SILVA FENNICA
Silva Fennica 40(3) research articles
www.metla.fi/silvafennica · ISSN 0037-5330
The Finnish Society of Forest Science · The Finnish Forest Research Institute

Natural Regeneration of Scots Pine and Norway Spruce Close to the Timberline in Northern Finland

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Juntunen, V. & Neuvonen, S. 2006. Natural regeneration of Scots pine and Norway spruce close to the timberline in northern Finland. Silva Fennica 40(3): 443–458.

Two different datasets were analyzed in order to clarify the factors that affect regeneration success of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) in the climatically extreme areas in northern Finland. First, pine seed maturity and the number of cones in the trees were investigated at five pairs of study sites during the period 1997–2003. Secondly, the rate of seedling establishment and seedling survival of Scots pine and Norway spruce were monitored and compared among three different timberline zones (forest zone, timberline, tree line) in 13 localities during the period 1983–1999. The first study showed that both cone production (bud formation) and seed maturity may be limiting factors for successful reproduction in the climatically marginal habitats. Seed maturity correlated well with the temperature sum of the summer, but variation in the number of cones had a periodic component rather than strictly following the temperature sum of the summer of bud formation. Monitoring surveys since 1983 showed that pine and spruce regenerated more or less regularly in all the zones during 1983–1999. However, seedling mortality of pines was much higher compared to spruce. In general, initially small sized seedlings showed higher mortality compared with larger ones. The results suggest that besides restrictions in reproduction, stand dynamics in the timberline habitats are strongly controlled by seedling mortality due to a variety of causes.

Keywords Scots pine, Norway spruce, regeneration, timberline, tree line, seed maturity, seedling mortality
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Received 18 April 2005 **Revised** 20 February 2006 **Accepted** 24 March 2006
Available at http://www.metla.fi/silvafennica/full/sf40/sf403443.pdf

1 Introduction

Uncertainty about future global climate warming and its consequences on northern boreal forests and the adjacent timberline ecotone has characterized timberline research over the previous decades. Responses of different models vary from drastic positive effects on boreal forests and the coniferous timberline (Kellomäki and Väisänen 1995, Kellomäki et al. 1997) to catastrophic incidents of dieback and regression of the timberline (Gates 1990, Hänninen 1991, Juday et al. 1997). Recent studies show that tree species respond individualistically to climatic variation (Brooks et al. 1997, Kullman 2001, Juntunen et al. 2002). Moreover, the responses are often regionally variable in magnitude and direction (Kullman 2001, Juntunen et al. 2002). Follow-up measurements on permanent plots since 1983 in Finnish Lapland have revealed that regeneration of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) has occurred in climatically extreme areas during recent decades suggesting that advancement of timberlines may occur in the near future (Juntunen et al. 2002).

Natural regeneration of Scots pine and Norway spruce consists of many phases, e.g. formation of regenerative buds, flowering, maturation, germination, early survival of seedlings. Certain climatic conditions must be fulfilled during several years before successful regeneration can take place (Sarvas 1962, 1970, Koski and Tallqvist 1978, Pukkala 1987). Generally, the potential regeneration rate of a stand of average stocking is enormous if all climatic, edaphic and ecological factors are optimal (Koski and Tallqvist 1978). In each phase, however, a large proportion of its total potential is normally lost, and this proportion increases the further north the stand is located.

It is commonly known that the numbers of male flowers and the amounts of pollen deposition, which are closely related, are low in timberline areas (Sarvas 1962, 1970, Hicks 2001). However, according to some researchers, a more crucial factor for successful reproduction is the number of female flowers since background pollination is high enough to fertilize the female flowers of trees even beyond the timberline (Hustich 1948, 1978, Sirén 1993b). The anatomical maturity of conifer seeds, which is a prerequisite for high germination percentages (Ryynänen 1980, Simak 1980), clearly depends on temperature. The temperature sum required to result in 50% of anatomically mature seeds varies according to different studies within the range of 790–950 degree days (d.d.; above the +5 °C threshold) for Scots pine (Pohtila 1980, Schildt 1985, Henttonen et al. 1986, Kortesharju 1991, Harju et al. 1996, Almqvist et al. 1998), and about 700–800 d.d. for Norway spruce (Almqvist et al. 1998).

The final success in regeneration is not only a function of reproduction rate but depends substantially on the survival of seedlings, too (Hustich 1948, Körner 1998, Lloyd 1998). Some studies show that high seedling mortality in climatically extreme areas might constitute the crucial obstacle to the advance of the timberline (Hustich 1978, Kullman 1993, 2001, Körner 1998, Lloyd 1998, Stöcklin and Körner 1999, Holtmeier 2000, Paulsen et al. 2000). Unfortunately, seedling mortality as a controlling factor of timberline dynamics has been neglected in many analyses.

The main objective of the present study is to analyze the regeneration success of pine and spruce in different timberline zones in Finnish Lapland. The present paper deepens the analyses of an earlier study (Juntunen et al. 2002) by focusing on small seedlings (<20 cm) and including data on seedling mortality in the analyses. In addition, data on seed maturation of Scots pine in relation to summer temperatures in the northern timberline (where forest canopy closure ceases) and tree line (beyond which coniferous trees taller than 2 m no longer exist) is presented.

2 Study Area and Methods

2.1 Temperature Measurements and Annual Variation in Temperature Sums

The present study focused on the transition between Scots pine's northern timberline and tree line in Finnish Lapland. Five pairs of study sites were established at regular intervals along the northern timberline ecotone of pine so that one site of each pair of sites was situated at the tree line and the other at the timberline (Fig. 1). The timberline sites were situated at the northern edge of the boreal coniferous forest. At the tree line locations, polycormic birches dominated the landscape and solitary pines occurred widely spaced over a long distance. The tree line sites were placed at the northern edge of this transition zone. The distance between the tree line and timberline sites varied from 7 km to 25 km.

