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# Isolated occurrences of spruce, Picea abies, in northernmost Fennoscandia in relation to the enigma of continental mountain birch forests

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In northern Fennoscandia, timberline forests are birch-dominated both in oceanic areas and in areas with relatively continental climate. In eastern Fennoscandia and northern Russia, weakly and moderately continental areas are characterized by spruce-dominated timberline forests. A similar situation prevails in parts of southern and central Scandinavia, too. Possible causes for the anomalous situation in northern Fennoscandia include (1) qualitative differences between the kind of continentality found in northern Fennoscandia and in other areas with similar values of conventional continentality indices, (2) differences between the ability of spruces to defend positions obtained during the hypsithermal and their ability to expand their range under current climatic conditions and (3) the existence of dispersal barriers between the present limit of continuous spruce forests and potential spruce areas north of it. The structure of the northernmost spruce outposts suggests that all three factors are involved, but available evidence is insufficient for judging their relative importances.

*Key words*: climate, continental, deciduous, evergreen, history, larch, mountain birch, oceanic, perfmarost, pine, spruce, timberline

## INTRODUCTION

Arctic and boreal-oroarctic timberlines are normally formed by spruces, often with an understory of shrubby birches (Hustich 1966, Larsen 1965, 1988, Norin 1961, Tihomirov 1970, Walter 1974). Timberline forests dominated by birches or other mesomorphic deciduous trees are typical for high-latitude areas adjacent to ice-free oceans (Ahti & Hämet–Ahti 1969, Hämet–Ahti 1978). Larches prevail at the timberlines of central and eastern Siberia, where conditions are extremely continental and the taiga is underlain by permafrost (Walter 1974). In Fennoscandia, spruce-dominated timberline forests are typical for small, isolated inl mountains (Haapasaari 1988, Wistrand Moreover, spruce forests frequently reac

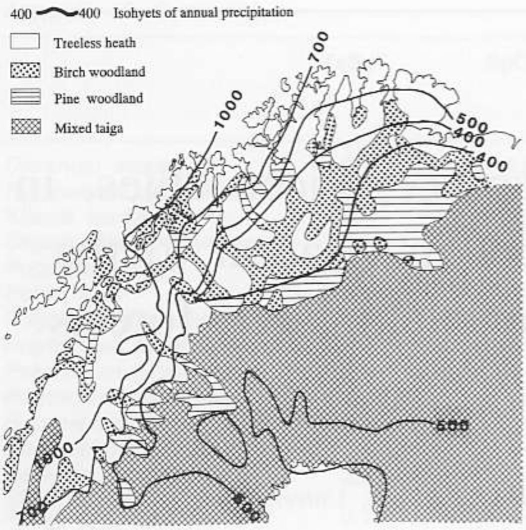

Fig. 1. Overview of the distribution of main habitat types in northern Fennoscandia based on Oksanen & Virtanen 1995, Anon 1978–1984 and Hesselman & Lundqvist 1935.

timberline or its vicinity in the Tröndelag-Jämtland gap, where the Scandinavian mountain chain is at its lowest, and along the southeastern edge of the mountains from Telemark to Dalarna (Anonymous 1978–84, own observations). In northern Fennoscandia, however, timberline forests are formed by mountain birches (*Betula pubescens* ssp. *czerepanowii* (Orlova) Hämet-Ahti) even in inland areas with relatively dry and continental climate (Fig. 1, see also Anonymous 1978–1984, Hustich 1961, Hämet–Ahti 1963, Tuhkanen 1980, 1984). Another area with extensive mountain birch forests even under relatively continental conditions lies in rain shadow of South Norwegian mountains (from Gudbrandsdalen to Härjedalen and southern Jämtland, Anonymous 1978–1984, own observations).

The continental mountain birch forests in Fennoscandia have been formed from mixed pine-birch forests as a result of withdrawal of the latitudinal and altitudinal limit of *Pinus sylvestris* after the hypsithermal (Kullman 1979, 1981, 1983, 1987ab, 1991a, Kullman and Högberg 1989). This recession of the latitudinal and altitudinal limit of coniferous forests represents a circumpolar trend which, however, has been more pronounced in Fennoscandia than in areas where spruces were present during the hypsithermal (Huntley 1987, Webb 1987). The occurrence of spruce and larch woodlands with shrubby birches north of and above the timberline of *Pinus sylvestris* is typical for the entire Eurasian taiga (Walter 1974). The geobotanically anomalous features of the two relatively continental parts of Fennoscandia thus lie in the low altitudinal and latitudinal limits spruce forests and in the reversal of the normal order in which *Pinus sylvestris* and *Picea abies* s.l. disappear at the transition from taiga to tundra. The scope of this paper is to formulate three alternative explanations for this geobotanical anomaly and to discuss them in the light of semi-experimental evidence provided by the spruce outposts of northern Fennoscandia.

