Dissertationes Forestales 396

Natural regeneration success of Scots pine and Norway spruce in continuous cover forestry in Finland

Petra Peltola

School of Forest Sciences
Faculty of Science, Forestry and Technology
University of Eastern Finland

Academic dissertation

To be presented, with the permission of the Faculty of Science, Forestry and Technology of the University of Eastern Finland, for public criticism in the auditorium AU100 of the University of Eastern Finland, Yliopistokatu 2, Joensuu, on 11th of September 2026, at 12 o' clock noon.

Title of dissertation: Natural regeneration success of Scots pine and Norway spruce in continuous cover forestry in Finland
Author: Petra Peltola

Dissertationes Forestales 396
https://doi.org/10.14214/df.396

Thesis Supervisors:
Professor Heli Peltola (main supervisor)
School of Forest Sciences, University of Eastern Finland, Joensuu, Finland

Professor Matti Maltamo
School of Forest Sciences, University of Eastern Finland, Joensuu, Finland

Research Professor Pasi Rautio
Natural Resources Institute Finland, Rovaniemi, Finland

Associate Professor Antti Kilpeläinen
School of Forest Sciences, University of Eastern Finland, Joensuu, Finland

Pre-examiners:
Professor Emeritus Pasi Puttonen
Department of Forest Sciences, University of Helsinki

Tenured Professor of Silviculture Hardi Tullus
Institute of Forestry and Engineering, Estonian University of Life Sciences

Opponent:
Professor Emeritus Tomas Lundmark
Department of Forest Ecology and Management, Swedish University of Agricultural Sciences

ISSN 1795-7389 (online)
ISBN 978-951-651-882-7 (pdf)

Publishers:
Finnish Society of Forest Science
Faculty of Agriculture and Forestry of the University of Helsinki
School of Forest Sciences of the University of Eastern Finland

Editorial Office:
Finnish Society of Forest Science
Viikinkaari 6, 00790 Helsinki, Finland
http://www.dissertationesforestales.fi

Peltola, P. (2026) Natural regeneration success of Scots pine and Norway spruce in continuous cover forestry in Finland. Dissertationes Forestales 396: 39 p.
https://doi.org/10.14214/df.396

ABSTRACT

Continuous cover forestry (CCF) may improve the overall production of ecosystem services compared to traditional rotation forestry. However, sustainable CCF requires successful natural regeneration. The aim of this research was to evaluate the success of the natural regeneration of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* [L.] Karst.), and determine the influencing factors, after CCF cuttings in Finland. In Studies I and II, the natural regeneration of pine seedlings was evaluated in northern Finland 12–34 years after selection cuttings (I), and of spruce seedlings in southern Finland 25 years after selection cuttings (II), using no mechanical site preparation. In Study III, the natural regeneration of pine seedlings was evaluated 3–4 years after small gap, selection and shelterwood cuttings in northern Finland, using different site preparation intensities (all unprepared, and track and patch scarification in small gap and shelterwood cuttings). In Studies I and II, the dense overstory reduced the number and height growth of the pine (I) and spruce (II) seedlings after selection cuttings. In Study I, a thick humus layer also reduced the number of pine seedlings. In Study III, the number of pine seedlings was highest in small gap cuttings with track preparation. In small gap cuttings, the number of pine seedlings also increased with distance from the forest edge and coverage of bare humus. In the selection and shelterwood cuttings (III), number of seedlings decreased with increasing stoniness and moss and bilberry cover. To conclude, the establishment and height growth (and also ingrowth) of the seedlings were slow after the selection cuttings (I and II). Mechanical site preparation improved seedling establishment in the small gap and shelterwood cuttings (III). The use of remote sensing showed potential for estimating the success of forest regeneration in small gaps (III).

Keywords: *Picea abies*, *Pinus sylvestris*, Uneven-aged management, Seedling number, Height growth, Overstory density

ACKNOWLEDGEMENTS

First and foremost, I want to thank Heli Peltola of the University of Eastern Finland (UEF). She always found time to supervise this thesis project and taught me how impactful research articles are written. This thesis work would not even have begun if she had not offered me a doctoral researcher position with a focus on silvicultural sciences. At first, I hesitated, not knowing if I had skills sufficient to carry out the work, or even if it was something I wanted to do after having been a remote-sensing person since graduating with my undergraduate degree. Two years later, here I am, finalising this thesis, and not at all regretting my decision. On the contrary, silviculture has turned out to be way more interesting than I could ever have imagined! Secondly, I want to thank Matti Maltamo (UEF), who encouraged me to test the applicability of remote sensing in estimating forest regeneration success during this research, which I'm very glad to have done. In this way, I was able to deepen my skills on remote-sensing-based forest inventory. Thirdly, I want to thank Pasi Rautio from the Natural Resources Institute (Luke) for making it possible for me to use some of Luke's unique study data in two of my research articles (I and II) and for providing me with a great deal of knowledge on how study designs are created, data collected and, most importantly, data analysed using statistical modelling. I also want to thank Antti Kilpeläinen (UEF) for providing insightful ideas and comments for improving this thesis summary and the related articles. I am also grateful to Ville Hallikainen (Luke) for teaching me the statistical modelling needed for this research and Laura Pikkarainen (UEF) for her valuable support in drafting and writing all my manuscripts. In addition, I would like to extend my gratitude to Aaron Petty, Fan Yang, Tuukka Poutiainen and Viivi Pääkkönen, who joined me in collecting field data for research article III and Jouko Haatainen for his contribution to Article II as part of his master's thesis. Kalle Eerikäinen and Niklas Björqkvist from Metsähallitus Metsätalous Ltd are acknowledged for participating in the planning of this research, as is Metsähallitus Metsätalous Ltd for their field surveys from managing all the study sites (Studies I–III). Sauli Valkonen (Luke) is acknowledged for providing additional information about the data included in research article II. A big thank you also goes to the UNITE flagship (funded by the Research Council of Finland) for financially supporting this thesis project. Finally, I want to thank my friends and family. I'm grateful to all my friends for providing support and a counterbalance to my work life. I want to thank my parents for always making me feel that I can succeed at anything I put my mind to. And especially, I want to thank my husband for being my best friend and biggest academic role model.

Miami, FL, USA, 13 April 2026

Petra Peltola

LIST OF ORIGINAL ARTICLES

This thesis is based on data presented in the following articles, referred to by Roman Numerals I–III in the text.

I. Peltola P, Pikkarainen L, Hallikainen V, Rautio P, Peltola H (2025) Natural regeneration and development of Scots pine seedlings in continuous cover forestry in northern Finland. Forest Ecology and Management 593, article id 122845. https://doi.org/10.1016/j.foreco.2025.122845.

II. Peltola P, Haatainen J, Pikkarainen L, Hallikainen V, Rautio P, Maltamo M, Kilpeläinen A, Peltola H (2026) Natural regeneration and development of Norway spruce seedlings in continuous cover forestry in southern Finland. Forestry (Manuscript).

III. Peltola P, Maltamo M, Poutiainen T, Pääkkönen V, Petty A, Yang F, Pikkarainen L, Korhonen L, Rautio P, Hallikainen V, Kilpeläinen A, Peltola H (2026) Natural regeneration of Scots pine seedlings in northern Finland after small gap, selection and shelterwood cuttings and site preparation. Forest Ecology and Management 617, article id 123929. https://doi.org/10.1016/j.foreco.2026.123929.

Petra Peltola was responsible for compiling and writing this thesis. For Articles I–III, the author participated in the conceptualisation of the all the studies, together with the co-authors (supervisors). She was responsible for processing and analysing the data, and drafting and writing the manuscripts for Articles I–III. She also led the field collection of data for Article III. The co-authors supported the data collection (III) and analyses, and participated in co-writing and/or commenting on the manuscripts.

