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Manipulating overstory density and mineral soil exposure for optimal natural regeneration of Scots pine

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ABSTRACT

In northern boreal region the growth of forests is slow, and yield and profit are low, which is why low reforestation costs are important for profitable forestry. If natural regeneration is successful, expensive artificial forest regeneration (planting or direct seeding) can be avoided. In this study, we look at the impact of overstory density and site preparation on natural regeneration and seedling growth of Scots pine. Study stands were established in different parts of Northern Finland and in each stand following treatments: 50, 150 and 250 trees ha^{-1} or unthinned control, where the stand density was $\geq$ 250 trees ha^{-1}, were randomly allocated to experimental plots. In addition, site preparation (disc trenching, 4000–5000 m ha^{-1}) was carried out on two experimental plots in which tree density was either 50 or 150 trees ha^{-1}. In the experimental stands seedling number, age and growth were monitored for 11 years. Monitoring revealed that the number of seedlings increased with decreasing tree density. Average seedling height growth was very low or even non-existent in the unthinned control and in the densest (250 trees ha^{-1}) treatment, but increased when the density of trees decreased. The highest seedling number and the highest growth were achieved when the tree density was 50 trees ha^{-1} and the soil was prepared to expose mineral soil. Achieving e.g. 2000 seedlings ha^{-1}, would need about 40% exposition of mineral soil. The required low tree density implies that not only seed supply from seed trees and site preparation is important for regeneration success in northern boreal Scots pine forests but also the reduction of competition by mature trees.

1. Introduction

The use of natural forest regeneration as an inexpensive regeneration method is particularly supported in northern part of Finland where the expected revenue is lower compared to the southern part of Finland where the forest growth is faster. Also the increased multifunctional use of forests and the need to keep forests increasingly tree covered throughout their life cycles are highlighted in the north. Many forms of forest use in northern Fennoscandia, such as tourism, reindeer herding and recreation, benefit from the preservation of more continuous forest cover through denser seed-tree and shelterwood stands compared to that used in practical forestry today (Hyppönen, 2002). That is why discussion about the benefits of Continuous-Cover Forestry (CCF) has intensified recently, especially regarding state owned forests, which are abundant in Finnish Lapland.

Natural forest regeneration with the seed-tree and shelterwood methods involves the retention of a moderate to large number of overstory trees throughout the restocking period. The retention trees, or part of them, may also remain on site for much longer for certain purposes, especially if aiming at the development of a two- or multi-storied stand in terms of Continuous-Cover Forestry as based on Northern German experience (Heinsdorf, 1994). However, Scots pine (*Pinus sylvestris* L) is a light-demanding species, and it is questionable how much shading and overstory competition is tolerated during the restocking period and the subsequent stages when seedling growth and survival are critical. In any case, a minor part of the original seed or shelterwood trees are supposed to be permanently retained throughout the management cycle and beyond.

In addition to light availability, natural regeneration in a pine forest is affected by multiple intertwined abiotic and biotic factors. This was

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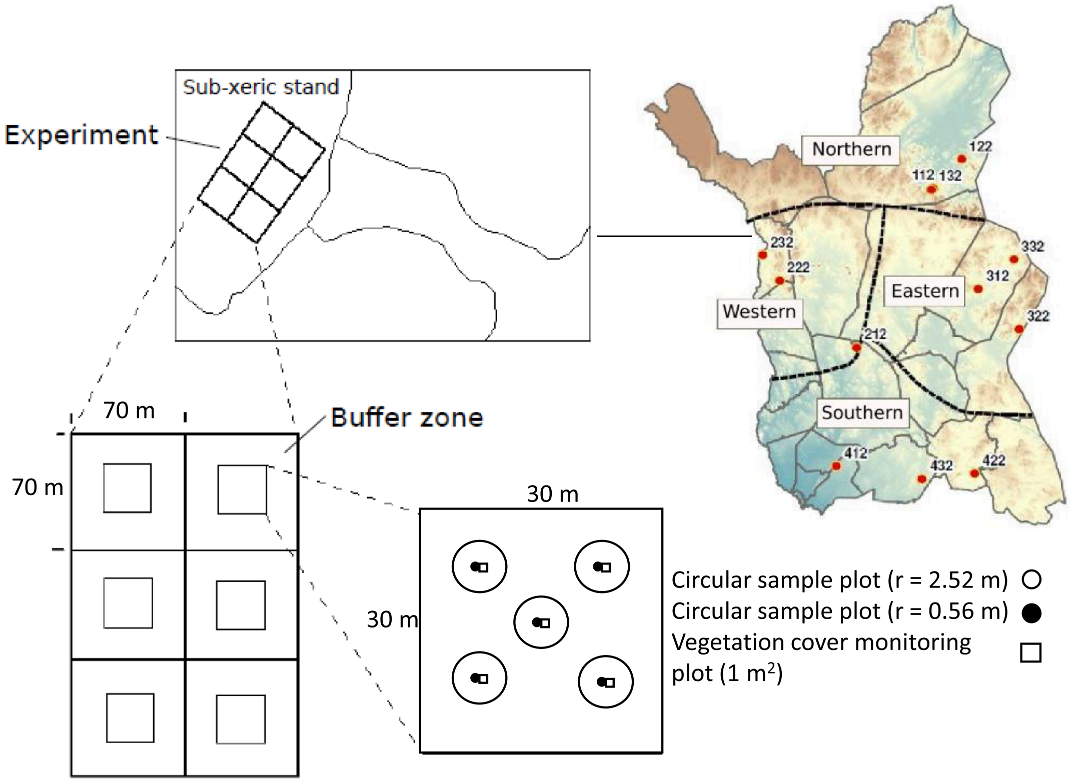

Fig. 1. Location of districts and experimental stands and study design in the stands.

clearly demonstrated in terms of the famous German "*Dauerwald* " management concept, where the shade tolerance, survival and growth of pine seedlings underneath pine overstories depended very much on site fertility and moisture (Wiedemann, 1925). Of such abiotic factors, soil properties like temperature, moisture, texture, water retention capacity and nutrient level are considered most important. Of biotic factors, competition between mature trees (e.g. Aaltonen, 1919; Hagner, 1962; Ackzell and Lindgren, 1992, Thishler et al., 2020), competing tree seedlings (Peet and Christensen, 1987; Nilsson and Albrektson, 1994; Ruano et al., 2013) and understory vegetation (Lehto, 1956; Hyppönen et al., 2013, Huth et al. 2022) are affecting regeneration. Further, the winter conditions are of especial importance in these northerly areas. For example, snow blight (caused by a pathogen *Phacidium infestans* P. Karst.) can kill snow-covered small pine seedlings and branches of trees of various size classes and cause big losses. The needles are infected in autumn and the pathogen is able to expand under the cover of snow even at –5°C. This pathogen causes losses nearly every year, and thus it is a very significant factor in natural selection of Scots pine seedlings (Jalkanen, 2003, 2007).