## Formulation of three hypotheses

Before the anomalous situation in northern Fennoscandia can be understood, it is necesary to have a plausible explanation for the general pattern of the occurrence of deciduous and evergreen trees along the arctic timberline. The traditional explanation for the prevalence of birches in the timberline areas of Fennoscandia is the intolerance of *Picea abies* to oceanic conditions (Tallantire 1972, Huntley 1987). This mechanism can indeed contribute to the vertical extent of deciduous timberline forests along the Norwegian coast. However, timberline forests dominated by mesomorphic deciduous trees are encountered in all high-latitude areas close to ice-free oceans (Ahti & Hämet–Ahti 1969, Hämet–Ahti 1978), even in the presence of spruces well adapted to oceanic climate (*Picea sitchensis* in Alaska, *P. jezoensis* in Far East, Hultén 1927, 1941). In order to explain the entire pattern, we thus need a causal mechanism based on the ecological advantages and disadvantages of the evergreen habit in different kinds of climate.

An obvious advantage of evergreens is their ability to start photosynthetizing in spring as soon as temperatures are sufficiently high and meltwater has percolated to the rhizosphere. In the vicinity of open oceans, however, mild temperatures are frequent in the middle of the winter, too, when light intensity is below the compensation point. This inflicts respiratory losses, which may outweigh the energetic gains of early spring photosynthesis. Another potential problem is generated by conditions continental enough to create periodic permafrost. Then, unavailability of water limits photosynthesis in early spring, and evergreens can be partially defoliated during periods of warm weather and frozen ground (Larsen 1965, Kullman 1989, 1991b).

Notice that the mechanisms outlined above do not require that the marginal populations of spruces would be necessarily subjected to heavy mortality or frequent, conspicuous damage of the kind recorded by Kullman (1989). As pointed out already by Cajander (1905), distributional limits of plants are rarely set by limits of their physiological tolerance. Normally, plants meet their limits of distribution when becoming outperformed by other species claiming similar sites. Evidence provided by cultivated plants may thus have limited relevance to issues of distribution and abundance and there need not be 'blood on the ground' at the natural limit of a given species' distribution.

The climatic equilibrium hypothesis of Kullman (1991b) and Kullman & Engelmark (1991) states that the distribution of spruce and birch dominated timberline forests in northern Europe can be explained on the basis of current climatic conditions. Conventional continentality indices fail to show any systematic differences between inland areas with birch-dominated and spruce-dominated timberline forests in northern Europe (Tuhkanen 1980, 1984). Consequently, the equilibrium hypotesis requires that the climatical factors determining the advantages and disadvantages of evergreenness are not adequately reflected by these indices. The Fennoscandian pattern alone requires factors, which favour spruces on hills and low mountains rising above their surroundings (in the Salla-Kuusamo, Tröndelag-Jämtland and Telemark-Dalarna areas) and birches on east slopes of tall mountains. Elevated areas are characterized by copious snowfall in winter and lack of ground frost in spring (Dahl 1957, Oksanen &Virtanen 1994, Solantie 1988). Thus, hills and mountains in inland areas, where temperatures are relatively high during the snowmelt, appear to provide optimal conditions for spruces. Conversely, the thin snow cover of rain shadow areas east of tall mountains leads to the development of at least periodic permafrost even in the vicinity of open oceans (Seppälä 1986, Kullman 1989, 1991b). Areas close to ice-free oceans are also subjected to periodic invasions of warm air masses. Due to the chinook (föhn) effect, temperatures rise even further when the air masses descend along the leeward side of mountains. Rain shadow areas close to open oceans might thus be characterized by a mixture of oceanic and continental factors maximally disadvantageous for evergreens, leading to respiratory losses in winter and permafrost-induced drought stress in spring.

The position defence hypothesis converges with the climatic equilibrium hypothesis with regards to the mountain birch forests in locally continental parts of Fennoscandia but interprets the spruce-dominated timberline forests of northern Russia as due to historical factors. According to paleoecological and paleoclimatical evidence (Bartlein et al. 1986, Huntley 1987), winters along the arctic timberline have become colder and drier after the hypsithermal. This has been reflected as a decline in the amount of spruce pollen along the arctic timberline in northern Russia (Huntley 1987). It is thus possible that the existence of spruce-dominated timberline forests between White Sea and the Urals is critically dependent on the ability of spruces to stand their ground thanks to their superb capacity for clonal growth. The position defence hypothesis thus implies that there are two alternative stable states for weakly continental areas along the European arctic timberline. Studies aiming to distinguish between the climatic equilibrium and position defence hypotheses should focus on the ability of spruces to re-colonize secondary birch forest (due to forest fires or logging) within spruce-dominated timberline areas.

