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Response of Scots Pine (*Pinus sylvestris*) to Warming Climate at Its Altitudinal Limit in Northernmost Subarctic Finland

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ABSTRACT. The present study aims to contribute to a fine regional differentiation of Scots pine (*Pinus sylvestris*) response to climate change at its altitudinal margins in subarctic Finland north of 69˚ N (Utsjoki) and to find out whether a prompt establishment of new pines in response to climate change can be expected above the old pine tree limit in and above the mountain birch zone. In 10 sampling areas, distribution, site characteristics, and condition (damage degree, growth forms) of the new pines (pines that have become established since the mid 20th century) were checked in a zone 50 m to the left and right of our field routes. The field routes extended from the scattered birch forest to the treeless alpine zone and mountaintops and covered a total area of more than 4 km^2. In total, 213 new pines were found. Tree height was measured and age estimated by counting the whorls. The degree of damage was estimated and then attributed to four damage classes. Pine establishment was most successful during the 1970s and up until the end of the last century. Pines younger than 10 years are rare (< 3%) in the study areas, with one exception (about 8%). Pine recruitment is comparatively intense in close proximity to old pines in the birch forest while it is sporadic within the scattered birch stands at higher elevations and in the alpine tundra. More than 80% of the new pines show disturbed growth forms due to frequent winter injury, reindeer, and moose. About 66% exhibit severe damage, and 15% have already died. On windswept terrain, microsite facilitation is essential for pine establishment. Lack of local seed sources and severe site conditions at high elevations have probably delayed pine altitudinal advance. New pine generations may become effective seed sources speeding up pine advance beyond the present seed trees. In view of the high proportions of severely damaged and dead new pines, we do not expect that climatic warming will bring about a rapid advance of the pine tree limit.

Key words: Scots pine, *Pinus sylvestris*, tree-limit, climate change, regeneration, growth forms, winter injury, reindeer damage, microsite facilitation

RÉSUMÉ. La présente étude vise à contribuer à une fine différenciation régionale de la réponse du pin écossais (*Pinus sylvestris*) au changement climatique à l'emplacement des marges altitudinales de la Finlande subarctique au nord du 69˚ N (Utsjoki) et à déterminer si on peut s'attendre à l'établissement rapide des nouveaux pins en réponse au changement climatique au-dessus de l'ancienne limite des pins située dans la zone des bouleaux de montagne et au-dessus de celle-ci. Dans dix lieux d'échantillonnage, la répartition, les caractéristiques du site et les conditions (ampleur des dommages, formes de croissance) des nouveaux pins (soit les pins qui se sont établis depuis le milieu du siècle précédent) ont été vérifiés dans une zone située à 50 m à la gauche et à la droite de nos voies d'accès. Ces voies commençaient à partir de la forêt parsemée de bouleaux et s'étendaient jusqu'à la zone alpine dépourvue d'arbres et aux pics montagneux. Elles couvraient une surface totale de plus de 4 km^2. En tout, 213 nouveaux pins ont été répertoriés. Nous avons mesuré la hauteur des arbres et évalué leur âge en comptant les verticilles. Ensuite, nous avons estimé le degré des dommages et les avons attribués à quatre catégories. L'établissement des pins a connu le plus de succès dans les années 1970 et jusqu'à la fin du dernier siècle. Les pins de moins de dix ans sont rares (< 3 %) dans les aires visées par l'étude, sauf une exception (environ 8 %). Le recrutement des pins est comparativement intense à proximité des anciens pins de la forêt de bouleaux, tandis qu'il est sporadique dans les peuplements de bouleaux épars des hautes altitudes et de la toundra alpine. Plus de 80 % des nouveaux pins affichent des formes de croissance instables attribuables à la destruction par l'hiver de même qu'à l'activité des rennes et des orignaux. Environ 66 % d'entre eux présentent des dommages prononcés, tandis que 15 % d'entre eux sont morts. Sur le terrain exposé au vent, la facilitation des niches écologiques est essentielle à l'établissement des pins. Le manque de sources de graines locales et les conditions sévères aux emplacements en haute altitude ont probablement eu pour effet de retarder l'avancement des pins en altitude. Les nouvelles générations de pins sont susceptibles de représenter des sources efficaces de graines, ce qui aurait pour effet d'accélérer l'avancement des pins au-delà des arbres semenciers actuels. À la lumière des fortes proportions de nouveaux pins gravement endommagés ou morts, nous ne nous attendons pas à ce que le réchauffement climatique se traduise par l'avancement rapide de la limite forestière des pins.

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Mots clés : pin écossais, *Pinus sylvestris*, limite des arbres, changement climatique, régénération, formes de croissance, destruction par l'hiver, dommages causés par le renne, facilitation de niche écologique

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INTRODUCTION

The warming after the Little Ice Age, in particular during the 20th century, has resulted in tree line rise in many regions of the Northern Hemisphere (see Holtmeier, 2009; Holtmeier and Broll, 2010). In Scandinavia and Finland, the tree line occurs as an altitudinal boundary. Because of its high latitudinal position, it is located at comparatively low elevations. The tree line has been advancing in pulses. Infilling of treeless gaps by new trees within the tree-line ecotone and tree establishment beyond the existing tree limit peaked during the favourable period from the 1920s to the 1940s (e.g., Hustich, 1937, 1942, 1948; Blüthgen, 1942) and resumed, after a break, in the 1970s. However, warming and tree-line advance were not always synchronous, and they occurred at different regional and local intensities (e.g., Kullman, 2001, 2004, 2007a, b; Juntunen et al., 2002; Holtmeier et al., 2003; Dalen and Hofgaard, 2005). Up until the 1960s, most pines that had invaded the alpine tundra in northernmost Finland during the favourable 1920s to 1940s were still protected under the winter snowpack. When they began projecting above the winter snowpack, they became heavily damaged by climatic influences. Thirty years later, most of the surviving pines (and also spruce on the more southern mountains) showed more or less disturbed growth forms or else had died (Kallio et al., 1971; Holtmeier, 2005a). Thus, the optimistic assumption that tree lines were progressing to their Holocene maximum positions, made by Blüthgen (1942) in view of abundant young growth during the favourable 1920s to 1940s period, had not materialized.