TABLE OF CONTENTS

INTRODUCTION

1.1 Continuous cover forestry cuttings and natural regeneration success

In Finland, for decades, the majority of forests have been managed using even-aged rotation forestry (RF) (Korhonen et al. 2024). Rotation forestry is distinguished by different stand development classes, such as open area, young sapling stand, young thinning stand and mature stand (Äijälä et al. 2019; Brunner et al. 2025; Lula et al. 2025). In RF, forest regeneration depends on the tree species and site fertility (and geographical location), and is done by either by planting, sowing or using natural regeneration with seed-tree or shelterwood cuttings (and with mechanical site preparation, except for with shelterwood cuttings). Forest regeneration activities are followed by precommercial and one to two commercial thinnings (at intervals of 15–25 years), with final felling typically occurring at the end of a rotation of 60–100 years (Äijälä et al. 2019).

However, in Finland, as with elsewhere in Northern Europe, the interest in uneven-aged continuous cover forestry (CCF) has increased. This is because maintaining a mixed stand structure (i.e. different tree species and size/age classes) is believed to enhance the overall production of ecosystem services compared to RF. As defined by Brunner et al. (2025) CCF refers to silvicultural systems that sustain continuous forest cover and thus such forests can be treated with selection or small gap cuttings. However, sustainable CCF relies entirely on natural regeneration and the ingrowth of seedlings, and greater numbers of younger compared to older trees should be maintained in such forests (Äijälä et al. 2019; Lula et al. 2025). In CCF, selection cuttings are typically conducted every 10–20 years (Äijälä et al. 2019).

In CCF selection cuttings, mainly larger individual trees are harvested, while keeping the forest relatively dense compared e.g. to typical RF cuttings. However, selection cuttings should be conducted often enough to keep the stand sparse enough to allow natural regeneration to occur under the canopy. In RF shelterwood cutting, the overstory stocking may be similar to the selection cutting in CCF. However, a greater number of overstory trees are left in the stand in shelterwood cutting of RF (and these are also larger than in RF seed-tree cuttings) to provide seeds as well as shelter for recently established seedlings. The overstory trees are removed when the sapling stand has become established. In small gap cuttings, the trees are entirely removed over a relatively small area. It should be noted that, if the clear-cut area is 0.3 ha or smaller, the forest owner is not required to actively regenerate the area, according to the Finnish Forest Act.

The use of CCF has, to some degree, increased in Finland over the last decade, after becoming legally acceptable in practical forestry in 2014 with the updating of the Finnish Forest Act (Brunner et al. 2025). However, from the 1940s to 2014, CCF was practically illegal in Finland due to fears that it would degrade the forests (Sarvas 1944; Brunner et al. 2025). Before that, something akin to CCF was practiced in Finnish forests, but in the 1950s, transformation into RF began (Leikola 1987). The move to RF was accelerated by Appelroth et al. (1948), who declared that the then-prevalent CCF methods were deteriorating Finnish forests. Transformation to RF was seen as the only option for ensuring a sufficient supply of timber for the rapidly growing economy. This was because poor regeneration in CCF forests in the early 1900s was expected based on the prevailing knowledge (Leikola 1987).

Nowadays, forests are expected to provide in a sustainable way multiple ecosystem services concurrently for the society, such as timber, carbon sequestration, biodiversity conservation and recreational value (Tuulentie et al. 2025). This way of using forests may especially benefit from CCF, which is the case, for example, in northern Finland, where the forests are important for reindeer husbandry and tourism (Hyppönen 2002; Ahtikoski et al. 2025). In addition, CCF can be a suitable and profitable option for low-profit stands with high forest management costs or stands on drained fertile peatlands (Äijälä et al. 2019; Rautio et al. 2023). However, while the interest in CCF has increased, its usage remains limited, with RF cuttings still being the most common management strategy (Korhonen et al. 2024; Brunner et al. 2025). According to the Forest Centre (2020) and Brunner et al. (2025), only about only 2.7% (in 2020) to 5%, respectively, of all annual cuttings in Finland in the last decade have been reported as CCF cuttings. This low implementation of CCF is partly due to a lack of knowledge concerning the preconditions needed for sustainable CCF, but also to the fact that the majority of forests in Finland are quite even-aged due to past management practices.

The long-term sustainability of CCF depends on the success of natural regeneration and the ingrowth of seedlings, which can be limited. Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* [L.] Karst.), which are the most economically important tree species in Finland, may require different kinds of CCF cuttings. Scots pine is a light-demanding species that benefits from sparse and open stand structures (Sarvas 1944; Kellomäki 2022; Lula et al. 2025). Therefore, small gap cuttings in CCF (and seed-tree cutting in RF) may be better suited to Scots pine-dominated stands than selective cuttings. Norway spruce, on the other hand, can regenerate relatively well under shadier conditions if its other environmental needs are met (Sarvas 1944; Kellomäki 2022; Lula et al. 2025). Therefore, selection cutting in CCF (and shelterwood cuttings in RF) may be suitable for Norway spruce-dominated stands, when forest regeneration relies on natural regeneration. However, for these two tree species, the establishment of seedlings, their growth and survival can differ remarkably after small gap, selection and shelterwood cuttings, as well as across different overstory densities in the latter two types of cutting (Nilsson et al. 2002; Lula et al. 2025).

Based on previous studies, the number of seedlings that naturally regenerate under CCF varies a lot, and their growth is slow compared to RF. For example, in northern Finland, Rautio et al. (2023) found, in Scots pine stands with an overstory density of 50–150 trees ha^{-1}, 2000–10 000 seedlings ha^{-1} over all vitality classes, depending on the site preparation intensity (i.e. either with or without), 11 years after selection cuttings. Lower stand densities and no site preparation also increased seedling height. Correspondingly, Saksa (2004) found 6000–25 000 Norway spruce seedlings ha^{-1} in southern Finland 6–8 years after selection cuttings, while Nilsson et al. (2002) found that a basal area of 10 m^2 ha^{-1} enhanced the natural regeneration of Norway spruce.

There is great variation in the number of naturally regenerated seedlings in Scots pine-dominated small gap cutting stands. Valkonen (2019) found 12 970 pine seedlings ha^{-1} 6–10 years after small gap cutting with site preparation in southern Finland. Hallikainen et al. (2019) recorded 22 000 pine seedlings ha^{-1}, with a mean height of 9.1 cm, 5 years after small gap cutting in northern Finland. Also, Eerikäinen et al. (2014) reported that the annual height growth was low, at only 2–4 cm, in naturally regenerated spruce seedlings in southern Finland.

1.2 Remote sensing

Field inventories are used to determine the number of seedlings and their rate of growth. The aim of lowering the costs associated with performing forest inventories has increased interest in applying remote-sensing techniques to the monitoring of forests. Remote-sensing applications, including airborne laser scanning (ALS), have become standard tools for predicting forest resources information in even-aged forests (Korhonen et al. 2013; Maltamo et al. 2023). However, research on the use of ALS in structurally complex CCF forests with multiple canopy layers is still limited compared to its application in RF forests (Bollandsås et al. 2008; Maltamo et al. 2023; Stoddart et al. 2023; Korhonen et al. 2024; Brunner et al. 2025). Recent developments in remote sensing have improved the potential applicability of ALS in CCF forests. The National Land Survey of Finland's (NLS's) new LiDAR campaigns and continuously updated datasets are presently providing high-density LiDAR data at up to approximately 5 pulses m^{-2} and, from 2026, even up to 20 pulses m^{-2}. Despite this dense ALS data, studies aimed at predicting the number of naturally regenerated seedlings are still rare (Bollandsås et al. 2008). Previous studies on sapling stands have mainly examined the need for tending operations under RF or have assessed the characteristics of more-advanced regeneration stages using ALS and other remote-sensing methods, but have not been focused on detecting early-stage natural regeneration success (Bollandsås et al. 2008; Närhi et al. 2008; Korhonen et al. 2013; Imangholiloo et al. 2019).

Most experimental findings regarding natural regeneration after CCF cuttings are based on a limited number of experimental stands with field inventories. Therefore, there is a need to broaden our understanding of natural regeneration and seedling growth, and particularly the transition of seedlings (i.e. ingrowth; the corresponding number of seedlings surpassing a height limit of 1.3 m) into established trees and the number of seedlings required to ensure the long-term sustainability of CCF. Although currently limited, in the future, field measurements may become routinely used in combination with open-source high-density ALS remote-sensing data, or ALS data may even be used alone, to evaluate natural regeneration success after CCF cutting.