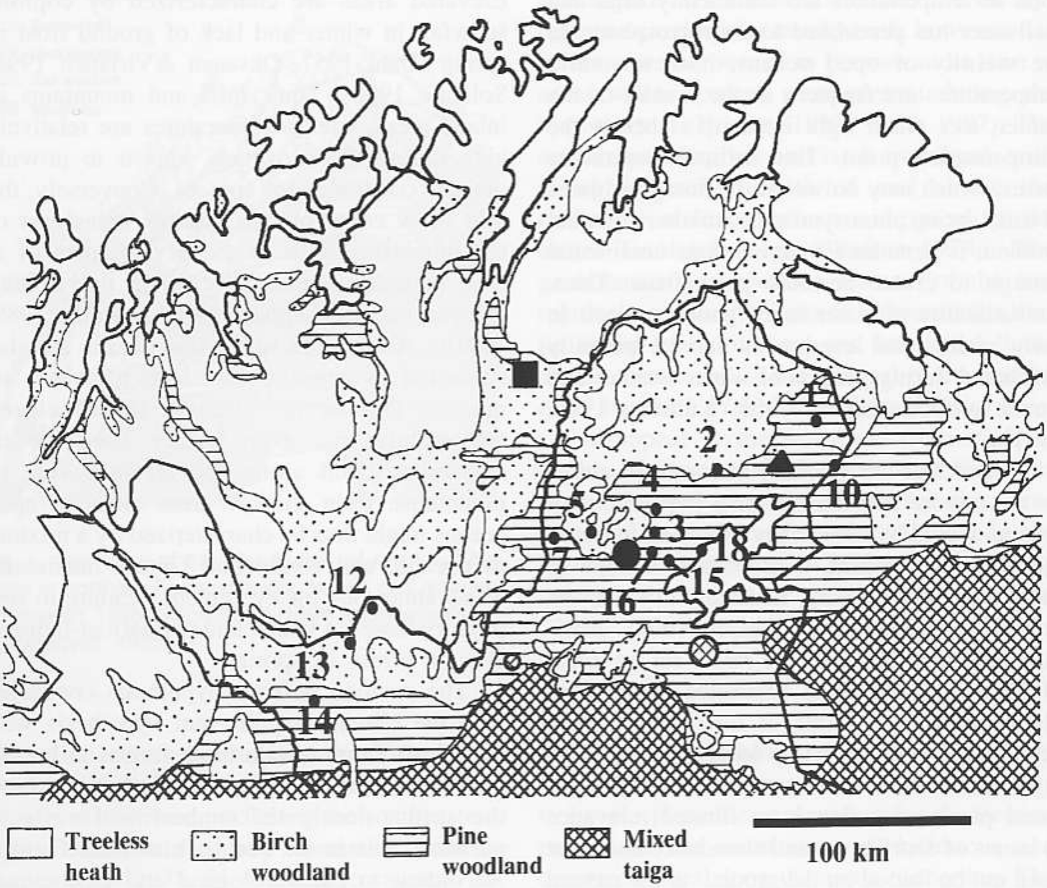

Fig. 2. Location of the isolated spruce stands included in the study (dots, numbers refer to Table 1) The big dot denotes the area with stands 6,8,9,11 and 17 (presented in detail in Fig. 3). The hatched circle marks the spruce forest of Ivalo. The sown spruces of Luovvusvárri are denoted by a square, the planted larches of Järvenpää by a triangle. The study area of Kullman & Engelmark (1991) lies in the SW corner of the figure. Based on Hustich 1961, Kallio et al. 1971, Seppälä & Rastas 1986, Kullman & Engelmark 1991, Hesselman & Lundquist 1935 and topographic maps.

The dispersal barrier hypothesis offers a third alternative. It can be developed from the arguments of Faegri (1950) and Moe (1970), who proposed that the lack of spruces from the interior parts of southwestern Norway is due to historical factors (either a pure non-equilibrium phenomenon or a consequence of dispersal barriers created by the cold and locally oceanic mountain climate). In its initial form, this view is clearly inapplicable to northern Fennoscandia, where the limit of continuous spruce forests is relatively stable (Kallio et al. 1971, Kullman & Engelmark 1991) and lies an area with continental climate (Fig. 1, Ahti et al. 1968, Tuhkanen 1980). However, Kullman (1989) found that *Pinus sylvestris* tolerates periodic permafrost better than *Picea abies*. Partially, this was due to lack of permafrost in pine-dominated sites, but also the characteristics of *P. sylvestris* (greater drought-tolerance, ability to obtain water through thin lenses of frozen ground by means of the long taproot) were probably involved. Thus, the pine-dominated continental lowlands with periodic permafrost might create a dispersal barrier between the northern limit of continuous spruce forests and potential spruce forest sites in higher country and in the interior parts of the fjordlands of northernmost Norway.