During the last three to four decades, new pines have become established at and above the upper limit of mature pine forest within the mountain birch tree-line ecotone and even in the alpine dwarf shrub–lichen heath on the mountains. Current climate change seems to be the driving factor (Juntunen et al., 2002; Autio and Colpaert, 2005; Holtmeier, 2005a; Juntunen and Neuvonen, 2006; Paus, 2010). The question now is whether these "young" trees will develop, and if so, whether they indicate a general lasting altitudinal advance of the pine limit in the long term, as is expected, for example, for the Swedish Scandes (Kullman, 2001, 2004, 2007a). However, varying local site and growing conditions (e.g., topographically controlled redisposition of snow and its side effects, moisture, availability of nutrients, damage caused to new pines by reindeer [*Rangifer tarandus*], moose [*Alces alces*], and the mountain hare [*Lepus timidus*]) may impede or even prevent pine expansion, thus overriding the positive effects of increasing temperature. The aim of the present study is to contribute to a fine regional differentiation of Scots pine response to climate change at its margins in subarctic Finland.

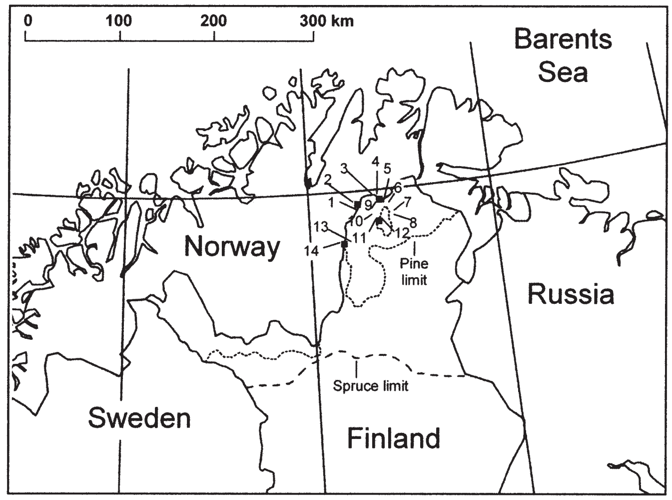

FIG. 1 Location of the study areas, villages mentioned in the text, and the Kevo Subarctic Research Station: 1) Rodjanoaivi (509 m), 2) Levajok village (Norway), 3) Kohappeloaivi/Staloskaidi (420 m), 4) Utsjoki village, 5) Ailigas (342 m), 6) Puollamoaivi (432 m), 7) Tšahkaltšohkka (376 m), 8) Kiđesjoktšielgi (335 m), 9) Riikkavarri (305 m), 10) southern drainage area of Pâdjeseävtteg (200–280 m, east of Utsjoki valley), 11) Jesnalvarri (330 m), 12) Kevo Subarctic Research Station, 13) Lánká (620 m), and 14) Karigasniemi village. The northern distribution limits of continuous pine and spruce forests are shown for Finland only. Local outliers of the boreal pine forest in northern Norway (cf. Hustich, 1958) are not considered.

STUDY AREAS

The northernmost study areas are located on mountains at nearly 70° N within the subarctic mountain birch zone (*Betula pubescens* ssp. *czerepanovii*) north of the continuous limit of the boreal pine forest (Fig. 1). We call the study areas located south of the Tenojoki valley and west and east of the Utsjoki valley "northern mountains" to distinguish them from Lánká Mountain, located farther south near Karigasniemi, which at 620 m is 200 to 300 m higher than the northern mountains.

On the northern mountains, mountain-birch forest gives way to open birch stands at an elevation of about 240–300 m. Birch groves and climatically stunted solitary birches can be found up to about 380 m. The upper pine limit formed by solitary trees is located within the birch forest at a lower elevation. Pines, a few of them several hundred years old, can be found there on the valley sides and in the valley head of the small tributary streams up to 240–260 m and locally even higher. Pines dating from the early and mid 20th century predominate. Pine afforestations dating from 1928 to the late 1960s (Holtmeier, 1974) are located on the river terraces in the Tenojoki and Utsjoki valleys. The afforestations, as well as the solitary old pines, act as seed sources that can also provide higher elevations with pine seeds.

On the western and southern sides of Lánká Mountain, the upper limit of scattered birches and birch groves is located at about 400 m. Solitary mature pines can be found up to about 350 m.

The only meteorological station that has continuously recorded weather data (since 1962) is located at the Kevo Subarctic Research Station in the relatively wind-protected Utsjoki valley (Fig. 1). The climate is subcontinental, with a mean annual temperature of -1.6˚C and mean annual precipitation of 415 mm (maximum July, minimum March). Summer temperatures are lower on the mountains than at the Kevo station because of the higher elevation and much windier conditions. Sudden changes in weather conditions are typical of subarctic Finland. In the winter, Atlantic air masses may cause the temperature to rise from -30˚C to above freezing within a few hours. In summer, by contrast, cold air from the Barents Sea may cause a sudden drop in temperature to below 5˚C.

Annual growing season mean temperatures (Fig. 2) at Kevo reflect relatively cool summers throughout the 1960s. After a prominent peak in the early 1970s, mean temperatures fluctuated around the mean of the period 1962–2008. From the end of the 20th century up to present, they have continuously been ranging above the average except in 1998 and 2008. Also, mean monthly winter temperatures (October–May) fluctuated greatly during the period from 1962 to 2008. Subsequent relatively warm winters with mean temperatures a little above the long-term average (7.3˚C) occurred from 1989 until 2008, except in 1998.

The study areas are characterized by more or less varying local topography. The soils, developed on sandy skeletal till, are usually acidic, well drained, and relatively poor in nutrients (Holtmeier et al., 2004; Broll et al., 2007; Anschlag et al., 2008). Hydromorphic soils have developed in shallow depressions. Some areas are covered with saprolite or have exposed bedrock.

METHODS

We had come across sporadic new pines accidentally during earlier field studies on the birch tree line (e.g., Holtmeier, 2005a; Holtmeier et al., 1996, 2003), so we expected that new pines had become established in the birch tree-line ecotone and lower alpine as a result of climatic warming during the last decades. We therefore checked the northern mountains and Lánká Mountain systematically for additional occurrences of new pines. The tree-line environment on these mountains is representative of this area. The field studies were carried out in 2007 and 2008.

We call all pines that have become established since the mid 20th century "new pines." These include seedlings and trees that have not yet reached conventional tree height (2 m; e.g., Juntunen et al., 2002). Much smaller pines may be 50 or even more than 100 years old.

All new pines were checked in a zone 50 m to the left and right of our field routes, which extended from the scattered birch forest to the treeless alpine zone and mountaintops. Most field routes were re-examined several times. Altogether, we examined an area of more than 4 km^2 and sampled a total of 213 new pines (including dead pines). The localities where new pines were found were marked on the topographic map and GPS data were taken. Pine regeneration at lower elevations (on the valley floors and lower mountain slopes) was not included. For characterization of the pine sites, we refer to our previous studies (e.g., Holtmeier et al., 2003; Holtmeier, 2005a).