1.3 Factors affecting the success of natural regeneration in continuous cover forestry

Natural regeneration occurs following a disturbance that alters stand structure and resource availability and is controlled by gap dynamics (Oliver and Larson 1996). Small gap and selection cuttings of CCF can be considered such disturbances. In both systems, gap dynamics are engaged, although gap size differs markedly: small gap cuttings typically create openings of up to approximately 0.3 ha, whereas selection cuttings form much smaller gaps, often corresponding to the removal of an individual tree. Following disturbance, a new generation of trees establishes and occupies these gaps in response to increased resource availability (Oliver and Larson 1996). Gap size regulates several key factors affecting natural regeneration, including seed crop and dispersal, competition from surrounding vegetation, and the availability of light and water (Figure 1).

Due to good seed-crop years being a rare occurrence, natural regeneration can be highly variable and slow (Kellomäki 2022; Lula et al. 2025). Good seed-crop years typically occur once in a 10-year period, less often in Norway spruce and slightly more often in Scots pine under southern and middle boreal conditions in Finland. However, good seed-crop years can be rare under northern boreal conditions, and germination may be delayed (Äijälä et al. 2019; Hallikainen et al. 2019; Kellomäki 2022). In addition, even when large numbers of seedlings germinate, their mortality rates can be substantial. High mortality rates of up to 80–99% have been reported in naturally regenerated spruce seedlings (Leemans 1991; Valkonen and

Maguire 2005). However, mortality decreases markedly once seedlings reach a height of approximately 10 cm (Saksa 2004; Lula et al. 2025).

The relationship between overstory density and regeneration success can be complex, with a dense overstory simultaneously restricting seedling germination and growth by limiting the available resources, while at the same time producing larger seed crops (Aaltonen 1919; Lehto 1956, 1969; Yli-Vakkuri 1961; Béland et al. 2000; Rautio et al. 2023). A denser overstory with less and smaller canopy openings restricts germination by causing belowground competition for water and nutrients and by restricting the available light (Aaltonen 1919; Lehto 1956; Kellomäki 2022).

By contrast, maintaining a sparser overstory for improved regeneration may be linked to reduced timber yields because stand volume, among other variables, such as site fertility, positively correlates with volume increment (Sarvas 1944; Lundqvist 2017; Ekholm et al. 2023). The relationship between stand density and ingrowth is also complex. Some studies have reported that ingrowth decreases with increasing stand density (Lappi and Pukkala 2020), whereas others have found no significant effect (Eerikäinen et al. 2014). However, it is known that the natural regeneration and ingrowth of spruce can be restricted under a dense canopy, and that canopy gaps larger than individual trees are needed to promote natural regeneration, although this may lead to more-uneven regeneration results (Aaltonen 1919; Lundqvist 1991; Oliver and Larson 1996; Lula et al. 2025).

The size of gaps (i.e. canopy openings) influences seedling density, with smaller gaps generally promoting higher seed germination rates (Hallikainen et al. 2019; Miettinen et al. 2024). With larger openings, the field layer hinders the growth of pine and spruce seedlings over time, and seed dispersal can be limited (Hertz 1932, 1935; Miettinen et al. 2024). Downey et al. (2018) found that seedling emergence peaked at 5 m from the forest edge in small gaps, whereas Aaltonen (1919) reported that seedling emergence peaked at 10 m from the forest edge of a gap (Figure 1).

In addition to the overstory density and environmental conditions, the ground- and field-layer vegetation and the thickness of the humus layer play important roles in seed germination and seedling growth. Their effects, however, vary widely between tree species and can sometimes go in the opposite direction. In some previous studies, several moss species, and a deep humus layer, have been shown to reduce seed germination and early seedling development (Hertz 1932, 1935; Yli-Vakkuri 1961; Hyppönen et al. 2013; Kyrö et al. 2022; Rautio et al. 2023). A thick humus layer limits germination primarily by preventing the seeds from reaching a mineral soil surface that enables water and nutrient uptake (Hertz 1935; Rautio et al. 2023). However, seedling mortality tends to be low on moist sites dominated by *sphagnum* mosses (Kyrö et al. 2022). By contrast, bilberry (*Vaccinium myrtillus* L.) and stony soil tend to make it difficult for seedlings to become established (Jäderlund et al. 1997; Downey et al. 2018). Some herbs may also restrict the development of seedlings (also being indicators of site fertility), especially in larger canopy openings (Aaltonen 1919; Hertz 1932; Oliver and Larson 1996; Kellomäki 2022). Whereas lichen coverage has been associated with the increased seedling density by preserving moisture (Yli-Vakkuri 1961; Miettinen et al. 2022).

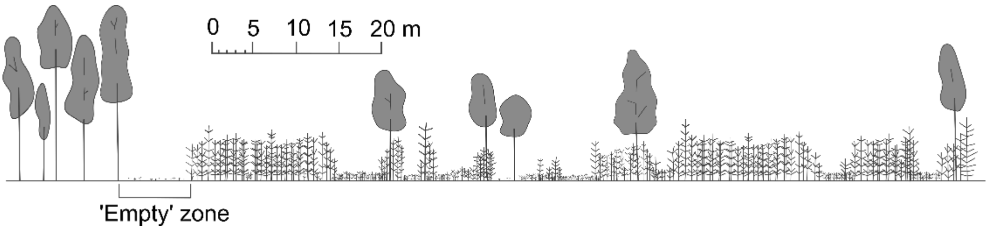

Figure 1. An illustration of how a forest edge and a gap influence seedling numbers, their spatial patterns, and their height, revealing a roughly 10 meter “empty” zone from the forest edge with few or no seedlings. Redrawn on the basis of Aaltonen (1919).

Mechanical site preparation is often used in RF because it has been found to improve the establishment, survival and growth of seedlings (Hertz 1932, 1935; Lehto 1956; Yli-Vakkuri 1961; Béland et al. 2000; Nygren 2003; Valkonen 2019). Site preparation reduces competition from other species, and increases the soil temperature and water and nutrient availability (Kyrö et al. 2022; Miettinen et al. 2022; Rautio et al. 2023). Disc-trenching and patch scarification are the site preparation methods typically recommended for natural regeneration because both techniques expose the mineral soil by removing the humus layer. In patch scarification, an excavator is used to uncover small areas of mineral soil, whereas track preparation uses the passage of a forwarder, which only slightly breaks the ground surface, exposing limited mineral soil and mostly humus (Miettinen et al. 2022). In CCF, mechanical site preparation is seldom used due to its high cost, even though it can enhance forest regeneration success, especially on mineral soils with thick moss layers (Miettinen et al. 2022; Rautio et al. 2023; Lula et al. 2025). It also should not be used after selection (or shelterwood) cuttings in Norway spruce-dominated stands because it increases the risk of root rot (*Heterobasidion* spp.) (Hantula et al. 2025), although moderate site preparation could improve regeneration results (Nilsson et al. 2002; Valkonen et al. 2011).

1.4 Aims, objectives and hypotheses of the study

The aims of this the research were to evaluate the success of natural regeneration in Scots pine and Norway spruce seedlings in Finland, and to determine the influencing factors after CCF cuttings. The objectives, addressed in three studies (I–III), were:

(i) To study the natural regeneration of Scots pine seedlings on xeric and sub-xeric sites in northern Finland 12–34 years after selection cutting, with no mechanical site preparation (Study I).

(ii) To study the natural regeneration of Norway spruce seedlings on mesic and herb-rich sites in southern Finland 25 years after selection cutting, with no mechanical site preparation (Study II).

(iii) To study the natural regeneration of Scots pine seedlings on xeric and mesic sites 3–4 years after small gap, selection and shelterwood cuttings in northern Finland under different site preparation methods (no preparation, and track and patch scarification in small gap and shelterwood cuttings) (Study III).

The factors influencing the success of the natural regeneration were examined in all three studies without using (I and II) or using (III) remote-sensing information. While the height growth of the seedlings was addressed in Studies I and II. In Studies I and II, a minimum height of 10 cm was used in counting the seedlings, whereas in Study III, naturally established Scots pine seedlings older than 1 year were counted. There was no minimum distance between the seedlings required in any of the studies. In all the studies, statistical modelling was used to identify the contributing factors and the direction of their effects because the establishment and growth of seedlings are driven by many factors, the interactions between which can be complex.

