salix lapponum)* and dwarf birches *(Betula nana)*. They usually grow on organic hummocks (50–60 cm) with other dwarf shrub species (such as *Empetrum hermaphroditum, Vaccinium uliginosum, Vaccinium myrtillus)*, mosses and a few lichens (mainly *Cladonia* spp.). Grass bogs occur at the wettest sites. Except for

Fig. 4. View of the west-facing slope of Ailakkavaara. Mountain birch advances to greater elevation in the shallow valleys. (Photo F-K Holtmeier, 2 August 1999).

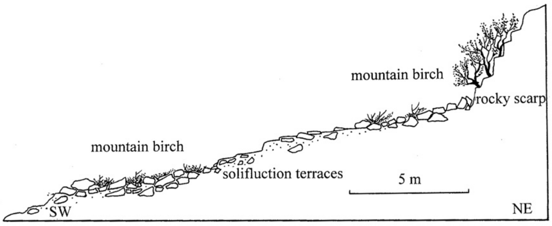



Fig. 5. Mountain birches growing in rocky scarp and between blocks (□1) on the west-facing slope of Ailakkavaara at about 675 m (schematically).

waterlogged sites, Podzols developed under the closed birch forest. On convex, sparsely vegetated topography we find Regosols. The bare mineral soil has been exposed by deflation that followed disturbance by reindeer grazing.

Birch seedlings are abundant in the valley birch forest up to about 580–600 m. At suitable sites, i. e. in low *Empetrum hermaphroditum* and *Vaccinium myrtillus* patches, eight to ten up to 30 cm high seedlings per square meter can be found, while almost no seedlings occur in taller *Betula nana* vegetation. Young growth projecting above the snow cover is usually more or less heavily damaged by reindeer.

At increased elevations, above the closed forest, seedlings are less frequent. The distribution pattern of the seedlings is closely related to microsite conditions (Fig. 6 a–d). Sites without any seedlings alternate with small patches of low to high seedling density. At the valley floor, most seedlings occur on relatively open patches close to the streams and other moist or wet sites covered by low grass and herb vegetation. The highest seedling density we found was eight seedlings on an area of 25 $m^2$. As a rule, seedlings are rooting in the thick organic layer or in fine mineral soil (Fig. 7, see also Fig. 6 b). Typically, seedlings can also be found between blocks, where organic matter and fine mineral material have accumulated, providing more favorable moisture conditions and nutrient supply (see also Fig. 6 c).

Conditions on the organic hummocks are somewhat different. On top of these hummocks, dense dwarf birch vegetation prevents any regeneration of mountain birch. However, at the base of the hummocks, usually covered by grasses and herbaceous vegetation, mountain birch seedlings occur (Fig. 6 d). On the other hand, the small furrows (troughs) between the hummocks are usually free of seedlings. On convex topography in the valleys seedlings are rare or missing.

On the wind-exposed mountain slope area between the valleys, almost no mountain birch seedlings could be found, except in wind-protected shallow depressions and block fields (see also Fig. 5). Close examination showed that some of these

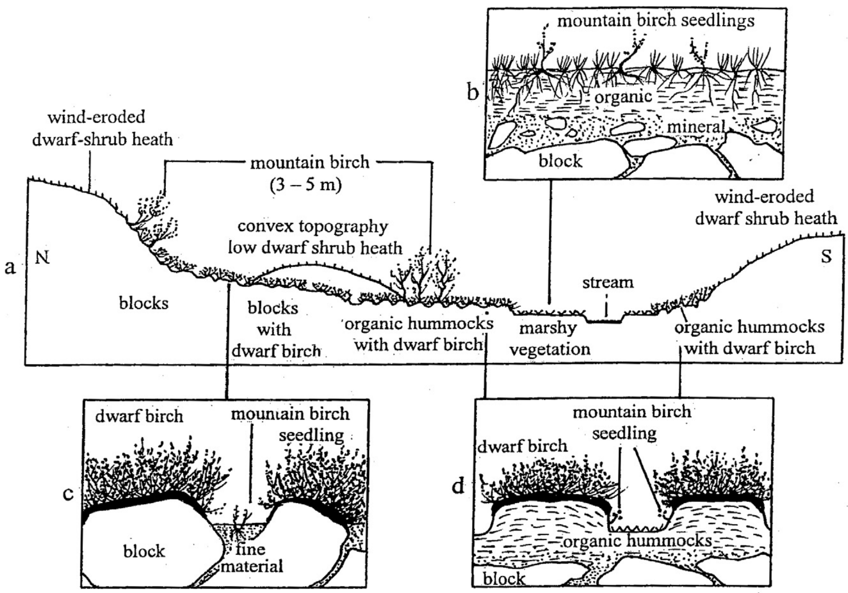



Fig. 6. Cross section (a) through a shallow, E-W-trending valley (□2) on Ailakkavaara (schematically) and distribution of mountain birch seedlings (b, c, d).

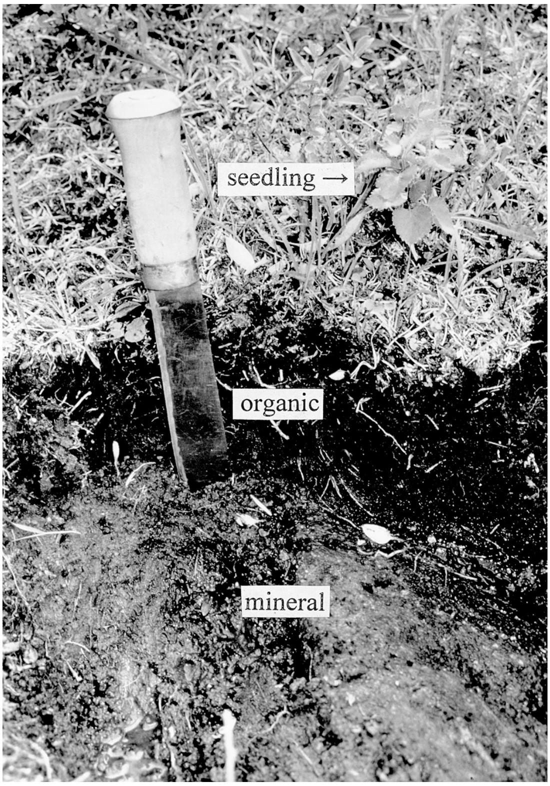



Fig. 7: Mountain-birch seedling rooting in the organic layer of a Gleysol at the stream side in a shallow valley on Ailakkavaara (for scale 30 cm long knife). (Photo F-K Holtmeier, 4 August 1999).

seedlings were basal sprouts thriving from older root stocks ("pseudo-seedlings"). Above the closed birch stands in the upper part of the valleys as well as on the mountain slope, seedlings are ten to twenty years old and up to 10 cm high. Older birch seedlings and young growth are rare. The comparatively high seedling density at the valley sites and the rare occurrence on convex slope topography can be attributed to the different soil moisture conditions, exposure to the wind, and height and duration of the snow cover. On the mountain slope and also on slightly convex topography in the valleys (cf. Fig. 4 and Fig. 6), water-holding capacity of the soil (sand and coarse material) is low. Also, snow cover in winter is low or even missing, and seedlings are exposed to strong desiccating and abrasive winds. At the same moisture conditions, temperature of the topsoil on wind-swept topography is relatively low in summer compared to more wind-protected sites. On the valley bottom, particularly close to the stream sites, and also on small alluvial flats, soil moisture is sufficient throughout the growing season. Waterlogging, on the other hand, does not obviously impede establishment of mountain birch seedlings as long as the uppermost soil is not continuously saturated.

## Pallastunturi

In the Pallastunturi study area (Fig. 8), closed forest (mountain birch, spruce, pine) ends at about 450–500 m and the treeline ecotone extends up to 700 m. The area was studied by the first author 30 years earlier (Holtmeier 1974). Thus, comparison could be made to the present situation. The uppermost limits of tree growth are stunted pines. They became established under comparatively favourable climatic conditions between the 1920s and 1940/50s (Hustich 1937, 1942, 1958; Blüthgen 1942; Holtmeier 1974; Müterthies & Stevens 1996). Spruces dating back to this period are less frequently represented. This could be due to gradual mortality. However, as was reported by Blüthgen (1942), spruce seedlings were comparatively rare even at that time. By 1969 most of these trees exhibited climatically shaped growth. Many had already died. Also, many of the younger trees still protected by the winter snow cover thirty years ago, were seriously damaged or killed when they started growing taller than the average snow depth. Some of the spruces that became established in the middle of the previous century have maintained themselves by layering (adventitious roots) and now form compact tree islands. These islands are more or less damaged by severe climatic factors (Fig. 9). None of these trees developed "normal" apical dominance growth forms.