The dispersal barrier hypothesis implies that the continental pine forests are in some sense vicarious to the larch forests of Siberia (Walter 1974) and continental mountain valleys in Central Europe (Ellenberg 1978). The hypothesis can thus be extended by postulating that the existence of spruce-free pine forests and the wide climatic amplitude of mountain birch forests in Fennoscandia are in fact due to two dispersal barriers: the continental inland climate of northern Fennoscandia stops the advance of spruces, while the suboceanic climate of the White Sea region (Ahti et al. 1968, Tuhkanen 1980, 1980), makes spruces competitively superior to larches, thus blocking the westward expansion of *Larix sibirica*. This version implies that the continental pine and mountain birch forests of northern Fennocandia include both potential light taiga and potential dark taiga. A weaker version of the hypothesis states that pines are maximally competitive in the kind of continental climate encountered in northern Fennoscandia, where permafrost is only periodic and permafrost lenses are thin, allowing pines to obtain water in early spring with their long taproots.

The dispersal barrier hypothesis predicts that spruces should be able to penetrate long ways northwards and westwards (to the timberline or to areas where birches start to prevail due to the oceanic climate), if they managed to cross the pine-dominated lowlands with periodic permafrost. This prediction is corroborated by the wedge of spruce forests, penetrating deep into the mountains of Sarek (Anonymous 1978–84, Hesselman & Lundquist 1935). The scope of the rest of this paper is to examine, whether a similar development is going on in northernmost Fennoscandia, too.

## MATERIAL AND METHODS

In 1974, I attempted to visit all known spruce stands in the northern part of the Anarjávri (Inarinjärvi) basin and on the Muotkiduottarat (Muotkantunturit) highland between Anarjávri and Anarjohkka (Inarinjoki), on the basis of information provided by Kallio et al. (1971) and Kallio (pers. comm.). Some small stands were missed due to partial lack of topographic maps. A few others were excluded for logistic reasons. Nevertheless, the sample includes the majority of known stands and two previously unrecorded ones. Only one known stand with more than 10 spruces was not visited, but I included it on the basis of the description of Kallio et al. (1971) and Kallio (pers. comm.). Three spruce outposts in Enontekiö were visited in 1976.

Within the visited stands, the following parameters were recorded: forest site type, number of spruces (if < 100), heights (measured with a hypsimeter) and breast-height circumferences of trunks, shapes of crowns, occurrence of vegetative reproduction (layering, development of branches of fallen spruces into secondary stems), numbers of generative and vegetative offspring (if < 100), growth in length during the latest 5 years (if the structure of the top was sufficiently clear), breast-height ages of older trees (isolated lone trees were not cored) and occurrence of dead trunks. All stands were mapped and photographed and the vegetation of the field layer was documented by Havas (1978a, see also Havas 1978b).

In addition to the natural outposts of spruces, I visited the sown *P. abies* stand on Luovvusvárri (Porsanger municipality, Finnmark county, Norway), established in 1933. As compared with other sown and planted spruce woodlots in northern Norway, this one is at exceptionally high latitude and altitude. The stand is also in an exceptionally continental area and mainly on an edaphically dry site. I took notes on other planted conifer stands within the study area as well.

## RESULTS

The locations of the spruce stands are presented in Figs. 2 and 3. Of the 18 spontaneous stands, 14 consist of fewer than 100 individuals. Their characteristics are summarized in Table 1. The four bigger stands are described in the Appendix, along with the planted Luovvusvárri stand (square in Fig. 2) and a stand of planted larches (*Larix sibirica*), encountered in the northeastern part of the Anarjávri basin (triangle in Fig. 2).

Seven spruce stands are within the pine forest limit. As a rule, they are on edaphically moist sites. The three big stands in the pine forests region (15, 16 and 18) are influenced by running water. One lone spruces (7) is on the bank of a river, another (14) stands the shore of a lake. A third lone spruce spruce (6), this