The hypotheses tested were:

(i) The establishment and growth of pine and spruce seedlings are slow after selection cuttings (Studies I and II).

(ii) The establishment and growth of seedlings are affected by overstory density, i.e. stand basal area (Studies I and II), ground- and field-layer vegetation hinder seedling establishment through competition (Study III), but indicate more fertile sites (Study I), coverage of exposed humus and a thinner humus layer improve establishment by enhancing seedbed moisture (Studies I and III).

(iii) Small gap cutting, mechanical site preparation and proximity to forest edge improve the establishment of seedlings (Study III).

(iv) Lidar and aerial image features can be used to estimate the number of newly established seedlings in small gaps (Study III).

2 MATERIALS AND METHODS

2.1 Study areas and experimental designs

In Study I, the stands were harvested by selection cutting once at establishment, between 1985 and 2007, and inventory data were collected in the autumn of 2019 (Figure 2). The location of the first sample plot in the stand was randomly chosen, the other two being located 50 and 100 m north of the centre of first plot (Table 1; Study I: Figure 1). The inner and outer dimensions of the sample plots depended on the number of trees observed in the plot. The target was to measure 100 trees per stand and 30–35 trees per plot. Each sample plot included four vegetation plots, from which average values were calculated (Table 1).

In Study II, the stands were harvested by selection cutting at site establishment, in 1992–1994 and then again in 2009–2010, during a 25-year inventory period (Figure 2). The inventory data were collected every 5 years in the autumn. All the trees were measured from the selection cutting treatment, harvested to the target basal area (Table 1; Study II: Figure 1). The seedlings were measured in 16 circular seedling plots located in selection cutting treatment surrounded by a buffer zone that was also harvested to the target basal area (Table 1).

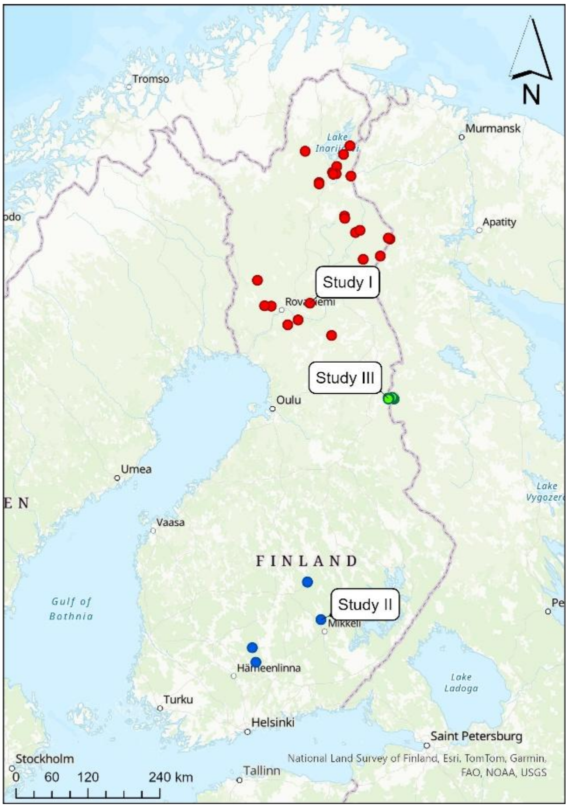

Figure 2. Locations of all the study sites from Studies I–III, marked with different colours. Study I included 27 stands in northern Finland, Study II five stands in southern Finland and Study III six stands in northern Finland.

In Study III, the stands were harvested by small gap, selection and shelterwood cuttings once at establishment, in 2020–2021, and the inventory data were collected in the summer of 2024 (Figure 2). The trees were measured from treemap plots using electronic callipers with GPS detection (Kostensalo et al. 2023; Maltamo et al. 2026) (Table 1). The seedlings were measured from a batch of nine circular seedling plots located in either a treemap plot or a small gap (Table 1; Study III: Figure 1). Each seedling plot included two vegetation plots, in which the coverage of different ground and field layers was visually evaluated as a percentage. The average value from these two vegetation plots was assigned to a seedling plot (Table 1).

2.2 Data collection and processing

The measured and calculated stand variables from Studies I–III are shown in Table 2. Stand variables were calculated for each stand and, in Study II, also for each inventory year. There was no minimum distance set between the counted seedlings in any of the three studies. In Study II, the ingrowth was measured by counting the number or seedlings surpassing a height limit of 1.3 m.

The share of empty plots in Studies I–III was computed by calculating how many seedling plots contained no seedlings of the given tree species and/or vitality classes. In Study III, the tree-level variables (Table 2) were measured from treemap plots. Because the accurate location of each tree was recorded on a treemap plot, the geometry of each treemap plot was created by each tree having a 10 m buffer.

In Study III, the stand attributes were predicted using remote-sensing data and an area-based approach (ABA) alongside stand attributes calculated based on treemap plot measurements (Nasset 2014). LiDAR data from the NLS were used, except for the easternmost stand, where a drone LiDAR survey was conducted and the point density reduced to that of the NLS LiDAR. The stand attributes estimated using the ABA were extrapolated for each stand surrounding the seedling plot batches. The extrapolated attributes were the height (metres), diameter (centimetres), volume (cubic metres per hectare), number of tree

Table 1. Description of plot types and study designs for Studies I–III.

Plot type	N	Size	Description
Study I			
Vegetation plot	324	1 m^2	4 pcs inside each seedling plot. Coverages of different ground and field layers
Seedling plot	81	50 m^2	1 inside each inner/outer plot. Seedling-level measurements
Inner and outer plot	81	~max. 0.2 ha, 30–35 trees	3 inside each stand. Stand-level measurements
Stand	27		Northern region 10 stands, western/southern region 7 stands, eastern region 10 stands Selection cutting, no site preparation
Study II			
Seedling plot	640	4 m^2	16 pcs inside 20 x 20 m grid in each selection cutting treatment. Seedling-level measurements
Selection cutting treatment	40	0.08–0.12 ha	8 pcs, 2 replicates of 8–25 m^2 ha^{-1} selection cutting densities inside study area. Tree-level measurements
Study area	5	80 x 100 m, 0.8 ha	1 per stand
Stand	5		Selection cutting, no site preparation
Study III			
Vegetation plot	414	0.25 m^2	2 pcs inside each seedling plot. Coverages of different ground and field layers
Seedling plot	207	20 m^2	9 pcs inside treemap plot or small gap. Seedling-level measurements
Treemap plot	14	~0.1–0.15 ha, 100–200 trees	1 inside site preparation segment, 2 per stand in unprepared stands. Stand-level measurements
Site preparation segment	15	~0.3–1 ha	3 per stand in shelterwood cutting and small gap cutting stands. No site preparation, patch scarification, track preparation
Stand	6		1 selection cutting stand, 2 shelterwood cutting stands, 3 small gap cutting stands

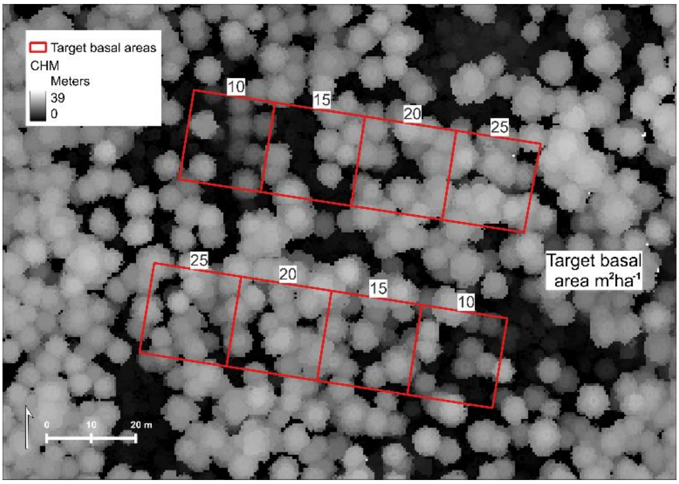

Figure 3. Illustration of different stand densities in a Norway spruce stand from Study II after selection cuttings and a canopy height model created from 5 pulses m⁻² ALS data.

stems (per hectare) and basal area (square metres per hectare). The species were not separated because the inventory area was highly dominated by Scots pine, which accounted for 88% of the trees, on average. First, the LiDAR features (5–95% percentiles, mean, standard deviation [SD] and maximum density, intensity and height) were calculated from the height-normalised LiDAR and aerial image features (minimum, maximum, median, mean and variance of the red–green–blue [RGB] and colour infrared [CIR] images [all bands] and the Normalised Vegetation Difference Index [NDVI]) from the NLS orthoimages to treemap plots. Then, simple generalised linear models were built to link the field-measured stand attributes to the remote-sensing features. The stands were divided into grids, and the models built using the treemap plots were used to predict the stand attributes in each grid cell. Finally, the stand attributes were extrapolated to the stands from these grid cells using zonal statistics. A canopy height model (CHM) was generated from the LiDAR data to determine the distance of the seedling plot to the forest edge in the small gaps (Figure 3).