Although all age classes are represented in the high-stemmed closed forest, seedlings were rare in this ecotone thirty years ago. Some information on increasing number of seedlings in the early 1970s is given by Tasanen et al. (1998). Since the mid-eighties, seedlings and young growth, mainly of spruce, increased considerably, while regeneration of pine is less conspicuous. However, the situation may be different in distinct areas in the Pallastunturi. Thus, on the southeast-facing slope of Suastunturi, for example, located about three kilometers north of our study area, abundant spruce and pine regeneration occurred between 1975–1985 and then almost ceased (Müterthies

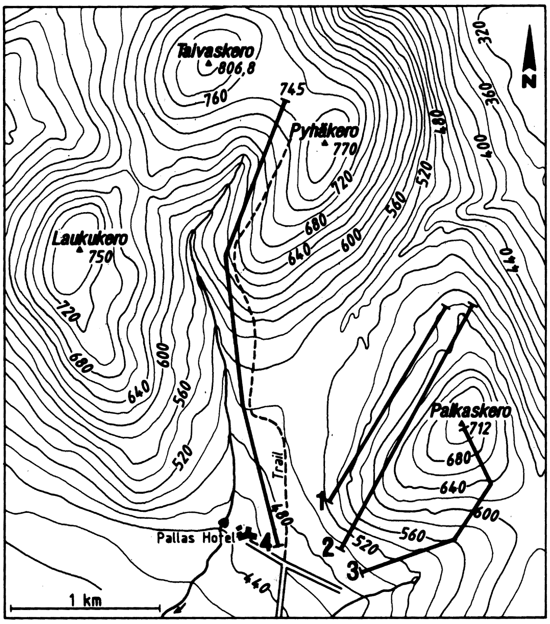



Fig. 8. Pallastunturi study area with transects. Map redrawn for Topographic Map of Finland 1: 20 000, sheet Pallastunturi, no. 274201

& Stevens 1996). On the other hand, Juntunen et al. (2002) found spruce seedlings having more than doubled from the early 1980s to 1999, what is in line with our observations.

On four transects (cf. Fig. 8) seedlings were mapped. On transects 1 and 2 (six metres wide) on the western slope of Palkaskero (712 m) seedlings of spruce prevailed (Table 1). Pine seedlings were by far less common, and birch seedlings were rare. The same was observed on transect 3 located on the southeast-facing slope of Palkaskero (Table 1). Spruce and pine seedlings younger than ten years were exceptional on these transects. The uppermost living pine seedlings (about 10 yrs) were found at 583 m, on a wind-exposed site, sparsely covered by patches of *Empetrum hermaphroditum* and *Loiseleuria procumbens* alternating with open mineral soil obviously influenced by frequent freeze-thaw events. At the same place several pines (about 60–70 cm high) that had become established during the favorable decades of the 20th century had died. A few 30–50 yrs old pines (30–40 cm high) were partly damaged by climate. On transect 3, seedlings of spruce, pine and birch are remarkably rare above 560 m. Below the upper limit of scattered birch and conifer trees (several meters high) at about 560 m, seedlings, in particular of birch, increase. In the open forest, real "carpets" of birch seedlings occur, and seedlings and young growth of spruce are very common below 520 m. However, increasing density of young growth favours snow fungi infection *(Herpotrichia juniperi, Phacidium infestans)* and thus may impede further establishment of spruce and pine.

On the six metres wide transect 4 on the west slope of Pyhäkero (Fig. 8) birch clearly prevailed compared to spruce and pine (Table 1) up to an

Fig. 9. Clonal group of Norway spruce on the southwest-facing slope of Palkaskero (Pallastunturi) at about 500 m. The terminal shoots, which are no longer protected by the winter snow cover, have lost almost all needles, and some shoots have died. (Photo F-K Holtmeier, 1 July 1970).

Table 1. Percentage of tree seedlings in transects of Pallastunturi.

| Tree species [%] | Transect 1 (Palkaskero) n=52 | Transect 2 (Palkaskero) n=84 | Transect 3 (Palkaskero) n=83 | Transect 4 up to 550 m n=37 | (Pyhäkero) 550–745 m n=15 |
|---|---|---|---|---|---|
| Norway spruce | 77 | 70 | 70 | 30 | 67 |
| Scots pine | 17 | 25 | 21 | 20 | 27 |
| Mountain birch | 6 | 5 | 9 | 50 | 6 |

elevation of 550 m, what is different from the other transects. At increasing distances from the seed bearing old trees, however, spruce seedlings were more frequent than those of pine. Birch again was almost missing. However, one birch seedling (8 cm high) was found in the saddle at an elevation of 745 m.

The uppermost, twelve to fifteen years old spruce seedling was found on the east-facing slope of Laukukero (735 m) at an elevation of 730 m, i. e. 80 m above the most advanced young pine, while birch seedlings did not occur above 550 m. Anyway, on this slope the number of conifer seedlings and young growth also declines drastically at the upper limit of the scattered, usually heavily stunted conifers (mainly pine), which date back to the favourable decades of the 20th century (1920s to 1950s). Young spruces are growing slower than young pines. Although these spruces and pines are not higher than 20–40 cm, most of them are severely damaged by climate or reindeer.

In general, birch seedlings are far less frequent in the middle and upper part of the ecotone than spruce and pine seedlings. Obviously, this also was the case when regeneration increased during the favourable decades of the previous century (cf. Blüthgen 1942). Birch seedling densities drastically decline a few meters distant from the seed source in the upper orchard-like birch stands. There, regeneration is abundant at open sites where competition by dwarf shrubs, grasses and herbaceous vegetation is reduced.

At its upper limit, birch reproduces mainly from basal sprouts, particularly after having been damaged by climatic influences or reindeer. Thus, multi-trunk birches prevail. However, it is almost impossible to calculate the very age of the initial tree. Generally, the living stems are not older than 50–80 years.

Waterlogged sites, shallow depressions and similar topography, are usually devoid of conifers and birch. Most favourable conditions for seedling establishment and young growth are on the deeper Podzols at wind-sheltered sites, protected by snow in the winter. Occasionally, however, conifer seedlings may also be found on open sites between patches of *Loiseleuria procumbens* and *Empetrum hermaphroditum*, though frost heaving may adversely affect seedling establishment.

## Northern Utsjoki

### Jesnalvaara

On Jesnalvaara (Fig. 10), the upper limit of the closed pine-birch forest is located at about 200 m. Solitary old-growth pines (six to eight meters high, up to several hundred years old) can be found up to 240 m. On the flat mountain top (330 m), scattered, low growing crippled pines and birches occur. Most of the pines – not taller than 40–80 cm – are growing between blocks and in cracks of bed rock outcrops, where they are at least partly protected from the strong winds (abrasion, desiccation) that blow the snow off from most of the mountain top in winter (Fig. 11). Brown leaders are very likely caused by a rapid drop of above-freezing temperature on a breezeless sunny day in spring-time to –10 ˚C or even –20 ˚C in the following clear and calm night (cf. Jalkanen 1993a). Also, frost drought (gradual desiccation because of transpiration at sunny conditions while water supply is inhibited by the frozen soil; cf. Holtmeier 1971; Tranquillini 1979) cannot be excluded.