The role of mature trees on regeneration is complex and contradictory. A higher density of shelterwood implies a higher seed yield and a higher number of pine germinants (Beland et al., 2000; Dovčiak et al., 2003). On the other hand, overstory trees tend to reduce seed germination as well as seedling survival and growth especially in the closest vicinity of the overstory trees through shading and competition for nutrients and water (Aaltonen, 1919; Lehto, 1956, 1969; Niemistö et al., 1993; Bassett and White, 2001; Hallikainen et al., 2007).

Emerging seedlings have not only the tree overstory trees to compete with but also other tree seedlings and forest floor vegetation. As an example of competition between tree seedlings, Nilsson and Albrektson (1994) found that in a high competition pine sapling stand (HCS, 40 000 stems ha^{-1}) compared to a low competition stand (LCS, 10 000 stems ha^{-1}) the mortality was about the same until 5 years of age but increased after that annually up to year 15 in HCS while remaining constant in the LCS. The noteworthy effects of dense brush of broadleaved species on the survival and growth of Scots pine seedlings and their dependence of the pine overstory density as commonly observed and accounted for in Central Europe (e.g. Lust, 1987; Lust and Geudens, 1998) are not common in Northern Fennoscandia where Scots pine management is not much practiced on mesic sites.

In case of forest floor vegetation, the pattern is much more complicated. Lehto (1956) reported the effect of understory vegetation and thickness of humus layer on seedling establishment being larger than the effect of overstory trees. But in fact, the forest floor vegetation as such can have a contradictory role on regeneration. Some species have been reported to have positive while others to have negative effects on seedling establishment. In a study by Hyppönen et al. (2013) the presence of crowberry (*Empetrum nigrum* ssp. *hermaphroditum*), feather moss (*Pleurozium shreberi*) or *Dicranum* moss species increased the mortality of pine seedlings, while the pine seedling density increased with the cover of heather (*Calluna vulgaris* L.). In contrast, Nilsson and Zackrisson (1992) found that heather was harmful to seedling establishment. Moreover, Hyppönen et al. (2013) found that heather decreased the height growth of pine seedlings while mitigating seedling establishment. Hertz (1934) reported that shrubs do not impair the establishment of seedlings. Similarly, to the results concerning the shrub layer, studies on the effects of ground layer on pine regeneration have also brought conflicting results. Brown and Mikola (1974) showed that lichens have negative allelopathic effects on mycorrhizas and tree seedlings but later on Steijlen et al. (1995) and Kytöviita and Stark (2009) have reported that the effects of lichens are neutral or even beneficial. Kyrö et al. (2022) showed that high coverage of hair mosses (Polytrichum spp.) was associated with poorer seedling survival.

Whatever the actual effects of tree overstory or forest floor vegetation on regeneration really are, in practical forestry the general assumption has been that their effect is competitive and negative to seedling establishment and growth (Hagner, 1962, Lehto, 1969,. Hence the silvicultural practice has been to decrease the degree of competition

Table 1
Data description. The ground cover (in %) and the values of other continuous explanatory variables. Measurement 1 denotes the measurement of the cover in the beginning and 2 denotes the measurement in the end of the inventory period, avg. being an average (used in the statistical models). All the variables were tested in the models in addition to the treatment effect, number of inventory, and the number of all seedlings in the 20 m^2 circular sample plot (in the case of the height model).

Variable	Mean	Median	Min.	Max.
Cover (%)				
Bilberry 1 (*Vaccinium myrtillus*)	5.48	1.00	0.00	50.00
Bilberry avg.	6.50	3.67	0.00	51.67
Bilberry 2	6.25	4.00	0.00	45.00
Cowberry 1 (*Vaccinium vitis-idaea*)	6.77	5.00	0.00	50.00
Cowberry avg.	8.68	7.00	0.25	43.33
Cowberry 2	9.32	7.00	0.00	45.00
Crowberry 1 (*Empetrum nigrun*)	4.21	1.00	0.00	50.00
Crowberry avg.	7.40	5.17	0.00	41.67
Crowberry 2	9.41	5.00	0.00	50.00
Heather 1 (*Calluna vulgaris*)	0.81	0.00	0.00	20.00
Heather avg.	2.07	0.00	0.00	21.67
Heather 2	2.88	0.00	0.00	30.00
Lichens 1	6.97	1.50	0.00	60.50
Lichens avg.	5.23	3.00	0.00	46.92
Lichens 2	4.91	3.00	0.00	50.25
Mosses 1	71.89	80.00	0.50	100.50
Mosses avg.	65.89	71.00	2.67	99.67
Mosses 2	65.08	75.00	0.50	102.00
Exposed mineral soil 1	9.18	0.00	0.00	100.00
Exposed mineral soil 2	5.97	0.00	0.00	60.00
Slash 1	5.36	1.00	0.00	100.00
Slash 2	4.46	2.00	0.00	55.00
Other continuous explanatory variables				
Number of seedlings (>10 cm) in 20 m^2 circular plots	6.48	1.00	0.00	168.00
Thickness of humus layer, mm	26.91	24.00	4.00	73.25
Stoniness (penetration of stick, cm)	24.59	23.12	2.50	62.50
Proportion of coarse sandy (2.0 – 0.2 mm), %	48.37	46.93	9.53	83.08
Proportion of fine sandy (0.2 – 0.06 mm), %	35.72	35.96	7.60	85.05
Proportion of silty (<0.06 mm), %	25.84	25.25	1.85	47.72
Temperature sum, d.d. (average of period 1981 – 2010)	747	726	638	925
Age of pine seedlings (years)	10.58	9.75	1.00	36.00

with thinning of the overstory and site preparation for the ground vegetation. These two methods are usually combined in the standard natural regeneration method of seed tree cutting, where mature trees are left at a density of 50–100 trees per hectare to produce a sufficient seed rain while exposing mineral soil for the seeds to germinate and for the seedlings to survive and grow. A seed tree cutting might be preceded by a preparatory cutting where > 200 mature trees are left to the stand in order to strengthen their roots and canopy for about 10–15 years (Hyppönen, 2002). Mineral soil exposure has been found to improve the emergence of pine seedlings on xeric and sub-xeric heaths. In practice, the share of the exposed mineral soil does not have to be very large for an improvement in seedling establishment, as an example Hallikainen et al. (2019) have found 10–15% mineral soil exposure of the ground surface area to be enough. Site preparation not only removes competition of field and ground layer vegetation, but also improves physical properties of the soil. Site preparation raises the temperature of the soil (Lähde, 1978; Örlander et al., 1990), and because the heat sum positively influences the result of regeneration (Hyppönen, 2002, 2005) the exposed mineral soil can also favor the emergence this way. Heiskanen et al. (2007) found that 21 years after site preparation the water retention at saturation and air-filled porosity at field capacity (10 kPa) were significantly higher and the bulk density lower in ploughed ridges than in the untreated intermediate areas. The fact that Forest floor vegetation can suppress seedlings and the humus layer prevents seed from entering a suitable germination surface in the mineral soil (Nygren and Saarinen, 2001).