2.3 Statistical data analyses and modelling

In Studies I–III, generalised linear mixed models (GLMMs) with negative binomial distribution assumptions and log-link functions were created to model the number of seedlings, as well as the ingrowth in Study II (Table 3). The GLMMs were built using the *glmmTMB* R software package (Brooks et al. 2017). In Studies I and III, four different models were built to model the number of seedlings. In Studies I and II, the height of the seedlings was modelled with a linear mixed model using log-transformation (Table 3). These models were created to determine, in more detail, which factors influenced seedling establishment and growth. A height model was created using the *nlme* R software package (Pinheiro et al. 2025). A ratio estimator was applied to the modelled mean heights in Studies I and II, and to the number of seedlings in Study I, because general or generalised models are inclined to underestimate the mean (Snowdon 1991). The probability of empty plots in Study II was modelled using a logistic GLMM via penalised quasi-likelihood using the R software package *MASS* (Table 3) (Venables and Ripley 2002).

Table 2. Measured and calculated variables for the sample plots from Studies I–III.

	Tree	Seedling
Study I	$d_{1.3m}$ ≥ 4.5 cm	d < 4.5 cm, h ≥ 10 cm
Measured	$location_I$, h_I (dm), $d_{1.3m}$ (mm), ch_I (dm), vitality (1–6 [healthy–dead/dying]), thickness of $bark_I$ (mm), age_I (years), annual growth of d_I (mm)	n ($plot^{-1}$), h (cm), age_P (years), $vitality_P$ (1–3 [good–dead])
Calculations	h_P (m), d_P (cm), V (m^3 ha^{-1}), N (ha^{-1}), BA (m^2 ha^{-1}), age_P (years)	total n ($plot^{-1}$), h_P (cm), age_P (years)
Species	Scots pine, other	Scots pine, Norway spruce, deciduous
Study II	h > 1.3 m	10 cm < h ≤ 1.3 m
Measured	location, h (dm), $d_{1.3m}$ (cm), ch (dm), vitality (0–3 [good–dead/dying])	n ($plot^{-1}$), h (cm), vitality (0–3 [good–dead/dying])
Calculations	h (m), d (cm), V (m^3 ha^{-1}), N (ha^{-1}), BA (m^2 ha^{-1}) and changes between inventory years, ingrowth (selection cutting $treatment^{-1}$)	total n ($plot^{-1}$), average h (cm)
Species	Norway spruce, Scots pine, deciduous	Norway spruce, Scots pine, birches, other deciduous, other conifers
Study III	$d_{1.3m}$ > 4.5 cm	age > 1 year, d ≤ 4.5 cm
Measured	location, h (m), $d_{1.3m}$ (cm), ch (m), sh (cm)	n ($plot^{-1}$), h (cm), age_P (years), $vitality_P$ 1 (1–3 [good–dead])
Calculations	h (m), d (cm), V (m^3 ha^{-1}), V dead trees (m^3 ha^{-1}), N (ha^{-1}), BA (m^2 ha^{-1})	total n ($plot^{-1}$), average h (cm), vitality (1–3), age (years)
Species	Scots pine, Norway spruce, deciduous	Scots pine, Norway spruce, deciduous, other

Note. BA = basal area, ch = canopy height, d = diameter, h = height, I = inner sample plot only, n = number of seedlings, N = number of trees, P = Scots pine seedlings only, sh = stump height, V = volume.

The models created for the number of seedlings were used to analyse the number of new seedlings despite their distance from each other and, in Study I, despite their vitality class. Thus, the models described the recruitment potential, not the number of developable seedlings. In Study III, models were created separately for small gap cutting stands and for selection and shelterwood cutting stands combined (because they did not statistically differ in their stand attributes).

Initial variables with at least a minor effect on the response variable were chosen for the models, while final variables and their interactions were chosen from amongst those variables after several include–drop phases. A variable was included if its p-value was <0.05 in the analysis of variance, its inclusion improved the coefficient of determination (R^2), it was ecologically reasonable, it did not correlate with other variables or its effect was of interest. Initial selection was conducted because the number of available fixed variables was too high

Table 3. Models created in Studies I–III.

Response variable	Details	Unit	Model, Distribution	Level
Study I				
Scots pine				
Number of seedlings	Emerged after cuttings, h > 10 cm, $d_{1.3m}$ < 4.5 cm	$plot^{-1}$	GLMM, negative binomial (NB2)	Experimental stand, plot
Height	Emerged after cuttings, h > 10 cm, $d_{1.3m}$ < 4.5 cm	cm	Linear mixed effect model, normal	Experimental stand, plot, seedling
Study II				
Norway spruce				
Number of seedlings	Living and dead or severely damaged, 10 cm < h ≤ 130 cm	$plot^{-1}$	GLMM, NB2	Study area, selection cutting treatment, plot
Height	Living, 10 cm < h ≤ 130 cm	cm	Linear mixed effect model, normal	Study area, selection cutting treatment, plot
Proportion of empty plots	No living seedlings, 10 cm < h ≤ 130 cm	%	Logistic GLMM via penalised quasi-likelihood, binomial	Study area, selection cutting treatment
Ingrowth	New living trees, h > 1.3 m	$plot^{-1}$	GLMM (Hurdle model), truncated NB2	Study area, selection cutting treatment
Probability of no ingrowth	No new living trees, h > 1.3 m	%	GLMM (Hurdle model, Bernoulli), binomial	Study area, Selection cutting treatment
Study III				
Scots pine				
Number of seedlings	Emerged after cuttings, age > 1 year, $d_{1.3m}$ < 4.5 cm	$plot^{-1}$	GLMM, NB1	Seedling plot

and the traditional way if selecting the fixed variables by building a full model, as suggested by Zuur et al. (2009), was not reasonable.

Multicollinearity in the GLMMs was tested using the *performance* R software package with a variance inflation factor of less than 5 (Lüdecke et al. 2021). The possibility of zero inflation in the models for the number of seedlings was tested using the *DHRMa* R software package, but it occurred only for ingrowth so therefore a Hurdle model was used for modelling it in Study II (Hartig et al. 2024). The R^2 values for those models with a negative binomial (NB2) parametrization distribution assumption and the height model in Study II were calculated using the *performance* R software package (Lüdecke et al. 2021). For models with NB1 distribution and the height model in Study I, the R^2 values were calculated using the *MuMIn* R software package (Bartoń 2025). For the model analysing the proportion of empty plots in Study II, the receiver operating characteristics were calculated using the R software package *ROCR* (Sing et al. 2005). Because Study II included measurements repeated over time, the temporality was managed using autoregressive correlation with one lag. In Study III, the model fit was also analysed using the root mean square error (RMSE), and the possible spatial correlation was checked using the R software package *nlme*, but this was found to be small and so was excluded (Pinheiro et al. 2025). Plots with 68–95% (1–2 SD) confidence intervals (CIs) were produced using the *ggeffect* and *ggplot2* R software packages (Wickham 2016; Lüdecke 2018) in all three studies.

