

Establishment and Height Development of Harvested and Naturally Regenerated Scots Pine near the Timberline in North-East Finnish Lapland

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Researchers and professionals in practical forestry have faced problems concerning the regeneration success of Scots pine in natural regeneration near the timberline in North-East Lapland. The aim of the study was to analyze the seedling establishment and seedling height development of Scots pine in seed-tree stands in the area. The average number of living pine seedlings in the study stands was about 1000 ha⁻¹, but there was considerable variation between the stands. The seedling density was modelled using a multinomial logistic regression with a random factor. Forest site type and the time since seed-tree cutting were the most significant explanatory variables in the model. The probability of reaching the acceptable seedling density was higher on dry site types than on the more fertile ones. The probability increased with the time elapsed since the regeneration activities. Effective temperature sum and the number of intermediate pines also positively affected the probability, but the presence of residual trees negatively. On northern and eastern slopes the probability was lower than on southern and western ones. Seedling height was modelled using a linear mixed model. The age of a dominant seedling was the most positively effective explanatory variable in the height development model. Other positively affecting significant predictors were time since seed-tree cutting, number of intermediate birches, and distance between a seedling and the nearest seed tree. Degree of paludification had a negative effect. The study suggests that the regeneration of Scots pine in North-East Lapland is a relatively slow process.

Keywords Scots pine, natural regeneration, seed-tree method, seedling establishment, density model, height development model, timberline

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1 Introduction

Natural regeneration accounted for 25–30% of the total regeneration area in Finland from the mid-1970s up until the early 1990s. Since then, natural regeneration has increased, especially in Finnish Lapland, where it accounted for 40–50% of the total regeneration area in the early 2000s (Finnish Statistical Yearbook of Forestry 1970–2004). The natural regeneration of Scots pine (*Pinus sylvestris* L.) is mostly achieved using the seed-tree method.

Despite the cool climate and short growing season, the capacity of Scots pine for natural regeneration is good in Finnish Lapland and elsewhere in northern Fennoscandia, especially on dry and dryish upland forest sites (Sarvas 1950). This is clearly evident in mature pine forests, where advance-growth seedlings are frequently present and they can be utilized for reforestation (Sundkvist 1993, Listov and Semyonov 1995, Hyppönen 2002). Therefore, the seed-tree method has considerable potential as a successful, cheap regeneration method even in the northernmost parts of the forested area. However, it should only be employed under favourable conditions, and using appropriate methods (Lehto 1969, Hyppönen et al. 2002, Varmola et al. 2004).

A higher seed-tree density usually induces the production of larger seed crops in Scots pine stands. Generally, 50–150 seed trees are retained per hectare in Northern Finland, but in many cases 20–50 trees per hectare seems to be enough on dry and dryish upland forest sites (Hagner 1962, Kubin 2000). Large variation in viable seed crops between years and between stands is a characteristic of Scots pine in the north (Heikinheimo 1932, 1937, Sarvas 1937, Pohtila 1980, Henttonen et al. 1986). In addition, there is a large number of ecological factors that influence the success of seedling establishment. For example, climatic conditions (Yli-Vakkuri 1961, Hagner 1962, 1965, Hyppönen 2002, Tegelmark 1998a, 1998b), site type and soil properties (Lähde 1974, Valkonen 1992, Kinnunen 1993), thickness of the humus and moss layers (Bergan 1981, Kinnunen 1993), and the ground vegetation (Räsänen et al. 1985, Beland et al. 2000), affect seedling establishment and mortality (Juntunen et al. 2002) and the initial height development of the seedlings.

Forest management activities strongly affect regeneration success (Bergan 1981, Ackzell 1993, Kinnunen 1993). Site preparation clearly improves seedling establishment (Yli-Vakkuri 1961, Ackzell 1993) and compensates for the poor seed crops especially in areas with a harsh climate and relatively high altitude (Hagner 1962, Skoklefeld 1995). Site preparation is especially necessary on moist and more fertile upland forest sites, with a thick humus layer, fine-textured soils or spruce dominated stands (Hagner 1962, Lähde 1974, Kinnunen 1993, Hyppönen et al. 2005). Furthermore, site preparation increases height growth and shortens the regeneration time (Hagner 1962, Ackzell 1993, Karlsson and Örlander 2000, Hyppönen 2002). Even with site preparation, natural regeneration often takes a long time in northern Fennoscandia (Ackzell 1993). Favourable conditions for germination are generally maintained on scarified sites for about ten years in the northern part of Fennoscandia (Hagner 1962, Valkonen 1992, Jeansson 1995). On the other hand, seed production culminates 4–5 years after establishment cutting (Karlsson 2000). Thus, if the soil is scarified, there are usually good possibilities for natural regeneration.

Professionals in practical forestry have faced severe problems in seedling establishment especially in North-East Finnish Lapland (Niemelä 2002). Additionally, a number of researchers have drawn attention to the problems in the natural regeneration of Scots pine near the northern timberline and at high elevations (e.g. Valkonen 1992, Hyppönen et al. 2005). On the other hand, the data of those studies were collected from different areas and under slightly different climatic and geographic conditions compared to North-East Lapland. Therefore, applicable research results about the environmental conditions affecting regeneration success in this particular study area are missing.

Earlier, the establishment and seedling height development have, in most cases, been modelled at the stand level using single-level data (e.g. Hyppönen and Hyvönen 2000, Hallikainen et al. 2004). During the last few years, multilevel modelling has become common (e.g. Hyppönen 2000, Hyppönen et al. 2002, 2005). The response variable has mostly been continuous but also categorical (Lexerød 2005). Multi-response multilevel modelling has also been used (Miina and Saksa 2006).

The purpose of the study was to construct explanatory models for the establishment and seedling height development in the natural regeneration of Scots pine using the seed-tree method in the especially harsh climatic conditions in North-East Lapland. The focus of the study was on analyzing the influence of certain important ecologically based variables and management activities that simultaneously affect seedling establishment and its progress over time, as well as the early height development of the seedlings. In addition, we attempted to illustrate the effects of explanatory variables by calculating the predictions of the models. Density and height development of the seedling stands are usually used as the principal attributes of regeneration success.