The aim of the present study was to find out how seedling establishment and growth are affected by silvicultural treatments optimizing competition by mature trees and ground and field layer vegetation. The study is based on a field experiment where we: 1) Manipulated the density of a mature pine stand, and 2) Partly removed the ground and field layer vegetation and the raw humus to uncover the mineral soil. Our hypotheses were: 1) Uncovering the mineral soil enhances seedling emergence with a multiplicative rather than just additive effects when combined with thinning in the overstory and 2) thinning in the overstory increases the number of seedlings and their growth. The results are based on data representing a monitoring period of 11 years on the experimental plots.

2. Materials and methods

2.1. Study area and experimental design

The study area covers the forested part of Finnish Lapland that is around 9 million hectares. The area was divided into four districts: southern, western, northern and eastern Lapland. Three experimental stands (replicates) were placed in each district (Fig. 1, Appendix Table A1). The experimental stands had to fulfill the following criteria: 1) sub-xeric site on mineral soil, 2) Scots pine dominated, 3) the number of Scots pine stems at least 250 trees ha^{-1}, 4) large enough for the experiment (at least three hectares of non-fragmented forest), 5) mature forest (up for final harvest and regeneration immediately or no later than 10 – 20 years according to the Finnish Best Practices (Äijälä et al., 2019). Due to long south-north distance the age of mature forest varies in the study area from 80 to 120 years. At the first stage of the experimental site selection, candidates were provided and examined using the geographic information system of Metsähallitus Forestry Ltd (responsible for the management of state-owned forests in Finland). Potential sites were checked in situ, and the best alternatives fulfilling the requirements were selected. Especially the size of the homogeneous forest stand played a major role in the selection process. If there were more than one more or less equal alternative pine stand in a district, the site was chosen randomly among these.

In each experimental stand, a set of six square treatment plots was placed in the central homogenous area. Each plot was 70 × 70 m in size. A core plot of 30 × 30 m was placed in the middle of each of the treatment plots, and all the measurements were carried out in the core plot. The rest of the plot thus constituted a buffer zone with a width of 20 m in all directions. The buffer zone was treated similarly as the core plot (Fig. 1). The treatments for the six treatment plots were randomized. The treatments were: 1) tree density 50 trees ha^{-1} without site preparation (50 NT in the figures), 2) tree density 50 trees ha^{-1}, with disc trenching (50 T), 3) tree density 150 trees ha^{-1} without site preparation (150 NT), 4) tree density 150 trees ha^{-1} with disc trenching (150 T), 5) tree density 250 trees ha^{-1} without site preparation (250 NT), 6) control, no cutting or site preparation (Control). Tree density in control plots was on average 439 trees ha^{-1}. Site preparation (disc trenching) was not applied with the tree density of 250 trees ha^{-1}, because the massive machinery would have been too difficult to operate among such a dense stand of trees. The number and diameter at breast height of trees with $d_{1.3} > 3$ cm was measured before and after cutting. Disc trenching was performed targeting 4000–5000 m site preparation tracks per ha with a track breadth of 60–80 cm, constituting to an exposed proportion of 24–40 % of area. The proportion of exposed mineral soil in different treatment is given in Appendix 1 (Table A2).

On each of the six treatment plots, five circular sample plots (20 m^2, radius 2.52 m) were placed in a systematic order on the core 30x30 m plot (Fig. 1) before cutting and site preparation. The number and height of the Scots pine seedlings (height $\geq$ 10 cm) were recorded in each subsequent seedling inventory on each circular sample plot.

All birch (*Betula* spp.) and Norway spruce (*Picea abies* (L.) H. Karst.) seedlings and all pine seedlings with a height over 0.5 m were removed from the circular plots at establishment, except for the control treatment that represented the forest without the effects of harvest operations and site preparation. Consequently, some seedlings (h less than 50 cm) remained on the circular sample plots – and on sample plots on control treatment also seedlings $h > 50$ cm - already from the beginning. The computed seedling count variable included all seedlings with height $\geq$ 10 cm on the sample plot in each measurement. The seedling height used here in the data analysis is the arithmetic mean of seedlings in a sample plot.

2.2. Data collection

Composition of the ground and field layer vegetation (% of ground cover) was measured on 1 m^2 square sample plots placed in the center of each 20 m^2 sample plot after the cutting and site preparation. Also, the proportion of scarified mineral soil and slash (harvest residue) were recorded in the same 1 m^2 square sample plots after cuttings (Fig. 1).

The vegetation cover was recorded for groups of species such as mosses, grasses, and lichens, and separately for the most common dwarf shrub species:cowberry (*Vaccinium vitis-idaea*), bilberry (*Vaccinium myrtillus*), crowberry (*Empetrum nigrum*) and heather (*Calluna vulgaris*). The vegetation and the proportion of scarified mineral soil were measured in the beginning of the experiment, and also in parallel with the last seedling measurement (Table 1). A rather long monitoring period during the experiment lead to challenges to describe the cover of the vegetation and the cover of exposed mineral soil because the vegetation succession proceeded during the monitoring period. Hence, the vegetation inventories were carried out in the beginning and in the end of the monitoring period, and the average of these two values were used in the models as potential explanatory variables (Table 1). The first measurement of the exposed mineral soil with the greatest variation (0 – 100 %) was used in the statistical models as explanatory variable. The cover of slash was about five percent in the beginning of the study period and decreased somewhat during the experiment (Table 1), hence we used the first measurement of slash in the statistical models.

In addition, soil type and thickness of humus layer were measured after cutting and site preparation on smaller circular plots (radius 0.56 m) adjacent to the square 1 m^2 ground and field vegetation monitoring plots. Soil type was denoted as by the proportions of coarseness fractions (%) of coarse sandy (2.00 – 0.20 mm), fine sandy (0.20 – 0.06 mm) and silty (less than0.06 mm). The proportions of the soil fractions were computed from the total mass of the sieved soil samples weighed in the laboratory. Soil samples for soil type determination were taken using soil corer. Humus thickness was measured from the same samples cored for soil type determination.

To better control the effect of variation in the environmental conditions between years (e.g. warm or cold summers or large/small seed crops), the start of the experiment was sequenced over three years. The experiment was started in 2004 in one experimental stand in each of the districts, second experimental stand in each district was managed in 2005 and third one in 2006. The seedlings in the 20 m^2 circular sample plots were inventoried annually for the first five years and with a three-year interval after that. All the experimental stands were inventoried seven times making the length of the whole monitoring period 11 years.

2.3. Statistical evaluation

The explanatory variables tested in the statistical models (in addition to the treatment effects) are listed in Table 1. The number of all the seedlings in the 20 m^2 circular sample plot in each inventory was tested in the height model as a potential predictor (indicating competition between tree seedlings).