In order not to destroy young pines by cutting for age control, we estimated their approximate age from the number of the whorls on the main stem. In young pines, age correlates well with the number of annual shoots (age = 1.069 · number of shoots; corr. Pearsson 0.63; SD = 20; Holtmeier et al., 1996; Müterthies, 2002). As a practical correction for the age at the early seedling stage, we added an extra seven years when whorls near the ground (< 15 cm above the surface) were not discernible. For severely stunted pines lacking the primary vertical leader, we counted the number of whorls on the second-order branches. However, heavily disturbed growth forms were often difficult or impossible to date reliably.

In addition to making detailed field notes on tree physiognomy, damage, and age, we took pictures of the pines for documentation and future comparisons. Some of the pines already checked before the last field campaign were revisited. They give evidence of sometimes rapidly changing tree physiognomy. The degree of damage was estimated according to the amount of needle loss and dieback of shoots and stems. Each tree was assigned one of four damage classes: undisturbed (0–10%), slightly to moderately disturbed (> 10–50%), severely disturbed (> 50%), and dead (100%).

RESULTS

Altitudinal Position of New Pines and Site Characteristics

Of 213 sampled new pines (dead pines included), 92 have established themselves above 300 m. The uppermost living new pine was found on Lánká Mountain at an elevation of 534 m (Fig. 3). Above 400 m, we came across many dead or seriously damaged pines dating from the favourable last decades of the 20th century. On the northern mountains (cf. Fig. 3), young growth of pine has become established mainly within the present birch tree-line ecotone, the upper specimens usually being between 260 and 340 m. Very few new pines have advanced to or beyond the upper birch tree limit. On Tšahkaltšohkka (376 m), a few new pines occur on the mountaintop. The uppermost living specimen (35 years old, 30 cm high) was found at an elevation of 412 m, just below the highest point of Koahppeloaivi-Staloskaidi (419 m).

In some places, a relationship between site characteristics and the distribution pattern of new pines is obvious.

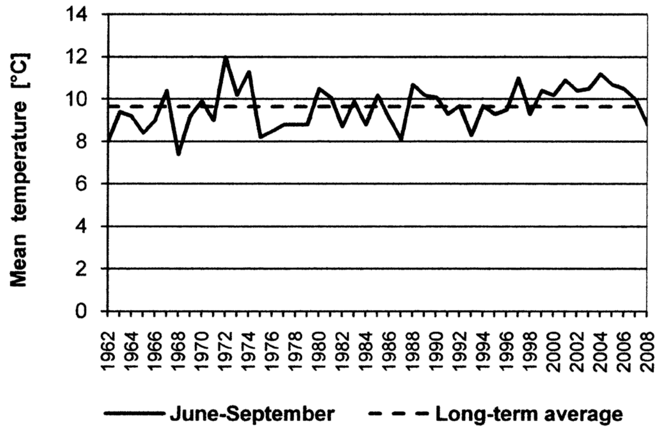

FIG. 2. Mean temperatures for June to September at the Kevo Subarctic Research Station, 1962–2008. (Data Kevo Research Station, 2009.)

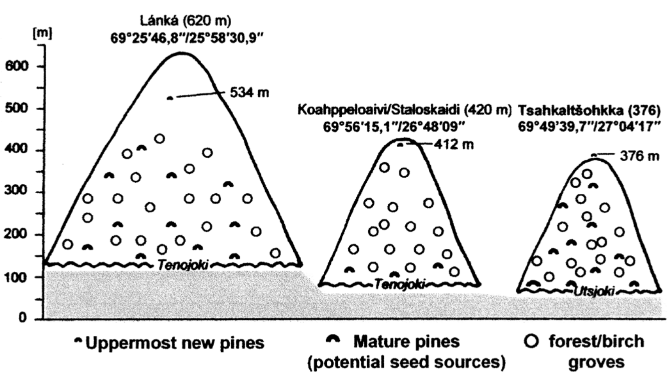

FIG. 3. Altitudinal position of the uppermost new pines found in the study areas.

Microsite types that facilitate pine establishment by providing shelter from the wind and accumulating snow in winter are shown in Figure 4. These types include (A) the lee sides of scattered blocks, (B and C) mountain birch stands, (D) leeward slopes of small ridges (e.g., eskers), and (E) bedrock clefts. Regarding the frequency of these different types of shelter-providing microsites with young pine occurrences, we must distinguish the closed birch forest from the upper zone of the birch tree-line ecotone, where windswept open terrain prevails. In the closed forest, Type C microsites dominate. In the zone above, Type B microsites are most common (ca. 40%), followed by D, A (ca. 20% each), and E (ca. 20%). Type E is restricted to windswept sites where erosion has exposed the crystalline, cleft-rich bedrock. The situation of pines will become critical when they begin to grow taller than the surrounding vegetation and microtopography (cf. Fig. 4A, B).

In our study areas, pines have not invaded sites with wind-eroded topography at high elevations in or above the birch tree-line ecotone. Such sites are relatively dry (highly permeable skeletal-sandy till, cf. Fig. 4D) and poor in nutrients, and they freeze to great depth in winter (Broll et al., 2007). Moreover, new pines were not found either at very snow-rich sites such as depressions and lower leeward slopes, or at foot zones of convex topography, where too short a growing season, snow blight infection (*Phacidium infestans*), or mechanical damage by settling snow and snow creep may destroy pine seedlings and saplings.