2 Material and Methods

2.1 Data

A stratified random sample of 62 seed-tree stands was selected from the Scots pine seed-tree stands harvested in 1986–1997 in state-owned forests in the municipality of Savukoski. The study stands were located near the timberline in the immediate vicinity of the protection forest area (Fig. 1). The protection forest area has been designated in northernmost Finland in order to prevent the deterioration of timberline forests as a result of uncontrolled cuttings, reindeer grazing, and forest fires (Varmola et al. 2004). The population was divided into 16 strata based on the regeneration

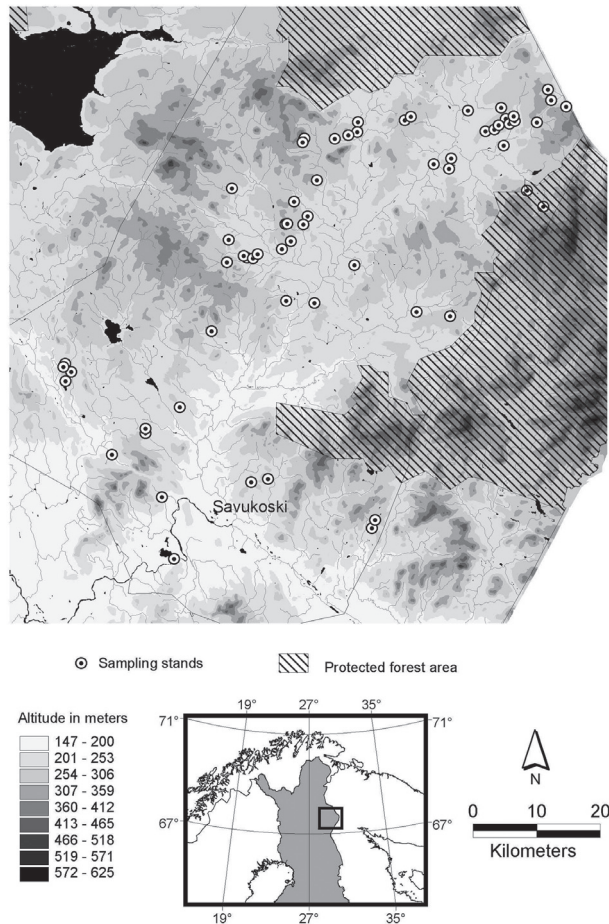


Fig. 1. The study area and the sample stands.

Table 1. The explanatory variables tested in the models. The variable types are continuous (cont.) and categorical (cat.). A large sample plot denotes a plot area of 1000 square meters and a small one of 50 square meters. The site types are the Cladina type (CIT), the Myrtillus-Calluna-Cladina type (MCCIT), the Empetrum-Myrtillus type (EMT), and the Ledum-Myrtillus type (LMT, see Cajander 1909, Kalliola 1973).

Variable	Sample plot	Type	Classification (categorical variables)	Additional information
Height of seed trees, m	Large	Cont.	-	-
Diameter of seed trees, cm	Large	Cont.	-	-
Number of seed trees ha ⁻¹	Large	Cont.	-	-
Number of intermediate Scots pines ha ⁻¹	Large	Cont.	-	-
Number of intermediate Norway spruces ha ⁻¹	Large	Cont.	-	-
Number of intermediate birches ha ⁻¹	Large	Cat.	None, 1–19 trees ha ⁻¹ , ≥20 trees ha ⁻¹	Categorized because of highly skewed distribution
Topography	Small	Cat.	Slope, dell, ridge, flat	-
Exposition	Small	Cat.	North-east, south-west, flat terrain	-
Stoniness	Small	Cat.	Yes, no	-
Paludified	Small	Cat.	Yes, no	-
Retained trees	Large	Cat.	Yes, no	-
Residual trees	Small	Cat.	Yes, no	-
Seed trees have competent crowns	Large	Cat.	Yes, no	-
Distance from the middle of the sample plot to the nearest forest edge	-	Cat.	<10 m, 10–29 m, 30–49 m, 50–99 m, ≥100 m	Measured as categorical
Site type	Small	Cat.	CIT, MCCIT (infertile) and EMT, LMT (sub-fertile or fertile)	Site type on a small sample plot
Soil type	Small	Cat.	Fine-textured, coarse-textured	Soil type on a small sample plot
Soil preparation	Small	Cat.	Prepared, not prepared	-
Proportion of exposed mineral soil, %	Small	Cont.	-	-
Thickness of humus layer, cm	Small	Cont.	-	-
Age of the maximum Scots pine seedling, years	Small	Cont.	-	-
Number of Norway spruces	Small	Cont.	-	-
Number of birches	Small	Cont.	-	-
Area of stand	-	Cat.	<5.0 ha, 5.0–9.9 ha, 10.0–19.9 ha, ≥20.0 hectares	Measured as categorical
Time since seed-tree cutting, years	-	Cont.	-	The regeneration period
Elevation, m a.s.l.	-	Cont.	-	-
Average temperature sum during the regeneration period, d.d.	-	Cont.	-	Calculated for each stand as the mean of the annual temperature sums

year (4 categories) and the size of the regeneration area (4 categories). Stratifying was used in order to ensure variation in the sample in terms of size and age (years since seed-tree cutting) of the cutting area. The number of seed-tree stands was 62 (3–4 stands/strata) and included a total of 413 sample plots (2–13 plots/stand).

The inventory method used was a systematic line survey with circular plots. The first line was located on the westernmost side of a seed-tree stand. The distance between the lines and sample plots was determined by dividing the total area in a stratum by 25, and then taking the square root of the quotient. Data were acquired from the sample plots within the stands. The size of a sample plot varied according to the information to be collected (Table 1). A part of the information was collected on the 50 m² sample plots (radius 3.99 meters), and a part on the 1000 m² plots (radius 17.84 meters). The midpoint of both kinds of plot was the same.