The number of seedlings on the 20 m^2 circular sample plots was modelled using generalized linear mixed models with the assumption of a negative binomial distribution. Four-level hierarchy (the levels nested within the others) and repeated time-dependent measurements (t) were used in the model from highest to lowest hierarchy levels: district, experimental stand, square 70x70m treatment plot and 20 m^2 circular sample plots.

The data consists of seven measurements during the 11-year monitoring period. Even though the time between the inventories (1 – 7) varied an auto-regressive correlation structure (AR(1)) was found to give the best fit for the repeated inventories. A negative binomial distribution was used in modelling the number of seedlings because it fitted best to the over-dispersed seedling count data. The model is:

$$y_{ijklt} \sim negativebinomial(\pi_{ijklt}, var_{ijklt}) \tag{1}$$

$$ln\left(\pi_{ijklt}\right) = f\left(X_{ijkl}, \beta\right) + \mu_i + \mu_{ij} + \mu_{ijk} + \mu_{ijkl},$$

where y denotes the number of seedlings on a plot. The negative binomial distribution assumption is defined with expected value (mean) π and variance (var). Furthermore, $ln(\pi)$ is a log-link function, and f(.) is a linear function with arguments X_{ijkl}(i.e. fixed predictors, measured from different levels of hierarchy) and β(i.e. fixed parameters). Subscripts i, j, k and l refer to the district, experimental stand, square treatment plot and circular sample plot levels, respectively. μ_i, μ_{ij}, μ_{ijk}, μ_{ijkl} denote random normally distributed between-district, between-stand, between-square treatment plot and between circular sample plot effects with the mean of 0 and constant variances. The residual in the repeated measurement (t, denoting inventory in time) is not presented in the formula 1, but the measurements were assumed to be correlated in time (AR(1)). The negative binomial variance (var) can be defined as $var = \pi + (1 + \frac{\pi}{k})$, where k refers to clumping parameter (theta). If $k = 1$, the distribution represents geometric distribution, and if $k \to \infty$, the distribution approaches Poisson distribution. Natural seedling recruitment might be spatially aggregated. This would tend to indicate over-dispersion, where the variance is larger than the mean. The fit of the negative binomial model to the data was estimated by simulating the distribution of expected counts and compare the values with those of observed counts. Estimated parameters of theta (size) describing the shape of the distribution and mu describing the estimated mean of the distribution were used in the simulation.

Furthermore, a model using normal distribution assumption for the average height of the Scots pine seedlings on a sample plot was computed. The average was based on all seedlings with $h \geq 10$ cm on a circular sample plot that had emerged at any point during the monitoring period. The response variable (seedling height) was log-transformed to normalize the distribution. The model can be described as:

$$ln\left(y_{ijklt}\right) = f\left(X_{ijk}, \beta\right) + \mu_i + \mu_{ij} + \mu_{ijk} + \mu_{ijkl} + \varepsilon_{ijklt}, \tag{2}$$

where y_{ijklt} is log-transformed response variable, seedling height in district i, experiment j, square plot k, circular plot l and inventory t. The other terms are similar to those described in formula 1, but ε_{ijklt} denotes normally distributed error variance with AR(1) correlation structure.

To find out the evenness of the regeneration we analysed what is the probability of a given 20 m^2 circular sample plot to have at least 1, 2, 3 or 4 seedlings (equal to 500, 1000, 1500 or 2000 seedlings /ha) by computing ordered cumulative mixed effects logistic model. The model is just an extension of a binary logistic model. The different intercept levels are computed for the ordinal categories k-1 and the coefficients of the independent variables remains the same for all the categories of response. The regression coefficients across the levels of response variable have to be parallel. This was tested using R package brand (Schlegel and Steenbergen, 2020). The coefficient of soil treatment was parallel across the response categories ($\chi^2 = 3.25$, df $= 3$, $p = 0.350$). The logit link function was used in the model and the random effects (variances) were estimated for all the nested hierarchy levels except the lowest level (circular sample plot).

The R package MASS and its function glmmPQL (Venables and

Table 2

Parameter estimates and tests of generalized linear mixed model (negative binomial) for the number of seedlings. Std. err. denotes the standard error of the estimates, t- and chi-squared values are the test values for the parameter estimates or type III Anova (deviance) tests, df denotes the degrees of freedom and cl the confidence intervals. R^2 (trigamma) for the marginal model was 45.2 % and that for the conditional model 61.9 %. For all fixed effects presenting a categorical variable also tests for the other treatment categories vs. a reference category (given in parenthesis) are presented.

Variable	Coefficient	Std. err.	df	t / chi-squared	p
Fixed effects					
Intercept	2.916	0.583	2154	5.000	< 0.001
Treatment (*ref. Control*)	–	–	5	40.204	< 0.001
– 250 non-scarified	−2.567	0.639	55	−4.021	< 0.000
– 150 non-scarified	−2.547	0.654	55	−3.896	< 0.001
– 50 non-scarified	−1.352	0.663	55	−2.038	0.064
– 150 scarified	−3.197	0.649	55	−4.925	< 0.001
– 50 scarified	−3.658	0.659	55	−5.552	< 0.001
Number of inventory	0.126	0.041	2154	3.066	0.002
Thickness of humus layer, mm	−0.074	0.019	279	−3.989	< 0.000
Cover of exposed mineral soil, %	0.015	0.006	279	2.616	0.009
Cover of slash, %	−0.012	0.006	279	−2.072	0.039
Cover of moss species, %	−0.010	0.004	279	−2.714	0.007
Treatment * Number of inventory			5	94.832	< 0.001
– 250 non-scarified	0.173	0.059	2154	2.925	0.004
– 150 non-scarified	0.252	0.059	2154	4.294	< 0.001
– 50 non-scarified	0.267	0.059	2154	4.518	< 0.001
– 150 scarified	0.448	0.058	2154	7.702	< 0.001
– 50 scarified	0.482	0.056	2154	8.315	< 0.001
Treatment * Thickness of humus layer	–	–	5	20.409	0.001
– 250 non-scarified	0.059	0.023	279	2.555	0.011
– 150 non-scarified	0.057	0.024	279	2.405	0.017
– 50 non-scarified	0.015	0.023	279	0.628	0.530
– 150 scarified	0.063	0.022	279	2.867	0.005
– 50 scarified	0.077	0.022	279	3.549	0.001
Random effects, phi (AR(1)) and theta	Value				
Theta (*k*)	0.357				
AR(1), phi	0.826				
District (variance)	0.205				
Experimental stand (variance)	0.275				
Square treatment plot (variance)	5.971e-3				
Circular sample plot (variance)	5.859e-8				

Ripley, 2002) was used in the modelling of count data, together with the R package glmmADMB and its function glmmadmb (Fournier et al., 2012). Package glmmADMB was used in the estimation of theta parameter because glmmPQL could not estimate the parameter, but the parameter estimate was needed in the glmmPQL negative binomial model. glmmADMB has a feature that it is not able to estimate an autoregressive correlation (AR(1)) structure (needed for the repeated measurements), but glmmPQL can do this. R package nlme was used in the computation of the general linear mixed model (Pinheiro et al., 2018). The coefficients of determination (R^2) were computed for the negative binomial model and the linear model using R package MuMIn (Bartoń, 2017). The fixed effects predictions with their 95 %'s confidence intervals were calculated and plotted using R package effects (Fox, 2003). The ordinal regression was computed using R-package ordinal (Christensen, 2019). All the analyses were made in the R statistical environment (R Core Team, 2016).