One temperature logger was installed at each study site in 1997/98. Thermometers measured the air temperature at the height of 2 m throughout the summer (May–September) at intervals of two hours. These measurements were continued until summer 2002 (inclusive).

Variation in the annual cumulative temperature sums during 1900–1982 (with threshold value +5 °C; d.d.) was estimated using the program developed by Ojansuu and Henttonen (1983). The mean temperature sums for the same locations during 1983–2002 were based on the program by Ojansuu and Henttonen for the period of 1983–1998 and on the data provided by thermometers for the period 1999–2002.

2.2 Cone Crop and Seed Maturation

The nearest ten mature trees from the thermometers (see above) were chosen to serve as sample trees. A tree was abandoned as a sample tree if it carried less than 30 cones and then the nearest

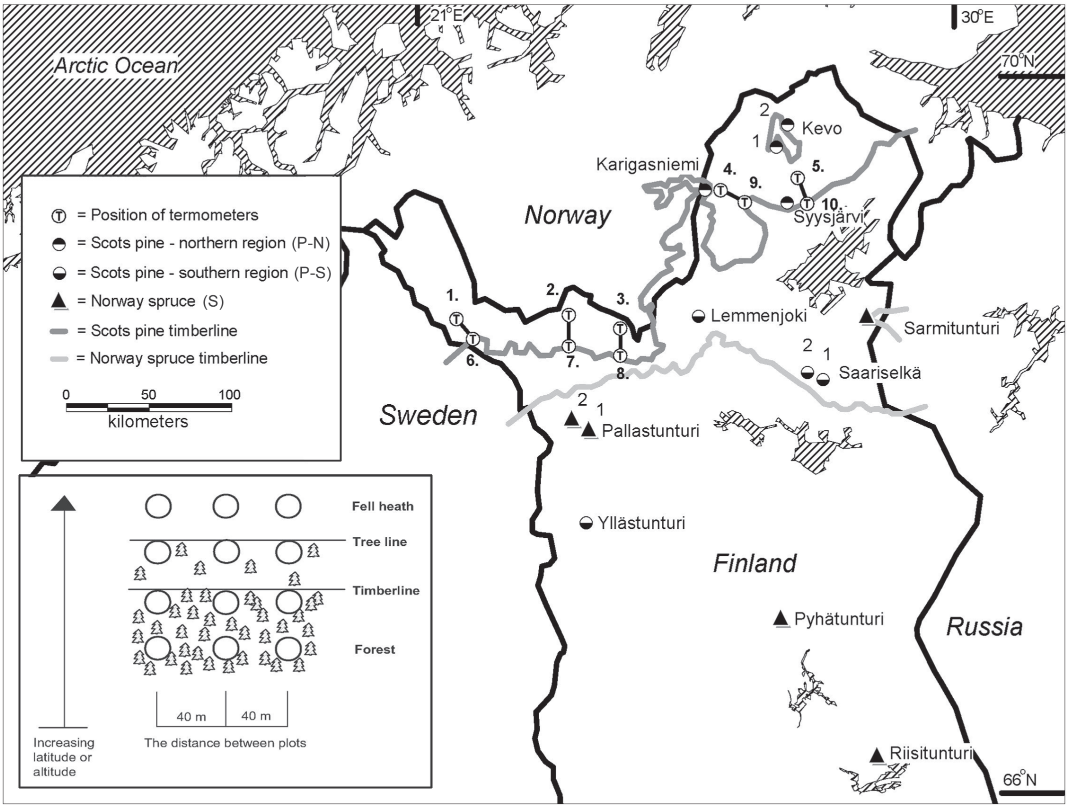


Fig.1. Map of the monitoring localities of "The Finnish Timberline Monitoring Project" and the experimental design in the localities. The locations of thermometers in the northern timberline and treeline of Scots pine describe the sites where cone samples for seed maturation analyses has been collected. The location of study sites mentioned in the text: 1. Luspa, 2. Pöyrisjärvi, 3. Kalmakaltio, 4. Karigasniemi, 5. Petsikko, 6. Järämä, 7. Leppäjärvi, 8. Nunnanen, 9. Kaamasmukka, 10. Syysjärvi.

next tree in the vicinity was chosen. The number of investigated trees varied between 15 to 30 in number on each of the study sites. The mean heights of the sample pine trees were 7.8 m and 6.3 m, and the mean diameters (at 1.3 m) were 25.9 cm and 25.0 cm at the timberline and tree line, respectively. The selected trees at the timberline sites occurred within an area of about 100 m × 100 m, while within the tree line the selected trees occurred normally within an area of 1 km × 5 km.

In the pilot study conducted in 1997, cones were collected from three tree line sites. A more systematic study at five tree line and five timberline sites was launched in the following year. At least 30 cones were collected annually from each sample tree in order to define seed quality and the expected germination percentage. The cones were collected from all sides of the crown and 30 cones were chosen as the minimum with the intention of obtaining at least 400 seeds for an x-ray radiograph. Seed quality was calculated by embryo classes, determined as the proportion of the embryo of the embryo cavity. The expected germination percentage was determined on the basis of the seed maturation analyses according to Simak (1980). Furthermore, the total cone number of each tree was estimated visually. However, trees with no cones were not noted down in 1997 and 1998, and therefore the results concerning the cone numbers for those years are probably slight overestimations.

2.3 Seedlings

Seedling densities and survival were monitored as a part of the Finnish timberline monitoring project launched in 1983 (Kallio et al. 1986, Juntunen et al. 2002). The main objective of the project is to monitor changes in the population structure of conifers within the different zones along the elevation gradient of the timberline ecotone, and to analyse the relations of these changes to climatic variability.

The monitoring network is comprised of 13 localities spread over Finnish Lapland (Fig. 1). Each locality has a row of three circular monitoring plots, 300 m^2 or 500 m^2 in area, situated along the slope transect in three or four zones within the timberline ecotone (see the insert in Fig. 1). A more detailed description of the monitoring set-up and of the characteristics of different study areas is given in Juntunen et al. (2002).