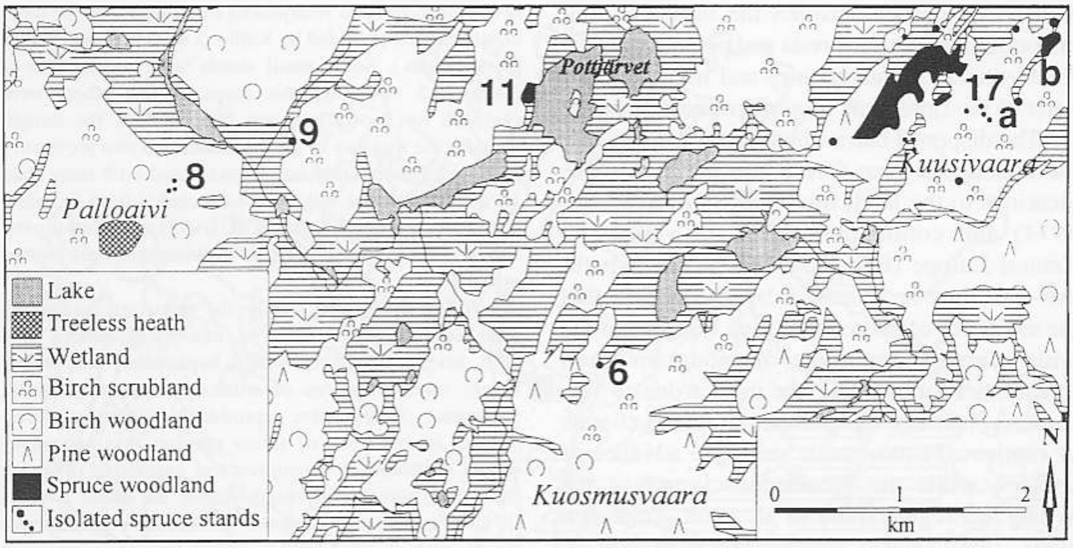

Fig. 3. Location of stands 6, 8, 9, 11 and 17 at the transition between pine-birch woodlands. Based on sheets 'Innihvaara' and 'Palloaivi' of the 1974 provisional topographic map of northern Finnish Lapland.

Table 1. Summary of attributes of the small isolated spruce stands of northernmost Finnish Lapland.

| Stand | Alt. m a.s.l. | Ft | Seed-lings | Rb | Veg.saplings of live trees | dead trees | Living trees (length in m) 2–5 | 5–10 | 10–15 | Dead trunks Natural | Cut | Ps | 5-year-growth (cm) | Coordinates |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1a[3] | c.150 | lh | | | | | 1 | | | | | * | 0 | 7724:582 |
| 2[1] | 220 | lh | | + | 7 | 3 | 3 | 8 | | 1 | 1 | + | 40–120 | 7696:537 |
| 3 | 320 | lh | | + | | | | 1 | | | | | nm | 7669:495 |
| 1b | c.150 | dh | | | | | | 1 | | | | * | 40 | 7724:582 |
| 4a | 320 | dh | | + | | | | 1 | | | | | 40 | 7671:491 |
| 5[2] | 400 | mh | | + | + | + | c.10 | c.20 | | 5 | 1 | | 75–120 | 7672:462 |
| 6[3] | 260 | mh | | | | | | | | 1 | | * | nm | 7657:482 |
| 7[4] | 250 | mh | | + | | | | 2 | 1 | | | * | 60 | 7672:449 |
| 8 | 290 | ph | | | | | | 1 | 2 | | | + | nm | 7658:479 |
| 4b | 320 | ph | | | | | | | 1 | | | | 80 | 7658:480 |
| 9[3] | 280 | ph | | | | | | 1 | | | | | nm | 7652:482 |
| 10 | c.250 | w | | | | | | | 1 | | | + | 60 | 7703:586 |
| 11 | 250 | w | 5 | + | 7 | 2 | | 8 | 3 | 1 | 1 | + | 30–80 | 7659:486 |
| 12 | 470 | ph | | | | | 1 | | | | | | nm | 7640:375 |
| 13 | 380 | dh–mh | | | | | | | 1 | | | | nm | 7626:364 |
| 14[5] | 290 | dh | | | | | | | 1 | | | * | nm | 7588:352 |

Ft = Forest types: lh = lichen heath (sEliT or MCClT), dh = dry dwarf shrub heath (sEMT or UVET), mh = moist heath (CoEMT or LMT), ph = paludified heath normally dominated by *Betula nana*, w = wetland. Rb = Rooted branches. Ps = Pine status: + = scattered, * = forest-building. 5-year-growth: nm = not measured.

[1] Part of the stand on a stony, weakly paludified lichen heath.

[2] Trees impossible to count due to the density of the clone.

[3] Previously unknown.

[4] On a riverbank.

[5] On the shore of a lake.

Fig. 4. The main part of stand 17, consisting of mixed birch-spruce woodlands (forest site type EMT-sEMT) on the level foreland of Kuusivaara.

one dead, stands on a moist heath close to the pine timberline (Fig. 3). Only one live stand (1, two small spruces 45 m from each other) in the pine forest region grows on dry heath without contact to surface water. Two of the large stands (15, 18) are mixed spruce-pine woodlands. The third one (16) represents a spruce swamp. These stands are relatively compact. No secondary stands were found nearby, in spite of the predominance of generative reproduction and frequent occurrence of spruce seedlings in the vicinity of the stands.