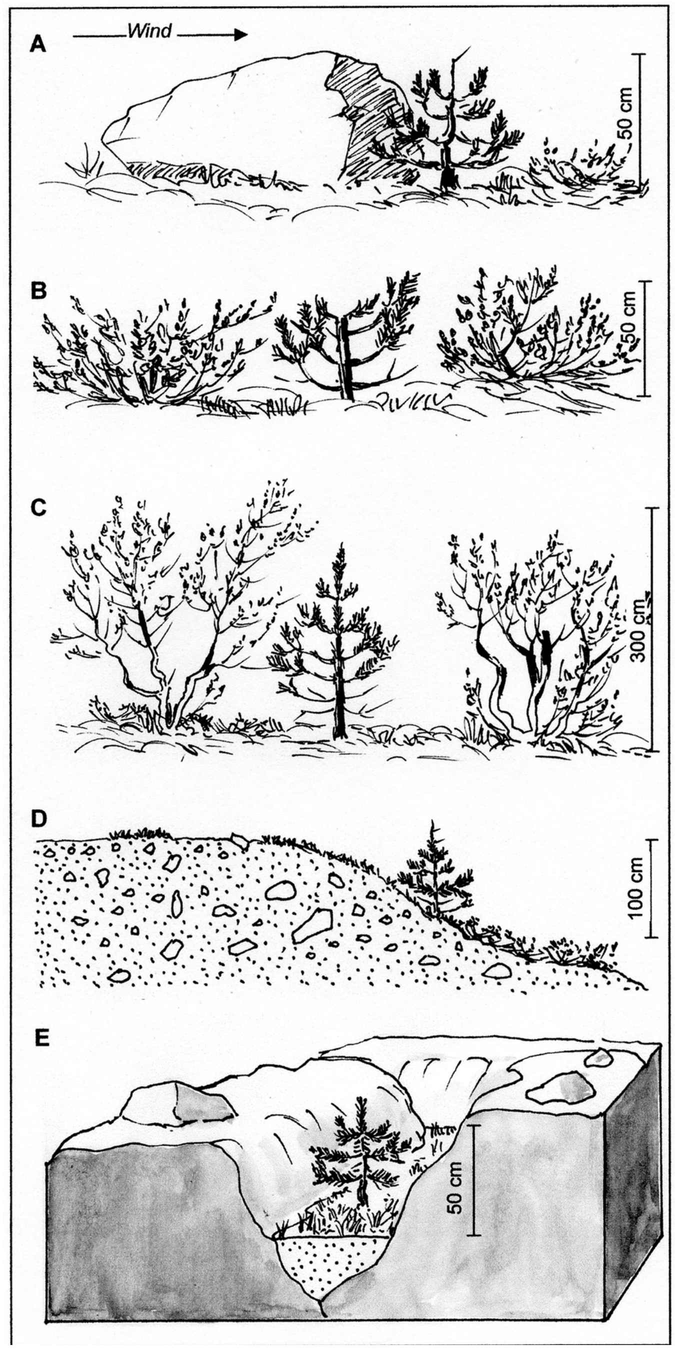

FIG. 4. Main types of microsite facilitation: A) block giving wind shelter to a new pine; B) dwarf birches (*Betula nana*) protect a new pine from wind as long as it does not project above the dwarf birches; C) within the stand of mountain birch (*Betula pubescens* ssp. *czerepanovii*), pines are not much affected by strong winds and may develop a normal growth form; D) on the lee slope of convex topography (esker), reduced wind velocity and accumulation of snow in the winter facilitate the establishment of a new pine; and E) in the bedrock cleft, the new pine enjoys warmer conditions and reduced mechanical and physiological stress caused by permanent winds. In winter, blowing snow accumulates in the cleft and is removed from the exposed bedrock surface. The snow protects the pine from winter climatic injury. Moreover, fine inorganic and organic matter accumulate in the cleft, improving moisture and nutrient supply for the pines

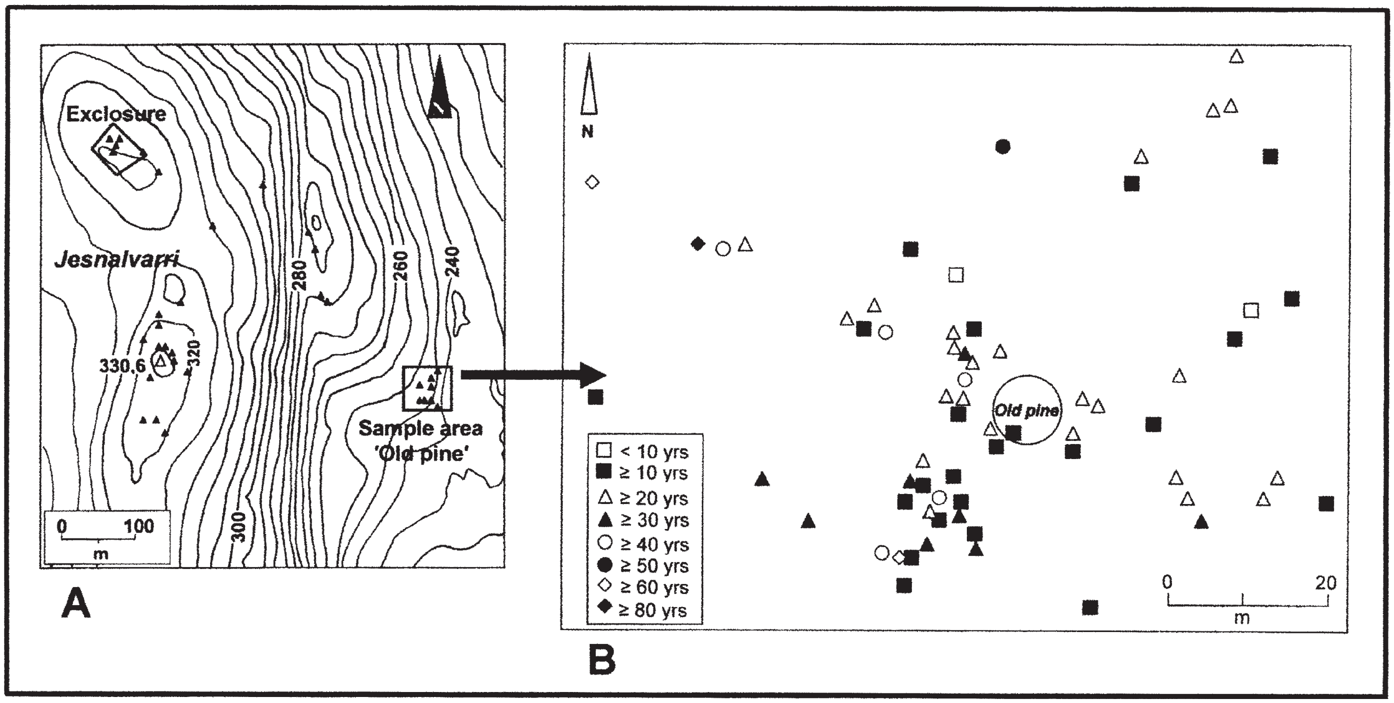

FIG. 5. Jesnalvarri, showing old and new pines. The old seed tree (B; cf. Fig. 6) and the pines that became established in the beginning or middle of the 20th century are very likely among the seed sources for the new pines on Jesnalvarri (A). The number of young pines around the old pine (B) rapidly decreases with the distance from the mother tree.