The first inventory was made in 1983/84. Within the plots, all the trees (height ≥ 2 m) and seedlings-saplings (height < 2 m) were mapped by measuring their direction and distance from the centre point, and their height and diameter were measured. Hereafter, we refer to seedlings smaller than 20 cm as ‘small seedlings’ and those from 20 to 199 cm as ‘tall seedlings’ or ‘saplings’. The seedlings shorter than five centimetres were only tallied as to their number. The plots were resurveyed in the same manner in 1994 and 1999, but with the exception that the minimum height limit of tallied seedlings was set at 20 cm (Juntunen et al. 2002).

2.4 Statistical Analyses

In the seedling data the numbers of small (0–19 cm) and tall (20–199 cm) seedlings were calculated in 1983, 1994 and 1999 on each plot. The changes in their numbers from 1983 to 1994, and from 1994 to 1999, were analysed in each region and zone. Before analysing each dataset, the homogeneity of variance was tested with the Levene test and the normal distribution with the Kolmogorov-Smirnov test (Sokal and Rohlf 1981). The effects of Region (R) and Zone (Z) and the interaction between R and Z on the change in the numbers of small and tall seedlings in all of the data were tested using ANOVA with a split-plot design, in which R and Z were treated as fixed effects, and in which Locality was a random effect and nested within R (see Potvin et al. 1990). The analysis was performed separately for the periods 1983–94 and 1994–99. Type III sum of squares was used. The analyses were performed on logarithmically transformed values ($\ln(x+20)$).

Seedling mortality values from the period 1983–1999 were based on the follow-up measurements of the seedlings. In 1983 seedlings smaller than 5 cm and in 1999 seedlings smaller than 20 cm were only tallied in numbers. Therefore, monitoring of those seedlings that were smaller than 5 cm in 1983 could not be performed and seedlings higher than 5 cm in 1983 but not found in the at-least-20 cm class in 1999 were classified as dead. According to the growth rate distribution of pine and spruce seedlings, our method may lead to slight (less than 2%) overestimation of mortality.

3 Results

3.1 Summer Temperature Variability

The estimated annual temperature sum for the location of thermometer at the pine northern timberline (Syysjärvi) (see Fig. 2) during the period 1900–1982 varied between 358 and 973 degree days (d.d.), with the average value being 647 d.d. Analogous values for the tree line site (Petsikko) were 329–900 d.d. with the average value being 592 d.d. The temperature sum of 845 d.d., which is a limiting value for 50% pine seed maturity according to Sarvas (1970), was reached eight times at the timberline and three times at the tree line, while the value of 800 d.d. (the limit for 50% seed maturity according to Harju et al. 1996) was reached twelve and five times at the same sites, respectively.

At the northern timberline of pine (Syysjärvi) (Fig. 2) there were seven periods during the 20th century when temperature sum exceeded 750 d.d. both in the first (bud formation) and third (seed maturation) summers (1920–22, 1922–24, 1934–36, 1936–38, 1945–47, 1970–72, 1972–74), but two of those periods were timed so that bud formation coincided with seed maturation of the former peak and thus it is uncertain if the crop could have been a rich one. Correspondingly, in the northern tree line of pine (Petsikko) the value of 750 d.d. was reached four times (1920–22, 1934–36, 1936–38, 1970–72).

The mean temperature sums for the same locations during 1983–2002 were 633 and 582 d.d. for the timberline and tree line, respectively, which is slightly below the average for the period 1900–

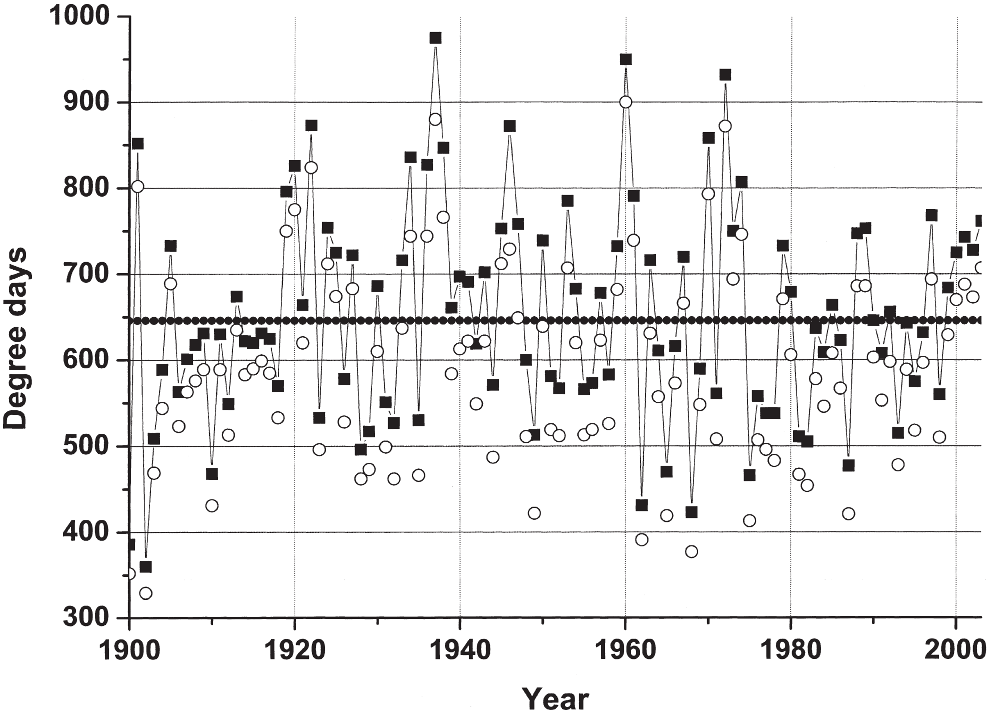


Fig. 2. The calculated effective temperature sum (+5 °C threshold) in degree-days for the timberline site of Syysjärvi during the period 1900–2002. The average value (647 d.d.) is shown by the dotted line. The temperature sums for the treeline are displayed by open circles 55 d.d. lower, on average, compared to the timberline.