The eleven stands encountered north of or above the pine forest limit cover the entire range of available site conditions, from lichen heaths (2) to wetlands (10, 11) and from the vicinity of pine forests (8) to the birch timberline (5) and open tundra (12). Four stands (9, 10, 12, 13) are lone spruces, which so far have not reproduced vegetatively. Six stands (2, 3, 4, 5, 8, 11) represent various stages of clone formation; stand 11 has also recently started to reproduce generatively. Stand 5 is still faithfully depicted by sketch map of Sandberg (1898). Stand 17 is a case in itself: a diffuse conglomerate of substands, spanning an area of about 2 km$^2$ and showing both vegetative and generative reproduction. Apparently, it started as a clone near the top of the hill (17a) about 500 years ago (evidence: still largely undecayed remains of an old, very big spruce, lack of remains of still older trees, see Appendix). The tallest spruces are on a slope mire (17b). The most rapid expansion is taking place on a level heath northeast of the hill, where various substands have merged to form a semi-continuous spruce-birch woodland of about 0.5 km$^2$ (Figs. 3 and 4). The prevailing site type of this substand is intermediate between sEMT and EMT. The stand is surrounded by several smaller outposts. Stands 6, 8, 9 and 11 are only 2–5 km from stand 17, and can thus be regarded as parts of the same diffuse occurrence (Fig. 3). Except for stand 9 (a previously unknown lone spruce), the stands above or north of the pine forest limit are striking features of the landscape, as the spruces are about twice as tall as the co-occurring mountain birches and occassional stunted pines.

The Luovvusvárri stand, sown in 1933, has survived well. Growth rate has been fairly high since 1970, especially in the most mesic sites. (see Appendix). Several spruces have started to reproduce, and spontaneous seedlings occur in the stand and its vicinity. The patches of equally old planted or sown *Picea abies* forest ('fredsskogene') along the Atlantic coast have grown considerably better than the Luovvusvárri stand (S. Spjelkavik and T. Dahl, pers. comm., own observations).

A stand of 14 planted larches (*Larix sibirica*) (triangle in Fig. 2) was encountered in the northeastern part of the Anarjávri basin, within the pine forest limit. The stand lies on potential lichen heath, though lichens are largely excluded by larch detritus (Appendix). The larches have already overtopped surrounding pines and continue to grow.

## DISCUSSION

The spruce stands within the pine forests of the Anarjávri lowlands are either composed of stunted specimens or occur in sites influenced by running water. The same is true of the relatively large, isolated spruce forest of Ivalo (Avvil), marked as a hatched circle in Fig. 2 (Kallio et al. 1971). In the bigger stands (15, 16 and 18), spruces reproduce generatively. Nevertheless there are no signs of rapid expansion (neither secondary stands nor wide zones with young trees around the core of the occurrence). Moreover, spruces do not form sufficiently dense stands to locally outcompete pines. A fundamentally different scene is displayed by the spruce outposts within mountain birch forests. Their distribution is haphazard with regards to site and altitude, indicating that spruces can survive and grow wherever their seedlings have become established. The Kuusivaara (Guossačorro, 17) stand is expanding, as demonstrated by the numerous secondary stands around the oldest one (17a).

The sown spruces of Luovvusvárri indicate that spruce seedlings can survive, grow and reproduce in typical heathland habitats in the interior parts of the fjordland of northernmost Norway. The increase in growth rates in early 1970s suggests that spruce seedlings require a critical size before starting to grow at a reasonable rapid rate in the conditions of northernmost Fennoscandia.

The isolated stands illustrate the problems that spruces have in crossing dispersal barriers. Due to the self-incompatibility of *Picea abies*, outposts created by a single dispersal event cannot normally produce seedlings. Moreover, well-growing spruces established at optimal sites normally lack branches with ground contact. Thus, they cannot reproduce vegetatively, either, unless they become felled by winds when still vigorous and manage to form secondary roots and tops along the trunk. The more likely fate of such isolated spruces is that they thrive as individuals but die without leaving offspring, as illustrated by the dead lone spruce of Kuosmusvaara (6).

The evidence summarized above and by Kullman and Engelmark (1991) suggests that all three hypotheses contain some realistic elements. Conditions prevailing in rain shadow areas of northern and central Fennoscandia appear indeed to be continental in a way which is periodically stressful for spruces (Kullman 1989, 1991b). Yet, spruce clones established in continental mountain birch forests appear to be practically immortal. Moreover, except for clones at or above the birch forest limit, the northern outposts are dominated by seemingly vigorous trees with regularly shaped crowns, whereas at their limits of physiological tolerance spruces normally grow as clusters stunted specimens with dead tops, irregular crowns and clear abrasion layers at the snow surface (Haapasaari 1988, ff. 103 & 104, see also Norin 1961, Payette et al. 1985). Moreover, spruces in the northern outposts normally overtop surrounding mountain birches by broad margin (above, Kullman & Engelmark 1991, f.3) and thus do not resemble the uppermost and westernmost spruce stands in Västerbotten where spruces are only slightly taller than mountain birches and have most of their needles below the foliage height of mature birches (own observations). Spruces thus seem to be able to defend established positions in northernmost Fennoscandia against the rigours of the physical environment and against mountain birches.