3 RESULTS

3.1 Natural regeneration of Scots pine seedlings after selection cuttings (Study I)

The number of Scots pine seedlings observed to have emerged after the selection cuttings was 2144 ha^{-1}, with the total number of Scots pine seedlings being 2778 ha^{-1} 12–34 years after the selection cuttings. Based on the observed number of pine seedlings, four different models were developed to evaluate the factors contributing to the number of established pine seedlings. Thickness of the humus layer was included as a fixed effect in all the models. The same random effects were included in all the models (Table 4). However, in Model 1, the fixed effects also included number of trees, in Model 2, basal area of trees, in Model 3,

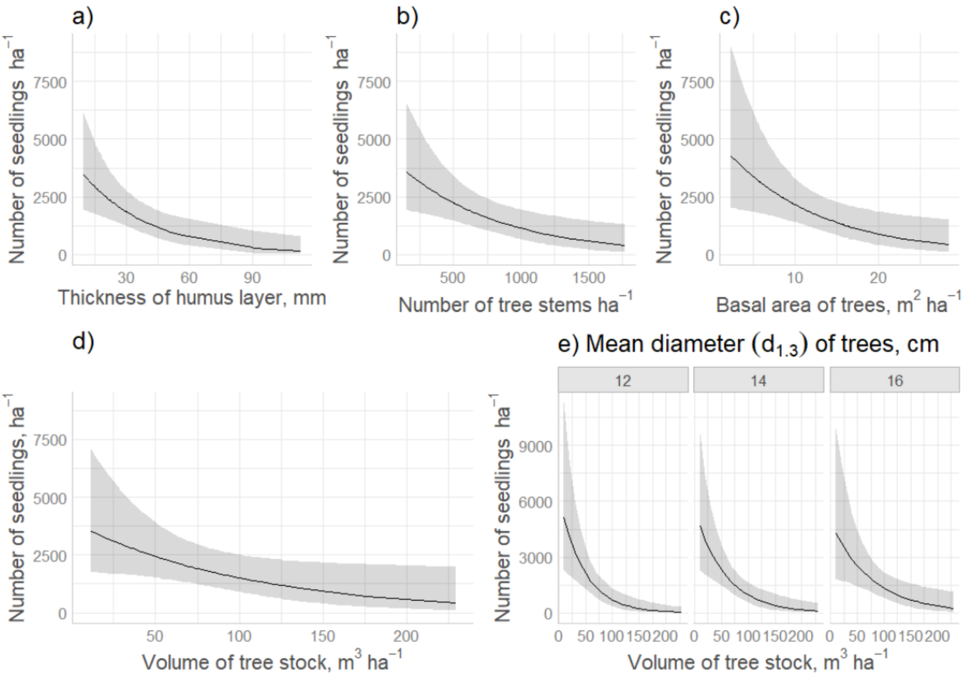

Figure 4. Predictions of the four best models for the number of naturally established Scots pine seedlings after selection cuttings, with point estimates and 95% CIs: (a and b) Model 1; (c) Model 2; (d) Model 3; and (e) interaction effects of Model 4.

volume of tree stock, and in Model 4, mean diameter and its interaction with volume (Table 4). Model 4 was considered the best because it had the lowest Akaike information criterion (AIC) value (Table 4). Thicker humus layer and larger overstory stocking (number of trees ha^{-1}, basal area [$m^2\ ha^{-1}$] or volume of growing stock [$m^3\ ha^{-1}$]) indicated fewer seedlings in all models (Table 4 and Figures 4a–d). According to Model 4, the number of seedlings was slightly higher when the overstory consisted of larger trees (Figure 4e). When the mean diameter was higher, the modelled number of seedlings was higher under the larger tree stock volume (Figure 4e). However, all the constructed models underestimated the number of established seedlings, the modelled mean being about 1700 ha^{-1}. The probability of having 1500 seedlings ha^{-1} was 5% and the share of empty plots was about 20% (Study I: Figure 3).

Based on the observed height of the pine seedlings emerged after selection cuttings, a model for the seedling height was developed to evaluate the factors contributing to the height. As fixed effects, the model included region (northern, eastern and western Lapland), volume of tree stock, seedling age, its transformation and interactions with region and volume of tree stock, and coverage of moss and herbs (Table 5). The seedling height established after the cuttings increased with volume of tree stock, coverage of herbs and moss, and transformation of seedling age and its interaction with region in the model (Table 5 and Figures 5a–c). However, coverage of herbs was, overall, small. The seedling height was decreased with seedling age with no transformation and its interaction with volume of tree stock (Table 5 and Figure 5d). Region alone decreased the seedling height, although only the eastern region compared to the northern region was statistically significant (Table 5). A height of 50 cm was reached in 16 years in the southern region, but in 20 years in the northern region (Figure 5c). Dense overstory hindered seedling height growth (Figure 5d).

Table 4. Study I model parameter estimates for the number of naturally established Scots pine seedlings after selection cuttings (using a NB2 parametrization distribution assumption).

Variable	Estimate	Standard error	z-value	p-value
Model, version 1: R^2 (marginal) = 24.6, R^2 (conditional) = 52.5, AIC = 521.2				
Fixed effects				
Intercept	3.868	0.507	7.627	0.000
Number of trees ha^{-1} (in 2019)	–0.001347	0.000	–2.777	0.005
Thickness of humus layer, mm	–0.03047	0.010	–3.074	0.002
Random effects, dispersal parameter				
Experimental stand, variance	0.4461			
Theta	0.8930			
Model, version 2: R^2 (marginal) = 22.6, R^2 (conditional) = 57.5, AIC = 522.3				
Fixed effects				
Intercept	3.889	0.555	7.008	0.000
Basal area of trees, m^2 ha^{-1} (in 2019)	–0.08857	0.036	–2.494	0.013
Thickness of humus layer, mm	–0.0274	0.0103	–2.650	0.008
Random effects, dispersal parameter				
Experimental stand, variance	0.6416			
Theta	0.953			
Model, version 3: R^2 (marginal) = 19.8, R^2 (conditional) = 56.4, AIC = 524.0				
Fixed effects				
Intercept	3.568	0.503	7.088	0.000
Volume of tree stock, m^3 ha^{-1} (in 2019)	–0.009611	0.005	–2.085	0.037
Thickness of humus layer, mm	–0.0268	0.015	–2.558	0.011
Random effects, dispersal parameter				
Experimental stand, variance	0.6643			
Theta	0.932			
Model, version 4: R^2 (marginal) = 32.8, R^2 (conditional) = 62.0, AIC = 519.7				
Fixed effects				
Intercept	5.035	1.558	3.232	0.001
Volume of tree stock, m^3 ha^{-1} (in 2019)	–0.04973	0.018	–2.818	0.005
Thickness of humus layer, mm	–0.02988	0.010	–2.986	0.003
Mean diameter of trees ($d_{1.3}$), cm	–0.06829	0.107	–0.639	0.523
Volume of tree stock: mean diameter of trees	0.0023	0.001	2.086	0.037
Random effects, dispersal parameter				
Experimental stand, variance	0.5685			
Theta	1.040			

Table 5. Study I linear mixed effects model for the (log) height of the Scots pine seedlings established after selective cuttings.