Seed Sources, Supply of Viable Seeds

On the northernmost mountains (Rodjanoaivi, Koahppeloaivi-Staloskaidi), old seed-producing pines are missing. On Rodjanoaivi, no living new pines were found although solitary mature pines appear in the Tenojoki valley, mainly near Levajok on the Norwegian side of the river. The few new pines that we found on Koahppeloaivi-Staloskaidi became established 3–4 km away from the nearest seed sources in the Tenojoki valley (Fig. 3).

The mountain slopes on both sides of the Utsjoki valley and its tributary valleys present a more favourable situation. In some places, old seed-producing pines occur up to an elevation of about 270 m, and locally even higher (e.g., at an elevation of 307 m on Kiđesjoktšielgi-Tšahkaltšohkka). In addition, a few new pines (about 30–40 years old; height about 50–60 cm) that became established within the birch tree-line ecotone during the second half of the 20th century have occasionally produced cones. As these trees do not usually rise above the birch stands, long-distance seed dispersal is unlikely. As a rule, the pine population within the mountain birch forest has been increasing mainly close to old seed trees (Fig. 5B; Fig. 6), while at greater distances from the seed trees, young pines are still sporadic.

On the west- and south-facing slopes of Lánká Mountain, the distance between the uppermost new pines (> 500 m) and the old seed trees at a lower elevation (350 m) is about 1–1.5 km. At an elevation of 440 m, we found one severely stunted multi-stemmed pine (height 120 cm, 60 to 70 years old) with a few cones on the lowest branches close to the ground. A higher number of new pines became established above the mountain birch tree line here than in the northern mountains.

FIG. 6. Old pine (ca. 400 years old) on Jesnalvarri at 240 m, with younger pines dating from the second half of the 20th century. The younger pines originated from seeds of the old tree (Photo: F.-K.Holtmeier, 31 August 2007).

Age Classes

Figure 7A shows the number of living pines per age class above the upper limit of mature pine stands on the northern mountains. On the mountains bordering the Tenojoki River (Rodjanoaivi, Koahppeloaivi-Staloskaidi, Ailigas) and also on Riikkavarri (260–320 m), new pines are still exceptional. On the other northern mountains (Puollamoaivi, Kiđesjoktšielgi-Tšahkaltšohkka, top of Jesnalvarri), pine recruitment has considerably increased during the last five

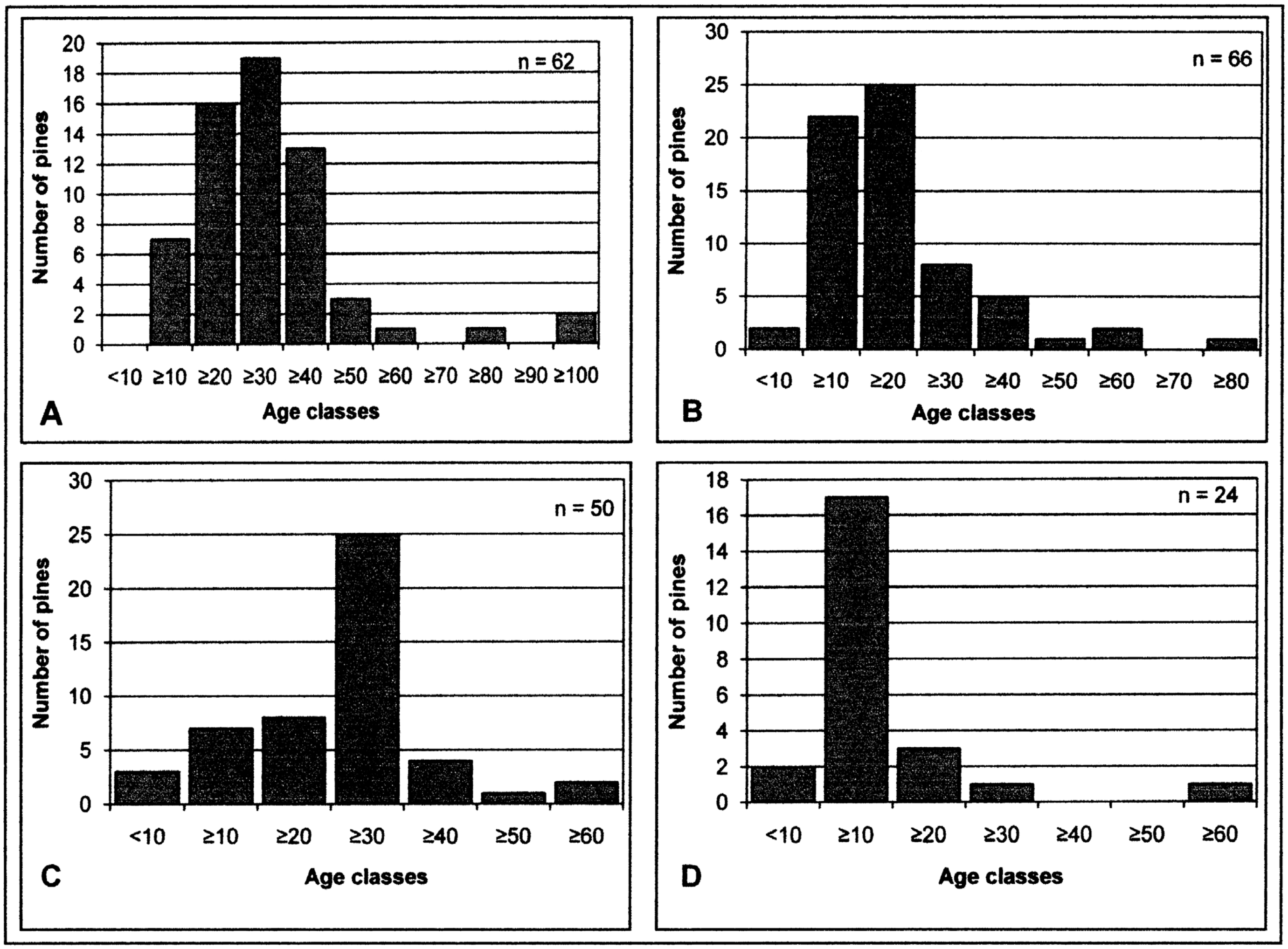

FIG. 7. Age distribution of living new pines. A) above the upper limit of old mature pine stands on the northern mountains (Koahppelolaivi/Staloskaidi, Ailigas, Puollamoaivi, Kidsjoktšieli/ Tšahkaltšohkka, Riikkavarri, Jesnalvarri top); B) the Old Pine site on the east slope of Jesnalvarri; C) the Pâdjeseävtteg site; and D) on Lánká Mountain.