The total number of living Scots pine seedlings was counted on each sample plot, and the height and age of a minimum, median and maximum Scots pine seedling was measured. The definition of a minimum, median and maximum (dominant) seedling was based on the height distribution.

The area of the seed-tree stands varied from 1.0 to 101.1 hectares. Almost all of the stands were classified as dry or dryish forest site types and only 7% as the moist *Hylocomium-Myrtillys* (HMT) and *Ledum-Myrtillys* (LMT) types. The proportion of the driest site type, *Cladina* type (CIT), was 5%, that of the dry *Myrtillys-Calluna-Cladina* type (MCCIT) 37%, and the proportion of the dryish *Empetrum-Myrtillys* type (EMT) was about half of the stands (for classification of the forest site types, see Cajander 1909, Kalliola 1973). In 76% of the stands, the soil was coarse-textured till, and in 21% of the stands fine-textured till. The soil was sand or silt in only 5% of the stands. Site preparation had not been performed in half (33) of the stands, and 22 of the sites had been disk-trenched, six scalped and one ploughed. The mean proportion of the exposed mineral soil was low, less than 10% (Table 2). The site had not been prepared in 62% of the dry sites and in 53% of the dryish or moist sites.

The seed trees had not been removed from the regeneration areas (Table 2). However, the seed-

tree stand in some of the areas had been thinned by storms. In addition to the seed trees, an average of twenty *intermediate trees* had been retained on the regeneration areas. An intermediate tree (pine, spruce, and birches) refers here to a tree that is larger and older than a seedling, but smaller and younger than a seed tree. The intermediate trees are old enough to produce seed, and they can increase the seed production in a seed-tree stand.

Residual trees and bushes, i.e. broadleaved trees but also spruce, refers to trees that are usually cleared after final cutting. Nowadays a few *dominant trees* are also permanently retained on regeneration areas for ecological and aesthetical reasons (Valkonen 2000).

It was not possible to use all of the sample plots for height modelling because, in some cases, there were no pine seedlings on a plot or the age of the seedlings could not be determined reliably enough. All the potential explanatory variables tested in the density and height models are presented in Table 1. The effective temperature sum for a seed-tree stand was calculated from the latitude, longitude, and altitude using the model of Ojansuu and Henttonen (1983).

2.2 Statistical Analysis

The data structure for the models was hierarchical with two levels: the seed-tree stands (independent observations) and the sample plots nested within the stands (correlated observations). Correlation was notified in the analysis.

The seedling density was modelled using multinomial logistic regression with a random factor (Goldstein 1995, Hox 2002, Rasbash et. al 2004, Snijders and Bosker 2003), where a seed-tree stand was used as the random factor. The random factor was needed in the model, because the data are hierarchical, and the tests for parameter estimates would have been biased without the random factor. The purpose of using multinomial logistic regression was to model the probability of a sample plot belonging to a certain seedling density category. A categorical response variable was used because of the high proportion of empty sample plots (plots without any seedlings), and because the use of a continuous response variable

Table 2. Description of the sample stands.

Variable	Minimum	Maximum	Mean	Standard deviation	95% CI for mean		Median
					Lower	Upper	
Seed trees							
– height, m	7.0	19.2	14.5	2.5	13.8	15.1	15.1
– diameter at 1.3 meters, cm	13.0	38.5	24.6	5.2	23.3	25.9	24.3
– number ha ⁻¹	4	175	31	25	25	37	27
Seedlings ha⁻¹ (alive)							
– Scots pine	0	5714	1021	1235	707	1334	580
– Norway spruce	0	2960	182	436	71	292	42
– Silver birch	0	800	41	145	4	78	0
– Pubescent birch	0	4356	380	844	165	594	11
– Total	0	7200	1623	1611	1214	1611	1083
Seedlings ha⁻¹ (dead)							
– Scots pine	0	3286	460	533	324	595	300
– Norway spruce	0	400	34	71	16	52	0
– Silver birch	0	2057	60	292	0	134	0
– Pubescent birch	0	2829	224	514	94	355	0
– Total	0	5428	779	902	549	1007	507
Height of median pine seedling, cm	7	400	50	80	26	73	22
Height of maximum pine seedling, cm	12	500	103	113	69	135	52
Height of minimum pine seedling, cm	3	300	32	49	17	46	15
Age of median pine seedling, years	2	50	10	8	7	12	8
Age of maximum pine seedling, years	3	50	15	9	12	17	13
Age of minimum pine seedling, years	1	58	7	9	5	10	5
Number of intermediate trees ha⁻¹							
– Scots pine	0	103	18	21	13	23	11
– Norway spruce	0	17	1	3	1	2	0
– Birches	0	60	4	9	1	6	0
– Total	0	120	23	24	17	29	16
Height of intermediate trees, m	0.0	9.2	3.4	2.6	2.8	4.1	3.5
Thickness of humus layer, cm	0.6	10.3	3.3	1.9	2.8	3.8	2.8
Proportion of exposed mineral soil, %	0	35	7.4	8.9	5.1	9.6	4.2
Altitude, m a.s.l.	170	320	253	29	246	261	255
Average temperature sum during the years 1984–1998, d.d	653	792	692	26	686	699	694
Time since seed-tree cutting, years	2	13	7	4	6	8	8

with the assumption of normal, Poisson or negative binomial distributions, which is often used in the modelling of count data (Goldstein 1995), proved in the pre-modelling analyses to be unsuitable. The use of ordered logistic regression was not possible because of convergence problems in estimating the parameters. Furthermore, we consider that a multinomial model is easier to interpret.

The categories of seedling density were:

- 1) ≥ 1200 seedlings ha⁻¹ (acceptable pine seedling density),
- 2) 1–1199 seedlings ha⁻¹ (supplementary planting will be needed), and
- 3) 0 seedlings ha⁻¹ (planting of the total area will be needed).