Variable	Estimate	Std. error	df	t-/chi-value	p-value
Fixed effects	**R^2 (marginal) = 62.6, R^2 (conditional) = 81.2**				
(Intercept)	–4.019	0.197	826	–20.446	<0.01
Region (ref. Northern)	—	—	2	4.458	0.108
– Eastern	–0.3185	0.151	22	–2.109	0.047
– Western/Southern	–0.1968	0.229	22	–0.859	0.400
Seedling age, years	–0.7082	0.114	826	–6.206	<0.01
Seedling age^0.9, years	1.163	0.161	826	7.208	<0.01
Volume of tree stock, m^3 ha^{-1} (in 2009)	0.000244	0.002	36	0.116	0.909
Coverage of herbs, %	0.1031	0.036	36	2.834	<0.01
Coverage of moss, %	0.006234	0.002	36	3.493	<0.01
Region: Seedling age	—	—	2	16.934	<0.01
– Eastern	0.02609	0.006	826	4.115	<0.01
– Western/Southern	0.02517	0.014	826	1.800	0.072
Seedling age: Volume of tree stock	–0.000249	0.000	826	–2.235	0.026
Random effects, variance					
Experimental stand	0.04942				
Sample plot	0.03211				
Residual	0.08288				

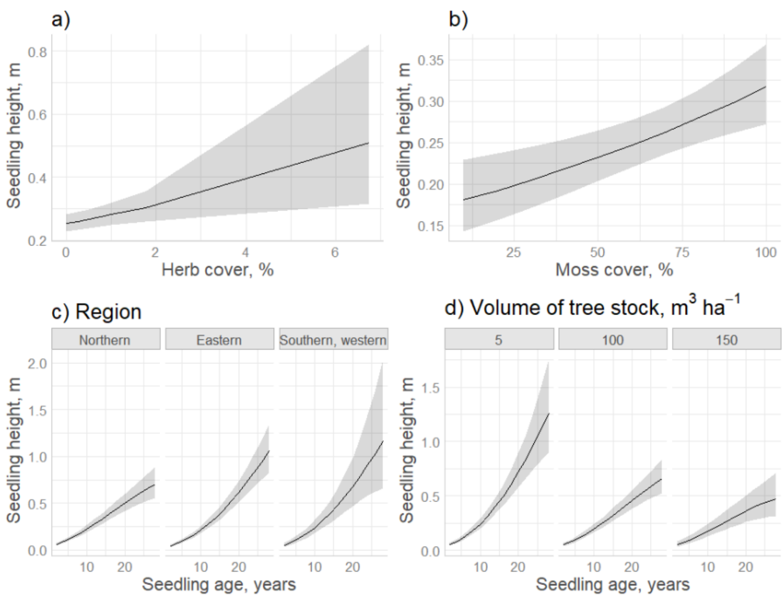

Figure 5. Predictions with 95% CIs of the height model for Scots pine seedlings established after selection cuttings from the explanatory variables and their interactions: (a) herb coverage; (b) moss coverage; (c) interaction between region and seedling age; and (d) interaction between volume of tree stock and seedling age.

3.2 Natural regeneration of Norway spruce seedlings after selection cuttings (Study II)

At the beginning of the inventory period, the observed number of living Norway spruce seedlings for all target basal areas was 9040 seedlings ha^{-1}, and at the end of the 25-year inventory period, it was 5270 seedlings ha^{-1}. The second selection cutting, in 2008, decreased the number of seedlings for all target basal areas. At the end of the inventory period, the observed proportion of plots with no living spruce seedlings was the lowest (25%) for a basal area of 16 m^2 ha^{-1} and the highest (62%) for a basal area of 10 m^2 ha^{-1}. The observed average height of living spruce seedlings at the end of the 25-year inventory period was 65 cm for a basal area of 10 m^2 ha^{-1} and 35 cm for a basal area of 25 m^2 ha^{-1}. The observed ingrowth was 49 trees ha^{-1} $year^{-1}$ with a basal area of 10 m^2 ha^{-1} and 13 trees ha^{-1} $year^{-1}$ with a basal area of 25 m^2 ha^{-1} over the inventory period.

Different models were developed, based on the observed number and height growth of the spruce seedlings established after the selection cuttings, to evaluate the factors contributing to the number, height and ingrowth of the newly established seedlings. Target basal area, inventory year and their interaction were included as the fixed effects in the models created for the number of living Norway spruce seedlings, their height and ingrowth (Table 6). In addition, in the model for the number of seedlings, the fixed effects included change in deciduous trees, mean diameter of trees and basal area of deciduous trees, and in the model for seedling height, the fixed effects were mean diameter, number of trees, their interaction and number of deciduous seedlings (Table 6). The random effects were the same for the seedling number and height models and partly the same for the ingrowth model, in which it excluded the lowest level of model hierarchy.

An increase in the target basal area decreased the number of living spruce seedlings, their height and ingrowth (Table 6 and Figures 6a–c). Inventory year (time since establishment of the experiment) increased the height of the seedlings and their ingrowth, but decreased the number of seedlings because they grew into trees (Table 6 and Figures 6a–c). Interaction between target basal area and inventory year increased the number of seedlings, their height and ingrowth (Table 6 and Figures 6a–c). The number of seedlings declined for all target basal areas over the 25-year inventory period (Table 6 and Figure 6a).

At the beginning of the inventory period, more spruce seedlings were established for smaller basal areas, but their number declined more rapidly during the inventory period (Table 6 and Figure 6a). Therefore, more seedlings existed at the end of the inventory period under larger target basal areas. The modelled number of living spruce seedlings had declined from 2800 to 1280 seedlings ha^{-1} for a basal area of 10 m^2 ha^{-1} and from 1890 to 1770 seedlings ha^{-1} for a basal area of 20 m^2 ha^{-1} by the end of the inventory period (Figure 6a). Similarly, ingrowth (i.e. the number of seedlings growing past 1.3 m) increased during the inventory period and was highest under smaller basal areas (Table 6 and Figure 6c). The modelled average ingrowth over the inventory period and for all target basal areas was 175 trees ha^{-1} 5 $years^{-1}$ (35 trees ha^{-1} $year^{-1}$).

The mean diameter of the overstory trees decreased both the number of living spruce seedlings and their height (Table 6). Also, a positive change in the number of deciduous trees indicated fewer and shorter seedlings and number of deciduous seedlings for shorter seedlings (Table 6). The basal area of the deciduous trees increased the estimated number of seedlings, while the number of trees and its interaction with diameter indicated for taller seedlings (Table 6). For smaller basal areas, the seedlings were taller at both the beginning and end of the inventory period (Figure 6b).

Table 6. Study II models and parameter estimates for the number of Norway spruce seedlings, for 5 years of spruce seedling ingrowth (using a [truncated for ingrowth] NB2 parametrization distribution assumption) and a linear mixed-effects model (log) for seedling height.

Variable	Estimate	Std. error	df	z-/t-/chi-value	p-value
Number of living spruce seedlings: R^2 (marginal) = 4.5, R^2 (conditional) = 84.8, AIC = 3723.3					
Fixed effects					
Intercept	121.1	19.98		6.062	<0.01
Change in dec. trees, ha^{-1}	–0.0004125	0.000		–7.212	<0.01
Mean diameter, cm	–0.06553	0.010		–6.510	<0.01
BA m^2 ha^{-1} deciduous	0.09135	0.029		3.117	<0.01
BA m^2 ha^{-1}	–5.791	0.994		–5.824	<0.01
Year	–0.06034	0.010		–6.057	<0.01
BA*Year	0.002886	0.000		5.825	<0.01
Random effects, variance and dispersal parameter					
Study area	0.271				
Cutting treatment	0.360				
Seedling plot	2.107				
Theta	2.4				
Height of living spruce seedlings: R^2 (marginal) = 14.0, R^2 (conditional) = 37.5, AIC = 2757.238					
Fixed effects					
Intercept	–10.95557	10.979	1514	–0.998	0.319
Mean diameter, cm	–0.008668	0.006	1514	–1.489	0.137
Trees ha^{-1}	0.000012	0.000	1514	0.410	0.682
Dec. seedlings plot^{-1}	–0.015531	0.004	1514	–3.611	<0.01
BA m^2 ha^{-1}	–1.696	0.586	1514	–2.893	<0.01
Year	0.007303	0.005	1514	1.333	0.183
Diameter*Number of trees	0.000039	0.000	1514	2.717	<0.01
BA*Year	0.000824	0.000	1514	2.828	<0.01
Random effects, variance					
Study area	0.004				
Cutting treatment	0.004				
Seedling plot	0.000				
Residual	0.5830336				
Average ingrowth ha^{-1} per 5-year period: R^2 (marginal) = 16.6, R^2 (conditional) = 58.5, AIC = 752.2					
Fixed effects					
Intercept	–0.737921	141.230		–0.005	0.996
BA m^2 ha^{-1}	–5.159081	7.601		–0.679	0.497
Year	0.002555	0.070		0.036	0.971
BA*Year	0.002515	0.004		0.666	0.505
Random effects, variance, and dispersal parameter					
Study area	0.695				
Cutting treatment	0.001				
Theta	1.1				

Note. BA = basal area, df = degrees of freedom.

