



# Natural regeneration and development of Scots pine seedlings in continuous cover forestry in northern Finland

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## ABSTRACT

Continuous cover forestry (CCF) is expected to enhance the overall production of ecosystem services compared to even-aged rotation forestry. CCF is relying on natural regeneration and the ingrowth of seedlings in small gap and selection cuttings. However, the factors affecting their success in CCF remain poorly understood, especially under the challenging climatic conditions and sparse stand structures typical in northern boreal forests. Here, we examined the natural regeneration and development of Scots pine (*Pinus sylvestris* L.) seedlings and the factors influencing them following selection cuttings across Northern Finland. The cuttings were done with varying intensity at 27 experimental sites between 1985 and 2007. The establishment and height growth of new Scots pine seedlings were inventoried in 2019. We used generalised linear mixed modelling to evaluate the establishment of new Scots pine seedlings in 50 m<sup>2</sup> study plots, and log-normal linear mixed modelling to evaluate their post-cutting height growth, and the affecting factors affecting them. In a post-cutting field inventory, it was found in the study plots on average, 2144 new pine seedlings ha<sup>-1</sup>, about 20 % of the plots having no new seedlings. By comparison, the constructed models underestimated this number (on average, 1700 seedlings ha<sup>-1</sup>). An increase in basal area, tree stock volume and number of overstorey trees reduced both the number of seedlings and their height. A thick humus layer reduced the number of seedlings. Denser moss and herb cover reduced the number of seedlings but increased their height. Also, the seedlings were shorter in the northern regions due to the harsher growing conditions.

## 1. Introduction

Boreal forests provide various ecosystem services, such as timber and non-wood products, carbon sequestration and maintenance of biodiversity and recreational environments. Continuous cover forestry (CCF) is expected to enhance the overall production of ecosystem services compared to even-aged rotation forestry (RF) (Díaz-Yáñez et al., 2019). Continuous tree coverage is important in forests for tourism, recreational areas and reindeer herding in Lapland, located in northern Finland. Therefore, interest has increased in preserving continuous forest cover in state-owned forests through denser seed-tree and shelterwood stands in RF, and selection and small gap cuttings in CCF (Hyppönen, 2002; Koivula et al., 2020; Hirvelä et al., 2022).

Due to Lapland's challenging growing conditions and low-fertility sites, the forests dominated by Scots pine (*Pinus sylvestris* L.), typically feature an uneven-aged, sparse and open stand structure. Scots pine, as a

light-demanding species, also requires relatively low stand densities for natural regeneration and ingrowth of seedlings in a stand (Pukkala et al., 2010; Lundqvist et al., 2019; Valkonen, 2020). On sub-xeric and xeric sites, natural regeneration of Scots pine, using the seed-tree method in RF or small gap and selection cuttings in CCF, is more profitable than planting and seeding in RF (Pukkala et al., 2010; Norokorpi and Lähde, 2013; Ahtikoski and Hökkä, 2019; Valkonen, 2020).

The natural regeneration and ingrowth of seedlings in CCF (as well as RF) are controlled by environmental factors (e.g. temperature, light, soil nutrient and moisture availability, and soil texture) and above- and belowground competition by overstorey and understorey trees and ground and field-layer vegetation, as well as the distance to the seed-producing mature trees (Downey et al., 2018; Rautio et al., 2023; Häggström et al., 2024). Overall, the competitive effects of overstorey trees on the germination of seeds and the further growth of seedlings can be very complex. A higher density of mature trees may indicate larger seed fall and

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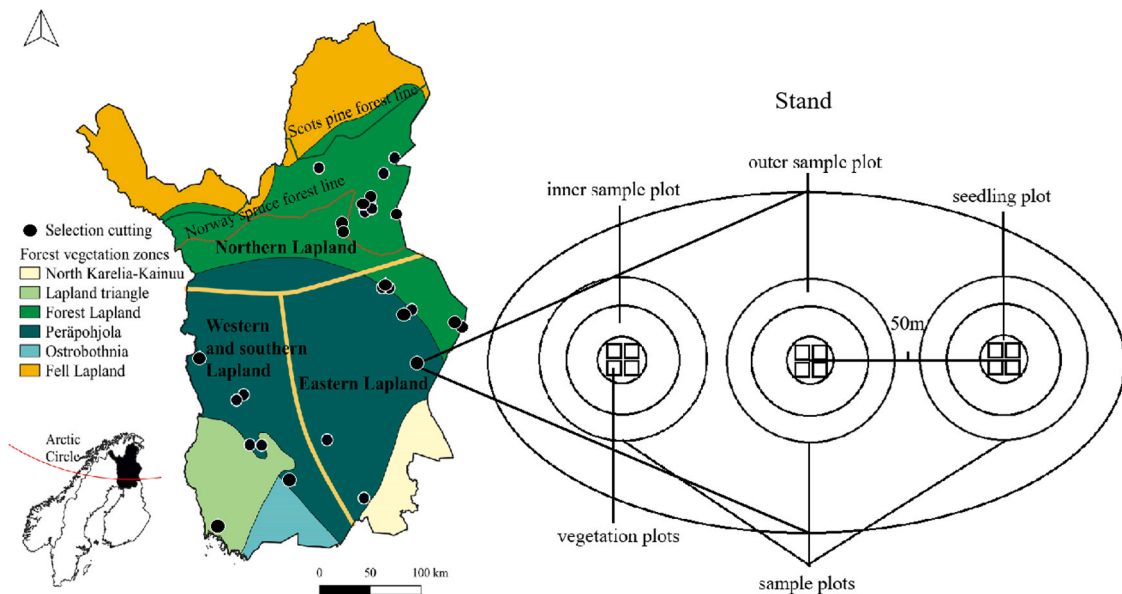


Fig. 1. Location of the study area and the studied stand layout. Map adapted from © Taru Rikkinen, Arctic Centre, University of Lapland 2021. Data from © the National Land Survey 2021 and © the Finnish Environmental Institute 2021.

germination potential, but a simultaneous limitation on seed germination and the ingrowth of seedlings due to the competition for growth resources (Lehto, 1969; Beland et al., 2000; Hallikainen et al., 2007; Stuiver et al., 2016; Rautio et al., 2023). While seedling density may remain relatively stable under higher stocking (basal area), older seedlings may continuously die as new ones emerge (Niemistö et al., 1993; Rautio et al., 2023). Seedling growth and development decline significantly within a 10-m radius of a single overstory tree due to strong below- and aboveground competition (Lehto, 1956; Valtanen, 1984; Axelsson et al., 2014; Häggström et al., 2024).

Ground and field-layer vegetation and the thickness of the humus layer affect seed germination and seedling development. However, the strength and direction of their effects can be very species-specific and sometimes even contradictory. For example, heather (*Calluna vulgaris* L.) can enhance the emergence (establishment) of Scots pine seedlings but decrease their growth as a competitive species (Lehto, 1956; Hyppönen et al., 2013). Meanwhile, depending on the study, lingonberry (*Vaccinium vitis-idaea* L.) either improves the emergence and growth of pine seedlings (Hertz, 1934; Hyppönen et al., 2013) or reduces their emergence (Wardle et al., 2008; Kyrö et al., 2022). Crowberry (*Empetrum nigrum* L.), many moss species and a thick humus layer have been shown to decrease seed germination and the development of pine seedlings (Hertz, 1934; Lehto, 1956; Nilsson and Zackrisson, 1992; Hyppönen et al., 2013; Kyrö et al., 2022; Rautio et al., 2023). A thick humus layer hinders seed germination by blocking the seeds from reaching a suitable mineral soil surface (Nygren and Saarinen, 2001). However, seedling mortality is typically low on moist sites with sphagnum mosses (Kyrö et al., 2022).

The natural regeneration and ingrowth of seedlings in CCF relies on small gap and selection cuttings without soil preparation. While much is understood about the factors affecting the success of Scots pine regeneration in RF, our knowledge concerning the factors involved in CCF remains limited, especially under the challenging climatic conditions and sparse stand structures typical in boreal forests in Northern Finland (Valkonen et al., 2020; Routa, Huuskonen., 2022). This is partly because CCF in Finland has only been permitted alongside the prevailing RF in practical forest management since the enactment of the New Forest Act in 2014. RF stands are often regenerated with clear cuts followed by soil preparation and artificial regeneration using planting or seeding to secure the seedling stand establishment. Alternatively, natural

regeneration using with soil preparation with seed tree cutting (Scots pine) or shelterwood cutting without soil preparation (typically Norway spruce, *Picea abies* Karst. L.) may be used in RF. The establishment of seedlings improves with soil preparation and planting or seeding of light demanding Scots pine in clear cut area compared to natural regeneration with seed trees and especially if no soil preparation is used (Lehto, 1969, Beland et al., 2000, Nygren, 2003).