The cutpoint between categories 1 and 2 is based on the forest management guidelines for the northern part of Finland (Hyppönen et al. 2001).

The multinomial logistic regression model presupposes the use of three response categories at least, which can be ordered or not (Allison 1999). The model consists of $t-1$ binary logistic regression models, where t is the number of response categories. The last category t (here 0 seedlings ha^{-1}) will be considered as a reference category, and a set of $t-1$ equations will be simultaneously estimated, contrasting each of the remaining response categories with the reference category.

The model for multinomial logistic regression with a random factor used in the analysis was:

$$\log\left(\frac{p_{ij}^{(s)}}{p_{ij}^{(t)}}\right) = \beta_0^{(s)} + \sum_{k=1}^l \beta_k^{(s)} x_{kij} + \sum_{k=1+1}^m \beta_k^{(s)} x_{kj} + u_j^{(s)}, s=1, \dots, t-1$$

where

- s and t = seedling density category indices
- k = explanatory variable index
- i = sample plot index
- j = seed-tree stand index
- $p_{ij}^{(s)}, p_{ij}^{(t)}$ = probabilities of a sample plot belonging to a seedling density category
- x_{kij}, x_{kj} = explanatory variables
- $\beta_0^{(s)}, \beta_k^{(s)}$ = fixed parameters
- $u_j^{(s)}$ = random seed-tree stand effect

The model was constructed using MlwiN statistical software (Rasbash et. al 2004). The estimation method was the second-order, marginal quasi-likelihood (MQL) method. Because our prime interest was fixed factors, random stand effects were not estimated. It was possible, using only the fixed part of the model, to calculate the predicted probabilities of a sample plot belonging to a seedling density category from the above equation as follows:

$$p_{ij}^{(s)} = \frac{\exp\left(\beta_0^{(s)} + \sum_{k=1}^l \beta_k^{(s)} x_{kij} + \sum_{k=1+1}^m \beta_k^{(s)} x_{kj}\right)}{1 + \sum_{r=1}^{t-1} \exp\left(\beta_0^{(r)} + \sum_{k=1}^l \beta_k^{(r)} x_{kij} + \sum_{k=1+1}^m \beta_k^{(r)} x_{kj}\right)}, s=1, \dots, t-1$$

and

$$p_{ij}^{(t)} = \frac{1}{1 + \sum_{r=1}^{t-1} \exp\left(\beta_0^{(r)} + \sum_{k=1}^l \beta_k^{(r)} x_{kij} + \sum_{k=1+1}^m \beta_k^{(r)} x_{kj}\right)}$$

where r, s and t are the seedling density category indices. The probabilities sum to 1, that is:

$$\sum_{r=1}^t p_{ij}^{(r)} = 1$$

The height of a dominant (maximum) seedling was modelled using a linear mixed model with the normal distribution assumption. The dominant seedlings' height was modelled because they were expected to keep their height position (see e.g. Gonzales-Martinez and Bravo 2001).

The linear mixed model used in the analysis was:

$$\log(y_{ij}) = \beta_0 + \sum_{k=1}^l \beta_k x_{kij} + \sum_{k=1+1}^m \beta_k x_{kj} + u_j + e_{ij}$$

where

- k = explanatory variable index
- i = sample plot index
- j = seed-tree stand index
- y_{ij} = height of a dominant (maximum) seedling
- x_{kij}, x_{kj} = explanatory variables
- β_0, β_k = fixed parameters
- u_j = random seed-tree stand effect (log-scaled variance σ_u^2)
- e_j = residual error term or random sample plot effect (log-scaled variance σ_e^2)

The model was constructed using the MIXED procedure of the SAS statistical software (SAS Institute Inc. 2002–2005). The estimation method was the restricted maximum likelihood (REML) method. As in the above, random stand effects were not estimated. Log-transformation was used to normalize the distribution of the residual error term. The predicted values of the fixed part of the model at the original scale were calculated using bias correction (Flewellling and Pienaar 1981) as follows:

$$y = \exp \left(\beta_0 + \sum_{k=1}^l \beta_k x_{kij} + \sum_{k=1+1}^m \beta_k x_{kij} + \frac{1}{2} (\sigma_u^2 + \sigma_e^2) \right)$$

The fit of the multinomial model was assessed on the basis of the classification table, and the fit of the linear model using the residual plot and by plotting the predicted values against the observed values. The models were not tested using independent data, because the goal in modelling was merely to describe the phenomena and to find explanatory variables, and not to make generalized predictions.

3 Results

3.1 Description of the Seedlings at Stand Level

The average number of living pine seedlings in the study stands was about 1000 ha⁻¹, and there was considerable variation between the stands. In a median seed-tree stand, there was only 600 pine seedlings ha⁻¹ (Fig. 2, Table 2). There were also a large number of dead pine seedlings in the study stands (Table 2). The natural regeneration

of Norway spruce, and especially silver birch and pubescent birch, made an important contribution to the total number (Fig. 2, Table 2).

A high proportion of the seedlings had become established as advance growth. Two thirds of the dominant (maximum) seedlings, one third of the median seedlings, and one fifth of the minimum seedlings had established as advance growth before the regeneration activities. Therefore, the height and age of the pine seedlings varied considerably between the stands (Table 2), and between the sample plots. The age distribution of the minimum pine seedlings suggested that reproduction of Scots pine had not occurred every year (Table 2). About one third of the minimum seedlings on the sample plots were at least five years old.

3.2 The Density Model

The final density model consisted of six explanatory variables, three of which were categorical ones. Site type and the number of years since seed-tree cutting were the most significant predictors in the model, but all the other variables were also highly significant, especially in sub-model 2 (model for predicting the density of ≥1200 seedlings ha⁻¹, Table 3).