Some of these pines date back to the beginning of the 20th century, a few are even older. About 90% of the pines, however, became established during the 1970s and in particular the 1980s (Holtmeier et al. 1996; Müterthies & Stevens 1996). Also, these relatively young pines display stunted growth caused by climatic injuries and

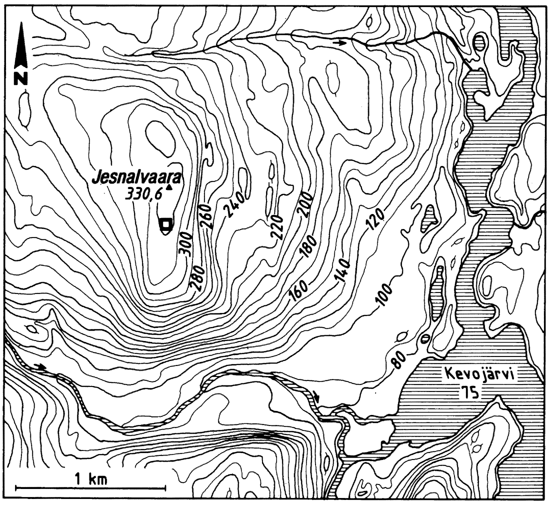



Fig. 10. Jesnalvaara study area. The open square (□) shows the location of figure 11. Map redrawn from Topographic Map of Finland 1:20 000, sheets Mielkejokskaidi, no. 391411, and Patoniva, no. 393202

reindeer. In 1997, 1998 and 1999 a few of the older stunted pines were found having produced cones. Older cones had fallen to the ground. Thus, it is not unlikely that these trees have become a seed source for regeneration of pine on the mountain top since the 1970s and may contribute to increasing pine density if favourable climatic conditions continue. Otherwise, sustainable regeneration depends on upslope seed dispersal from the tall pines at lower elevations.

Birch stands on Jesnalvaara were severely damaged by complete defoliation during the mass-outbreak of the autumnal moth *(Epirrita autumnata)* in the mid 1960s, when more than 50% of the damaged forests were completely defoliated (Holtmeier 1973, 1974; Kallio & Lehtonen 1975; Lehtonen 1987; Lehtonen & Heikkinen 1995). Most of the trees have at least partly developed from thriving basal shoots. While birches on the most wind-exposed sites only developed low growth forms, the better wind-protected trees grew taller (up to two meters height) being more or less shaped by climatic influences when they started to project above the snow surface (Fig. 12). Many tree tops have already died. Birch seedlings are abundant, except for sites covered by dense low alpine heath, but are severely damaged by reindeer grazing and trampling.

Regeneration of pine and birch on top of Jesnalvaara, which is exposed to winds from all directions, appear to be favoured by the very locally varying microtopography – thin till alternating with many crystalline outcrops – that provides wind sheltered sites and also suitable moisture conditions between the blocks and in shallow depressions (cf. Fig. 11). On the other hand, the stunted growth forms of pine and birch clearly mirror the so-called "Gipfel-Phänomen" (in the sense of Scharfetter 1938; see also Holtmeier 1974, 1989) – i. e. on comparatively low mountains climatic conditions are less favourable to tree growth than on higher mountains at the same elevation. As to seedling establishment and survival, the "Gipfel-Phänomen" is alleviated by the locally favourable microsite conditions (see above).

## Koahppeloaivi and Staloskaidi

In the Koahppeloaivi-Staloskaidi study area, the mountain slope is covered for the most part by sandy, two to three meters thick glacial till. Locally, small bedrock outcrops (granodiorite) project trough the till. Field work was done mainly on the east-facing slope (Fig. 13), which is dissected by several west-east oriented small valleys, alternating with somewhat convex slope topography (interfluves). These areas are characterized by hillocks and small closed or open depressions.

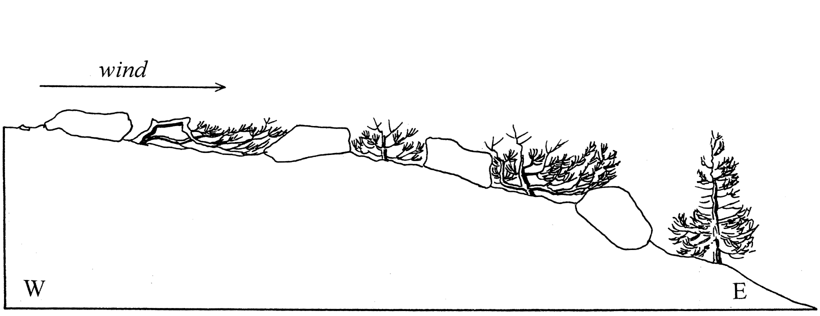



Fig. 11. Growthforms of "young" Scots pines on the top of Jesnalvaara related to decreasing (from left to right) wind exposure.

Fig. 12. Mountain birches on Jesnalvaara thriving from the remaining root stocks after the initial trees had been killed by Epirrita autumnata 1965/1966. (Photo F-K Holtmeier, 29 August 1996).

The closed birch forest (4–6 m high) ends at about 220–300 m giving way to low alpine dwarf shrub-lichen heath. The shallow valleys and other concave topography are partly waterlogged and covered by hummocks with dwarf shrubs, lichens and mosses on top. Small grass bogs occur in low gradient sections. Within the valleys, at moderately wet sites, solitary birch trees (2–4 m high) as well as birch groves are found up to 360 m elevation. Commonly, convex topography between the shallow valleys and depressions is heavily eroded by strong winds, mainly from the north and northwest (Fig. 14). The sandy substrate drains rapidly and thus is highly susceptible to deflation. This deflation makes the situation different from the Ailakkavaara, the Pallastunturi and also the Jesnalvaara study areas. On extremely windy sites, bare mineral soil (sandy-skeletal till) is exposed, and small patches of the low alpine heath (mainly *Empetrum hermaphroditum*, *Arctostaphylos alpina*, *Loiseleuria procumbens*, *Diapensia lapponica*, *Carex bigelowii* and also low mats of *Betula nana)* are left. These frequently exhibit few centimeters high wind-scarps at their windward edge (Fig. 15). Sand particles blown along the surface during storms play an important role as abrasive agents at such sites. Deflation occurs at the upper edge of the closed forest al-

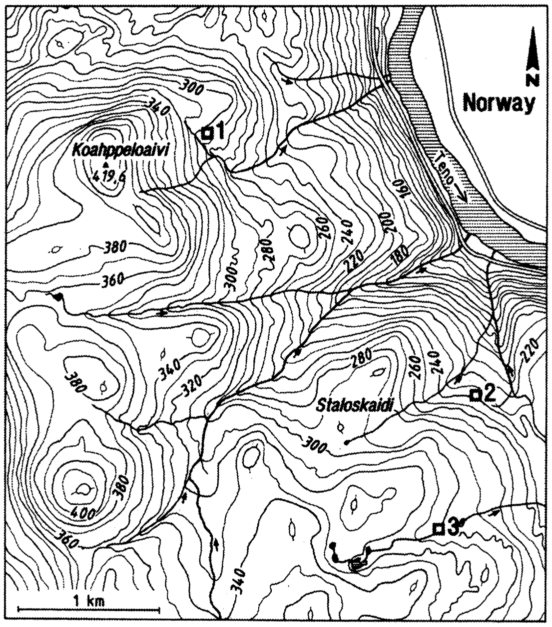



Fig. 13. Kohappeloaivi-Staloskaidi study area. The open squares show the location of the study sites. □1 and □2 – temperature recordings, soil sampling, measuring soil moisture, sampling of mountain birch seedlings for age determination (cf. Figs. 14–21). □3 – location of Fig. 23. Map redrawn from Topographic Map of Finland, sheet Koahppeloaivi, no. 392310, and Roavveoaivi, no. 391412

Fig, 14. Organic layer and top soil have been mostly eroded on this wind-exposed till-covered convex topography (327 m) on the north-eastern slope of Koahppeloaivi (cf. Fig. 15). (Photo F-K Holtmeier, 26 July 1998).

Fig. 15. Detail of figure 14. No mountain-birch seedlings occur in the eroded patches left of the wind-scarps shown here. (Photo F-K Holtmeier, 1976).

ready, also observed at Staloskaidi. Single stunted birches occur on the leeward side of little knolls and in shallow, wind-sheltered depressions.