The objective of this study was to examine the natural regeneration and development of Scots pine seedlings and the factors influencing them after selection cuttings across Lapland, in Northern Finland. This was done to provide new ecological insight into natural regeneration under continuous tree covers. In selection cuttings single large overstory trees are typically removed to enhance natural regeneration and ingrowth of seedlings under the forest canopy (Äijälä et al. 2019). Selection cuttings were performed in this study depending on the stand with varying intensity once at each 27 experimental sites between 1985 and 2007. The establishment and height growth of new Scots pine seedlings were inventoried in 2019. We used generalised linear mixed modelling to evaluate the establishment of the new seedlings (in study plots of 50 m<sup>2</sup>) and log-normal linear mixed modelling to determine their height growth after the cuttings, and the factors affecting them. We hypothesised that: 1) the natural regeneration and ingrowth of pine seedlings are slow and poor after selection cutting; 2) a dense overstory reduces the establishment and growth of pine seedlings; and 3) the establishment and growth of pine seedlings are affected by the thickness of the humus layer and the ground and field-layer vegetation.

## 2. Materials and methods

### 2.1. Study area, experimental design and data collection

The study area considered the entire forested region of Finnish Lapland, which is around 9 million ha. Overall, Lapland experiences harsh and humid climatic conditions, but the soil and vegetation in Southern Lapland are generally more fertile than in the northern regions. The annual average temperatures at the Sodankylä meteorological station in Central Lapland ranged from  $-3.5$  to  $2.0$  °C, with precipitation varying between 400 and 740 mm (Finnish Meteorological Institute, 2024).

Data were collected from 27 selection cutting stands from three

**Table 1**

Description of the variables considered in the modelling, including all the experimental stands (total 27), sample plots (total 81) and seedlings or trees (total 1535).

Variable	Min	Q1	Median	Mean	Q3	Max
<i>Forest stand level</i>						
Average temperature sum 1983–2019, d.d.	719	769	800	848	974	1065
Average temperature sum 2009–2019, d.d.	753	802	824	877	990	1089
Cutting time, year	1985	1995	1999	1998	2000	2007
Time since cutting, years	12.0	19.0	20.0	21.3	24.0	34.0
<i>Sample plot level</i>						
Number of Scots pine seedlings	0	2	8	14	18	84
Number of Scots pine seedlings after cutting	0	1	5	11	11	84
Number of all seedlings	0	5	11	17	22	85
Basal area of trees, m <sup>2</sup> ha <sup>-1</sup> (in 2019)	2.3	8.4	11.9	12.1	16.2	28.4
Basal area of trees, m <sup>2</sup> ha <sup>-1</sup> (in 2009)	1.3	4.8	7.2	8.3	11.0	24.2
Number of trees ha <sup>-1</sup> (in 2019)	158	410	628	679	892	1770
Number of trees ha <sup>-1</sup> (in 2009)	158	358	570	618	764	1770
Volume of tree stock, m <sup>3</sup> ha <sup>-1</sup> (in 2019)	11.4	48.6	74.4	79.1	108.0	229.0
Volume of tree stock, m <sup>3</sup> ha <sup>-1</sup> (in 2009)	4.8	18.4	40.7	49.5	69.8	174.0
Thickness of humus layer, mm	9.8	22.0	28.5	31.9	39.4	113.0
Stoniness, depth of steel bar, cm	3.0	9.6	17.1	21.7	30.3	70.0
Cover of lichens, %	0	0.8	4.0	9.0	11.0	53.8
Cover of mosses in mineral soil, %	4.3	55.0	80.0	68.8	87.3	98.0
Cover of bilberry, %	0	1.0	2.8	4.5	6.5	20.5
Cover of cowberry, %	1.5	4.3	9.5	13.3	19.8	43.8
Cover of heather, %	0	0	1.0	6.8	9.0	51.3
Cover of crowberry, %	0	3.5	8.3	11.0	15.8	38.8
Cover of herbs, %	0	0	0.5	0.7	1.0	8.5
<i>Tree and seedling level</i>						
Age of Scots pine trees or seedlings, years	2.0	9.0	16.0	38.1	54.8	398.0
Height of Scots pine trees or seedlings, m	0.1	0.2	0.4	3.2	5.2	19.9
Height of Scots pine trees, m	1.1	7.2	10.1	10.5	13.5	19.9
Age of Scots pine trees, years	39.0	70.1	92.6	101.0	113.0	398.0
Diameter (d1.3) of Scots pine trees, cm	4.3	9.2	13.7	15.0	19.6	43.8

regions, Northern (10), Western/Southern (7) and Eastern (10) Lapland (see, e.g., Rikkinen et al., 2023; Supplementary data Table A1 and Fig. A1). Stands were located mostly on either dry or dryish pine forest types, i.e. xeric and sub-xeric stands, where field layer is dominated by heather or lingonberry. No site preparation was undertaken at any of these stands which is prevailing practice in CCF. Each stand included three sample plots, which were further divided into outer and inner sample plots for the tree inventory (see Fig. 1). Seedling plots (radius

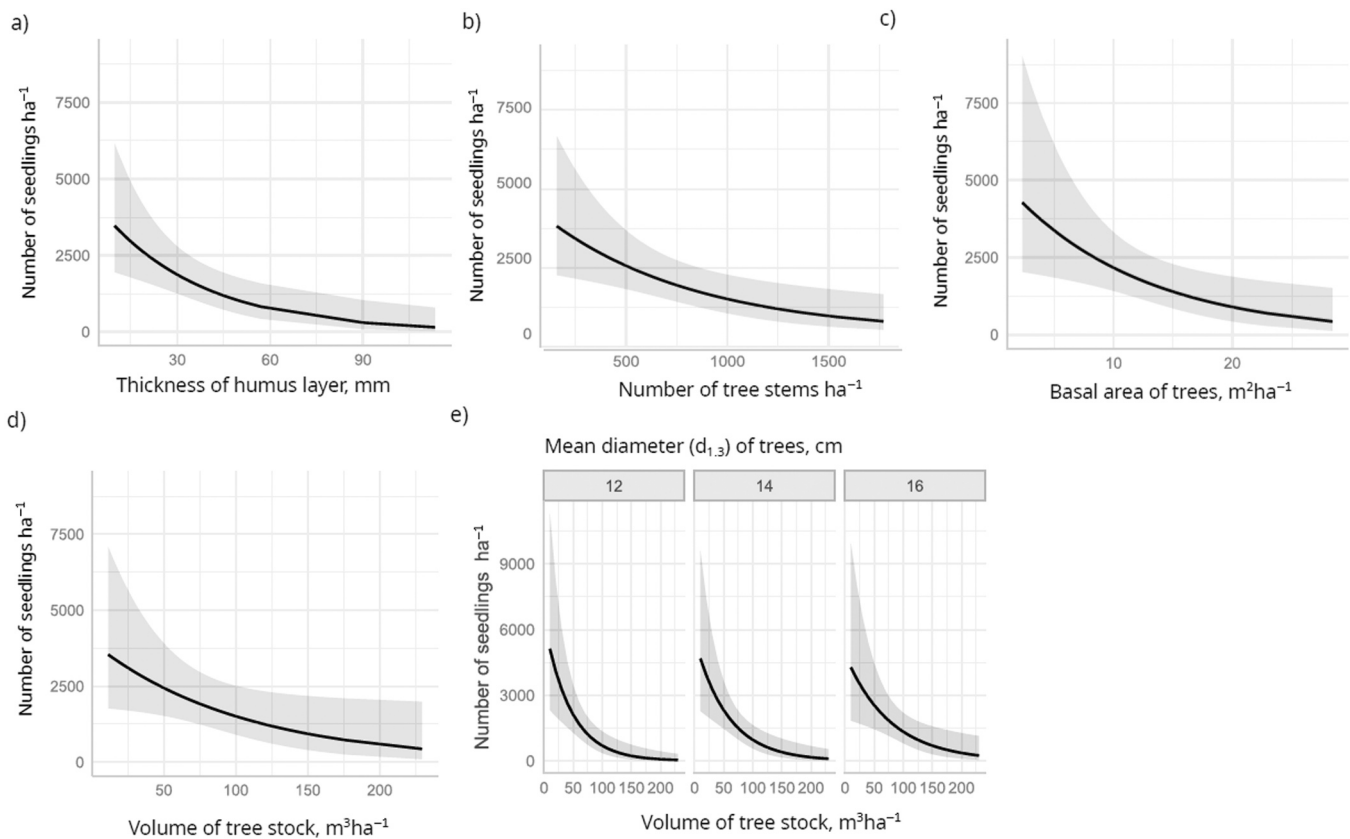
**Table 2**

Parameter estimates of the models for the number of naturally established Scots pine seedlings after selection cuttings (using a negative binomial [NB2 parametrisation] distribution assumption).