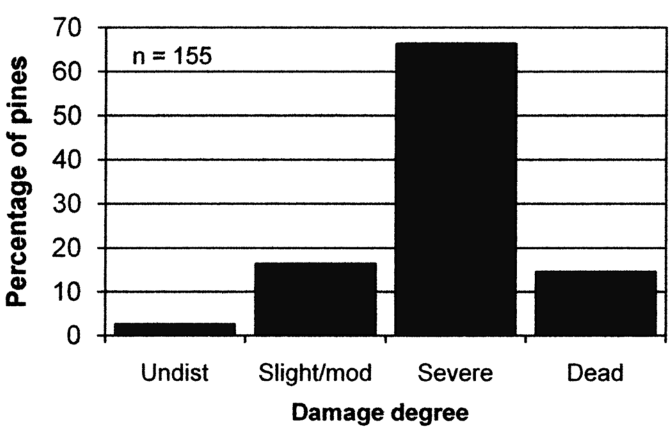

FIG. 8. Damage degree in new pines on the northern mountains and Lánká (without the Jesnalvarri Old Pine site and the Pâdjeseävtteg site). Undist = undisturbed, and Slight/mod = slightly to moderately disturbed.

decades, with peak recruitment from the 1970s to the turn of the century. Pines younger than 10 years appear to be very rare. At the upper limit of scattered mature pine stands on the east slope of Jesnalvarri (220 – 260 m, Fig. 7B; see also Fig. 6), pine establishment has gradually increased since the 1960s, and most of the new pines date from the late 1970s to the 1990s (see also Holtmeier, 2005a; Holtmeier et al., 1996). A few specimens established themselves during the last 10 years. In the Pâdjeseävtteg study area (200–280 m; Fig. 7C), pine has regularly regenerated since the late 1960s, with a peak during the 1970s. However, a few seedlings less than 10 years old were found. On Lánká Mountain (Fig. 7D) most of the scattered pines date back to the 1990s. A few older specimens dating from the mid 20th century were found in the upper birch tree-line ecotone and in the alpine tundra, but new seedlings less than 10 years old are rare.

Growth Forms and Damage Degree

Most new pines growing within and above the birch tree-line ecotone are shaped by climatic injuries and other external factors. The height of the pines is highly variable, even in trees of the same age. More than 80% of the new pines exhibit disturbed growth forms (Fig. 8). On all mountains (Lánká Mountain included), only about 7% of the new pines (≤ 60 yr) found at an elevation above 300 m had attained 2 m in height, while at lower elevations, 37% (Jesnalvarri "Old pine area") and 26% (Pâdjeseävtteg site) had reached or exceeded this size.

In all of our study areas, the local wildlife species (reindeer, moose, mountain hare), as well as climatic injury, impede new pines from developing their "normal" growth form. A few pines growing within the more than 30-year-old fenced exclosure (IBP site) on the windswept top of Jesnalvarri have escaped damage by mammalian herbivores and show symmetric growth. The oldest and tallest of these pines has reached more than 3 m in height even though there is no shelter from the prevailing strong winds.

Conspicuous annual shoot elongation was measured in pines 40 to 50 years old at the Pâdjeseävtteg site (200 – 280 m). Up to the end of the 20th century, these pines had survived as suppressed shrubby growth forms no higher than about 100 cm. The strongest terminal leaders have shot up since the late 1990s, reaching 200 – 250 cm in height in 2008. Maximum shoot extension occurred in 2005. In some pines, the annual shoot of 2005 measured more than 30 cm in length.

Relatively long annual shoots from 2005 are also common in many pines in the other study areas, irrespective of different site conditions and age class. Annual shoot extension corresponds to the mean temperatures in July and August of the previous year ($r^2 = 0.51$ $p = 0.03$; Fig. 9), and this growth pattern was obvious in 42 of 48 randomly sampled pines from six different places. In the other new pines, shoot elongation was different because of other factors that we were not able to identify.

In many new pines, even in exposed sites, living terminal shoots and needle foliage appear relatively healthy when not affected by reindeer or other herbivores.

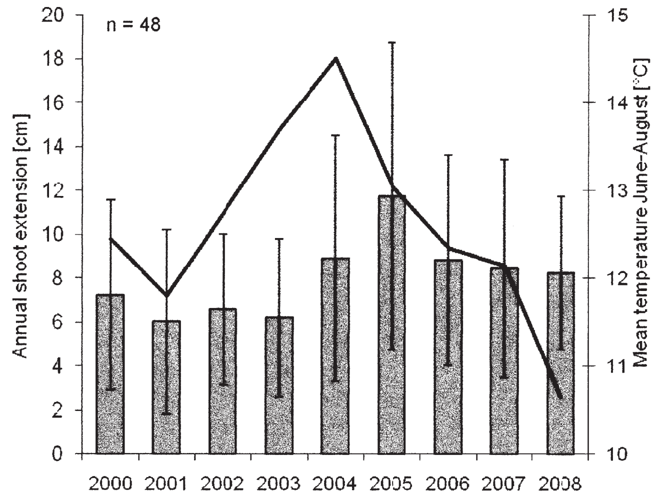

FIG. 9. Annual extension (with standard deviation) in randomly sampled new pines corresponds ($r^2 = 0.51$ $p = 0.03$) to the mean temperature July-August of the preceding year at the Kevo Subarctic Research Station. The very warm summer in 2004 caused maximum shoot extension in 2005. (Data Kevo Research Station, 2009.)

DISCUSSION

Altitudinal Position of New Pines and Thermal Conditions

The uppermost living new pine was found on Lánká Mountain at an elevation of 534 m (Fig. 3) while Luoto and Seppälä (2000) reported pine seedlings (up to 60 cm high) occurring even at 600 m on the mountaintop. However, we did not find any specimen there. The relatively low upper limit of pine young growth on the northern mountains is the result not only of the higher latitude, but also of the low elevation, compared to the Lanká Mountain or to the high mountains in western Central Finnish Lapland (e.g., the Pallastunturi area). On these high mountains, microtopography facilitates establishment of pines far above the elevation of the tops of the northern mountains (Holtmeier, 1974).