Very likely, reindeer grazing and trampling were the factors triggering deflation after the former birch forest had been destroyed, probably by mass-outbreaks of the autumnal moth *(Epirrita autumnata)* or/and by human impact such as firewood cutting. As is obvious from the many more or less rotten root stocks, wooden remains overgrown by lichens and dwarf-shrub vegetation and also from standing dead trees, most of the present treeless areas were covered with an open birch forest at least up to 340 m. Radiocarbon-dated wood from Staloskaidi provides some evidence that the birch forest declined during the last 150 years. Occasionally, basal shoots thrive on old, partly rotten root-stocks. Their chance of surviv-

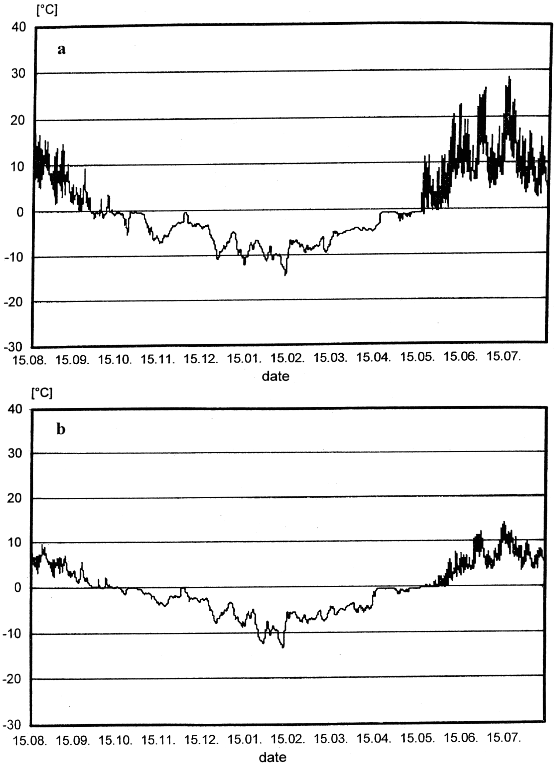



Fig. 16. Soil temperatures (1998–1999) at 2.5 cm depth at an eroded (a) and a non-eroded (b) site on Koahppeloaivi (cf. Figs. 14 and 15).

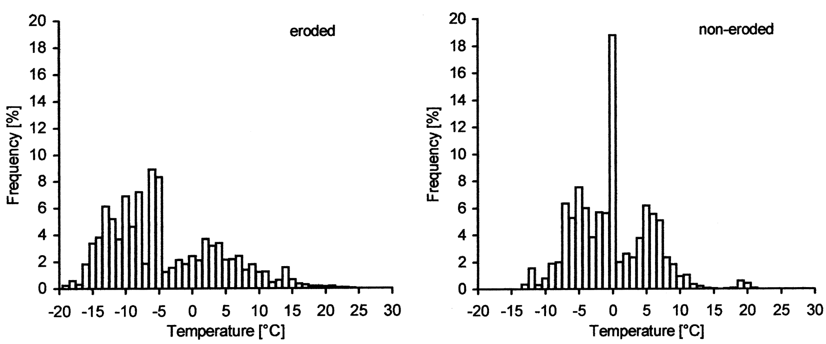
al, however, is reduced by root rot (e.g. *Armillaria borealis, Cerrena unicolor*; pers. comm. Y. Mäkinen) that may spread from the root-stock into the shoots.

From August 1998 to August 1999, soil temperatures (2.5 cm depth) were recorded on Koahppeloaivi at different sites on the knoll shown in figure 14. At one site the sandy mineral soil is exposed by wind erosion, while the other site – a few meters downwind – is not eroded and covered by a scattered mountain birch stand with dwarf shrub and lichen undergrowth (cf. Fig. 15). At both sites, soil (at 2.5 cm depth) was frozen for about two thirds of the year (Fig. 16 a and 16 b). At the eroded site, soil temperature did not rise above zero before the middle of May and ranged between 0 °C and 10 °C until early June, followed by further temperature increases. Maximum temperatures of 22 °C to almost 30 °C at 2.5 cm depth were recorded on clear days, in spite of the loss of sensible heat through turbulent mixing. Soil temperature did not drop below 5 °C from June 15 to almost the end of July. During the growing season, soil temperatures were five and more degrees centigrade on 120 days – considerably warmer than at the adjacent vegetated site (Fig. 17).

We measured soil moisture at these Koahppeloaivi plots and on comparable eroded and non-eroded plots at Staloskaidi (about 2.5 km northeast, cf. Fig. 13). At the non-eroded plots soil moisture was 5–12% (vol.) higher than at the eroded sites (Fig. 18). Because of the sandy till, plant available water depends almost completely on humus content. Organic carbon is less than 1% at the eroded plots (0–4 cm depth) and about 10% at the non-eroded plots (cf. Table 2).

Our analysis of soil samples from Koahppeloaivi, Staloskaidi and Rodjanoaivi showed distinct differences in soil acidity, cation exchange capacity, organic matter and plant-available nutrients between wind-eroded and non-eroded plots (Table 2). At the eroded site, pH ranges from 4 to 5, while it is about 3.5 at the site covered by

Fig. 17. Frequency (%) of degrees of temperature (1998–1999; 0.5 °C intervals) at 2.5 cm depth at a wind-exposed, heavily eroded site (310 m, left) with bare mineral soil and in a small birch stand (310 m, right) with low dwarf-shrub undergrowth, a few meters distant from the eroded site (see also Fig. 14).



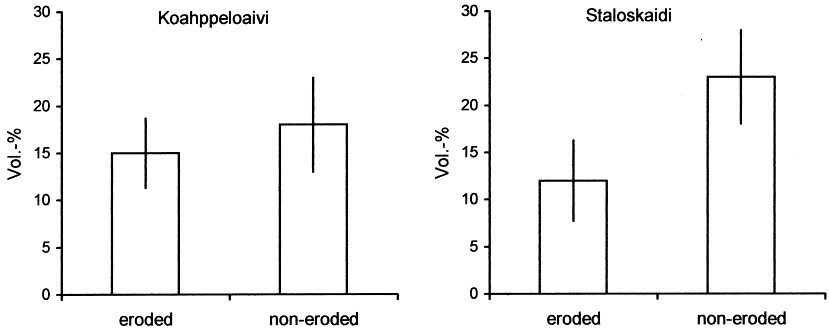



Fig. 18. Water content (Vol. %) on eroded and non-eroded sites. Koahppeloaivi (1 August 1998), Staloskaidi (2 August 1999).

Table 2. Results of soil analyses.

| Soil data | Eroded plots at | | | Vegetated plots at | | |
|---|---|---|---|---|---|---|
| | Koahppeloaivi | Staloskaidi | Rodjanoaivi | Koahppeloaivi | Staloskaidi | Rodjanoaivi |
| pH ($CaCl_2$) | 4.7 | 4.8 | 4.7 | 3.3 | 3.7 | 3.5 |
| P [mg $kg^{-1}$] | [a] | [a] | [a] | 13 | [a] | 4 |
| K [mg $kg^{-1}$] | 4 | 2 | 5 | 95 | 8 | 22 |
| $C_{org}$ [%] | 0.5 | 0.6 | 1.1 | 10.4 | 1.4 | 4.7 |
| $N_{total}$ [%] | 0.06 | 0.04 | 0.07 | 0.42 | 0.06 | 0.16 |
| $C_{org}/N_{total}$ | [b] | [b] | [b] | 25 | 23 | 29 |
| CEC [$cmol_c$ $kg^{-1}$] | < 1.0 | [b] | [b] | 9 | [b] | [b] |
| Base saturation [%] | < 1.0 | [b] | [b] | 18 | [b] | [b] |

[a] below the detection limit
[b] not determined

low dwarf shrub heath. At the vegetated plots, the leached topsoil is still in place, while at the eroded plots the former subsoil is exposed. Consequently, the cation exchange capacity is almost undetectable on the eroded plots. At the vegetated downwind plots it is about 9 $cmol_c$ $kg^{-1}$. At all study sites, organic carbon and total nitrogen are very low at the eroded plots compared to the vegetated plots. Plant available phosphorus and potassium are extremely low at all eroded plots. The vegetated plot on Koahppeloaivi exhibits relatively high organic matter content compared to the vegetated plots on Staloskaidi and Rodjanoaivi. Consequently, plant available phosphorus and potassium are also relatively high compared to the vegetated plots of Rodjanoaivi and Staloskaidi. Although being two to three times higher than at the eroded site it is very low. Altogether, these soil chemical conditions at the eroded plots are unfavourable to seedling establishment.

While birch seedlings occur in great numbers in the forest and also within a narrow belt above the closed forest, regeneration from seeds is very rare in the more wind-exposed ecotone. However, there are exceptions. Locally, seedling clusters (up to ten, a few cm high individuals per square metre) occur on open ground between the dwarf shrub vegetation, while dense plant cover prevents seeds from reaching a suitable seed bed. Also, solitary seedlings can occasionally be found on bare mineral soil at wind-exposed sites.