Variable	Estimate	Standard error	z-value	p-value
<b>Model, version 1: R<sup>2</sup> (marginal model) = 0.246, R<sup>2</sup> (conditional model) = 0.525, AIC = 521.2</b>				
<i>Fixed effects</i>				
Intercept	3.868E+00	5.071E-01	7.627	0.000
Number of trees ha <sup>-1</sup> (in 2019)	-1.347E-03	4.849E-04	-2.777	0.005
Thickness of humus layer, mm	-3.047E-02	9.913E-03	-3.074	0.002
<i>Random effects, dispersal parameter</i>				
Experimental stand, variance	4.461E-01			
Theta	8.930E-01			
<b>Model, version 2: R<sup>2</sup> (marginal model) = 0.226, R<sup>2</sup> (conditional model) = 0.575, AIC = 522.3</b>				
<i>Fixed effects</i>				
Intercept	3.889E+00	5.549E-01	7.008	0.000
Basal area of trees, m <sup>2</sup> ha <sup>-1</sup> (in 2019)	-8.857E-02	3.552E-02	-2.494	0.013
Thickness of humus layer, mm	-2.740E-02	1.034E-02	-2.650	0.008
<i>Random effects, dispersal parameter</i>				
Experimental stand, variance	6.416E-01			
Theta	9.530E-01			
<b>Model, version 3: R<sup>2</sup> (marginal model) = 0.198, R<sup>2</sup> (conditional model) = 0.564, AIC = 524.0</b>				
<i>Fixed effects</i>				
Intercept	3.568E+00	5.034E-01	7.088	0.000
Volume of tree stock, m <sup>3</sup> ha <sup>-1</sup> (in 2019)	-9.611E-03	4.610E-03	-2.085	0.037
Thickness of humus layer, mm	-2.680E-02	1.048E-02	-2.558	0.011
<i>Random effects, dispersal parameter</i>				
Experimental stand, variance	6.643E-01			
Theta	9.320E-01			
<b>Model, version 4: R<sup>2</sup> (marginal model) = 0.328, R<sup>2</sup> (conditional model) = 0.620, AIC = 519.7</b>				
<i>Fixed effects</i>				
Intercept	5.035E+00	1.558E+00	3.232	0.001
Volume of tree stock, m <sup>3</sup> ha <sup>-1</sup> (in 2019)	-4.973E-02	1.764E-02	-2.818	0.005
Thickness of humus layer, mm	-2.988E-02	1.001E-02	-2.986	0.003
Mean diameter of trees (d1.3), cm	-6.829E-02	1.069E-01	-0.639	0.523
Volume of tree stock: mean diameter of trees	2.300E-03	1.102E-03	2.086	0.037
<i>Random effects, dispersal parameter</i>				
Experimental stand, variance	5.685E-01			
Theta	1.040E+00			

3.99 m, area 50 m<sup>2</sup>) were placed at the centre of the sample plots (81 sample and seedling plots in total). Each sample plot included four vegetation plots (1 × 1 m) around the centre of the inner plot (324 vegetation sample plots in total). In vegetation plots percentages of different coverages (e.g. plant species, debris) were visually evaluated. Thus, the central point of the outer, inner and seedling plots was the same.

The location of the first sample plot in each stand was randomly selected, with the subsequent plot aligned 50 m to the north and the last one 50 m to the north of that one. The distance was calculated from the centre of the previous plot to the centre of the next plot. The size of the outer and inner sample plots varied depending on the number of trees found in the stand. The total target number of trees was 100 in the study stand and in a range of 30–35 in the sample plots (breast height diameter [d1.3] > 4.5 cm). However, the maximum radius of the outer plot was



**Fig. 2.** Predictions of the four best models for the number of naturally established Scots pine seedlings after selection cuttings, with point estimates and 95 % confidence intervals: (a and b) Model 1; (c) Model 2; (d) Model 3; and (e) interaction effects of Model 4 (see Table 2).

25 m, and the area of the inner plot was at least one-third that of the outer plot (Supplementary data Table A2). The aim was to measure 30–35 trees from the outer plot, and then depending on the radius of the plot, sample trees in more detail from the inner plot.

The study data was collected in September and October 2019. Data collected from the outer plot included tree species, diameter (at  $d_{1.3}$ ) and vitality. While data from the inner plot included more specific tree-level data i.e. tree-wise measurements including location of the tree, height, canopy height, diameter (at  $d_{1.3}$ ), thickness of bark, age and annual growth of diameter. Moreover, based on these measurements, stem count, basal area, log count, and timber volume were calculated at the plot level. The ages of the trees were counted from sample cores drilled with an increment borer. The diameters were measured based on two measurements taken at a  $90^\circ$  angle. Tree heights were measured using a Haglóf Vertex and diameter with measuring scissors. Tree level data included 934 trees in the inner plots, which comprised 81.9 % Scots pine, 9.2 % deciduous species and 8.9 % Norway spruce.