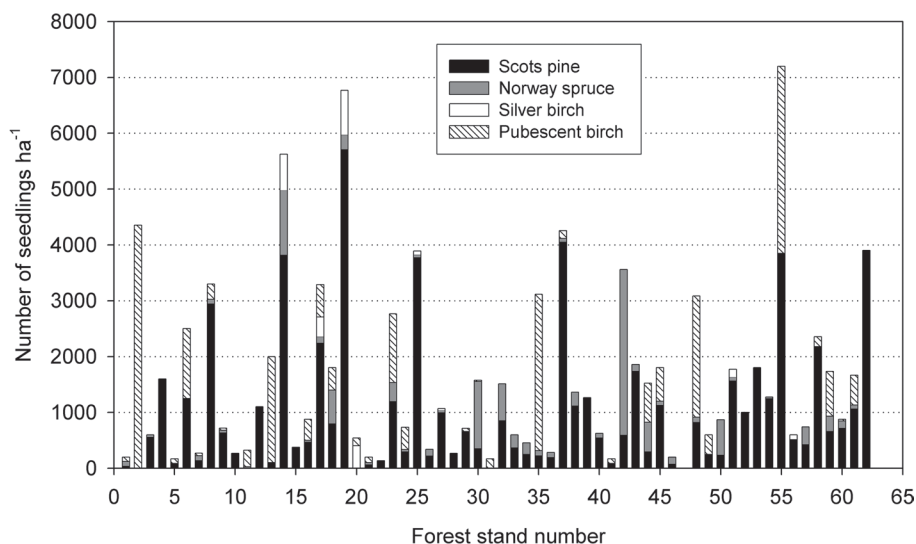


Fig. 2. The number of seedlings in the sample stands.

Table 3. The multinomial logistic regression model with a random factor for predicting the probability of a sample plot belonging to a seedling density category: ≥ 1200 seedlings ha^{-1} , 1–1199 seedlings ha^{-1} and 0 seedlings ha^{-1} (reference category). The χ^2 -test value corresponds to the value of the Wald test. Joined Wald tests are calculated for the categorical variables in order to test the significance of the variable in the model.

Explanatory variable / Parameter	Estimate	Std error	χ^2 -value	Odds ratio	df	p
Sub-model 1: Seedling density 1–1199 seedlings ha^{-1} (reference: 0 seedlings ha^{-1})						
Intercept	-9.458	3.307	0.000	6.172	1	0.013
Time since cutting, years	0.255	0.044	1.290	34.292	1	0.000
Temperature sum, d.d.	0.012	0.005	1.012	5.269	1	0.022
Intermediate pines ha^{-1}	0.009	0.003	1.009	7.274	1	0.007
Site type (ref. EMT, LMT)		Joined		44.429	1	0.000
– CIT, MCCIT	1.704	0.256	5.496	44.429	1	0.000
Residual trees (ref. Not present)		Joined		5.153	1	0.023
– Present	-1.003	0.442	0.367	5.153	1	0.023
Exposition (ref. South, West)		Joined		13.035	2	0.001
– North, East	-1.048	0.331	0.351	10.015	1	0.002
– Not defined	-0.877	0.278	0.416	9.964	1	0.002
Sub-model 2: Seedling density ≥ 1200 seedlings ha^{-1} (reference: 0 seedlings ha^{-1})						
Intercept	-23.371	5.757	0.000	16.479	1	0.000
Time since cutting, years	0.479	0.068	1.614	49.320	1	0.000
Temperature sum, d.d.	0.026	0.008	1.026	11.766	1	0.001
Intermediate pines ha^{-1}	0.019	0.004	1.019	24.659	1	0.000
Site type (ref. EMT, LMT)		Joined		73.290	1	0.000
– CIT, MCCIT	3.241	0.379	25.559	73.290	1	0.000
Residual trees (ref. Not present)		Joined		18.095	1	0.000
– Present	-2.575	0.605	0.076	18.095	1	0.000
Exposition (ref. South, West)		Joined		17.174	2	0.000
– North, East	-1.572	0.395	0.208	15.803	1	0.000
– Not defined	-1.026	0.321	0.358	10.240	1	0.001
Random part of the models: the variance (Var) and the covariance (Cov) of the random seed-tree stand effects (u) for the sub-models 1 and 2						
Var($u^{(1)}$)	0.511	0.218	-	5.474	1	0.019
Var($u^{(2)}$)	1.560	0.520	-	8.995	1	0.003
Cov($u^{(1)}, u^{(2)}$)	-0.614	0.282	-	4.753	1	0.029

The probability of reaching the acceptable seedling density increased with the time elapsed since the regeneration activities. The difference between the site types was considerable (Fig. 3a and 3b). Thirteen years since seed-tree cutting gave a probability of 70% of having an acceptable seedling density on the dry sites (Fig. 3a), but the probability on dryish or more fertile sites was only 30% (Fig. 3b). The expected probability of an empty sample plot on dryish or more fertile sites was extremely high, about 70% immediately after seed tree cutting (Fig. 3b).

The adverse effect of residual trees on regeneration was considerable, and it increased with time. The expected probability of an acceptable seedling density was about 30 percent-units lower on a 13-year old regeneration area with residual trees compared to one without any residual trees (Fig. 3c and 3d).