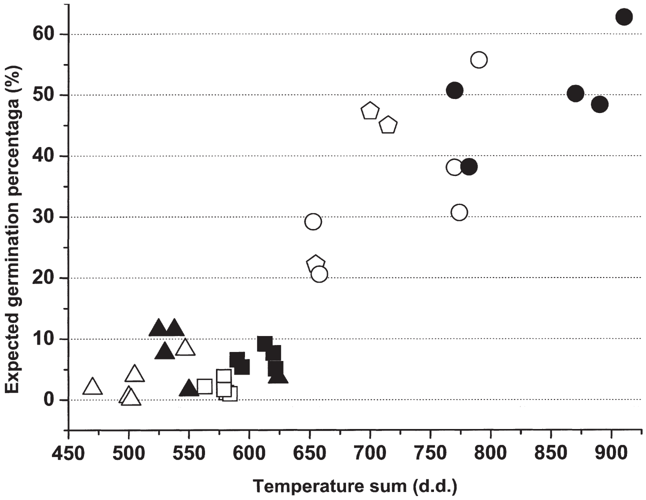


Fig. 3. Expected germination percentage (based on the seed maturation analyses according to Simak 1980) and annual temperature sums expressed in degree-days (calculated from the data of the thermometers) in the northern timberline and treeline of Scots pine during 1997–2002. There were no cones in the trees in 2000 and 2001 so seed samples could not be collected. Open symbols represent the treeline, and filled years, the timberline; pentagon = 1997, triangle = 1998, square = 1999, circle = 2002).

1982. The period 1983–2002 was characterized by low variation between the years, i.e. there were no unusually warm or cold summers (Fig. 2). The value 800 d.d. was not achieved in the tree line during this project.

Summer temperatures during the monitoring of seed production and seed maturation in the years 1997–2002 showed that the summers were warm in 1997 and 2002 (temperature sums 766 d.d. and 782 d.d., respectively, at the pine northern timberline in Syysjärvi). Meanwhile, the summer of 1998 was much colder than average (558 d.d). Also, the summer of bud formation (1995) for the cone production of 1997 was quite cold (573 d.d.). The temperature sums for the summers 1996 and 1999 were slightly below the long-term average, while the summers 2000 and 2001 were slightly above the average.

3.2 Seed Production and Maturation during 1997–2002

The formation of generative buds, and the number of cones in the trees two years later, were not completely dependent on the temperature sum of the summer of bud formation. The number of cones in the trees showed relatively modest variation in 1997, 1998 and 1999 (Table 1), although the summers 1995, 1996 and 1997 essentially differed (Fig. 2). Meanwhile, after the summers of 1998 and 1999, when temperature sums remained below average, there were no cones in the trees at all in 2000 and 2001. There were again some cones in 2002, but the number was lower than in the period 1997–1999.

Seed maturation directly correlated with the temperature sums throughout the summers. In 2002, when the temperature sum of 750 d.d. was achieved in most of the localities, the average expected germination percentage rose up to 50% at the timberline and to 35% at the tree line (Table 1). In 1997 (710 d.d. at the tree line), seed samples were only collected from three tree line sites, but the expected germination percentage reached 45% in two of them (Fig. 3). In 1998 and 1999, the summers were relatively cold, and therefore seed maturation was generally very poor. In 1998, the average expected germination percentages at timberline and tree line sites were

Table 1. Number of sample trees (N), average number of cones in the trees, expected germination percentage based on the seed maturation analyses according to Simak (1980) and standard deviation of expected germination percentage. The number of cones in different years are not fully comparable because sample trees varied from year to year. Moreover, in 2002 larger areas were used to include sample trees with enough cones so values are high compared with other years.

Site	1997				1998				1999				2002			
	N	Number of cones	Exp. germ%	Std	N	Number of cones	Exp. germ%	Std	N	Number of cones	Exp. germ%	Std	N	Number of cones	Exp. germ%	Std
Luspa	4	225	45.0	35.1	8	293	8.3	9.0	10	243	3.8	2.4	92	90	55.7	20.7
Pöyrisjärvi					8	269	0.5	1.0	11	143	1.2	2.0	7	71	30.7	13.4
Kalmakaltio	5	208	47.3	8.9	8	269	0.1	0.1	10	151	1.0	1.2	5	74	38.1	23.3
Karigasniemi	6	312	22.2	30.9	8	72	4.0	10.3	11	143	2.2	2.2	8	88	29.2	11.7
Petsikko					8	143	1.9	4.1	10	136	1.7	1.3	3	59	20.6	5.2
Järämä					8	289	7.7	4.6	10	117	5.1	2.6	9	140	62.8	17.3
Leppäjärvi					8	189	3.7	2.8	10	115	7.7	7.8	7	121	48.4	21.3
Nunnanen					6	233	1.6	1.8	10	144	5.4	1.9	9	148	50.2	11.9
Kaamasmukka					8	161	11.5	11.4	10	183	6.6	2.4	10	80	50.7	20.1
Syysjärvi					6	-	11.5	10.4	10	262	9.2	2.9	10	137	38.2	16.1

7.3% and 3.0%, respectively. In 1999, the corresponding values were 6.8% and 2.0% (Table 1). Summer temperatures in 2000 and 2001 were slightly above the long-term average, but as there were no cones in the trees, seed samples could not be collected.

The seed maturity after the warm summers in 1997 and 2002 varied among the sites within each zone from 22 to 47% and from 21 to 58%, respectively (Table 1). However, there was higher variation between trees within the sites; the expected germination percentage between trees on the same site varied from 0% to 80%. After the summers in 1998 and 1999, there were no trees with high maturity levels, but a lot of trees with an expected germination percentage of 0%.