Both the general linear model for the seedling height and the negative binomial model for the number of seedlings predicted the observed values rather well. Both models slightly underestimated the mean values and predicted better the highest values of the response variable distribution than the lowest values (Appendix: Fit of the models and Table A3).

3. Results

3.1. *Number of seedlings*

The proportion of Scots pines of all seedlings was 99.4 %. The number of Scots pine seedlings increased throughout the 11-year monitoring period (Table 2; Fig. 2a). Site preparation was associated with a greater increase. The number of seedlings was around 10 000 ha^{-1} at the end of the period when the site preparation was done and 2 000–4 000 ha^{-1} in corresponding treatments without site preparation (50 and 150 stems ha^{-1}). The overstory density of 250 ha^{-1} had on average substantially lower number of seedlings at the end of the period compared to 50 and 150 ha^{-1} (Fig. 2a). On the control plots the number of seedlings increased just slightly during the period. The estimates shown in Fig. 2a were computed using the mean value of 2.7 cm for the thickness of humus layer.

The thickness of humus layer affected the number of seedlings differently in the treatments. Thicker humus layer was associated with a significantly smaller number of seedlings in the control and in the tree density of 50 trees ha^{-1} without soil treatment (Fig. 2b). However, humus layer thickness did not have a substantial effect in treatments with site preparation, or with a greater overstory density.

A greater proportion of exposed mineral soil resulted in a greater number of seedlings. If the mineral soil was covered with vegetation or bare humus, the predicted number of seedlings was 1111 seedlings ha^{-1}, but if the mineral soil was completely exposed, the predicted number was about five-fold, 5081 seedlings ha^{-1}. If the proportion of exposed mineral soil was 10% (that is about the mean observed in the 20 m^2 plots), the corresponding number of seedlings was 1204 seedlings ha^{-1}.

A higher coverage of slash reduced the number of seedlings as well. With no slash (0% coverage), the predicted number of seedlings was 1364 seedlings ha^{-1}, the corresponding value at the mean slash coverage (5.3%) was 1278, and with 100% coverage the predicted seedling number decreased to 401 seedlings ha^{-1}.

A greater coverage of mosses reduced the number of seedlings substantially. With the minimum coverage of 3%, the predicted seedling number was 2334 ha^{-1}, decreasing to 1487 with 50% and 921 seedlings

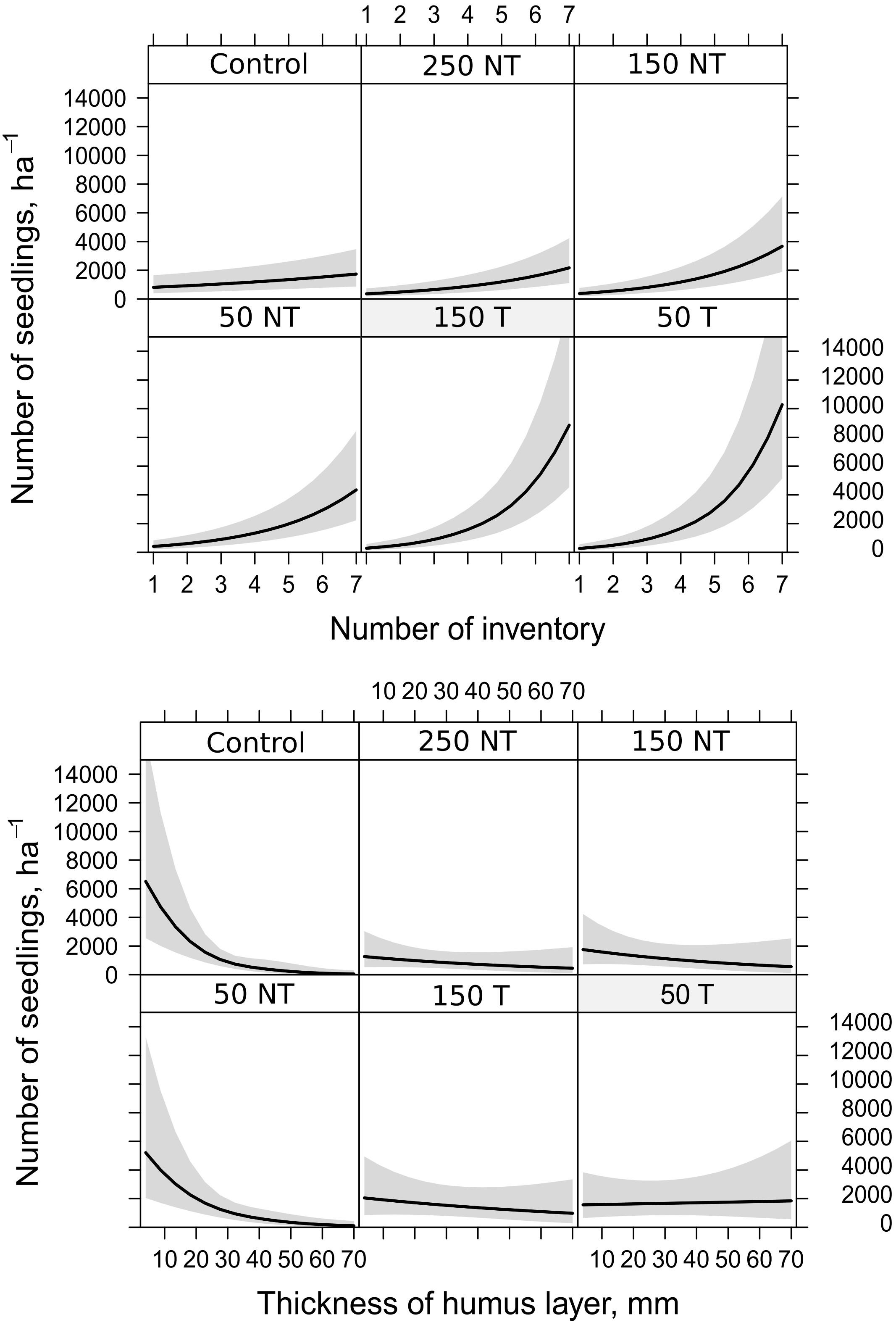

Fig. 2. Model predictions of the seedling density (number of Scots pine seedlings ha^{-1}) according to a) number of inventory and b) thickness of the humus layer. Point estimates and 95 % confidence intervals are presented. Numbers 50, 150 and 250 signify stand density ha^{-1}. NT = no soil treatment, T = soil is treated (disc trenching).

ha^{-1} with 100% coverage, respectively.