The structure of the Kuusivaara occurrence suggests that there are areas within the current mountain birch formation which could develop towards mixed spruce-birch forests if invading spruces became cross-fertilized. Notice, however, that the Kuusivaara area is elevated and indications of permafrost (such as palsas in wetlands) do not occur (own observations). The case of Kuusivaara must thus not be uncritically genralized to lowlands in the rain shadow of the Scandinavian mountains where spruces appear to be restricted to edaphically moist sites (Kullman & Engelmark 1990). Kullman and Engelmark also present other arguments for relative stability of the spruce limit in northernmost Swedish Lapland. They point out that no advances can be documented by comparing the current spruce limit with historical records obtained 100–150 years ago, and they demonstrate that the age structure of these spruce outposts is approximately log-linear, which they regard as evidence for stability.

These arguments for the stability are, however, somewhat unconvincing. Kullman & Engelmark (1991) studied subjectively selected spruce stands, whereas firm conclusions on habitat distribution would require random sampling or systematical studies of all outposts within a given area. Moreover, it is not self-evident that advances of spruces could be detected in the time scale of 100–150 years without detailed maps as a point of reference. The rarity of old spruces and virtual absence of dead ones in the stands studied by Kullman (1991a) and Kullman & Engelmark (1991) indicates recent advances of the spruce limit, as noted by Kullman & Engelmark (1990) themselves. The log-linear age structure, in turn, indicates constant rate of population growth and constant mortality across age classes, not stability of population size. Log-linear age structure could be generated, for example, by exponential population growth and zero mortality.

Available evidence thus appears to suggest that spruces might be able to invade continental mountain birch forests after penetrating across the pine-dominated lowlands with periodic permafrost. The rate of expansion seems, however, to be very slow, and the geographical extent of potential spruce forest areas currently occupied by mountain birches is unclear. The occurrence of potentially larch-dominated areas in Fennoscandian rain shadows is purely conjectural. Studies performed so far must thus be regarded as only a modest beginning in our effort to understand the role of historical and ecological factors in shaping out the continental mountain birch forests in Fennoscandia.

## Management perspectives

It might be possibile to grow spruce within parts of current subcontinental and suboceanic mountain birch forests. In the most continental basins and valleys of northern Fennoscandia, Siberian larches could provide an interesting alternative for forestry. There is, however, need for further descriptive and experimental studies, before we can judge whether and where such forestation projects are viable, and whether they are desirable anywhere. The ability of spruces to grow above the pine forest limit on highlands warns against attempts to convert high-altitude spruce forests to pine (or larch) forests by clear-cutting and planting. Highlands with snowy winters, largely unfrozen ground and relatively humid summers provide conditions where spruces are likely to outperform pines and larches. Moreover, some high altitude spruce forests might be defending positions in an area which only mountain birches can invade under current climatic conditions.

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## APPENDIX

Descriptions of isolated spruce stands with more than 100 trees, the sown Luovvusvárri spruce stand in northernmost Norway and the planted larch stand of Järvenpää, Inari. The numbers after the stand name refer to position in the Finnish uniform cooordinate system.

*Stand 15, Peskaoja (Beaška-aja, 7657:496)* Relatively large (25 ha) stand on moist heath (LMT), herb-rich vegetation locally present along a creek, part of the stand on a mire. Mixed pine-spruce forest. Altitude 230 m, within pine forest limit. Tallest spruces 17–18 m, maximum breast height circumference 107 cm, maximum recorded breast height age 170 yr. Vigorous stand, consisting on monocormic, regularly shaped trees. No abrasion layer at snow surface. Seedlings and young spruces common within the stand and in the surrounding area; vegetative reproduction uncommon. Trunks of dead spruces present.

*Stand 16, Pesälahti (Beasseluokta, 7660:491)*. Small patch (1 ha) of densely forested spruce swamp within a sedge-willow mire. Altitude 200 m, well within the pine forest limit but in a site, where pines do not grow. Maximum height of spruces 15 m, maximum breast height circumference 116 cm, maximum breast height age 265 yrs. Shapes of spruces variable, normally with clear abrasion layer at snow surface. Seedlings common but have difficulty getting above the snow surface (often malformed and/or with dried tops). Vegetative reproduction uncommon. Dead trunks common.