Seedlings (n = 46) were sampled at a few wind-eroded and wind-sheltered sites in shallow valleys (depressions) on Koahppeloaivi-Staloskaidi (cf. Fig. 13). Stem length varied between two and twenty-seven centimeters. About two thirds ranged between five and twenty centimetres. Only three stems were longer. Stem length, however, should not be confused with height of the seedlings, because on wind-exposed topography they usually are growing prostrate along the surface, in particular the longer ones. Also, there is only a low correlation between stem length and seedling age (Fig. 19). Many seedlings in this area are intermediate forms resulting from genetic interference of *Betula pubescens* and *Betula nana*

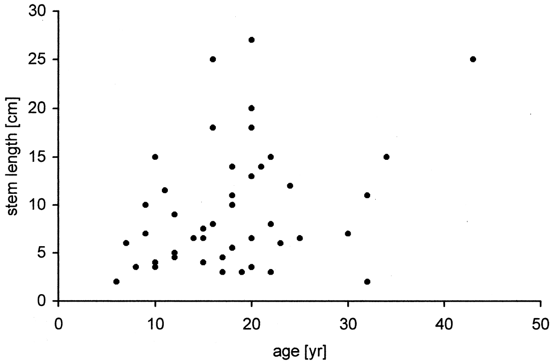



Fig. 19. Stem length of mountain birch seedlings as related to age of mountain-birch seedlings on Koahppeloaivi (northern Utsjoki).

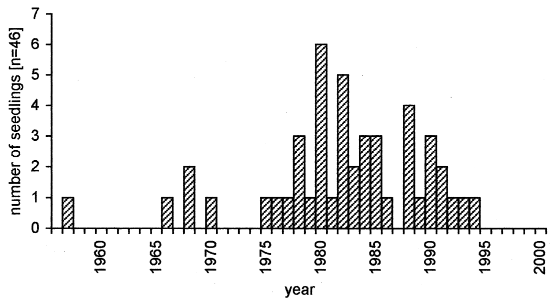



Fig. 20. Years of establishment of mountain-birch seedlings on Koahppeloaivi (northern Utsjoki).

(cf. Kallio & Lehtonen 1973; Vaarama & Valanne 1973; Sulkinoja et al. 1981; Kallio et al. 1983; Hämet-Ahti 1987), what also could explain prostrate growth and production of suckers from basal burls at the climatically extreme sites. For example, we found intermediate forms to be more common on the northern fells than on Ailakkavaara.

Seedling age was determined by tree ring analysis. Most living seedlings became established between the late 1970s and the beginning 1990s. Seedlings younger than five years (in 2000) were practically non-existent (Fig. 20). This might be attributed to unfavourable thermal conditions reflected in ring-width analyses of old birches. Decrease of diameter growth is obvious since the beginning of the 1950s and continues to the present (Fig. 21). The same trend was found in ring-width analyses of old-growth at Jesnalvaara and also Pallastunturi (Holtmeier et al. 1996).

Cold spells (mean day temperature < 5 °C) in northern Utsjoki occurred at relatively high frequency during the growing season from the mid-1980s to the early 1990s (Fig. 22; Müller 1999) and since then have decreased. This did not impede regeneration of birch. In contrast, one could suppose that comparatively high precipitation and reduced evaporation, usually combined with cold waves, alleviated the moisture stress at rapidly drained sites, even though the percolating water would have been available to the seedlings for a very short time.

On wind-exposed topography with rapidly

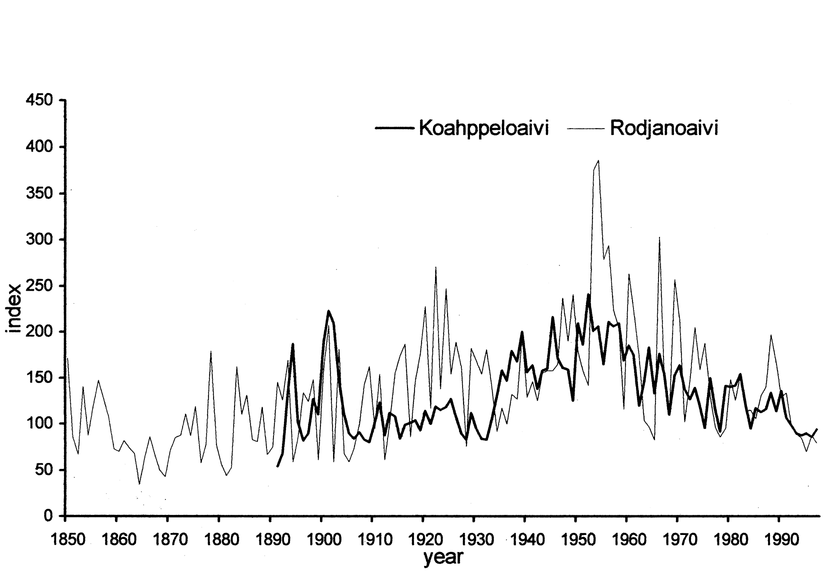



Fig. 21. Annual growth increment of mountain birches in the treeline ecotone on Koahppeloaivi and Rodjanoaivi.

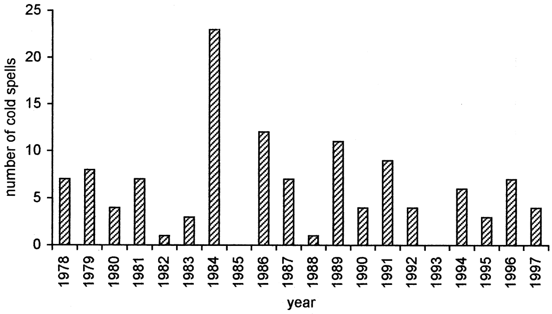



Fig. 22. Cold spells (mean daily temperature < 5 °C) at Kevo (northern Utsjoki) in summer (1978–1997; Müller 1999). Summer is defined as the warm season with mean daily temperatures ranging usually above 5 °C.

drained sandy soils, most birch seedlings have an extended root system. The longest main root we found was about 265 cm, while the above ground stem was six centimetres only. In many cases the roots are growing more or less horizontally a few centimetres below the soil surface before turning into greater depth (30 cm). Beneath stones, dense root mats develop because of the preferential flow at the stone surfaces (see also Broll 1994).

Main roots near the surface are often exposed by deflation, thus looking like prostrate stems. Their wood (tissue) structure, however, is different. Some of the older seedlings (> 10 yrs) exhibit a burl-like stem base, that very likely results in response to repeated damage by reindeer. At a close sight, however, many of them turn out to be sprouts emerging from buried old root stocks. Most sprouts are damaged by reindeer frequenting windy topography to escape the myriads of mosquitos and bot-flies *(Oedemagena tarandi,* Oestridae). In addition, the establishment of birch seedlings is impeded on heavily wind-eroded convex topography and other wind-exposed topography because of the coarse sandy mineral soil (and low humus content), which retains very little soil moisture (very often dropping to less than 20% vol.). Severe microclimatic conditions and lack of available nutrients also impede establishment of seedlings (Holtmeier 2000).

In the shallow valleys and depressions, except for snow beds, young birch seedlings (most of them 10–20 yrs old) are abundant and there is little reindeer damage. Reindeer do not like to graze on these wind-sheltered, mosquito-rich sites. However, these seedlings did not grow faster in length than those seedlings on wind-exposed and heavily eroded topography. This may be attributed to the shorter growing season and also to frequent waterlogging in valleys and other depressions. Temperature inversions are not very likely at such shallow concave topography during the growing season. In contrast to usually prostrate seedling growth at wind-exposed sites, upright (vertical) growth prevails at the better protected places.

Notably, extremely high densities (20–30 seedlings per square meter) of very young seedlings (up to 5 yrs old) were observed at wet places close to little streams (Fig. 23). Here, dense willow and dwarf-birch thickets give way to open and less competitive sedge and herb vegetation. Obviously, temporary flooding and waterlogging do not impede seedling establishment. However, older seedlings and young growth did not occur at these sites.