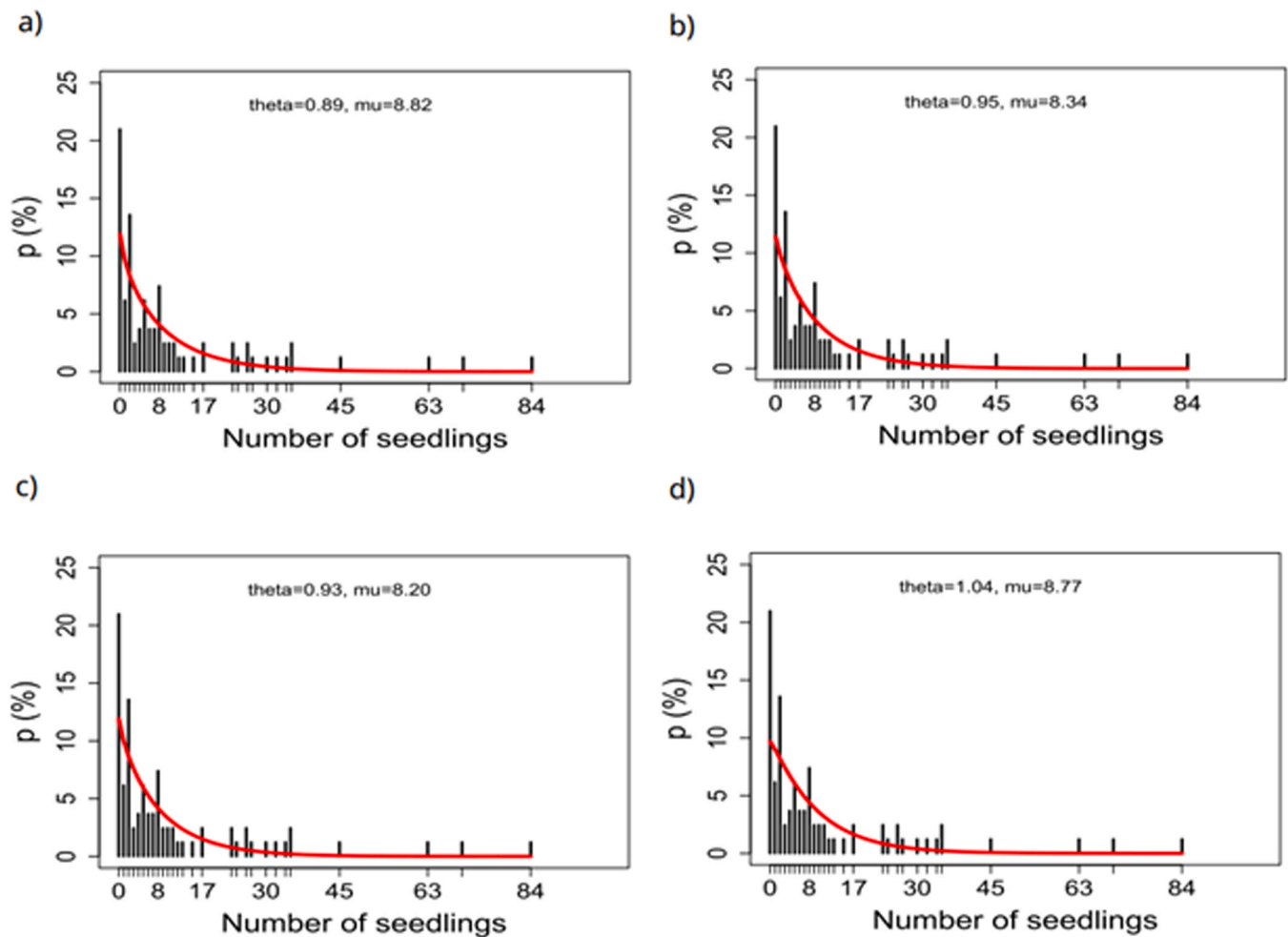
In the seedling plots, all seedlings with a diameter of  $<4.5$  cm (at  $d_{1.3}$ ) and a minimum height of 10 cm were counted. For the Scots pine seedlings, height, age and vitality were determined (for the other tree species, only the height was recorded). In addition, the coverages of stumps, fallen deadwood and stones were measured in the seedling plots (excluding the vegetation plots). The vegetation cover in the sample plot was calculated as the average of the four vegetation plots. In the vegetation plots, the ground-layer coverage was assessed for mosses, lichens, litter, deadwood (fallen and standing), exposed soil and humus layer, rocks and stumps. The field-layer coverage measurements included vascular plants — bilberry (*Vaccinium myrtillus* L.), cowberry (*V. vitis-idaea*), heather and crowberry, and herbs (including grasses).

## 2.2. Statistical data analysis

We used generalised linear mixed modelling to evaluate the number of all established new Scots pine seedlings (despite their vitality or position) in the  $50\text{ m}^2$  circular plots, which revealed the recruitment potential. The height of the seedlings recruited since cutting was modelled using a log-normal linear mixed model. In this modelling, we used a negative binomial distribution assumption, log-link function and considered two hierarchical levels, experimental stand and circular sample plot, nested within the stand. The models were computed using the R package glmmTMB (Brooks et al., 2017). In the glmmTMB negative binomial model, the quadratic variance function NB2 was used. Because general or generalised linear mixed models tend to underestimate the mean value, as also was found in this study, a ratio estimator (ratio of the observed and predicted means) (Snowdon, 1991) was computed and used as the correction coefficient for estimating expected value  $\mu$ .

The explanatory variables tested in the statistical modelling are listed in Table 1. Because of the great number of potential independent fixed variables, the model building could not start with the full model of all the candidate variables and all their interactions, as explained by Zuur et al. (2009). Instead, those variables that contributed at least slightly to the response were pre-selected. Then, the selected potential candidate variables and their possible two-way interactions were tested simultaneously in the models using several include-drop stages. Variables were added to the models and checked if they had p-values  $< 0.05$  in analysis of variance or improved coefficient of determination ( $R^2$ ). Depending on the result, variable was then dropped or included in the model.

A possible multicollinearity in the main-effects models between the selected variables was tested using the R package performance (Lüdtke et al., 2021). All the variance inflation factor values had to be  $<5$  (Hair



**Fig. 3.** Observed and simulated values from the models for the number of Scots pine seedlings established after cuttings illustrating the model fit to the data: (a) Model 1; (b) Model 2; (c) Model 3; and (d) Model 4 (see Table 2).  $p$  (%) means probability for number of seedlings in percentage.

et al., 2021). The glmmTMB package allowed zero-inflation modelling. The possible existence of a zero-inflation problem was tested in the count models. But zero inflation, in terms of excess zeroes, was not an obvious problem in these data, as tested by the R package DHRMA (Hartig, 2021). The (pseudo) $R^2$ -values for the negative binomial models were computed using the wide-functioning performance package (Lüdecke et al., 2021).

The hierarchy in the models was experimental stand, circular sample plot nested within the stand, and seedling or tree nested within the circular sample plot. In addition to the age of the seedlings, variables referring to the site type, the cover of different plant species, the geographical sub-regions of the study area and the other potential explanatory variables (see Table 1) were tested in the models.

The linear models were computed using the R package nlme (Pinheiro et al., 2020). The  $R^2$  values were computed using the R package MuMin (Bartoń, 2020). The predictions of the models with 95% confidence intervals were computed using the R package ggeffect (Lüdecke, 2018) and the prediction graphics were drawn using ggplot2 (Wickham, 2016). The model predictions were computed and drawn using the R packages ggeffects (Lüdecke, 2018) and ggplot2 (Wickham, 2016).

### 3. Results

#### 3.1. Number of pine seedlings established after selection cuttings

The average number of pine seedlings established after the selection

cuttings was 2144  $\text{ha}^{-1}$ . The total average number of all pine seedlings was 2778  $\text{ha}^{-1}$ , which includes also those established before the cuttings. The proportion of plots without any seedlings was about 20 %. In Table 2, the four best predictive models are shown for the number of pine seedlings established in a plot following the cuttings. The models considered both the fixed effects of the explanatory variables (main effects and significant interactions), such as tree basal area or thickness of the humus layer, and the experimental stand as random effects. Among these models, the model fit and Akaike information criterion (AIC) were best for Model 4, in which thickness of humus layer, volume of tree stock, mean diameter and interaction of volume and diameter were used as the fixed variables and experimental stand as a random variable. For marginal Model 4, the fit was 32.8 %, and for conditional Model 4, it was 62.0 %. The single most influential factor affecting seedling establishment based on this model was volume of overstorey tree stock, followed by thickness of humus layer.

An increase in humus layer thickness decreased the number of established seedlings (Table 2 and Fig. 2a). When the number of overstorey trees (trees  $\text{ha}^{-1}$ ) (Fig. 2b), basal area of trees ( $\text{m}^2 \text{ha}^{-1}$ ) (Fig. 2c) and/or volume of tree stock volume ( $\text{m}^3 \text{ha}^{-1}$ ) (Fig. 2d) increased, the number of seedlings decreased. For example, with 500 overstorey trees  $\text{ha}^{-1}$ , basal area of 8  $\text{m}^2 \text{ha}^{-1}$  or tree stock volume of 50  $\text{m}^3 \text{ha}^{-1}$ , the number of established seedlings reached 2500  $\text{ha}^{-1}$ . When the mean diameter was higher, the number of seedlings was higher in the larger tree stock volume (Fig. 2e). With a tree stock volume of 50  $\text{m}^3 \text{ha}^{-1}$ , there were 2000 seedlings  $\text{ha}^{-1}$  with a mean diameter of 12 cm and almost 3000 seedlings  $\text{ha}^{-1}$  with a mean diameter of 16 cm. The

**Table 3**

Linear mixed effects model for the (log) height of the Scots pine seedlings established after selective cuttings. Marginal model  $R^2 = 0.626$  and conditional model  $R^2 = 0.812$ .