The temperature sum had a strong influence on regeneration success (Fig. 3e). The probability of reaching the acceptable seedling density in the temperature sum conditions near the timberline (650 d.d.) was about 35 percent-units lower

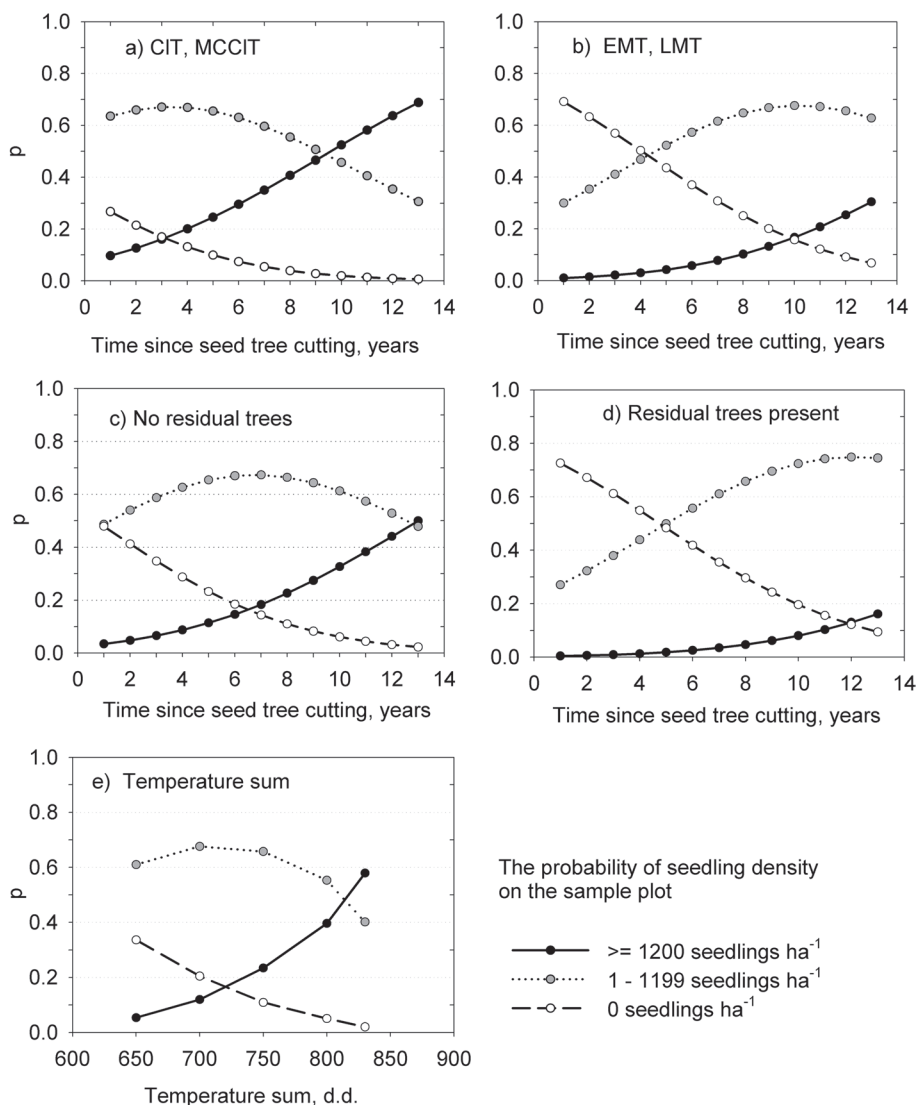


Fig. 3. The influence of the time since seed-tree cutting on the probability (p) of the classified seedling density by forest site types (a, b) and the existence of residual trees (c, d), and the influence of temperature sum on the probability of the classified seedling density (e).

than in the favourable conditions of the study area (800 d.d.) seven years after seed-tree cutting (mean value). However, the probability of no seedlings was about 35%, and of a seedling density of 1–1199 seedlings ha^{-1} was about 60% in the severe temperature conditions near the timberline (Fig. 3e).

An increasing number of intermediate pines

increased the probability of reaching the acceptable seedling density. The increase in the probability was 20% when the number of intermediate pines increased from 0 to 100 stems ha^{-1} . Furthermore, the probability of the acceptable seedling density was about 10 percent-units higher on south–west slopes compared to north–east slopes.

Table 4. Classification table of the multinomial logistic regression model. The predicted categories (columns) have been calculated using the fixed part of the model. The values, except for the number of sample plots, are row percents. The overall classification efficiency is 60.8%.

Seedling density	0 seedlings ha ⁻¹	1–1199 seedlings ha ⁻¹	≥ 1200 seedlings ha ⁻¹	Number of sample plots
0 seedlings ha ⁻¹	65.4	27.8	6.8	133
1–1199 seedlings ha ⁻¹	20.8	57.2	22.0	168
≥ 1200 seedlings ha ⁻¹	1.8	38.4	59.8	112

Table 5. Tests for the explanatory variables of the log-transformed height development mixed model.

Explanatory variable	Numerator df	Denominator df	F-value	p
Age of the seedling ^{-0.5} , years	1	134.0	890.60	0.000
Distance from the nearest seed tree, m	1	128.0	12.95	0.001
Time since seed tree cutting, years	1	39.9	6.81	0.013
Intermediate birches (not any, 1–20 ha ⁻¹ , >20 ha ⁻¹)	2	123.0	4.07	0.019
Paludification (paludified, not paludified)	1	133.0	8.62	0.004

Table 6. The parameter estimates for the log-transformed height development mixed model.

Explanatory variable / Parameter	Estimate	Std error	df	t-value	p
Intercept	0.339	0.235	138.0	1.44	0.152
Age of the seedling ^{-0.5} , years	0.745	0.050	134.0	29.84	0.000
Distance from the nearest seed tree, m	0.018	0.005	128.0	3.60	0.001
Time since seed tree cutting, years	0.030	0.011	39.9	2.61	0.013
Intermediate birches (reference category is ‘not any’)					
– >20 trees ha ⁻¹	0.332	0.149	111.0	2.22	0.028
– 1–20 trees ha ⁻¹	0.224	0.099	133.0	2.26	0.025
Paludification (reference category is ‘not paludified’)					
– paludified	–0.531	0.181	133.0	2.94	0.004
Random part of the model				z-value	
Seed-tree stand variance, σ_u^2	0.044	0.018		2.43	0.008
Residual variance, σ_e^2	0.097	0.014		6.97	0.000

The classification efficiency of the model in the data was relatively good. About 60% of the sample-plots were classified into the correct category. In addition, the efficiency was relatively stable in the three categories, the classification efficiency being almost the same in all the categories (Table 4).