Pine advance to greater elevations and increasing pine recruitment around old seed trees appear to be promoted by climatic warming (Holtmeier and Broll, 2007). Although correlating growth processes such as annual shoot extension with temperature data from Kevo is problematic because the meteorological station is located about 150 – 270 m below most of the sampled new pines, it would appear that mean monthly temperatures at higher elevations have been fluctuating similarly to those at Kevo. Conspicuous above-average shoot elongation with a maximum in 2005, as well as the presence of three to four generations of healthy, bright-green needle foliage, even in otherwise strongly distorted pines, may reflect improved thermal conditions.

New pines, being still of short stature, are living in a comparatively warmer ground surface microclimate, which is almost decoupled from the free atmosphere (e.g., Wegener, 1923; Grace, 1988). They also enjoy facilitation by microtopography (saprolite, blocks, hummocks, etc.) and dwarf-shrub vegetation.

Age Structure, Reproduction, Seed Sources, and Establishment

Altogether, establishment of new pines within and above the upper birch tree-line ecotone has not been very intensive. It was most successful from the 1970s to the end of the last century. In all study areas, there are fewer trees under 10 years old than can be found in mature stands at lower elevation.

Although pine reproduction and establishment are controlled by thermal conditions, they obviously do not require exceptionally warm summers, as we can conclude from the age of the new pines in our study areas, where pines became established just as successfully during the less favourable periods from the mid 1970s through the 1980s (see also Juntunen et al., 2002; Juntunen and Neuvonen, 2006). Furthermore, cold spells (mean day temperature < 5°C) that occurred with relatively high frequency during the growing season from the mid 1980s to the early 1990s (F.-K. Holtmeier, unpubl. data) did not impede regeneration. However, the relatively warm summers—in particular, June, July, and August in 1972 – 74 and some above-average summers (mainly June and August) during the 1990s and in 2004—are likely to have favoured production of viable seeds and seedling establishment. However, we found only a few new pines dating from the relatively favourable last decade. The impact of natural factors (climate, reindeer, moose, snow fungi) cannot explain with certainty the comparatively low number of very young pines (< 10 yr). We may have overlooked small pines that were not noticeable among dwarf shrubs.

Pine recruitment varies locally. This variation is attributed to factors having negative effects on seed germination, seedling establishment, growth, and survival: missing or insufficient microsite facilitation; uprooting by frost-heave; competition for light, nutrients, and moisture with the dwarf-shrub vegetation; or allelopathic effects of the associated dwarf shrubs (*Empetrum hermaphroditum*) and lichens (in particular, *Cladonia stellaris*, *Cladonia arbuscula*, and *Cladonia rangiferina*; Nilsson et al., 1993). On wind-eroded topography (litter layer and topsoil missing; e.g., Holtmeier et al., 2003, 2004; Broll et al., 2007; Holtmeier, 2010), a possible lack of mycorrhiza may be a critical factor for nutrient uptake (Holtmeier, 2009 and further references therein). Last but not least, an insufficient supply of viable seeds is an important obstacle to pine recruitment at higher elevations (see also Juntunen and Neuvonen, 2006). Such factors may override the positive effects of the warming climate, as became apparent from modeling the possible response to increased temperatures of prostrate mountain pine (*Pinus mugo*) in the limestone Alps (Dullinger et al., 2004).

As there are no seed-producing old pines in or above the upper birch tree-line ecotone in our study areas, seed supply depends mainly on wind-mediated upslope transport of viable pine seeds from mature pine stands at lower elevations. However, the mountain birch forest surrounding the mature pines and the steep topography of the lower mountain slopes (valley sides) impede wind-mediated seed dispersal. Moreover, wind carries light seeds over greater distances than heavy seeds. As energy content and germination capacity of wind-dispersed seeds are positively correlated with seed size (Sveinbjörnsson et al., 1996), the amount of viable seed decreases with the distance from the seed sources (e.g., Lehto, 1957; Kuoch, 1965; Kullman, 1984; Norton and Schönenberger, 1984). Thus, on the northernmost mountains (e.g., Koahppeloaivi-Staloskaidi and Rodjanoaivi), the reason for the scarcity of pine seedlings and saplings in the birch tree-line ecotone is more likely to be the long distance from a seed source rather than the paucity of suitable sites. One may safely assume that more seedlings would have become established at the sites where we found new pines if enough viable seeds had been available. The sites do not differ enough to prevent a higher seedling density in these and other comparable places. The same argument probably holds true for Riikkavarri as well as for Ailigas, Puollamoaivi, and Kiđesjoktšielgi-Tšahkaltšohkka east of the Utsjoki valley, although the distance from seed trees is shorter than on the mountains bordering the Tenojoki. Seedling mortality is generally high during the first years in northern and alpine tree-line environments (e.g., Junttila and Skaret, 1990; Mellmann-Brown, 2005; Juntunen and Neuvonen, 2006). Thus it is possible that seedlings had died before we visited these locations. However, if that were the case, we would have expected to find at least their remains, which we did not. Moreover, pine seedlings would probably not become established or even survive (see also Paus, 2010) on the wind-eroded convex areas with exposed mineral soil and little or no snow cover in winter, even with a sufficient supply of viable seeds.

As to a viable seed supply, the situation on Jesnalvarri appears to be more favourable than on most of the other study areas. This is because the mature pines that have been reproducing fairly well during the last decades occur relatively close to the mountaintop (cf. Fig. 5; Holtmeier et al., 1996; Holtmeier, 2005a). New cone-bearing pines on the relatively flat mountaintop may also have acted occasionally as a seed source. Maturity and seed production of the present new pines may become increasingly important for further altitudinal migration of the pine limit (Holtmeier et al., 2003; Kullman, 2007a, b). Moreover, abundant microsite facilitation by bedrock outcrops, blocks, and crevices in the bedrock has obviously encouraged establishment and growth of relatively numerous pines on this windswept mountaintop. However, on Kiđesjoktšielgi-Tšahkaltšohkka, for example, despite similar microsite facilitation, pine could not spread at a comparable intensity. Thus, on Jesnalvarri the increased supply of viable seeds turns out to be a relatively important factor. In any case, the number and quality of microsites offering shelter from wind, moisture, and nutrient supply have not increased. Regeneration from seed banks is unlikely, as Scots pine seeds usually germinate within a short time after dispersal, and seeds do not live longer than 10 to 16 months (Granström, 1987). On Lánká Mountain, mature pines (at about 350 m) at the present birch forest limit produce viable seeds, at least in favourable years. Seed supply from these pines (and a few new pines at higher elevations) is very likely as important as seed transport from the pine forests on the lower mountain slope and the Tenojoki valley.