There were only a slight difference in seed maturity and no difference at all in the numbers of cones in the trees between the timberline and tree line sites. However, due to a significant difference in population density, total reproduction potential is far greater near the timberline compared to the tree line zone. For example, in 2002 the average density of trees with cones was about 10 trees/ha in the timberline sites while in the tree line sites it was only about 0.1 trees/ha. Calculations using the values of 67 and 53 cones per tree (20 seeds/cone), and an expected germination percentage of 50% and 35% for timberline and tree line sites, respectively, gives a total reproduction rate of 6700 germinated seeds per hectare in the timberline and 37 in the tree line. This calculation is only a rough estimation, and the values rather describe the scale of difference between the zones than absolute reproduction volumes.

3.3 Seedling Establishment during 1983–1999

In 1983, the average density of small pine seedlings (<20 cm) within the forest zone was about the same for both the Pine-North (P-N) and Pine-South (P-S) regions. However, variability between localities was much higher in the P-N region (Table 2; Fig. 4). At the timberline and tree line, small seedlings appeared more numerously in the P-S region. Small spruce seedlings (S region) slightly outnumbered others in the forest zone and by several times in the upper zones compared to

Table 2. Number of small and tall seedlings in the measurements of 1983, 1994 and 1999 in different zones. Regions: P-N = Pine-North, P-S = Pine-South, S = spruce.

Region	Zone	N	1983				1994				1999			
			Small		Tall		Small		Tall		Small		Tall	
			Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std
P-N	Forest	12	569	1034	442	560	1177	2254	658	895	883	1701	1217	1939
	Timberline	12	158	304	194	198	108	150	212	232	61	94	256	206
	Treeline	12	8	21	42	105	0	0	84	104	0	0	39	85
P-S	Forest	12	594	451	1217	875	156	117	778	1195	194	143	500	425
	Timberline	12	333	374	522	786	147	309	267	277	281	599	197	263
	Treeline	12	88	143	105	107	112	189	47	83	95	147	142	167
S	Forest	15	727	940	104	98	504	707	173	190	467	697	376	471
	Timberline	15	1251	1839	242	311	1149	1579	816	1403	996	1527	1584	2660
	Treeline	15	425	526	126	82	412	331	583	632	316	280	888	826

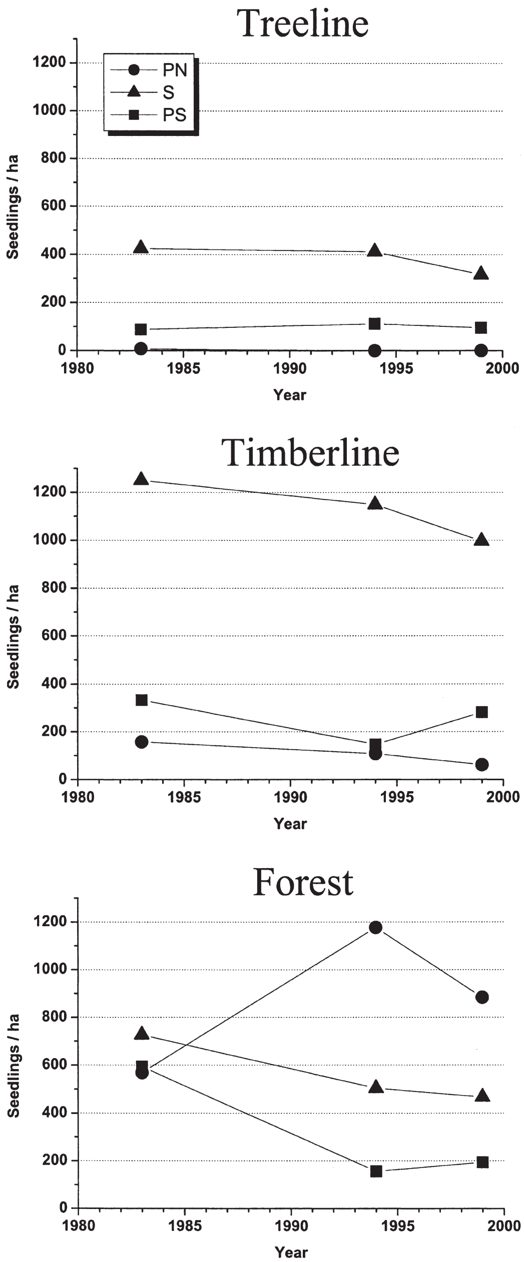
Table 3. Effect of region, zone, locality (nested within region) and the interaction between regions and zones on the changes in small (0–19 cm) and tall (20–199 cm) seedling density from 1983 to 1994 and from 1994 to 1999.

			Small	Small	Tall	Tall
			1983–94	1994–99	1983–94	1994–99
	df	df_e	F	F	F	F
Change	1	10[b]	2.02	0.05	1.73	4.33
Region × Change	2	10[b]	2.63	1.16	7.03*[a]	2.41
Zone × Change	2	98[c]	4.24*	2.93	7.86**	4.68*
Locality × Change	10	98[c]	4.74***	2.65**	3.77***	6.06***
Zone × Region × Change	4	98[c]	3.81**	1.29	0.69	2.13
Error	98					

[a] : *: $p<0.05$; **: $p<0.01$; ***: $p<0.001$
[b] : Error term = MS(Locality(Region))
[c] : Error term = MS(error)

the P-N and P-S regions. The average number of small pine seedlings decreased linearly from the forest zone up to the tree line in both the P-N and P-S regions. Small seedlings in the S region, meanwhile, appeared most numerously at the timberline, and the average density at the tree line was near the density observed in the forest zone (Table 2).