Many of the sample plots did not have any seedlings, and the number of the empty sample plots varied a lot between the treatments. In the intact control most (70%) of the sample plots were empty and also in the treatment 250 trees ha^{-1} (76.7%). In the other treatments without site preparation the proportion of empty plots was 56.7% with 150 ha^{-1} and 51.7% with 50 ha^{-1}. With site preparation the proportion of empty plots was much lower: 26.7% with 150 trees ha^{-1} and 16.7% with 50 trees ha^{-1}. Another way of looking at the effect of site preparations is to calculate how much mineral soil surface would need to be exposed to

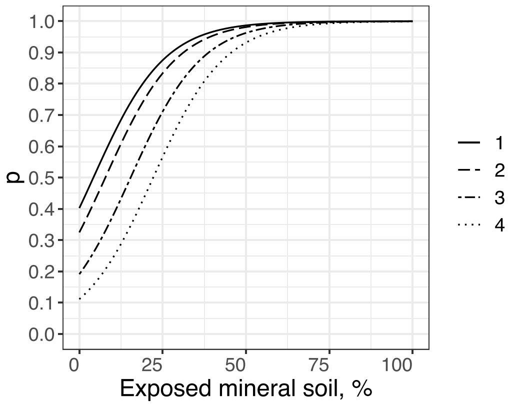

Fig. 3. The prediction of the ordered cumulative mixed effects logistic model for the probability that a given sample plot has 1, 2, 3 or 4 seedlings (that equals to 500, 1000, 1500 and 2000 seedlings ha^{-1}) in the function of proportion (%) of exposed mineral soil.

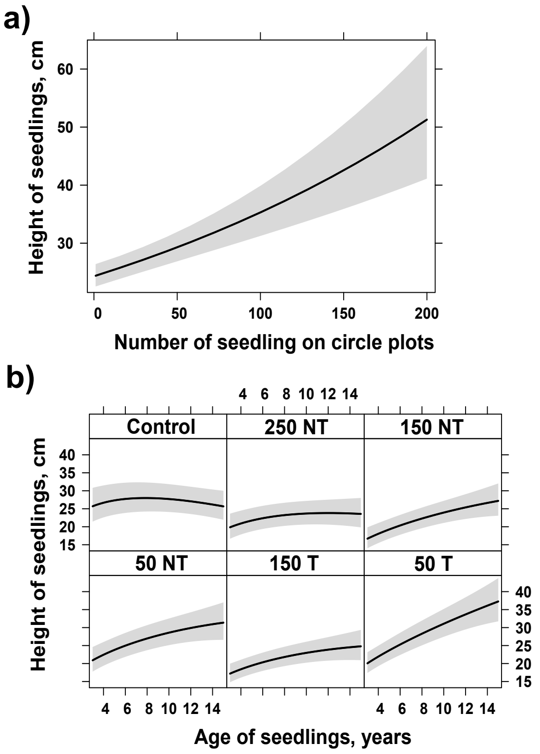

Fig. 4. The predictions of the seedling height model (average height of Scots pine seedlings on a circular sample plot) according to a) number of seedlings on sample plots and b) age of seedlings. Point estimates and 95 % confidence intervals are presented. Numbers 50, 150 and 250 signify stand density ha^{-1}. NT = no soil treatment, T = soil is treated (disc trenching).

achieve a certain probability of getting, as an example, one seedling per 20 m^2 circular sample plot corresponding to 500 seedlings ha^{-1}, or four seedlings per sample plot that corresponds a target density of 2000 seedlings ha^{-1} according to the Finnish Best practices (Äijälä et al., 2019). According to this approach treating the soil surface by disc trenching so that mineral soil is exposed in 25% of the area yielded at least 1 seedling on a sample plot (corresponding to 500 seedlings ha^{-1}) with the probability of nearly 90% (Fig. 3). To reach the same 90% probability to have at least 4 seedlings in a sample plot (corresponding to 2000 seedlings ha^{-1}) would require around 44% mineral soil exposition (Fig. 3, for formal statistical test see Appendix: Table A4).

3.2. *Seedling height*

Seedling height increased constantly throughout the monitoring period. The increase was greatest with 50 overstory trees ha^{-1}, clearly smaller with 150 and ha^{-1}, and very small or non-existent in 250 trees ha^{-1} and in the control (Fig. 4b). Site preparation increased seedling height with 50 ha^{-1} but not with 150 ha^{-1}. A greater number of seedlings was associated with a greater mean height (Table 3, Fig. 4a). Increasing number of seedlings in the sample plots increased the average height of the pine seedlings on the sample plots at the mean age of the seedlings (about 11 years, Table 3).

4. Discussion

On average, the number of seedlings increased throughout the study period (Fig. 2), which shows that new seedlings emerged even over 10 years after the thinning (and site preparation). The role of years of abundant seed crops in Northern Finland has often been emphasized in silvicultural research and practice (Henttonen et al., 1986; Hilli et al., 2008). The present results with steadily increasing seedling number through the study period rather support the viewpoint that gradual and constant seedling emergence is possible on favorable seedbeds as some viable seeds are produced in most years (Heikinheimo, 1932, 1937) and seedling number tends to increase constantly in time (e.g. Hyppönen et al., 2005).

The single most influential factor affecting seedling establishment was the removal of ground layer vegetation and humus layer by site preparation (disc trenching). In the overstory densities of 50 or 150 trees ha^{-1} where site preparation was applied or not applied, seedling density was over two times higher in treatments with site preparation than without it. This confirms many earlier experiments in which the decisive role of site preparation has been shown (Karlsson and Örlander, 2000; Hyppönen et al., 2005; Nilsson et al., 2002; Hyppönen et al., 2013; Hallikainen et al., 2019; Sikström et al., 2020; Kyrö et al., 2022). Site preparation has been found to be especially beneficial if the mineral soil is covered with a thick humus layer and a thick moss cover. Accordingly, we found that both the thickness of humus layer and cover of mosses decreased the number of seedlings. Winsa (1995) has shown that continuous supply of capillary water from mineral soil is very important for the germination of Scots pine, because the species germinates slowly at the low temperatures of northern Europe and the radicle cannot tolerate to be dried out. The humus layer blocks the seeds' contact with capillary water. Further, the humus layer dries out quickly and seedlings without root contact with the mineral soil easily die out during drought periods (Oleskog and Sahlén, 2000). According to Hertz (1934) and Yli-Vaakkuri (1961) moss and lichen surfaces are poor for emergence because they can completely trap and evaporate meagre rainfall. Oinonen (1956) found that a uniform and thick moss surface is a particularly poor germination medium when there is raw humus underneath. In this study, the humus layer was not particularly thick (less than 3 cm on average) but moss coverage was high at around 70%. Also Steijlen et al. (1995) have found, in both forest and laboratory, that pine seedlings experience significantly higher mortality on moss cover (*Pleurozium schreberi*) compared to lichen cover (*Cladina* spp.).