Surprisingly, we found three about 20 to 40 years old pines (40–60 cm high) at altitudes of 255 m, 260 m and 300 m in the treeline ecotone on Staloskaidi. They were growing on the leeward slope of slightly convex topography, about four to five kilometers distant from the next seed source on the banks of the Tenojoki. These pines developed several stems, probably after the apical shoots had been damaged. Although slightly discolored, the annual growth of present terminal

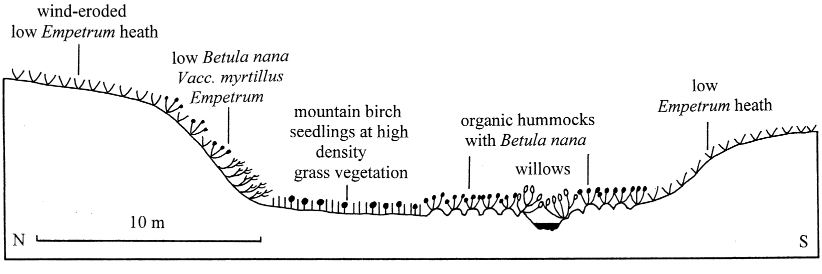



Fig. 23. Occurrences of mountain-birch seedlings in a small valley on Staloskaidi at about 300 m (schematically, for location see Fig. 13).

Fig. 24. Solitary Scots pine about 40 years old heavily damaged by reindeer on Staloskaidi at about 260 m. (Photo F-K Holtmeier, 2000).

shoots in 1998 and 1999 was twice to three times as much as ever before. However, when they grow above the average snow cover they will be increasingly exposed to the harsh winter climate and become crippled. In 2000, the tallest of these pines was heavily damaged by reindeer and died in the following year (Fig. 24). In 2003 we found a solitary 20–30 years old pine (30 cm high) on Koahppeloaivi at an altitude of even 414 m (!), also a few kilometers distant from the next seed trees. This pine is growing between scattered blocks, which provide some protection from the strong winds on the mountain top (420 m). The upper, more exposed needles and terminal shoots, however, had already been killed by frost or frost drought, while the foliage close to the ground had remained undamaged.

It would be too optimistic to take these solitary young pines on Staloskaidi and Koahppeloaivi as an indicator of climatically driven pine forest advance to higher elevation. An advance of pine forest would require high seedling density and seedling survival. However, because there are no pine seed trees in the treeline tundra ecotone regeneration depends totally on wind-mediated seed dispersal from the seed sources in the Tenojoki valley. Obviously, long-distance seed dispersal is not very effective. Otherwise more pine seedlings should have become established during the climatically favorable periods of the previous century, at least on the relatively suitable, wind-sheltered sites. Anyway, in case these few pines that were found on Staloskaidi and Koahppeloaivi survive, they may become a seed source some day that could encourage pine invasion into the ecotone, as observed on Jesnalvaara and Pallastunturi. Seed years are less frequent in pine than in birch (Holtmeier 1974), and regeneration from seed bank is very unlikely because Scots pine usually germinates within a short time after dispersal, and seeds do not live longer than 10 to 16 months (Granström 1987).

At present, many factors prevent birch from invading the heavily eroded treeless areas in the ecotone on Koahppeloaivi and Staloskaidi: In particular, 1) extreme microclimatic conditions (long-lasting frozen soil), 2) at least temporary insufficient soil moisture due to coarse soil texture and lack of humus, 3) deficiecy of available nutrients mainly because of deflation of the organic layer and 4) intense reindeer grazing. Thus, birch forest is very unlikely to invade these areas within the foreseeable future. In the wind-sheltered shallow valleys and depressions, however, regeneration may result in a gradual forest advance up to the present tree limit.

## Rodjanoaivi

In the Rodjanoaivi area, the study sites are located on the northwest-facing slope of the mountain (500 m) at an elevation of 300–390 m (Fig. 25). The till cover is dissected by shallow and – in their upper section – low gradient valleys (small tributaries of the Tenojoki), separated by gently sculptured convex topography (Fig. 26). At an altitude of 300 m the closed birch forest locally merges into more open, orchard-like stands. The forest limit is located at about 330 m. In the shallow valleys and depressions, however, solitary birches and birch groves (up to five meters high, diameter up to 20 cm) occur up to 380 m altitude. Low alpine dwarf shrub-lichen heath covers the

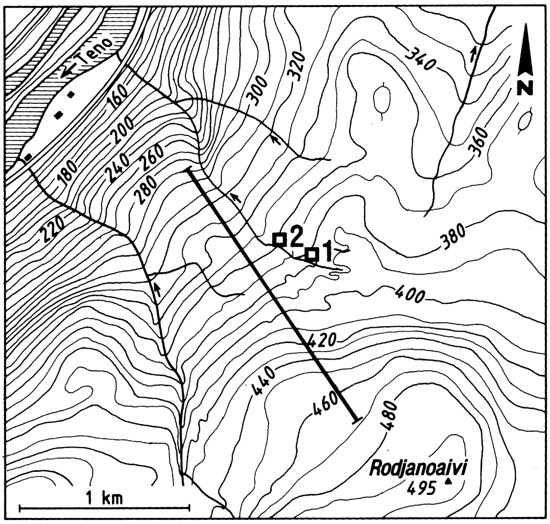



Fig. 25. Rodjanoaivi study area. Transect and study sites (□1 – location of Fig. 28 , □2 – soil sampling site, cf. Table 2). Map redrawn from Topographic Map of Finland 1:20 000, sheet Rodjanoaivi, no. 391406.

mountain slope above the birch forest limit. The valleys and depressions are characterized by hummocks and grass bogs.

On convex slope topography, mainly on small till-covered knolls or ridges projecting above the surface, the bare mineral soil (sand and coarser material) is partly exposed by strong winds from the west. Typically, wind erosion is strongest at the upper edge of the wind-exposed valley sides (Fig. 27). The topsoil has largely gone, while the illuvial horizon of the former Podzol has remained. Wind-scarps (10–20 cm high) are gradually "migrating" downwind. However, wind erosion is not as conspicuous as was observed on Koahppeloaivi and Staloskaidi. Very likely, the destruction of the dwarf shrub, lichen and moss vegetation by reindeer (trampling and grazing) has been, and obviously still is, the factor triggering deflation. Many of the present treeless areas between the valleys with high-reaching open birch stands once were covered with birch forests at least up to 380 m, as is evidenced by the many rotten root stocks that became overgrown by lichen vegetation *(Ochrolechia frigida, Cetraria nivalis, Cladonia stellaris, Cladonia rangiferina, Cladonia gracilis, Cladonia pyxidata, Cladonia mitis* etc.). We found dead wood even up to an elevation of 395 m. One piece taken from a peat hummock at 30 cm depth has a radiocarbon-age of 950 ± 60 yr. Two other samples taken from rotten root stocks at five to ten cm depth in the present treeless areas at about 360 m and 366 m have a radiocarbon-age of 555 ± 55 yr respectively. The average age of the living trees in the open birch stands ranges between 80 and 90 years, a few are up to 200 years old. The oldest birch we found (Rodjanoaivi, at 358 m) was 225 years old.

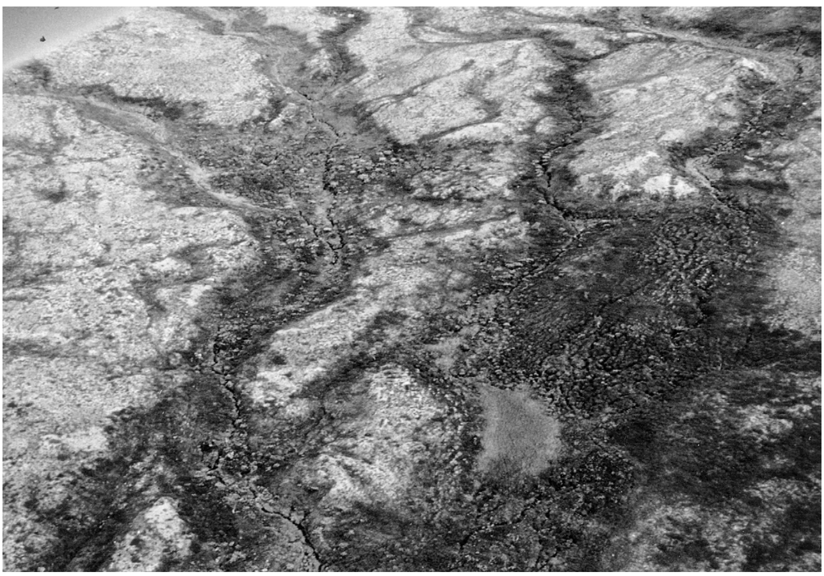


Fig. 26. View from a low-flying aircraft (250–300 m above ground) of the northwest-facing slope of Rodjanoaivi (northern Utsjoki) (view to the southeast). Convex topography (light grey areas) is covered by dwarf shrub-lichen heath or more or less wind-eroded. (Photo F-K Holtmeier, 5 August 1998)