Variable	Estimate	Std. error	df	t-/chi-value	p-value
<i>Fixed effects</i>					
(Intercept)	-4.019E+00	1.966E-01	826	-20.446	<0.001
Region (reference category Northern)	—	—	2	4.458	0.108
- Eastern	-3.185E-01	1.510E-01	22	-2.109	0.047
- Western/Southern	-1.968E-01	2.290E-01	22	-0.859	0.400
Seedling age, years	-7.082E-01	1.141E-01	826	-6.206	<0.001
Seedling age <sup>0.9</sup> , years	1.163E+00	1.613E-01	826	7.208	<0.001
Volume of tree stock, m <sup>3</sup> ha <sup>-1</sup> (in 2009)	2.440E-04	2.110E-03	36	0.116	0.909
Cover of herbs, %	1.031E-01	3.637E-02	36	2.834	0.008
Cover of moss, %	6.234E-03	1.785E-03	36	3.493	0.001
Region: Seedling age	—	—	2	16.934	<0.001
Eastern	2.609E-02	6.339E-03	826	4.115	<0.001
Western/Southern	2.517E-02	1.399E-02	826	1.800	0.072
Seedling age: Volume of tree stock	-2.490E-04	1.115E-04	826	-2.235	0.026
<i>Random effects, variance</i>					
Experimental stand	4.942E-02				
Sample plot	3.211E-02				
Residual	8.288E-02				

constructed models (Fig. 3) somewhat underestimated the number of seedlings (1700 seedlings ha<sup>-1</sup>) compared to the observed number (2140 seedlings ha<sup>-1</sup>). With zero seedlings in the plot, the performance of the prediction was less good.

### 3.2. Height of pine seedlings established after selective cuttings

In Table 3, model for height of the pine seedlings is shown. The model fit for the marginal model was 62.6 % and for the conditional model 81.2 % for the height of the pine seedlings established after selective cuttings. The height model included the fixed effects region, seedling age and its transformation, interaction between region and seedling age, volume of tree stock and its interaction with seedling age, and cover of moss and herbs, and as random effects, experimental stand and sample plot. The single most influential factor affecting seedling height was seedling age and its interaction with region, followed by cover of moss.

The transformation to the power of 0.9 of seedling age increased the height estimate in the model, whereas seedling age with no transformation slightly decreased it. The effect of herb or moss cover (as a percentage) was also significant, their increase increasing the seedling height (Fig. 4a and b). A seedling height of 0.3 m was reached with 1.5 % herb cover and 90 % moss cover. However, the herb cover was small and its confidence interval wide. Region also affected the height of the seedlings, with the same height reached faster in the southern and western regions than in the northern and eastern regions. In the northern region, a height of 0.5 m was reached when the seedlings were approximately 20 years old, whereas in the southern region, the same height was achieved by the age of 16 years (Fig. 4c). A large overstorey tree stock volume seemed to decrease the height of the seedlings. When the tree stock volume was 5 m<sup>3</sup> ha<sup>-1</sup>, a 20-year-old seedling had a height of 0.75 m, whereas, at the same age, a seedling had a height of 0.35 m when the tree stock volume was 150 m<sup>3</sup> ha<sup>-1</sup> (Fig. 4d).

## 4. Discussion

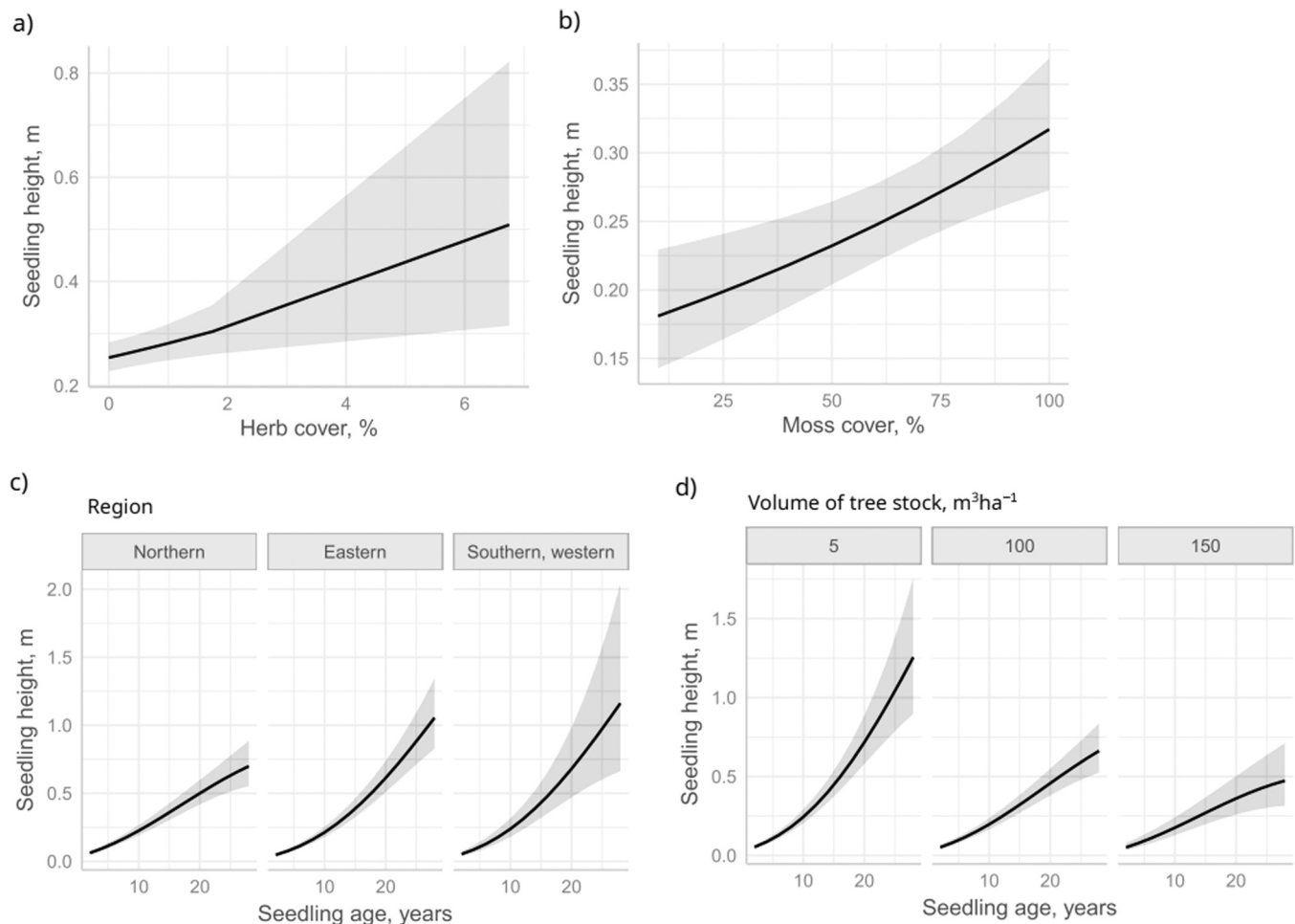
In our study, a minimum height of 10 cm was used in counting the seedlings, but no minimum distance between the seedlings was required. Also modelled seedling numbers represented all the seedlings with height >10 cm, and despite their vitality or distance to each other. In our study, the average number of new Scots pine seedlings was 2140 ha<sup>-1</sup>, 12–34 years after the selection cuttings, in different study sites of Northern Finland. The total number of all Scots pine seedlings was, on average, 2778 ha<sup>-1</sup>, including also the seedlings established before the selection cuttings. No soil preparation was used in the selection cuttings. In the model predictions, the number of new seedlings decreased from 3000 to 625 ha<sup>-1</sup> as the basal area increased from 5 to 25 m<sup>2</sup> ha<sup>-1</sup>. Based on the best constructed model (Model 4), the probability of having 1500 seedlings ha<sup>-1</sup> was approximately 5 %, whereas the probability of having 3000 seedlings ha<sup>-1</sup> was only about 2 %. The modelled number of new seedlings (about 1700 ha<sup>-1</sup>) was lower than the inventoried number, regardless of the predictive variables used in the models. The number of empty plots (i.e. plots with no seedlings) was also about 20 %. The lower modelled number of seedlings per hectare indicates that the models underperformed, potentially causing underestimation.

In a recent study on Northern Finland, Hallikainen et al. (2019) reported 22,000 Scots pine seedlings ha<sup>-1</sup> in a Scots pine stand 5 years after gap cuttings with site preparation. In a follow-up study, 5 years later, Miettinen et al. (2024) reported 29,100 seedlings ha<sup>-1</sup> from the same experimental sites. However, in these studies, a minimum height of 1 cm was used in counting the Scots pine seedlings, and no minimum distance between them was required. Rautio et al. (2023) reported in Northern Finland around 10,000 seedlings ha<sup>-1</sup> with site preparation and 2000–4000 seedlings ha<sup>-1</sup> without it in Scots pine, 11 years after cutting and with an overstorey density range of 50–150 trees ha<sup>-1</sup>. When the overstorey density was 250 trees ha<sup>-1</sup>, the number of seedlings was substantially lower. Similar to our study, a minimum height of 10 cm was used in counting the Scots pine seedlings, and no minimum distance between them was required. Based on these studies, seedlings may emerge well after cutting, but most die, and the establishment of stable seedling crops requires 5–10 years.