*Stand 17, Kuusivaara (Guossačorro 7657–7659:484–486)*. A large, diffuse occurrence, consisting of a large number of more or less distinct substands (Fig. 3). Spruces are mainly encountered as subordinate components of various types of mountain birch forest (Fig. 4). Latitudinally at the pine forest limit, vertically above it, with relatively few pines with maximum height of about 10 m. Spruces reproduce both generatively and vegetatively. Within the ocurrence, there are two relatively dense stands. *Stand 17a, sEMT heath* near the top of the hill (altitude 300 m), appears to be the core of the entire occurrence. It consists of about 20 full grown trees with varying shapes (maximum height 15 m, maximum breast height circumference 127 cm, maximum breast height age 155 year) and of remains of a few equally tall but still thicker dead spruces (height of the largest dead specimen had been about 15 m, breast height circumference 146 cm; the circumference of a still thicker, partially living spruce could not be measured, due to dense cover of hanging branches). *Stand 17b, slope mire* (altitude 260 m), is exceptionally dense and consists of about 40 spruces, mostly monocormic and with regular shapes, growing in a moist *Betula nana* scrubland. The trees are tall (maximum height 17 m, maximum breast height circumference 121 cm), but relatively young (maximum breast height age 115 yrs). No remains of dead trees were found.

*Stand 18, Siuttajoki*. Mixed pine-birch-spruce forest. The stand is a mosaic of moist heath forest (LMT) and meadow forest (GMT), partially paludified. Altitude 155 m. About 200 spruces, the majority well-growing, with regular crowns. Seedlings present, vegetative reproduction uncommon. Not visited. Information from Kallio et al. (1971) and P. Kallio (pers. comm.)

*The sown spruce stand of Luovvusvárri*. Location: Porsanger munincipality, Finnmark county, Norway (square in Fig. 10), on both sides of E6 highway 8 km south of Skoganvárri, latitude 69° 45′, altitude 270 m. The stand lies above the current pine forest limit, but pines were present before the war. Sown in 1933 from seeds collected in Helgeland, 300–400 m.a.s.l. (Ruden, pers. comm.). Forest type: mainly dry heath, intermediate between sEMT and sELiT, coverage of fruticose lichens up to 40%; a small part of the stand in a more mesic site (intermediate between sEMT and CoEMT). In 1974, the stand consisted of several hundreds of spruces. The heigt of the tallest one (in a moist site) was 5 m, length growth during 1969–1974 was 230 cm. Trees on dry sites were 1–3 m tall, length growth during 1969–1974 in our sample ranged from 33 to 140 cm. The stand was partially thinned. In the thinned part, the spruces had regular crowns, except for occassional double tops, due to snowbreaks. In the unthinned part, spruces grew as dense groups and had frequently irregular shapes. Some spruces had brown lower branches, due to fungal diseases, but most were healthy. The stand had produced numerous 20–30 cm tall seedlings. Vegetative reproduction was not observed.

The stand was revisited in 1994. I then measured the lengths and breast-height circumferences of ten uppermost spruces (site sELiT), ten spruces immediately below the road (site sEMT), and ten spruces furthest down the slope (site sEMT-GMT). In the upper group, the heights of the spruces ranged from 3.2 m to 6.2 m (mean 4.1 m, standard deviation 1.1 m). Breast-height circumferences ranged from 6 cm to 32 cm (mean 18 cm, standard deviation 8 cm). In the middle group, heights ranged from 4.6 m to 7.8 m (mean 5.7 m, standard deviation 1.3 m). Breast-height circumferences ranged from 17 cm to 47 cm (mean 30 cm, standard deviation 12 cm). In the lower group, the heights of the spruces ranged from 4.4 m to 8.5 m (mean 6.3 m, standard deviation 1.4 m). Breast-height circumferences ranged from 17 cm to 51 cm (mean 34 cm, standard deviation 10 cm). The stand was partially overdense; competitive suppression accounted for the variability of tree sizes within each group. Except for specimens growing too close to each other, spruces had regularly shaped crowns. No snow-breaks were observed, and there were no indications of abrasion layer along the snow surface. Spruces had started to overtop mountain birches growing in the same area. Seedlings were common. The development during 1974-1994 indicates that spruces are capable of becoming dominating trees in the conditions prevailing on the highland between Skoganvarre and Karasjok.

*The planted Larix sibirica woodlot of Järvenpää (Jávrregeahčči)* Location: NE-end of Suolisjärvi (Čuolisjávri), Inari, Finnish Lapland. Altitude ca. 160 m; within the pine forest limit. 14 specimens as an overdense stand on an area of 9 by 6 m in pine forest near the Järvenpää house, on dry heath (probably MCClT — difficult to determine, due to copious amounts of larch needle detritus, giving very little space for dwarf shrubs and lichens to grow). Age of the plantation unknown. Straight specimens with regular trunks, growth rates vary due to intense competition. Heights range from 4.75 to 9.75 m, generally taller than the surrounding pines, breast height circumferences range from 12.5 to 46.0 cm. No seedlings or vegetatively produced offspring observed; one larch has a branch which lies partially buried in detritus, but the tip protudes up — probably initial stage of vegetative reproduction. In addition, there is one 4.8 m. tall specimen on grassy field at the Järvenpää house, with several trunks, breast-height circumference of the main trunk 36 cm.