Some authors (e.g., Körner, 1998; Moen et al., 2008) consider seed supply to be only of minor importance for tree-line advance. Nevertheless, in most of our study areas, a limited supply of viable seeds appears to be as important as any other factor that is adverse to pine tree-line migration to higher elevations. It is not a lack of suitable sites that is inhibiting the establishment of pine seedlings beyond the existing pine limit. Site conditions do become increasingly important as the young pines start growing above the ground-level microclimate and shelter-providing microsites (cf. Fig. 4). When young pines grow taller than their protective environment and become fully exposed to climatic agents, they depend on hardiness for their survival.

Growth Form Development and Controlling Factors

Most new pines growing within and above the birch tree-line ecotone are shaped more by climatic injuries and other external factors than might be expected in view of the warming climate and from reports of observations of tree-line areas in more southern areas of Fennoscandia (e.g., Kullman, 2004, 2007a; Holtmeier and Broll, 2005). Disturbed growth forms prevail. These forms may be attributed to frost, winter desiccation, or abrasion by wind-driven ice and mineral particles, which affect shoots and needle foliage projecting above the winter snow surface (e.g., Holtmeier, 1971, 2005b, 2009, 2010; Bigras et al., 2001; Repo et al., 2001; Smith et al., 2003; Paus, 2010). Kullman (2007a) attributes a near 50% loss of the initial pine population established during 1941 – 55 at the tree line in the Handölan valley, southern Swedish Scandes, to subsequent winter mortality. Recurrent climatic injuries are probably among the main factors to which we may attribute the very low number of new pines taller than 2 m growing above 300 m in a permanently windy environment.

Deep, wet snow due to increased snowfall in spring (Solantie, 2000) increases the risk to young pines within the birch forest, where they might be growing at higher densities: they subsequently become victims of snow blight and mechanical damage by settling snow and snow creep. In open birch stands, however, new pines still benefit from shelter provided by the birches.

While current climatic warming is promoting pine advance into the birch tree-line ecotone and alpine tundra on the northern mountains, reindeer are probably one of the most adverse factors. In Utsjoki, the reindeer population more than doubled after the mid-1970s and peaked in the 1980s and early 1990s (e.g., Kumpula and Nieminen, 1992; Oksanen et al., 1995; Kashulina et al., 1997; Colpaert et al., 2003; Helle and Kojola, 2006). Recent summer stocking densities in the study area are 3.5 – 4.5 reindeer km^{-2} (Solberg et al., 2005). Reindeer may scrape or dislodge pine seedlings buried under the winter snowpack by pawing through the snow for lichens (e.g., Skuncke, 1969), and they injure saplings mainly when cleaning their antlers. This kind of damage is as important as climatic injury and is probably the main reason for the high incidence of disturbed growth forms within birch forests used by reindeer. The existence of a few normally grown pines inside the more than 30-year-old fenced exclosure (IBP site; cf. Fig. 5A) on the windswept top of Jesnalvarri supports this conclusion. Young pines less than 150 cm high are at constant risk of being affected by reindeer. At fully wind-exposed sites in the upper zone of the birch tree-line ecotone (e.g., Puollamoaivi, Koahppeloaivi-Staloskaidi, Lánká), no pines exceed this height. Most of them are much smaller and thus risk disturbance or even destruction by reindeer. In the other study areas as well, about 50% (Pâdjeseävtteg area) to 60% (Jesnalvarri) of the new pines are still smaller than 150 cm. It is possible that moose (*Alces alces*), which have considerably increased in the Utsjoki area during the last three decades (http://riistaweb.riista.fi/riistatiedot/riistatietohaku.mhtml, 16 December 2010), have already impeded pine advance to higher elevations. Moose are invading northernmost Finland mainly from northern Norway across the Tenojoki River. Moose browse pine (e.g., Löyttyniemi, 1985; Bergström and Hjeljord, 1987; Nikula, 1992; Heikkilä and Härkönen, 1996; Stöcklin and Körner, 1999) particularly during the winter because pine tissue, with its high nitrogen content and low concentrations of total phenolics and condensed tannins, is highly digestible (Stolter et al., 2009).

Damage to most new pines by climatic influences or animals was also observed by the present authors in the Pallastunturi area (Holtmeier et al., 1996; Holtmeier et al., 2003), whereas Juntunen et al. (2002) did not find any signs of growth form regression at their monitoring sites. Thus, local differences may be paramount.

Decline of high-elevation mountain birch forests, due to defoliation by the mass outbreaks of the autumnal moth (*Epirrita autumnata*) and the winter moth (*Operophtera brumata*) combined with excessive reindeer grazing (Helle, 2001; Helle and Kajala, 1992; Holtmeier and Broll, 2006; Oksanen et al., 1995;Väre et al., 1996), might also have an adverse effect on upslope migration of pine. Wind removes much of the winter snow from the destroyed birch stands, thus exposing young pines in the understory to winter injury, as has also happened to juniper (Holtmeier, 2005b). On the other hand, expansion of the mountain birch forest to higher elevations would probably encourage altitudinal advance of the pine limit except in the valley sites, where deep and late-lying snow might prevent pine establishment. Although pine is a light-demanding species, new pines growing within shelter-providing open birch stands were not affected by competition for light.

CONCLUSIONS

The warming climate has encouraged recent pine establishment above the upper limit of old pines in subarctic Finland since the 1960s. Lack of local seed sources delays pine advance to higher elevations irrespective of other factors. New pine generations may become effective seed sources above the present seed trees and will probably encourage an upward shift of the pine tree limit.

Obviously, warming has not yet been favourable enough for undisturbed growth on the northern mountains and cannot compensate for growth disturbances caused by winter injury and biotic factors. Stunted new pines may survive for decades as suppressed growth forms waiting for enough favourable years to allow undisturbed height growth and the attainment of tree size. However, sudden dieback due to extreme climatic events, such as extremely snow-rich winters or winters with almost no snow, cannot be excluded.

Microsite facilitation is essential to new pine sapling survival in the open above the closed mountain birch forest. Smooth surfaces may be less favourable for the survival of pine seedlings than varying microtopography offering more intermediate shelter-providing sites. The relative importance of microsite facilitation will increase in parallel to possible future upslope migration of the pine tree limit into a much windier environment. Reindeer and moose, if not reduced to lower numbers, will continue to seriously impede the development of new pines and delay the rise of the pine tree limit.

If we apply a conventional minimum tree height of 2 m to the new pine populations we found above an elevation of 300 m, then pine tree limit advance in our study areas cannot be considered to have taken place as yet. Continued warming will probably cause the pine tree line to shift to a higher elevation. A rapid advance, however, is not very likely.

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