Our findings represent selection cuttings with no soil preparation and, on average, the older and more stabilised seedling crop phase. This is because the establishment of new seedlings was inventoried 12–34 years after the selection cuttings. Some of our study sites were also located further north than the experimental sites of Hallikainen et al. (2019) and Miettinen et al. (2024). Overall, due to the severe climate in Northern Finland, good seed years there are rare, which affects the number of established new seedlings (Lula et al., 2025). By comparison, Valkonen (2019) reported an average of 1530–1760 Scots pine seedlings ha<sup>-1</sup> and 16–17 % of empty plots, 6–10 years after gap cuttings in Southern Finland at sites with similar fertility or more fertile than in our study. However, in that study, a minimum distance of 50 cm was used between the counted seedlings. Considering the very northern location of our study stands and the relatively low basal area, particularly in the northernmost stands, the regeneration result appears acceptable.

The establishment of seedlings is affected largely by site conditions. Humus layer thickness affects the establishment of seedlings, with a thick humus layer decreasing their numbers per unit area, especially with no soil preparation (Rautio et al., 2023). A thick humus layer hinders seedlings getting access to capillary water (Oleskog and Sahlén, 2000). Even when seedlings establish contact with the humus layer as a substrate, they cannot tolerate the capillary water blockage that a thick humus layer causes (Winsa, 1995). Seedlings growing in a thick humus layer might have difficulties growing roots through this layer to reach the mineral soil, and because the humus layer dries out easily during dry periods, such seedlings are more prone to drought (Winsa, 1995).

The growing conditions of seedlings are also affected by the characteristics of the overstorey forest. Larger numbers of mature trees may



**Fig. 4.** Predictions with 95 %'s confidence intervals of the height model for Scots pine seedlings established after selective cuttings from the explanatory variables and their interactions: (a) herb cover; (b) moss cover; (c) interaction of region and seedling age; and (d) interaction of volume of tree stock and seedling age. Predictions other than seedling age were computed for the mean age of the seedlings (11 years).

provide larger seed crops (Beland et al., 2000). However, a large number, basal area and volume of overstory tree stock can decrease the number of seedlings per unit area through the competition for growth resources (Rautio et al., 2023), which also we observed in our study. Additionally, this can affect the diameter and height growth of seedlings, as reported by Rautio et al. (2023). An abundant overstory compared to open area absorbs most of the light and blocks rainfall from reaching seedlings (Lehto, 1969; Nygren, 2003). The growing conditions of seedlings affect both the number of seedlings that can become established and their height development. Dense herb or moss cover, typical at more fertile sites, may result in lower numbers of taller seedlings, as we found. These findings are in line with those of Hallikainen et al. (2019) and Miettinen et al. (2024). In our study, the seedlings were also shorter in the northern region due to the harsher growing conditions there. Lower numbers and smaller diameters or heights of seedlings can also be caused by self-thinning in dense sapling stands, such as in older forests (White, 1981).

The minimum accepted level for the remaining overstory after selective cutting is 5–6 m<sup>2</sup> ha<sup>-1</sup> in Northern Finland on xeric and sub-xeric sites, depending on the region (Äijälä et al., 2019). Based on our results, an average of at least 3000 Scots pine seedlings ha<sup>-1</sup>, with a minimum height of 10 cm (but with no minimum distance required between seedlings), can be achieved with the overstory basal area (stand density) typically left in seed tree cuttings (50–100 seed trees ha<sup>-1</sup>) in RF (Äijälä et al. 2019). According to Rautio et al. (2023), achieving in Northern Finland 2000 Scots pine seedlings ha<sup>-1</sup>, with a height of at least

10 cm (no minimum distance requirements) would require an approximate 40 % exposition of mineral soil. In their study, the highest number of seedlings and height growth were achieved when the overstory density was 50 Scots pine trees ha<sup>-1</sup> and the site preparation involved exposing the mineral soil. This implies that not only seed supply (from seed trees) and site preparation are important for regeneration success, but also the reduction of competition from mature trees.

In the natural regeneration or seeding of Scots pine in RF, the aim is to obtain at least 3000 viable seedlings ha<sup>-1</sup>, which are also relatively evenly distributed (>50 cm minimum distance between seedlings), according to Finnish forest management guidelines (Äijälä et al., 2019). The Finnish Forest Act does not set any requirements after selection or gap cuttings for a minimum number of viable seedlings or their spatial distribution within a certain time span. By comparison, the Finnish Forest Act (11 §) requires that 20–25 years after forest regeneration cutting in RF in Northern Finland, there should be at least 1200 viable seedlings per ha<sup>-1</sup> with a mean height of 0.5 m. They should also be relatively evenly distributed in a forest regeneration area. Our results indicate that the quite the same number of seedlings which is required in natural regeneration in RF may be achieved in CCF, if the stand is enough sparse. Based on our findings, pine stands should, however, be selection cut as sparse as legally possible for CCF in practical forestry to enhance natural regeneration and ingrowth of seedlings.

To conclude, the constructed models somewhat underestimated the number of new seedlings established compared to our observations. Overall, natural regeneration was relatively poor, and the growth of the

pine seedlings was slow after the selection cuttings. However, the overstorey characteristics and growing conditions affected them greatly. The dense overstorey reduced the establishment and growth of the Scots pine seedlings. Also, a thick humus layer and dense moss and herb cover reduced their establishment. However, based on our findings, it was not possible to predict how many seedlings would grow into mature trees under varying overstorey densities and growing conditions. Our study excluded soil preparation, but this can significantly improve natural regeneration and the growth of seedlings after gap and selection cuttings, as in RF, and should be evaluated in future studies.

#### CRedit authorship contribution statement

**Heli Peltola:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Formal analysis, Conceptualization. **Pasi Rautio:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Ville Hallikainen:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Laura Pikkariainen:** Writing – review & editing, Writing – original draft. **Petra Peltola:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization.

#### Declaration of Generative AI and AI-assisted technologies in the writing process

During the writing of this study, the authors occasionally used

Microsoft Copilot and openAI ChatGPT to improve the grammar, spelling and readability, and reviewed and edited the content as needed. The authors take full responsibility for the content of the published article.