Fig. 27. Varying local topography on the northwest-facing slope of Rodjanoaivi at about 350 m (view north). On convex areas (soil sampling site, cf. Fig. 25 and Table 2), the bare mineral soil (sandy-skeletal till) is exposed by wind-erosion and trampling by reindeer. (Photo F-K Holtmeier, 29 July 1998)

The birch forest had disappeared maybe because of unfavourable climate conditions or repeated defoliation by the autumnal moth. In this area mass outbreaks were reported for 1855, 1905–1909, 1927 and 1955 (cf. map in Kallio & Lehtonen 1975; see also Kalliola 1941; Nuorteva 1963; Holtmeier 1974; Kallio & Lehtonen 1973). The closed birch forest at lower elevation was not affected by *Epirrita autumnata*, probably because extreme cold (cold air layers) killed the eggs or prevented the development of the embryos (Tenow 1972, 1975; Niemelä 1979; Tenow & Holmgren 1987; Neuvonen et al. 1996; Tenow 1996; Neuvonen et al. 1999). Because the upper limit of closed birch forest is higher on the mountain slope on the Norwegian side of the Tenojoki opposite to Rodjanoaivi it cannot be excluded, however, that also humans removed much of the previous forest (e. g. fuel). This is particularly obvious because of close vicinity of many human homesteads on the banks of the Tenojoki (Kallio et al. 1969). Even today one third of the households in Utsjoki heat with wood (Mattson 1995).

In the birch forest, particularly in the open stands, regeneration by seedlings and also from basal shoots is abundant. Seedling density decreases abruptly within a distance of about 100 m from the upper limit of the open birch forest from four seedlings to less than one per 100 m$^2$. On a ten meters wide and 1900 m long transect (reaching from 267 m to 470 m, cf. Fig. 25) 38 birch seedlings were found. In one third of the seedlings the tips of the little stems were dry or broken. Seedling height does not usually exceed 5 cm, most individuals are smaller. Anyway, seedlings occur more frequently compared to Koahppeloaivi–Staloskaidi. The distribution of seedlings is mostly irregular. However, on open mineral soil between patches of the dwarf shrubs, and also behind small microtopography (small hummocks, solifluction terraces, stones) seedlings may occur at greater numbers. These sites provide shelter from strong wind and high soil moisture (accumulation of snow, low evaporation loss). Dead seedlings and young growth are at least as frequent as living ones. Moreover, as has also been observed in the other study areas, many “seedlings” turn out to be “pseudo-seedlings” that originated from old buried root stocks or basal burls (see also Vaarama & Valanne 1973; Kallio et al. 1983).

High seedling density – twenty-five and even more seedlings (up to 5 yrs old) per square metre – was locally observed comparatively in wet places close to little streams up to an altitude of 380 m (Fig. 28). This contrasted with seedling densities on adjacent convex topography. In these wind-sheltered mosquito-rich valleys, reindeer damage (grazing, trampling) to seedlings is usually confined close to reindeer paths. However,

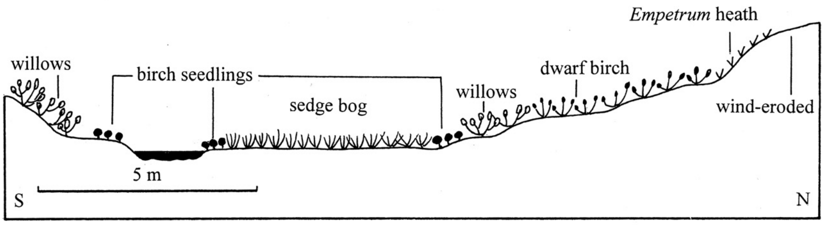



Fig. 28: Occurrences of mountain-birch seedlings in a shallow valley on Rodjanoaivi at about 370 m (schematically, for location see Fig. 25).

young growth older than five to eight years is still very rare.

At more favorable conditions, an invasion of birch into the present treeless areas between the valleys and advance of the birch forest to higher elevation could be expected in the shallow valleys and similar depressions. Birch will not likely invade the convex topography, mainly because of dry and windy conditions and reindeer grazing. Also, voles and snow hares damage birch seedlings.

## Discussion

Changes in the treeline ecotone are characterized by episodic invasions of seedlings. Many of them died or became crippled by climate and reindeer. The distribution pattern of treeless areas and forested patches in the ecotone did not change significantly during the last hundred years and seems to have become almost "stationary" in relation to the local topography and its effects on site conditions. This is in accordance, for example, with the observations of Holmgren & Tjus (1996) at the upper treeline in the Abisko area. These authors concluded that increase of mean summer temperature since about 50 years may have been too small to induce a significant altitudinal advance. Alexandersson & Dahlström (1992) could not find evidence of a clear warming trend during this period in northern Sweden. Sonesson & Hoogesteger (1983), however, reported an altitudinal expansion of the birch forest (birch thickets) since the 1940s into areas that were only sparsely covered by birches before. They attributed this expansion to improved sexual and vegetative reproduction of the mountain birch. In interior northern Norway reduced grazing pressure has obviously triggered birch forest advance to higher elevation (Odland et al. 1992).

As to the future development in the treeline ecotone, potential changes in the high climatic variability (Blüthgen 1952; Holtmeier 1974) and their effects on tree vegetation should be carefully studied (see also Holmgren & Tjus 1996; Tasanen et al. 1998; Holtmeier 2000). Also alternating periods of above-average (e.g. 1964–1968) and below-average precipitation (1969–1980) are typical of northern Lapland and an important factor influencing soil moisture conditions and thus regeneration. Since 1992 the annual precipitation was relatively high while the negative deviations were close to the long-term average.

Apparently, the mountain birch treeline ecotone in our study areas and at Abisko is different from the treeline in the more southern Swedish Scandes. There, the upper limit of the mountain birch is reported to have risen more than 100 m during the 20th century (Kullman 2000, 2002). This would correspond to a tree-limit position not exceeded during the last 4000–5000 radiocarbon years (Kullman & Kjällgren 2000). This tree-limit "advance", however, mainly results from the changing physiognomy of already existing, but low growing birches. They have grown taller than two meters during relatively favourable years and are now considered "right trees" (e. g., Kullman 1989; see also discussion on the term "tree" in Holtmeier 2000, 2003).

In all our study areas a bundle of physical and biological factors is impeding forest advance to treeless areas within the ecotone and above the present treeline. Reindeer grazing turns out to be the factor most adverse to seedling establishment. Originally, reindeer were an integral component of the subarctic birch forest and fell tundra ecosystem. Kankaanpää (1999), for example, considers the existence of open woodland below the treeline a truly natural situation (see also Oksanen et al. 1995). The population of semi-domestic reindeer, however, has grown beyond the natural carrying capacity of the treeline ecotone (Holtmeier 1974, 1999, 2002; Heikkinen & Kalliola 1989; Evans 1995). Since the mid-seventies the reindeer population in northern Finland has more than doubled (Kumpula & Nieminen 1992). Reindeer population in northern Utsjoki (ca. 3 reindeer/km$^2$ after Kashulina et al. 1997, or 5–10 reindeer/km$^2$ after Oksanen et al. 1995) is the highest in Finland. The drastic increase in reindeer numbers is caused by a number of factors, among them reduced mortality due to winter-feeding with hay (Burgess 1999). According to Käyhkö & Pellikka (1994), however, the impact of reindeer grazing on natural vegetation is not necessarily a consequence of excessive numbers of reindeer, but rather has to be attributed to the lack of seasonal grazing practice, which would reduce the summer grazing pressure. In the opinion of Helle (2001), the greatest threat to birch at timberline is the combination of high reindeer population and extensive *Epirrita autumnata* damage (see also Holtmeier 1974, 1999, 2004; Kallio & Lehtonen 1975; Oksanen et al. 1995).