The zone × region × change interaction for small seedlings (<20 cm) was significant from 1983 to 1994 but not from 1994 to 1999 (Table 3). In the forest zone, the numbers of small seedlings doubled in the P-N region by 1994, but decreased to one fourth in the P-S region (Table 2). At the timberline of the P-N region, the numbers decreased evenly from 1983 to 1999, while in the P-S region the numbers first decreased strongly by 1994, but then increased by 1999 close to the level of 1983. At the tree line, the numbers of small seedlings remained at very low levels for both the P-N and P-S regions throughout the monitoring period. In the S region, the numbers of small seedlings decreased smoothly and evenly in all the zones from 1983 to 1999. The change among the zones over all regions was significant from 1983 to 1994, such that the numbers of small seedlings decreased most intensively at the timberline. Due to high variability among the



Treeline

Timberline

Forest

Fig. 4. Number of seedlings (< 20 cm) per hectare in the measurements of 1983, 1994 and 1999 in different regions and zones.

localities, the change among the regions was not statistically significant.

There was no significant zone × region × change interaction to be observed in regard to the numbers of saplings (20–199 cm), but the change differed significantly among the regions from 1983 to 1994, and among the zones from 1983 to 1994 and from 1994 to 1999. The main trend was that the number of saplings increased strongly in the S region, but decreased steeply in the P-S region. In the P-N region, essential increases occurred in the forest zone, but at the timberline and tree line the numbers of saplings remained quite stable.

3.4 Seedling Mortality

In 1983, seedlings shorter than five centimetres were only tallied in terms of their numbers and so the development (growth and survival) of these seedlings over the study period could not be followed (17.7% of the seedlings in the P-N region, 3.5% in the P-S region and 15.6% in the S region). In 1983, there were 418, 1056 and 1237 seedlings between 5–199 cm in height in the P-N, P-S and S regions, respectively. The size distributions of the seedlings were roughly similar in the P-N and P-S regions, but strongly skewed in the S region, where 80% of the seedlings were in the size class 5–19 cm (Fig. 5). Therefore, the results concerning taller size classes should be viewed with caution.

Seedling mortality from 1983–1999 was highest in the P-S region, especially in the size classes up to 80 cm (overall mortality 78%) (Fig. 5). In the P-N region, mortality was considerably lower and it decreased evenly in relation to initial height (overall mortality 32%) (Fig. 5). The size-related mortality trend in the P-N region and high seedling mortality up to 80 cm in the P-S region were quite similar in all the zones. Overall, spruce seedling mortality (S region) was 48%. This was highest in the size class 5–19 cm and lowest in the size class 80–199 cm. The overall seedling mortality (5–199 cm) in the different localities within the regions varied between 29%–39% in the P-N region, 51%–94% in the P-S region, and 30%–55% in the S region.

Pine seedlings up to 80 cm in height were most susceptible to damage at the timberline, while

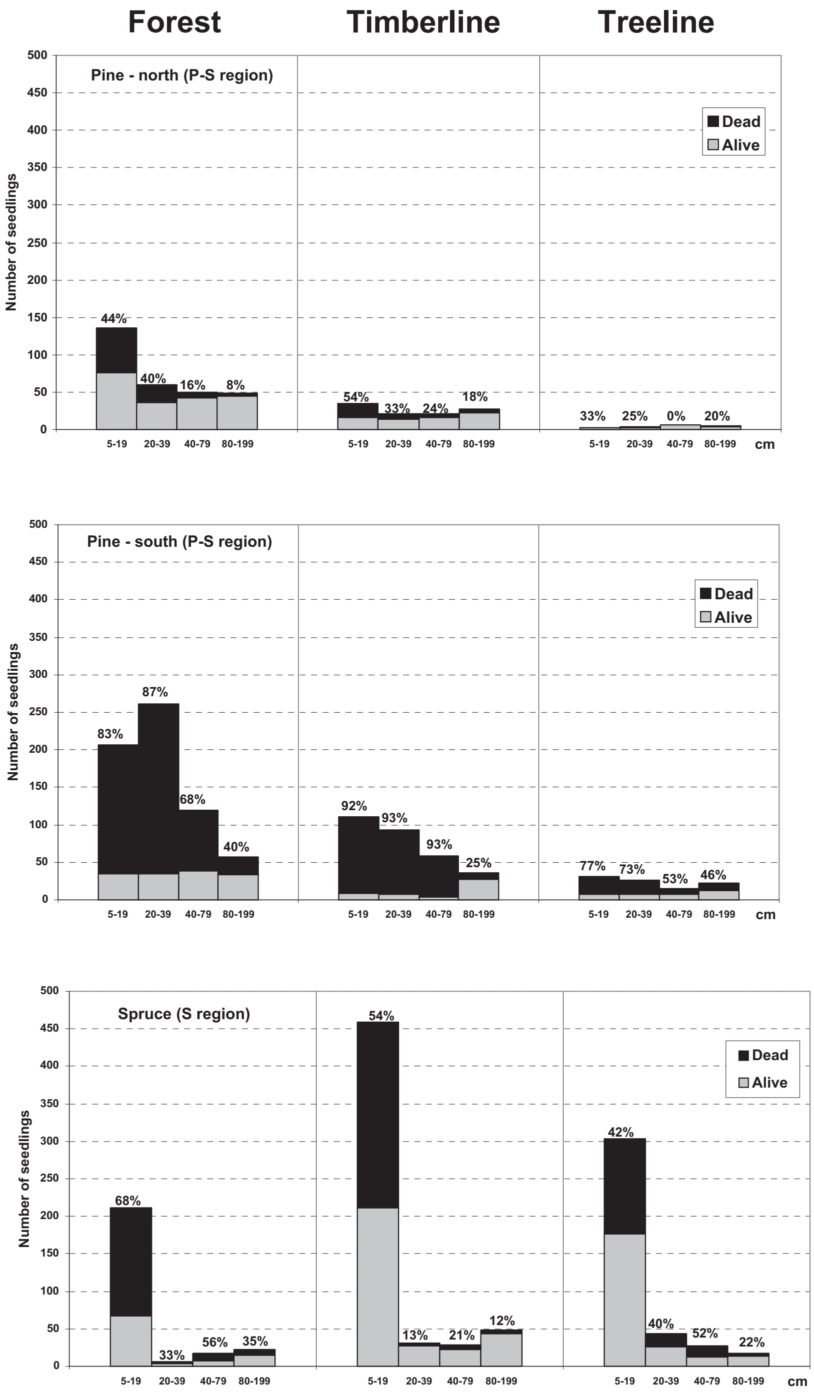


Fig. 5. Seedling mortality of Scots pine and Norway spruce from 1983 to 1999 in different size classes. Total bar height describes the amount of seedlings and saplings (height of 5–199 cm) in 1983, and the outcome in 1999 has been described by the black and grey fills. Seedling mortality has also been expressed by the values above the bar.