#### 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.

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#### Appendix

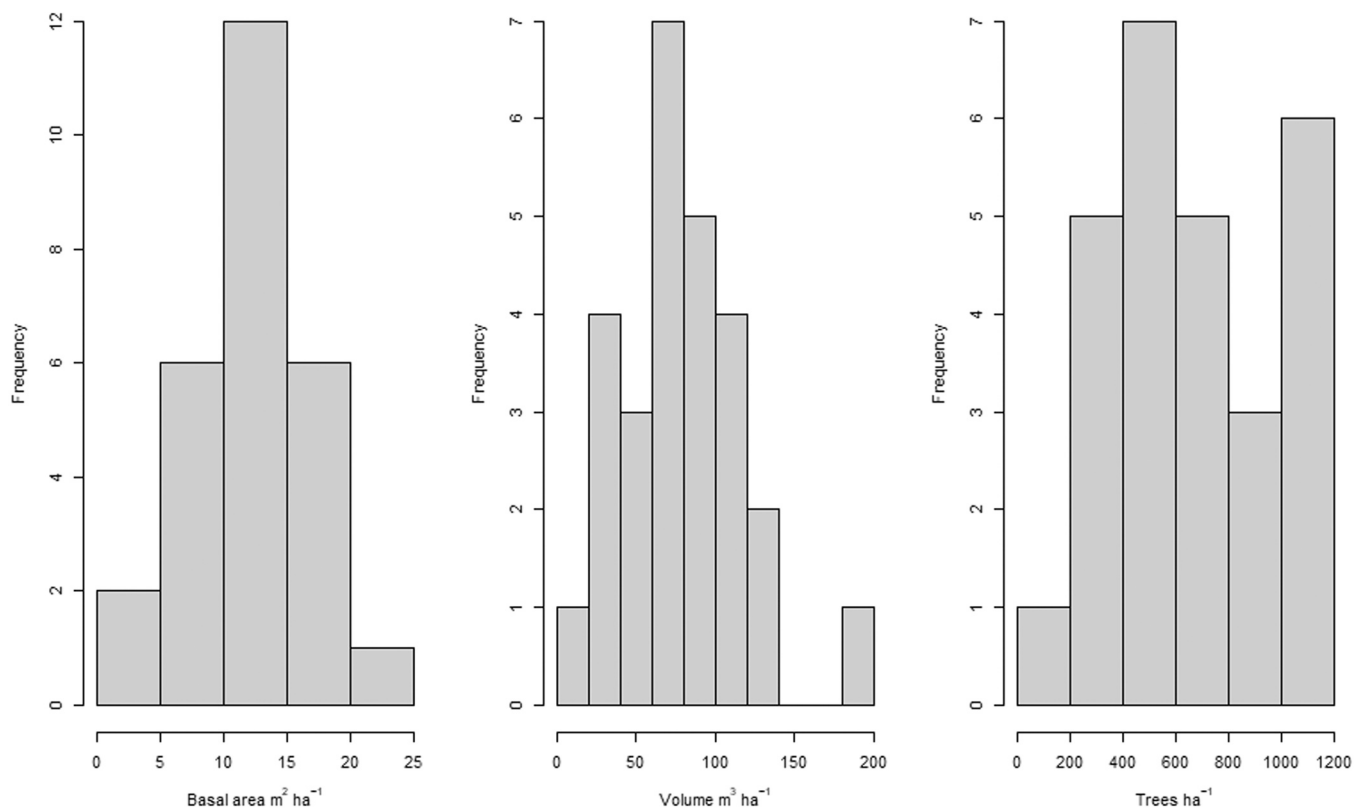


Fig. A1. Stand attributes as histograms in 2019

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2025.122845](https://doi.org/10.1016/j.foreco.2025.122845).

### Data availability

Data will be made available on request.