The impact of reindeer on the treeline ecotone is very complex. Reindeer influence seedlings, young growth and dwarf shrub-lichen heath directly by grazing (consuming living organic matter, mechanical damage by trampling) and indirectly by changing soil ecological conditions (Holtmeier 1974, 2000, 2003, 2004; Broll 2000). Reindeer browse especially the tips of basal sprouts (Haukioja & Heino 1974; Tenow 1996), as was also observed by the present authors. The slow growth of seedlings and sprouts makes them available to reindeer for many years. Lehtonen (1987), in contrast, does not consider reindeer browsing to be a factor limiting shoot formation. It is mostly on rapidly draining, sandy substrate (till, eskers etc.) that reindeer seriously enhance soil erosion (Holtmeier 1974; Haapasaari 1988; Evans 1995). Once the dwarf shrub-lichen heath is destroyed, soil organic matter and, consequently, field capacity and soil moisture decline. Although soil moisture was not measured on Ailakkavaara and Pallastunturi, we suppose that on loamy sands severe microclimate rather than insufficient soil moisture is impeding seedling establishment on convex topography.

Soil temperature at sites with bare mineral soil are higher in summer and lower in winter compared to sites covered by heath vegetation (cf. Figs. 16 and 17; Broll 2000; Holtmeier 2000). Under clear weather conditions, the drained topsoil (reduced heat conductivity) may quickly warm up to relatively high temperatures, even at wind-exposed sites. This was obvious from the soil temperatures recorded on Koahppeloaivi site (310 m; cf. Fig. 16). During the growing season soil temperatures were considerably higher on the knoll compared to its more wind-protected leeward slope covered by dwarf shrub vegetation and scattered mountain birches.

Generally, at temperatures below 5 ˚C mineralization and nutrient uptake rapidly decline (e.g., Retzer 1974). For example, at the upper limit of the mountain birch forest at Abisko (Sweden), at soil temperature below 5 ˚C nutrient uptake and seedling growth almost ceased (Karlsson & Nordell 1996; Karlsson & Weih 1996). Similar results were found at the upper *Nothofagus solandri* timberline on the south island of New Zealand (Benecke & Havranek 1980; Wardle 1985). Thus, at the given soil temperatures on the Koahppeloaivi site, conditions could be comparatively favourable to seedling establishment and growth. However, rapidly draining, subsequent drought, and lack of organic matter override the potential positive effect of the soil temperature conditions and hamper mineralization and seedling growth. Particularly during dry periods soil moisture deficiency may become critical to the seedlings and prevent successful regeneration (Kallio & Lehtonen 1973). This has also been reported for rapidly draining sites at the upper timberline in other mountains (e.g. Kalela 1941; Kullman 1986; Holtmeier 2000). Yet, it cannot be excluded that in the long term (we recorded temperatures through one year only) seedling establishment and growth may be impeded or even prevented by low soil temperatures during the growing season. In addition, where topography limits snow accumulation, shallow roots of seedlings may be damaged by occasional deep freezing temperatures (see also Jalkanen 1993b). For comparison, at snow-rich timberlines, such as in the Alps, for example, convex topography is usually more favourable to seedling establishment than depressions (short growing season, avalanches, sliding snow etc.; cf. Holtmeier 2000, 2003; Hiller et al. 2002).

Competition for light and nutrients does not play an important role on wind-exposed and only sparsely vegetated convex topography in our study area. However, it may impede or even prevent seedling establishment at sites covered by closed dwarf shrub heath (see also Holm 1993; Kallio & Lehtonen 1973; Weih & Karlsson 1999; Holtmeier 2000, 2003 and references therein). On experimental sites near Toolik Lake (50 km north of the treeline on the northern foothill zone of the Brooks Range, Alaska), Hobbie & Chapin III

(1998) found that tree growth could be increased by removing the competing tundra vegetation rather than by artificial warming. As also reported by Kallio & Lehtonen (1973), continuous dwarf shrub and moss cover may almost totally exclude any seedlings, while greater numbers of seedlings were found in eroded places. Especially during the first growing season competition may be critical to seedlings. Thus, in our study areas, reduced competition for nutrients and light may be the main reason for the occurrence of seedlings on small patches of open soil interspersed in the subarctic dwarf shrub heath. Moreover, wind-dispersed seeds may more easily reach a seed bed in the open patches, compared to densely vegetated sites.

Invasion of treeless areas depends on availability of viable seeds. Generally, production of viable seeds declines by increasing elevation (Holtmeier 1993; Sveinbjörnsson et al. 1996), and the uppermost treeline birches do not produce fertile seeds (Kullman 1984; Lehtonen & Heikkinen 1995). Viable seeds may be dispersed from lower elevation to treeline though. Also, a small percentage of birch seedlings may originate from seed banks, as birch seeds retain viability for two to three years after dispersal (Granström 1987). However, in central Sweden Kullman (1981, 1993) not only observed a drastic decrease of seedlings above the closed birch forest but also found that at sites without seedlings the seeds were empty. We did not prove the fertility of birch seeds, but at the high seedling density on wind-protected valley sites, the scarcity of birch seedlings on adjacent convex topography (at almost the same elevation) and the supply of fertile seeds do not seem to be an essential factor preventing birch forest from invading these areas.

## Conclusions

What are the perspectives now? The high seedling density in the wind-sheltered, snow-rich and moist, shallow valleys crossing the present treeline ecotone on Ailakkavaara and in northern Utsjoki might by considered as the beginning advance of the birch forest to higher elevation. If climate became more favourable to seedling growth for the long-term, a higher density of mountain birch could be expected mainly in the valleys. The situation of the wind-exposed convex slope topography is totally different. Severe site conditions such as thin or temporarily missing winter snow cover, deep-frozen soil, ice particle abrasion, upfreezing, and moisture stress, partly due to eroded soils (mainly in northern Utsjoki) impede the establishment of birch seedlings and advance of the birch forest to higher elevation. In contrast, at sites covered by dwarf shrub heath, conditions for regeneration by seedlings are more favorable, if not prevented by competition.

In the Pallastunturi area and also on Jesnalvaara, the negative influence of wind-eroded soils on seedling establishment is far less important as such sites are comparatively rare. However, seedlings and young growth of pine and spruce are limited mainly by severe local climatic influences when the young trees begin to project above the winter snow cover. Thus, some of the pines and spruces will develop more or less stunted growth forms and – under eventually more favourable conditions – may act as a seed source in the ecotone. It remains an unsolved question why mountain birch is less successful than spruce and pine in invading the treeless areas of the treeline ecotone on Pallastunturi. As to the future development in the middle and upper zone of the treeline ecotone on Pallastunturi one should not be too optimistic, as was, for example, Blüthgen (1942). He wrote that in view of the intensive regeneration during the favourable period of the previous century pine forests were advancing to their uppermost and northernmost Holocene position. As has been shown above, many of those "young" trees that became established during the "thermal optimum" of the 20th century died or became crippled without recovering from the damage caused by external factors (climate, snow, reindeer, snow fungi). The same could happen to the more recent young growth, if growing conditions will not considerably improve and extreme events will not occur. Increment cores taken from old pines (age-trend removed) in the lower part of the treeline ecotone give some evidence of decreasing growth rates during the late 1970s (cf. Holtmeier et al. 1996).

Decreasing diameter growth has become common almost everywhere in the northern hemisphere since the 1960s, except for a few regions (Schweingruber 2000). It has been speculated that the climate, air pollution or other factors are causing the decline (Briffa et al. 1998a, 1998b; Vaganov et al. 1999). However, as far as air pollution is concerned, Pallastunturi is located in one of the cleanest areas of continental Europe (Mylona

1993, Hatakka et al. 1997). Kashulina et al. (1997) do not believe that air pollution from Kola causes significant damage to the ecosystems in northern Finland.

Altogether, our studies do not support the optimistic forecasts of a rapid advance of timberline in the near future (e.g., Roos et al. 1996; Kellomäki et al. 1997). Even at generally expected warmer conditions the adverse effects of factors described earlier would override at least for decades the effect of slight temperature increases. Modest increases in temperature during the growing season can hardly compensate for the deterioration of the site conditions that occurred on convex topography after the birch forest had gone; gone because of human activity or mass outbreaks of the autumnal moth. On the other hand, higher spring temperatures resulting in more and wet snow in spring would strongly influence the ecological conditions. Typically, the effects would be strongest at the present sites already characterized by deep and long-lasting snow cover rather than on wind-exposed convex topography. Future studies should focus in particular on regeneration related to microsite conditions rather than on growth trends in mature trees. Also, the relative importance of site conditions at different stages of tree development should be considered.

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