the mortality of seedlings higher than 80 cm was most extensive at the tree line. A noteworthy observation was that seedling mortality in the timberline zone of the P-S region was over 90% in the size classes 5–19, 20–39 and 40–79 cm. Basically, spruce seedling mortality, regardless of initial height, was most extensive in the forest zone. Seedling mortality decreased up to the timberline in all the size classes, but it was relatively high in the tree line in the size classes 20–39 and 40–79 cm.

4 Discussion

4.1 Seed Production and Maturation

The dominant role of temperature sum for successful reproduction was clearly observed in our study (see also Henttonen et al. 1986, Harju et al. 1996, Kellomäki et al. 1997). After the cold summers in 1998 and 1999, seed maturity and total seed crop remained very low. Moreover, generative bud formation was close to zero which culminated in the summers of 2000 and 2001 when there were no cones in the pine trees at all. However, the results support the notion of Sarvas (1966) that northern pines have become adapted to some extent to the local climatic conditions, and that the same amount of heat as in more southern areas is not needed to produce viable seeds. The summers of 1997 and 2002 were not exceptionally warm (about 700 d.d. at the tree line), but solitary tree line pines were even then capable of producing matured seeds and the expected germination percentage rose above 30% in most of the localities.

Periodicity obviously characterizes reproduction in the temperature-constrained environments (Renvall 1912, Hustich 1948, Kullman 1992, Sirén 1993a). For example, during the six-year monitoring period of 1997–2002, successful reproduction was impeded by low seed maturity in 1998 and 1999, and the cone crop came close to nil in 2000 and 2001. In 2002, high seed maturity would have enabled abundant reproduction to occur, but due to the poor cone crop, the amount of germinating seeds remained at low level. Thus, only the summer of 1997 produced a moderate amount of maturated seeds, but overall, no seed years, i.e. years with abundant seed production, eventuated. The result is in agreement with Henttonen et al. (1986), Sirén (1993a) and Kellomäki et al. (1997) in that suitable conditions for proper seed years occur only a few times in a given century.

However, although seed years occur rarely, seeds are also produced to some extent in typical years within the northern timberline areas. Some years after previous abundant flowering, trees normally produce generative flower buds even during a summer with an average temperature sum (Lindgren et al. 1977, Kärkkäinen 1992). Moreover, the result that there was high variation in seed maturity is in agreement with Ryynänen (1982) and Harju et al. (1996). According to Ryynänen (1982), variation in seed quality between trees is high especially in the northern areas. The greatest variation (between trees) occurs when the annual temperature sum ranges from 700 d.d. to 850 d.d. (Harju et al. 1996). According to Schildt (1985) and Numminen (1989), a temperature sum of 500 d.d. is a limiting value for zero-germination. The results of this study substantiate this notion.

4.2 Seedling Establishment

Basically, trees in the timberline and tree line respond more sensitively to climate warming than to climate cooling (Kullman 1990). The most sensitive response to climate warming is the establishment of new seedlings and closer spacing of seedling populations. The response in terms of the numbers of small seedlings (0–19 cm) clearly indicates the reproduction capacity of the site over the last few years, as pines in the timberline areas attain a height of 20 cm by the age of 8–10 years (Hustich 1958, Kullman 1981) on average, and spruces attain the same height a few years later. Nonetheless, variation in initial development between individual seedlings is high.

Pine and spruce have regenerated more or less regularly during the monitoring period, and this is demonstrated in the numbers of small seedlings in the different years (Table 3). However, this does not mean that sexual reproduction has occurred annually, but rather it indicates that there have been some years of moderate reproduction before each measurement (c.f. Hustich 1958).

The results agree with the observations made by Holtmeier (1995) in Finnish Lapland. However, the reproduction pattern in the plots of this study differ from those observed in Swedish Scandes Mountains, where sexual reproduction of pine close to the tree line did not occur at all during the 1970s and the1980s (Kullman 1990, 1991) while a period of intensified reproduction prevailed during the 1990s (Kullman 2000, 2001). Spruce reproduction there was observed to have been almost continuous during the past 20 years (Kullman 2000). These different responses provide further support for the view that timberline areas are not always the equal of one another, but may instead have varying types of climatic control and that local results may not be representative of a larger area (Holtmeier 1995, 2000).

The numbers of small spruce seedlings were regularly higher than the numbers of small pine seedlings at the timberline and tree line. This might be partly related to the capacity of spruce to regenerate vegetatively (Kullman 1981) and partly to its lower temperature requirement for seed maturation (Almqvist et al. 2000). Meanwhile, there were no significant differences between pine (P-N and P-S) and spruce with respect to the change in small seedling numbers from 1983 to 1999. This suggests that both species, regarding reproduction pattern, have responded in a similar manner to climatic fluctuations during the monitoring period.