3.3 The Height Model

Seedling age was the most effective explanatory variable in the height model (Tables 5 and 6). Time since seed-tree cutting also affected the height of a dominant seedling (Tables 5 and 6). The effect of time since seed-tree cutting on the mean height of a seedling was about 1 cm a

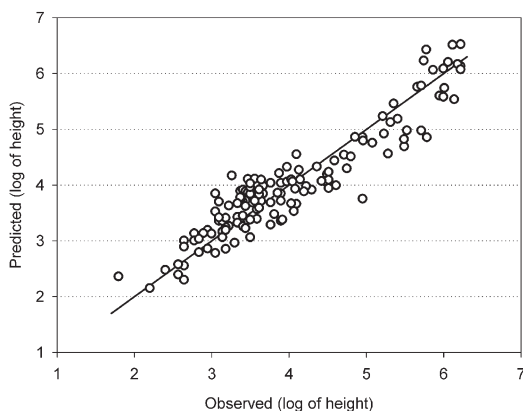


Fig. 4. The fit of the height model.

year, when the other explanatory variables were fixed at their mean values and the site was not paludified.

Paludification was a highly significant predictor in the model (Tables 5 and 6), since the seedlings were about 17 cm smaller on paludified sites. The number of intermediate birches was positively correlated with the height of the pine seedlings (Tables 5 and 6). Forest site type was not a significant predictor, and no significant relationship was found between the site type and the number of intermediate birches.

The distance between a seedling and the nearest seed tree had a significant influence on seedling height (Tables 5 and 6). If the distance was one meter, then the average height of a seedling was 35 cm when the effects of the other variables were fixed to the mean (e.g. mean age of the seedlings was 15 years) values and the site was not paludified. The predicted heights corresponding to distances of 10, 20 and 30 m were 41, 49 and 60 cm, respectively.

The fit of the model was fair as far as the observed and predicted values were concerned (Fig. 4). On the original scale, however, the residuals increased considerably when seedling height was more than 50 cm. Thus, the prediction accuracy for taller seedlings was not as good as that for shorter ones.

4 Discussion

The models should primarily be considered as explanatory models, because the main purpose was to find the explanatory variables affecting the regeneration success and height development of pine seedlings. The most important result of this study was the complexity (many variables affecting together) of the environmental factors, which simultaneously (tested in the same model) affected regeneration success and seedling height development under the harsh conditions of North-East Finnish Lapland. The inventory data provided a suitable means to study the complexity of the factors. The inventoried forest stands are a random sample of the regeneration areas in North-East Lapland. Thus, the models can be generalized for all the similarly regenerated stands in the study area. However, the coefficients for the predictors and the calculated predictions should be considered as indicative only. The predictions approximately illustrate the effects of the explanatory variables on the regeneration success and seedling-height development.

Based on the classification efficiency table for the multinomial model (Table 4) and observed versus predicted values for the linear model (Fig. 4), the fit of the models in the dataset is relatively good. However, the model was not tested using any independent validation method, independent data or cross-validation etc. (e.g. Snee 1977). This dataset was too small and unbalanced for such purposes. In further studies, the ability of the model to provide accurate predictions and wider generalizations in similar timberline conditions should be tested.

Regression models with random factors and a normal or Poisson distribution assumption have been used e.g. by Hyppönen et al. (2005), and a binary response logistic model in the modelling of empty versus recruited sample plots e.g. by Lexerød (2005). Because regression models with random factors and a normal or Poisson distribution assumption could not be used, a categorical response was the only possibility. The multinomial logistic regression models are an expansion of the binary logistic models. Thus, a multinomial model will give more detailed information compared to a binary logistic one. A linear regression model and a Poisson model will

predict the number of recruited seedlings under certain environmental conditions. A multinomial model predicts the probability to achieve a certain number of seedlings under certain environmental conditions. This information can be considered as important for decision-making in forest management (e.g. how probable it is to achieve a seedling density of at least 1200 seedlings ha⁻¹ during the seven-year period since seed-tree cutting). The multinomial regression models without a random factor have already been in use for a rather long time. However, the random factor was needed in this study because of the multi-level data. The multinomial logistic regression model with random factors represents a new approach in the modelling of forest regeneration. Development of the method, its algorithms, and the model evaluation routines are currently in progress (see Rashbash et al. 2004).

Although the study area is not located in the protection forest area, most of the study stands were located at high elevations far to the north in the immediate vicinity of the protection forest area and timberline. High elevation and northern location are associated with a low effective temperature sum. Both high elevation and low temperature sum are associated with poor regeneration results, i.e. a lack of mature seed crops, low emergence rate, and high seedling mortality (Varmola et al. 2004). The success of natural regeneration in the protection forest area has generally been satisfactory (see Varmola et al. 2004). Hyppönen (2002) found that 20% of the natural regeneration area in a dataset collected in the protection forest area was classified as unsuccessfully established. The regeneration success in this study was poorer, the proportion being as low as 50%. This suggests that environmental conditions in the area may be more difficult than in the areas mentioned above.

The effective temperature sum during the growing season needed for the formation of flower buds, which are of course a prerequisite for abundant flowering, must be at least 910 d.d. (Sarvas 1950). Furthermore, the temperature sum during the growing season needed for 50% ripening of the seed crop must be at least 845–890 d.d. (Pohtila 1980, Henttonen et al. 1986). However, some incompletely matured seed is produced every year even along the timberline (Heikinheimo 1932,

1937). Gradual establishment had also occurred in the study stands, despite the fact that the average temperature sum in the study area did not reach these limits during the study period.

Juntunen et al. (2002) reported that the high mortality of pine seedlings restricted regeneration at the high-elevation and low-temperature conditions on the timberline. The abundance of dead pine seedlings in this study also indicated a relatively high seedling mortality under the harsh conditions of North-East Lapland.