### References

- Ahtikoski, A., Hökkä, H., 2019. Intensive forest management—does it pay off financially on drained peatlands? *Can. J. For. Res.* 49, 1101–1113. <https://doi.org/10.1139/cjfr-2019-0007>.
- Äijälä, O., Koistinen, A., Sved, J., Vanhatalo, K., Väisänen, P., 2019. Metsänhoidon suositukset [Finnish Forest Management Recommendations] (in Finnish). Tapion julkaisuja, Helsinki. (<https://metsanhoidonsuosituks.fi/fi>).
- Axelsson, E.P., Lundmark, T., Högberg, P., Nordin, A., 2014. Belowground competition directs spatial patterns of seedling growth in boreal pine forests in Fennoscandia. *Forests* 5, 2106–2121. <https://doi.org/10.3390/f5092106>.
- Bartoń, K., 2020. MuMIn: multi-Model Inference. R package version 1.43.17 [software] <https://CRAN.R-project.org/package=MuMIn>.
- Beland, M., Agestam, E., Ekö, M., Gemmel, P., Nilsson, U., 2000. Scarification and seedfall affects natural regeneration of Scots pine under two shelterwood densities and a clear-cut in southern Sweden. *Scand. J. For. Res.* 15, 247–255. <https://doi.org/10.1080/028275800750015064>.
- Brooks, M.E., Kristensen, K., van, Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R. J.* 9, 378–400. <https://doi.org/10.32614/RJ-2017-066>.
- Díaz-Yáñez, O., Pukkala, T., Packalen, P., Peltola, H., 2019. Multifunctional comparison of different management strategies in boreal forests. *For. Int. J. For. Res.* 1, 84–95. <https://doi.org/10.1093/forestry/cpz053>.
- Downey, M., Valkonen, S., Heikkinen, J., 2018. Natural tree regeneration and vegetation dynamics across harvest gaps in Norway spruce dominated forests in southern Finland. *Can. J. For. Res.* 48, 524–534. <https://doi.org/10.1139/cjfr-2017-0358>.
- Finnish Meteorological Institute, 2024. (<https://en.ilmatieteenlaitos.fi/statistics-from-1961-onwards>) (Accessed 24 October 2024).
- Häggström, B., Gundale, M.J., Nordin, A., 2024. Environmental controls on seedling establishment in a boreal forest: implications for Scots pine regeneration in continuous cover forestry. *Eur. J. For. Res.* 143, 95–106. <https://doi.org/10.1007/s10342-023-01609-1>.
- Hair Jr, J.F., Hult, G.T.M., Ringle, C.M., Sarstedt, M., Danks, N.P., Ray, S., 2021. Partial Least Squares Structural Equation Modeling (PLS-SEM) Using R. A Workbook. Springer, Berlin. <https://doi.org/10.1007/978-3-030-80519-7>.
- Hallikainen, V., Hyppönen, M., Hyvönen, J., Niemelä, J., 2007. Establishment and height development of harvested and naturally regenerated Scots pine near the timberline in north-east Finnish Lapland. *Silva Fenn.* 41, 71–88. <https://doi.org/10.14214/sf.308>.
- Hallikainen, V., Hökkä, H., Hyppönen, M., Rautio, P., Valkonen, S., 2019. Natural regeneration after gap cutting in Scots pine stands in northern Finland. *Scand. J. For. Res.* 34, 115–125. <https://doi.org/10.1080/02827581.2018.1557248>.
- Hartig, F., 2021. DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.4 <https://CRAN.R-project.org/package=DHARMA>.
- Hertz, M., 1934. Tutkimuksia kasvualustan merkityksestä männyn uudistumiselle Etelä-Suomen kangasmailla [Studies of the importance of a substrate on the regeneration of Scots pine in the upland forests in South Finland] (in Finnish with German summary). *Commun. Insitituti For. Fenn.* 20, 1–98.
- Hirvelä, H., Karvinen, S., Kilpeläinen, H., Korhonen, K.T., Kumpula, J., Laitila, J., Mutanen, A., Nöjd, P., Pekkarinen, A.J., Rätty, T., Tuulentie, S., Tyrväinen, L., Viitanen, J., 2022. Metsiä hyödyntävät elinkeinot [Businesses that utilize forests]. In: Aro, K., Karvinen, S., Pynnönen, S., Soini, K., Vehmasto, E. (Eds.), *Näkökulmia metsäalan kestävyyskeskusteluun: Systemien lähestymistapa* [Perspectives on the Sustainability Discussion in the Forestry Sector: A Systemic Approach] (in Finnish). Luonnonvara- ja biotalouden tutkimus 85/2022 Luonnonvarakeskus, Helsinki. (<http://urn.fi/URN:ISBN:978-952-380-526-2>).
- Hyppönen, M., 2002. Männyn luontainen uudistaminen siemenpuunetelmällä Lapissa [Natural regeneration of pine using the seed tree method in Lapland] (in Finnish). *Metsäntutkimuslaitoksen Tied.* 844, 1–69. (<http://urn.fi/URN:ISBN:951-40-1824-9>).
- Hyppönen, M., Hallikainen, V., Niemelä, J., Rautio, P., 2013. The contradictory role of understorey vegetation on the success of Scots pine regeneration. *Silva Fenn.* 47, 903. <https://doi.org/10.14214/sf.903>.
- Koivula, M., Silvennoinen, H., Koivula, H., Tikkanen, J., Tyrväinen, L., 2020. Continuous-cover management and attractiveness of managed Scots pine forests. *Can. J. For. Res.* 50, 819–828. <https://doi.org/10.1139/cjfr-2019-0431>.
- Kyrö, M.J., Hallikainen, V., Valkonen, S., Hyppönen, M., Puttonen, P., Bergsten, U., Winsa, H., Rautio, P., 2022. Effects of overstorey tree density, site preparation, and ground vegetation on natural Scots pine seedling emergence and survival in northern boreal pine forests. *Can. J. For. Res.* 52, 860–869. <https://doi.org/10.1139/cjfr-2021-0101>.
- Lehto, J., 1956. Tutkimuksia männyn luontaisesta uudistumisesta Etelä-Suomen kangasmailla [Studies on the natural reproduction of Scots pine on the upland soils of southern Finland] (in Finnish with English summary). *Acta For. Fenn.* 66, 1–106. <https://doi.org/10.14214/aff.7472>.
- Lehto, J., 1969. Tutkimuksia männyn uudistamisesta Pohjois-Suomessa siemenpuu- ja suojuupunenetelmällä [Studies conducted in Northern Finland on the regeneration of Scots pine by means of the seed tree and shelterwood methods] (in Finnish with English summary). *Commun. Inst. For. Fenn.* 67, 1–140. (<http://urn.fi/URN:NBN:fi-metla-201207171099>).
- Lüdecke, D., 2018. ggeffects: Tidy data frames of marginal effects from regression models. *J. Open Source Softw.* 3, 772. <https://doi.org/10.21105/joss.00772>.
- Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., Makowski, D., 2021. Performance: an R package for assessment, comparison, and testing of statistical models. *J. Open Source Softw.* 6, 3139. <https://doi.org/10.21105/joss.03139>.
- Lula, M., Holt, K., Hanssen, M., Goude, M., Hökkä, H., Valkonen, S., Brunner, A., Rautio, P., Erefur, C., Granhus, A., 2025. Regeneration. In: Rautio, P., Routa, J., Huuskonen, S., Holmström, E., Cedergren, J., Kuehne, C. (Eds.), *Continuous Cover Forestry in Boreal Nordic Countries. Managing Forest Ecosystems*, 45. Springer, Berlin, pp. 45–72. <https://doi.org/10.1007/978-3-031-70484-0>.
- Lundqvist, L., Ahlström, M.A., Axelsson, E.P., Mörling, T., Valinger, E., 2019. Multi-layered Scots pine forests in boreal Sweden result from mass regeneration and size stratification. *For. Ecol. Manag.* 441, 176–181. <https://doi.org/10.1016/j.foreco.2019.03.044>.
- Miettinen, J., Hallikainen, V., Valkonen, S., Hökkä, H., Hyppönen, M., Rautio, P., 2024. Natural regeneration and early development of Scots pine seedlings after gap cutting in northern Finland. *Scand. J. For. Res.* 39, 89–100. <https://doi.org/10.1080/02827581.2024.2303022>.
- Niemistö, P., Lappalainen, E., Isomäki, A., 1993. Mäntysiemenpuuston kasvu ja taimikon kehitys pitkätyn luontaisen uudistamisvaiheen aikana [Growth of Scots pine seed bearers and the development of seedlings during a protracted regeneration period] (in Finnish with English summary). *Folia For.* 826, 1–26 <http://urn.fi/URN:ISBN:951-40-1350-6>.
- Nilsson, M.-C., Zackrisson, O., 1992. Inhibition of Scots pine seedling establishment by *Empetrum hermaphroditum*. *J. Chem. Ecol.* 18, 1857–1870. <https://doi.org/10.1007/bf02751109>.
- Norokorpi, Y., Lähde, E., 2013. Jatkuva kasvatusta pohjoisen männiköihin [Continuous cover forestry for northern pine forests] (in Finnish). In: Lähde, E., Pukkala, T. (Eds.), *Alikasvokesta ylispuuksi [From Understorey to Overstorey]*. Joen Forest Program Consulting. Nordprint, Helsinki, pp. 37–46.
- Nygren, M., 2003. Metsäpuiden siemenopas [Handbook to seeds of forest trees] (in Finnish) Metsäntutkimuslaitoksen tiedonantoja 882, 1–144. <http://urn.fi/URN:ISBN:951-40-1869-9>.
- Nygren, M., Saarinen, M., 2001. Itäminen ja taimettumisasusta [Germination and seedling substrate] (in Finnish). In: Valkonen, S., Ruuska, J., Kolström, T., Kubin, E., Saarinen, M. (Eds.), *Onnistunut metsänuudistaminen [Successful Forest Regeneration]*. Metsäntutkimuslaitos, Metsälehti Kustannus, Karisto Oy, Hämeenlinna, pp. 83–90. (<http://urn.fi/URN:NBN:fi-fe2018092036228>).
- Oleskog, G., Sahlén, K., 2000. Effects of seedbed substrate on moisture conditions and germination of *Pinus sylvestris* seeds in a clearcut. *Scand. J. For. Res.* 15, 225–236. (<https://doi.org/ezproxy.uef.fi:2443/10.1080/028275800750015046>).
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R. Core Team, 2020. nlme: linear and nonlinear mixed effects models. R package version 3.1-150 [software] <https://CRAN.R-project.org/package=nlme>.
- Pukkala, T., Hokkanen, T., Nikkanen, T., 2010. Prediction models for the annual seed crop of Norway spruce and Scots pine in Finland. *Silva Fenn.* 44, 629–642. <https://doi.org/10.14214/sf.131>.
- Rautio, P., Hallikainen, V., Valkonen, S., Karjalainen, J., Puttonen, P., Bergsten, U., Winsa, H., Hyppönen, M., 2023. Manipulating overstorey density and mineral soil exposure for optimal natural regeneration of Scots pine. *For. Ecol. Manag.* 539, 120996. <https://doi.org/10.1016/j.foreco.2023.120996>.
- Rikkinen, T., Turunen, M., Hallikainen, V., Rautio, P., 2023. Multiple-use forests and reindeer husbandry – case of pendulous lichens in continuous cover forests. *For. Ecol. Manag.* 529, 120651. <https://doi.org/10.1016/j.foreco.2022.120651>.
- Jatkuvaiteitten metsänkasvatus: Synteesiraportti [Continuous Cover Forestry: A Synthesis Report] (in Finnish). In: Routa, J., Huuskonen, S., Routa, J., Huuskonen, S. (Eds.), 2022. Luonnonvara- ja biotalouden tutkimus 40/2022. Luonnonvarakeskus, Helsinki. (<http://urn.fi/URN:ISBN:978-952-380-427-2>).
- Snowdon, P., 1991. A ratio estimator for bias correction in logarithmic regressions. *Can. J. For. Res.* 21, 720–724. <https://doi.org/10.1139/x91-101>.
- Stuiver, B.M., Wardle, D.A., Gundale, M.J., Nilsson, M.-C., 2016. Seedling responses to changes in canopy and soil properties during stand development following clear-cutting. *For. Ecol. Manag.* 378, 31–43. <https://doi.org/10.1016/j.foreco.2016.07.009>.
- Valkonen, S., 2019. Pienaukkojen ja osittaishakkuuaukkojen taimettuminen Häiriödynamiikka -hankkeen tutkimusalueilla [Regeneration in DISTDYN study areas after gap and partial felling] (in Finnish). Luonnonvara- ja biotalouden tutkimus 69/2019. Luonnonvarakeskus, Helsinki. (<http://urn.fi/URN:ISBN:978-952-326-837-1>).

- Valkonen, S., 2020. Metsän jatkuvasta kasvatuksesta [Continuous cover forestry] (in Finnish). *MetsäKust. Nat. Resour. Inst. Finl.*
- Valtanen, J., 1984. Männyn luontaisen uudistamisen mahdollisuudet [Possibilities for the natural regeneration of pine] (in Finnish). *Metsäntutk Tied.* 158, 37–50. (<http://urn.fi/URN:ISBN:951-40-0944-4>).
- Wardle, D.A., Lagerström, A., Nilsson, M.-C., 2008. Context-dependent effects of plant species and functional group loss on vegetation invasibility across an island area gradient. *J. Ecol.* 96, 1174–1186. (<https://doi-org.ezproxy.uef.fi:2443/10.1111/j.1365-2745.2008.01437.x>).
- White, J., 1981. The allometric interpretation of the self-thinning rule. *J. Theor. Biol.* 89, 475–500. ([https://doi.org/10.1016/0022-5193\(81\)90363-5](https://doi.org/10.1016/0022-5193(81)90363-5)).
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York. (<https://doi.org/10.1007/978-0-387-98141-3>).
- Winsa, H., 1995. Influence of rain shelter and site preparation on seedling emergence of *Pinus sylvestris* L. after direct seeding. *Scand. J. For. Res.* 10, 167–175. (<https://doi.org/10.1080/02827589509382881>).
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and their Extensions in Ecology with R*. Springer, Berlin. (<https://link.springer.com/book/10.1007/978-0-387-87458-6>).