The numbers of small pine seedlings decreased linearly on moving into upper zones. Basically, the reproduction dynamics of pine and spruce in marginal habitats is foremost a function of summer temperatures (Kullman 1992). However, the decrease in the numbers of small pine seedlings occurred in conjunction with a decrease in the basal area of matured pines. Thus, it can be assumed that, besides the thermal constraint, lack of local seed source is an important obstacle to high reproduction rates occuring in the upper zones. Spruce reproduction rates along the vertical transect clearly differed from those of pine. The numbers of small spruce seedlings were highest at the timberline, while the numbers at the tree line were close to the level of the forest zone. This supports the hypothesis that reproduction in different zones is controlled by different factors, which are characteristic to each species (Lloyd 1998). Inside the spruce forest, shading and competition from closely-spaced mature trees is often too great for seedlings (Örlander and Karlsson 2000). Moreover, thick moss and humus layers often impede seed germination. Further up the slope, where mature trees occur more sparsely, open space enables high seedling numbers to develop if there is enough local seed available.

A notable feature was that the change in the numbers of small seedlings from 1983 to 1999 displayed substantially different magnitudes or direction in neighbouring localities. Great variability in this was characteristic especially of pine. According to Kullman (2000), local variability in the magnitude of reproduction reflects the fact that air temperature may not be a directly limiting factor under all topographic, edaphic and historic conditions. Thus, stand dynamics are largely controlled by local factors rather than by the macroclimate alone.

4.3 Seedling Mortality

Initially, small seedlings showed higher mortality than larger ones. This was common for both pine and spruce seedlings. The result agrees with a number of studies stating that mortality declines in relation to seedling size (Kullman 1981, Junttila and Skaret 1990, Persson 1998). Kullman (1981) suggested that an increased mortality occurs at the height interval of 80–150 cm, when seedlings project above the maximum wintertime snow-cover and that once a height of 150–200 cm is exceeded mortality declines considerably. Our data does not show any signs of increased mortality at the height interval of 80–150 cm.

Mortality was lower for spruce than pine seedlings, especially among seedlings shorter than 40 cm. The first part of the 1980s has been reported to have been a period of high mortality for pine seedlings in northern Scandinavia (Kaitera and Jalkanen 1992, Hansson and Karlman 1997, Mäkitalo 1999). The summers in the early 1980s were relatively cool and well above normal humidity. Thus, the conditions were favourable for the spread of fungal pathogens, such as snow blight and Scleroderris canker. This would appear to be in agreement with the result that the dramatic decrease in the numbers of pine seedlings, especially at the timberline of P-S region, occurred between the measurements of 1983 and 1994. The difference between pine and spruce seedling mortality from 1983 to 1999 especially at the timberline can also be seen as a difference in sensitivity to climatic stress (Kullman 1997). According to Kullman (1991, 1997) pine seedlings are more predisposed than spruce to various kinds of weather-damage during the late winter and spring. Frost drought is a regular phenomenon in timberline areas and catastrophic frost droughts have been reported to have occurred, especially in 1987, throughout all northern Fennoscandia (Kullman and Högberg 1989, Kullman 1990, Ritari 1990).

Regional variability in pine seedling mortality was clear in all the size classes. Mortality was highest in the southernmost localities (P-S region), where the transition from coniferous forest to open fell heath is abrupt and mountain birch occurs sparsely. Meanwhile, in the northernmost localities (P-N region), where the closed mountain birch belt is well developed above the coniferous timberline, pine seedlings survived well, even if they are numerically few (cf. Holtmeier 1995). This implies that pine seedlings benefit from birch shelter. This might be connected to the favourable microclimatic conditions created by birch through higher minimum air temperatures, which reduce the risk of frost injury compared with open areas (Örlander and Karlsson 2000). However, at the later stage of seedling development, intensive competition might be a crucial obstacle to pine advancing into the mountain birch belt (Kullman 2001). Spruce seedling mortality was quite the same in the localities. Seedling mortality was highest at the forest zone. This may be due to increased overstorey competition, which reduces seedling growth and survival (Lloyd 1998, Saunders and Puetmann 1999).

4 Conclusion

During the monitoring period, a lot of of the pine seedlings died, but new seedlings emerged to take their place. This dynamic process was most evident at the timberline. The number of pine seedlings is currently quite low at the timberline with most seedlings being smaller than 40 cm. Therefore, despite frequent reproduction during previous decades, the change in ecological boundaries may be delayed by high seedling mortality. Analogous processes of continuous reproduction and high mortality during the past decade have been reported in the Swedish Scandes Mountains and in North America (Lloyd 1998, Kullman 2000, 2001).

The response of spruce was different to that of pine. These monitoring surveys since 1983 show reproduction rates much higher than mortality rates. Half of the seedlings died, but due to new seedling establishment, restocking of previously sparse timberline and tree line sites has occurred. By 1999, the density of spruce seedlings less than 2 m in height was 1200 per hectare at the tree line, compared with 550 per hectare in 1983. Development of the size distribution from 1983 to 1999 reveals that ecological transformations have been under way in most spruce dominated localities. In 1983, the timberline ecotone was characterized by having a fresh expansion of small seedlings and lack of tall seedlings. By 1999, tall seedlings appeared numerously in all the zones and in all the localities, enabling a widespread upward/northward timberline and tree line advancement to occur in the near future.

Population densification, and subsequent timberline advancement, can occur only through successful reproduction, and thus it is often hypothesized that they are exclusively dependent on summer temperatures. However, although successful reproduction has occurred, even short-term climatic extremes or epidemics of fungal pathogens can cause catastrophic havoc among the seedling populations and put a stop to promising advancement processes. Therefore, as the results of this study suggest, stand dynamics in high-altitudinal habitats are also powerfully controlled by seedling mortality (see also Lloyd 1998). In this respect it can be deduced that besides summer temperatures, late winter/spring weather conditions are also of great importance.

Acknowledgements

The timberline monitoring project is being carried out by the Finnish Forest Research Institute and the northern field stations of the universities of Helsinki, Oulu and Turku. We would like to thank all persons who have contributed to data collection. We also gratefully acknowledge Jari Hietanen for the finalizing of the figures and Anneli Kurkkio for carrying out the laboratory analyses. Useful comments from two anonymous reviewers are highly appreciated. Thanks also due to Erkki Pekkinen for his checking the English manuscript.

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Total of 56 references