Elevation has earlier been used as one of the explanatory variables in models for predicting seedling establishment (Hyppönen et al. 2002, 2005). In our study, elevation was not a significant predictor in the density model, which is probably due to the narrow elevation range in the data. However, elevation is closely correlated with temperature sum, and it was a statistically significant predictor in this study. In addition, exposition was found to have an effect on seedling establishment; the difference between south–west and north–east -slopes was as expected. For example, Çolak (2003) found a corresponding difference between slopes with different exposition in the regeneration success and development of Scots pine in the mountains of northern Anatolia.

The study area is dominated by dryish sites that are relatively poor in nutrients. The proportion of dry upland forest sites in the region is higher, and the proportion of moist and fertile ones is lower than elsewhere in northern Lapland or in Lapland in general (Kinnunen et al. 1998, Sandström et al. 2000). Hence, the site properties required for successful pine regeneration should be better than the average in northern Lapland.

Despite the low site fertility, there was a considerable admixture of Norway spruce and birch seedlings among the pine seedlings. The quality and production of spruce and birch seedlings are usually economically unsatisfactory on forest sites like these. In Lapland, the production of birch and spruce is lower than that of pine even on moist fertile *Ledum-Myrtillus* (LMT) or *Hylocomium-Myrtillus* (HMT) site types (Ilvessalo 1970). In addition, birch seedlings are often damaged by reindeer grazing (Mäkitalo et al. 1997). However, both spruce and birch seedlings can contribute to the stand structure and production. Birch also improves the soil properties (Berg and Cortina

1995), and this can be assumed to be especially important on dry, coniferous-dominated sites.

Site type considerably influenced the regeneration success, as has been reported in many other studies in northern Europe (e.g. Kinnunen 1993, Hyppönen et al. 2005). In this study, dry and dryish site types differed from each other irrespective of whether they were prepared or not, which is the opposite to the report of Hyppönen et al. (2005) in which they did not differ. In their study, unprepared moist site types differed from prepared moist site types and all the dryer ones irrespective of whether they were prepared or not. Site fertility is reflected by the ground layer vegetation, and this has been found to play an important role in seedling establishment in boreal forest ecosystems (Nilsson and Wardle 2005).

On the dry sites, a high proportion of the seedlings needed to reach the acceptable seedling density had already become established as an understorey before seed-tree cutting, in contrast to the more fertile sites. On those site types, the number of understorey seedlings was lower. In addition, a part of the seedlings had probably been destroyed during site preparation, in contrast to unprepared dry sites. A higher density of natural understorey seedling-stands on dry sites compared to that on dryish and moister sites has been reported in a study carried out in northwest Karelia, Russia (Volkov et al. 2000).

The probability of reaching the acceptable seedling density increased gradually during the period after seed-tree cutting. According to the Forest Act, satisfactory seedling establishment must be achieved within seven years after seed-tree cutting in Finnish Lapland (Metsäläki 1996). The results of this study suggest that there is only a slight chance of reaching the required establishment rate within this time frame without supplementary artificial regeneration, especially on dryish and moist sites. The probability of reaching the required establishment result would require at least ten years. The results obtained by Hyppönen et al. (2005) suggested that the acceptable seedling density could be obtained during the seven-year period in most other parts of Lapland.

Contrary to the results obtained in some other studies carried out in Lapland (e.g. Hyppönen 2002, Hyppönen et al. 2002, 2005), site preparation had no statistically significant effect on the

regeneration success. One explanation for the conflicting results may be that the regeneration period is too short in the harsh climate conditions of this area. Site preparation always destroys a part of the advance growth, and it takes a number of years before the seedling density even returns to the level prevailing before site preparation.

The presence of a small residual stand, mostly broadleaved trees, which is usually cleared after seed-tree cutting, had a negative influence on the seedling establishment of pine. This is a surprising result, because the residual stand was not abundant. On poor sites in the north, a residual stand may result in a high level of root competition, and inhibit seedling establishment and the initial development of pine seedlings (see Aaltonen 1919). The negative effect of a hardwood residual on the natural regeneration success of Scots pine has also been reported in some other studies (González-Martínez 2001).

In the north, the natural pine forests are sparse, and their canopy cover is not closed. Despite this, the mature trees present on the site inhibit the growth of seedlings (Hyppönen and Hyvönen 2000). Seed trees have been found to have a negative influence also on height growth (Hyppönen et al. 2005). It is obvious that root competition retards the growth of seedlings more than the lack of light (see Aaltonen 1919, Goomies and Grubb 2000, Vikberg 2004). The wide-ranging effect of the nearest seed tree on seedling height development, found in our study, confirms the effect of root competition.

Site type did not affect the seedling height in this study. The result was supported by some earlier studies (Hyppönen et al. 2005). On the other hand, conflicting results have also been obtained (Hyppönen 2002).

The positive relationship found between the number of intermediate birches and the height of the pine seedlings may be an indication of specific soil characteristics that promote both the height development of pine seedlings and the presence of birches in the same microhabitat. Birch litter contains relatively large amounts of rapidly released nutrients and this may have enhanced the growth of the pine seedlings as well (see Berg and Cortina 1995). Although the growth-promoting effects have not been widely studied, it is evident that the species composition of forest litter has an

effect on growth. For example, a mixture of birch and black crowberry (*Empetrum hermaphroditum* Hagerup) has been reported to have a promoting effect on the growth of pine biomass (Nilsson et al. 1999).

The study suggests that, in North-East Lapland, the regeneration of Scots pine is generally more problematic and slower than in other parts of northern Lapland near the timberline (Hyppönen 2002, Varmola et al. 2004). The time required to reach an acceptable seedling density is much shorter in the southern part of Lapland than in North-East Lapland. The results suggest that successful regeneration usually requires more than ten years. In addition, the mortality rate of the seedlings is considerable in the north. The difference between different site types is also considerable. Especially on the dryish and more fertile sites, seedling recruitment has been too low despite site preparation. The effects of the ground vegetation, the chemical and/or physical soil properties, and fungal infections on the establishment and development of seedlings should be studied in the future (see Nilsson and Wardle 2005).

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