Although more seeds are produced with an increasing number of seed trees and more seedlings have been found to emerge with increasing density of seed trees (Beland et al., 2000), greater overstory density may also limit their germination and the survival of the emerged seedlings. A denser overstory reduces the amount of light and rainfall achieving the ground level (Lehto, 1969; Nygren, 2003). This may explain why regeneration was more abundant with lower than higher densities (cf. Valkonen, 1992). Furthermore, more efforts are needed to find out the effects of different winter conditions on small seedlings and saplings in the vicinity of mature trees.

The number of the established seedlings per hectare alone is not a sufficient indicator for regeneration success. After regeneration there

Table 3

Parameter estimates and tests of the general linear mixed model (*normally distributed*) for the height development of seedlings. Age of the seedlings that were included in the model varied from 4 to 15 years. Std. err. denotes the standard error of the estimates, t- and chi-squared values are the test values for the parameter estimates or type III Anova (deviance) tests, df denotes the degrees of freedom. R^2 for marginal model was 17.8 % and that for conditional model 32.05 %. For all fixed effects presenting a categorical variable also tests for the other treatment categories vs. a reference category (given in parenthesis) are presented.

Variable	Coefficient	Std. err.	df	t / chi-squared	p
Fixed effects					
Intercept	2.637	0.267	750	9.858	< 0.001
Treatment (*ref. Control*)	–	–	5	22.528	< 0.001
– 250 non-scarified (NS)	−0.301	0.134	54	−2.244	0.029
– 150 non-scarified (NS)	−0.554	0.134	54	−4.132	< 0.001
– 50 non-scarified (NS)	−0.308	0.129	54	−2.393	0.020
– 150 scarified (S)	−0.493	0.124	54	−3.978	< 0.001
– 50 scarified (S)	−0.402	0.121	54	−3.325	0.002
Age of seedlings, years	−0.075	0.032	750	−2.349	0.019
Sqrt age of seedlings, years	0.420	0.180	750	2.330	0.020
Number of seedlings on sample plot	0.004	0.001	750	6.509	< 0.001
Treatment * Age of seedlings, years	–	–	5	35.306	< 0.001
– 250 non-scarified (NS)	0.014	0.011	750	1.364	0.173
– 150 non-scarified (NS)	0.041	0.011	750	3.791	0.000
– 50 non-scarified (NS)	0.034	0.010	750	3.341	0.001
– 150 scarified (S)	0.031	0.010	750	3.040	0.002
– 50 scarified (S)	0.052	0.010	750	5.403	0.000
Random effects and autoregressive correlation	Value				
AR(1), phi	0.633				
District (variance)	3.617e-3				
Experimental stand (variance)	2.674e −10				
Square treatment plot (variance)	0.020				
Circular sample plot (variance)	1.009e −9				
Residual	0.112				

should be enough seedlings evenly distributed in the stand area. This means that in the stand there are no large gaps without seedlings. In this study this was best achieved in the treatment with 50 trees ha^{-1} combined with site preparation, where about 80% of the sample plots had at least one seedling. In contrast, 70–75% of the sample plots in the control and 250 trees ha^{-1} treatments were empty, which is a poor result. The treatments with 50 and 150 stems ha^{-1} without site preparation were only slightly better with about half of the plots empty. Another way to look at the effect of site preparation is to estimate the probability of a single sample plot to be regenerated as a function of the proportion of mineral soil exposed by the soil treatment. According to our results, exposing mineral soil in 25% of the stand area yields a 90% probability that sample plots has at least one seedling. This, however, is not sufficient level of regeneration, as the Finnish Forest Act (Forest Act, 2014) requires that when using natural regeneration in Northern Finland at least 1200 main crop seedlings ha^{-1} needs to be present no later than 20–25 years after the regeneration cutting to secure the legally mandated forest regeneration. In our data this would require an average of 2.4 seedlings on 20 m^{-2} circular sample plots that would be achieved on around 90% probability by exposing around 30–35% of the mineral soil (Fig. 3). Achieving 2000 seedlings ha^{-1}, that is recommended minimum density for pines when using planting according to the Finnish best practices for forest management (Äijälä et al., 2019), would need about 40% exposition of mineral soil. On the other hand, in natural regeneration and direct seeding the recommended density is 4000–5000 seedlings ha^{-1} (Äijälä et al., 2019). However, the fact that exposing mineral soil dramatically improves germination probability indicates that, by optimizing the spatial distribution of exposed mineral soil patches, better regeneration could be achieved with less soil disturbance. This could be achieved by, for example, intermittently created planting spots using mounding or soil inversion (Sikström et al., 2020) or, in the near future, by automated machines that optimise the location of exposed soil patches with the help of environmental sensing, machine vision and artificial intelligence (Rautio et al., 2023). By decreasing the soil disturbance, one could better secure many other ecosystem services, like recreation, berry picking and reindeer herding (Rautio et al., 2023). Another way to avoid excess site preparation, to secure other ecosystem services, would be supplementary planting in places that have not regenerated naturally (in other words, using assisted regeneration). This would naturally increase the costs but if the natural regeneration has in general been satisfactory, the need for planting would be limited and potentially recompensed by the other ecosystem services.

Between measurements some seedlings died, and new ones grew of emerging seedlings that were less than 10 cm tall in the previous measurement. Consequently, the seedling mean height tended to develop slower than that of the dominant (tallest) seedlings. The consequences of such dynamics were strikingly expressed in the control treatment. The average height of seedlings at age 14 was basically at the same level as it was in the beginning at age 4 (Fig. 4b). In other words, even though it seems that the number of the seedlings doesn't change much in the control plots there are constantly seedlings dying and new ones established. However, these two processes seem to balance out each other so that when the older, and larger, seedlings died they were replaced by new shorter ones in the population. Kyrö et al. (2022) observed by monitoring the establishment and survival of individual pine seedlings for 11 years in some of the study stands used here, that the predicted probability of mortality approaches zero after five years while the cumulative number of seedlings steadily increases. Accordingly, Niemistö et al. (1993) found that in stands where the seed trees were retained for a long time the average seedling age increased rather slow in for the same reason, i.e. older ones are dying and new seedlings emerging all the time.

Thinning and site preparation had a clear positive effect on the height development of seedlings. On the heavily thinned and soil-prepared plots, the seedlings at age 6 were about the same height as the 14-year-old seedlings in the control and in the 250 trees ha^{-1} treatment. In fact, the difference to the untreated control was even higher than this, as in all the treatment plots except the control plots all seedlings exceeding 50 cm height were removed before starting the monitoring. This finding is consistent with previous studies, as in northern Finland where forests are sparse, canopy growth has been found to limit the growth of seedlings (Hyppönen and Hyvönen, 2000). Root competition has also been found to affect seedling growth, even more than lack of light (Aaltonen, 1919; Hagner, 1962; Ackzell and

Lindgren, 1992; Strand et al., 2006; Hallikainen et al., 2007). Site preparation generally improves the growth of seedlings (e.g. Hyppönen and Kemppe, 2001; Varmola et al., 2004; Hyppönen et al., 2005; Hyppönen et al., 2008), but our results show that site preparation needs to be combined with heavy thinning to have an effect on growth. When the stands were thinned to 150 trees ha^{-1} the site preparation did not result in any additional growth in the seedlings, whereas in 50 trees ha^{-1} the effect of site preparation yielded on average 10 cm additional growth at the age of 14 years (Fig. 4b).

In conclusion, our results confirmed the importance of competition by mature trees as well as field and ground layer vegetation on natural regeneration and seedling growth in northern pine forests. The number of naturally regenerated seedlings and seedling growth increased with decreasing tree density and increased mineral soil exposure. According to our results, the seed supply is enough to achieve successful natural regeneration even if the number of seed trees is low, as long as proper exposure of mineral soil is carried out. Further studies are needed on what is the most appropriate site preparation technique to achieve the optimal pattern and degree of mineral soil exposure for establishing the required number and growth of seedlings, but also their optimal spatial coverage.

CRediT authorship contribution statement

Pasi Rautio: Conceptualization, Methodology, Formal analysis, Validation, Investigation, Project administration, Writing – original draft. **Ville Hallikainen:** Conceptualization, Methodology, Formal analysis, Software, Validation, Investigation, Data curation, Writing – review & editing. **Sauli Valkonen:** Investigation, Formal analysis, Writing – review & editing. **Johanna Karjalainen:** Methodology, Formal analysis, Validation, Investigation, Data curation, Writing – review & editing. **Pasi Puttonen:** Investigation, Writing – review & editing. **Urban Bergsten:** Formal analysis, Investigation, Writing – review & editing. **Hans Winsa:** Investigation, Writing – review & editing. **Mikko Hyppönen:** Conceptualization, Methodology, Investigation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A

Material and methods

Study area

Table A1

Table A2

Table A1
Coordinates (X and Y in WGS84) of the experimental stands (location number refers to the numbers in the Fig. 1) and the year of establishment.

District	Location	Established	WGS84 X	WGS84 Y
Northern Lapland	112	2004	27.4403057	68.4833221
	122	2005	28.1187229	68.7366409
	132	2006	27.3981457	68.4689407
Western Lapland	212	2004	25.7364845	67.0729370
	222	2005	23.9756012	67.6385422
	232	2006	28.4430008	67.5883484
Eastern Lapland	312	2004	23.5592079	67.8579483
	322	2005	29.3234501	67.2219772
	332	2006	29.2637272	67.8377457
Southern Lapland	412	2004	25.3679123	66.0192719
	422	2005	28.2749653	65.9586716
	432	2006	27.1641579	65.9127502

Table A2
Proportion of exposed mineral soil of the ground cover (in %) in different treatments. Numbers 50, 150 and 250 signify stand density / ha. NT = no soil treatment, T = soil is treated (disc trenching).

Treatment	Mean	Median	Min	Max
Control	0	0	0	0
250 NT	0.83	0	0	30
150 NT	0.67	0	0	40
50 NT	0.42	0	0	25
150 T	23.80	19.00	0	65
50 T	29.35	22.50	0	100

Fit of the models

The number of seedlings predicted by the model was somewhat lower on the average (mean values) compared to the observed numbers, if the predictions were calculated using only the fixed effects of the model (Table A3). The pseudo R^2-values of the seedling number model were satisfactory, but the R^2-values of different distributions could not be compared to each other. If the fit of the seedling density model was evaluated using the simulated negative binomial distribution using the model parameters (theta and mu), the model fit was good, although the proportion of the zero counts was slightly underestimated and the proportion of the highest values underestimated (Fig. A.1).

The model for the height development predicted on the average (mean) slightly less than 1 cm lower heights, and the lowest predicted values were a bit higher and the highest predicted values quite much lower than the observed values. However, the predicted values at 3rd quartiles were rather close to the observed values, similar to the 1st quartiles and medians (Table A3). The R^2 value was rather low, suggesting that other natural conditions than the measured ones were affecting the height development. By leaving the sqrt-term out of the height model would have improved slightly in the highest values (by about two centimetres) but the fit of the model would have been significantly poorer (using AIC and difference in likelihood ratio tests) compared to the presented model. The sqrt-term was selected after testing the power from 0.1 to 2 (step 0.1). The residuals of the height model were pretty unbiased, although the residual variation was great.

Table A3
Observed and predicted distributions described by the base statistics for the models of the numbers of seedlings (negative binomial model, Table 2) and height development (normally distributed linear model, Table 3). The values in the number of seedlings model were computed for a 20 m^2 sample plot. The correspondence to a hectare needs multiplication by 500. Marginal model predictions denote that the predictions are computed using only the fixed part of the model.

	Minimum	1st quartile	Median	Mean	3rd quartile	Max
Model for the number of Scots pine seedlings (trigamma R^2, marginal model = 45.2 %)						
Marginal model (only fixed effects)	0.09	1.14	2.43	5.09	5.09	91
Observed	0.00	0.00	1.00	6.44	5.00	168
Model for the height development (R2, marginal model = 19.2 %)						
Marginal model	15.90	21.64	24.14	24.76	27.11	42.56
Observed	10.00	18.26	23.50	25.76	30.12	102.06

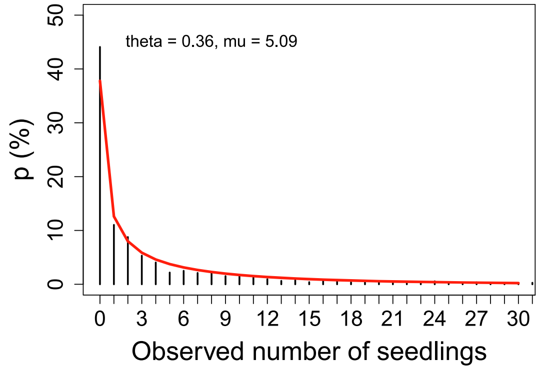

Fig. A1. The observed (vertical bars) and simulated (red line) distributions of the negative binomial model for seedling count (seedling density). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Results

See Table A4

Table A4
The parameter estimates for the cumulative ordinal logistic mixed effects model for the probability that a given sample plot has at least 1, 2, 3 or 4 seedlings (that equals to 500, 1000, 1500 and 2000 seedlings ha^{-1}) in the function of soil treatment (% of exposed mineral soil). Std. error denotes standard error. Nagelkerke's pseudo R^2 = 11.09.

Model effects	Coefficient	Std. error	z-value	p-value
Fixed effects				
Intercept >=4	−0.395	0.399	−0.991	–
Intercept >=3	−0.732	0.405	−1.807	–
Intercept >=2	−1.443	0.425	−3.395	–
Intercept >=1	−2.078	0.447	−4.644	–
Soil treatment	0.094	0.024	3.904	0.000
Random effects				
Variance of district	5.836e-12			
Experimental stand	5.094e-01			
Square treatment plot	2.106e + 00			

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