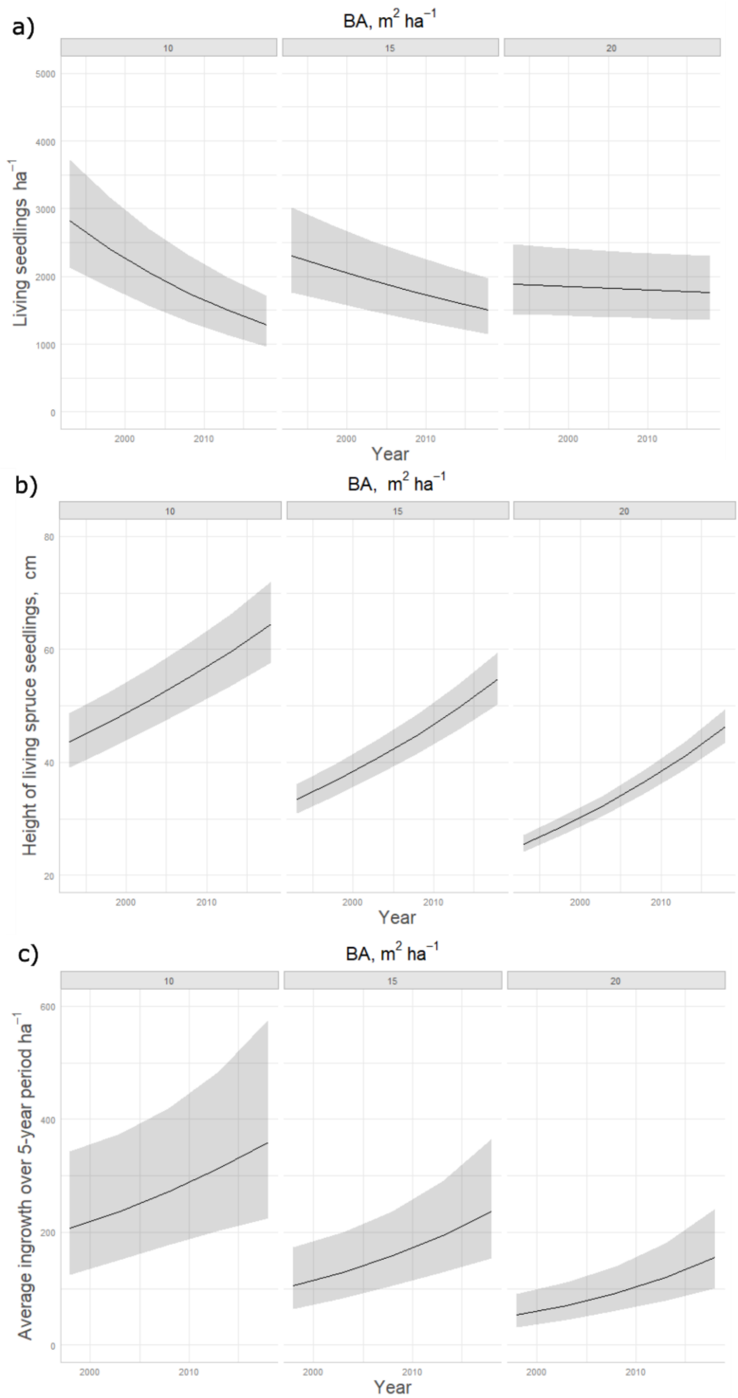

Figure 6. Predictions for different basal areas (10–20 m^2 ha^{-1}) of (a) the number and (b) the height of naturally established Norway spruce seedlings. (c) Ingrowth of Norway spruce seedlings after selection cuttings, with point estimates and 68% CIs.

3.3 Natural regeneration of Scots pine seedlings after gap, selection and shelterwood cuttings (Study III)

In the small gap cutting stands, the number of seedlings (1971 ha^{-1}) was the lowest with no site preparation (537 ha^{-1}) and the highest with track preparation (3407 ha^{-1}). In the shelterwood cutting stands, the number of seedlings (1204 ha^{-1}) was, likewise, the lowest with no site preparation (389 ha^{-1}) and the highest with track preparation (1417 ha^{-1}). In the selection cutting stands with no site preparation, the number of seedlings was 1417 ha^{-1}.

To evaluate the factors contributing to the number of newly established pine seedlings after the cuttings, four different models were created that separately considered small gap cutting stands and the combined shelterwood and selection cutting stands. All the models included site preparation and distance from forest edge in the small gap cutting stands as fixed effects, and plot as a random effect (Study III: Tables 4 and 5). The best model, with the lowest RMSE, was Model 4 for both the small gap and combined selection and shelterwood cutting stands (Tables 7 and 8). The models with the smallest AIC values were Model 1 for the small gap cutting stands and Model 4 for the selection and shelterwood cutting stands. Model 1 included LiDAR and aerial image features (95% percentile of the last echo density, minimum NDVI value, minimum red band value, red band variance and 30% of the first echo density) as the fixed effects, and Model 4 had ground- and field-layer coverage (exposed humus, lichen, stoniness, moss and bilberry). All the models slightly underestimated the number of seedlings.

In Models 1 and 4 for the small gap cutting stands, the number of Scots pine seedlings was increased by site preparation, with track preparation the most, and by distance from the forest edge, although this was not a statistically significant variable (Table 7 and Figure 7). The modelled mean from Model 4 for small gaps with no site preparation was 460 seedlings ha^{-1}, for small gaps with patch scarification, 1310 ha^{-1}, and with track preparation, 1850 ha^{-1} (Table 7 and Figure 7). In addition, in Model 4 for small gap cutting stands, the coverage of exposed humus and lichen increased the number of seedlings emerged after the cuttings (Table 7 and Figure 7). Additionally, in Model 1, the 95% percentile of the last echo density, minimum NDVI value, minimum red band value and red band variance all increased the modelled number of seedlings (Table 7).

In Model 4, for the combined selection and shelterwood cutting stands, the number of new Scots pine seedlings was decreased by the coverage of mosses and bilberry as well as stoniness. Site preparation improved the regeneration and track preparation improved it the most, although the differences were moderate, and this was not a statistically significant variable (Table 8 and Figure 8). The modelled mean from Model 4 was 787 seedlings ha^{-1} in segments with no site preparation, 815 ha^{-1} in the patch scarification segments and 911 ha^{-1} in the track preparation segments (Table 8 and Figure 8).

Table 7. Study III models and parameter estimates for the number of Scots pine seedlings established after small gap cuttings (using a NB1 parametrization distribution assumption).

Variable	**Estimate**	**Std. error**	**Chi-/z-value**	**p-value**
Model 1: R^2 (marginal) = 51.0, R^2 (conditional) = 72.4, AIC = 351.7, RMSE = 5.5				
Fixed effects				
Intercept	–148.7	44.88	–3.313	<0.01
l_p95	145.6	44.81	3.248	<0.01
ndvi_min	4.008	1.828	2.193	0.03
rgb1_min	0.02167	0.009	2.345	0.02
cir2_var	0.003034	0.001	3.269	<0.01
Distance from forest edge, m	0.03045	0.0241	1.260	0.208
Site preparation (ref. Unprepared)	—	—	—	<0.01
– Patch scarification	1.410	0.432	3.267	<0.01
– Track preparation	1.529	0.420	3.641	<0.01
Random effects, dispersal parameter				
Seedling plot, variance	0.470			
Theta	2.6			
Model 4: R^2 (marginal) = 38.7, R^2 (conditional) = 54.9, AIC = 355.0, RMSE = 4.5				
Fixed effects				
Intercept	–0.642920	0.415	–1.550	0.121
Coverage of lichen, %	0.753284	0.201	3.747	<0.01
Coverage of exposed humus, %	0.017049	0.007	2.355	0.019
Distance from forest edge, m	0.041383	0.022	1.921	0.055
Site preparation (ref. Unprepared)	—	—	—	<0.01
– Patch scarification	1.045976	0.414	2.529	0.011
– Track preparation	1.391824	0.420	3.315	<0.01
Random effects, dispersal parameter				
Seedling plot, variance	0.323			
Theta	1.4			

Note. cir2_var = red band variance, l_p95 = 95% percentile of last echo density, ndvi_min = minimum NDVI value, rgb1_min = minimum red band value.

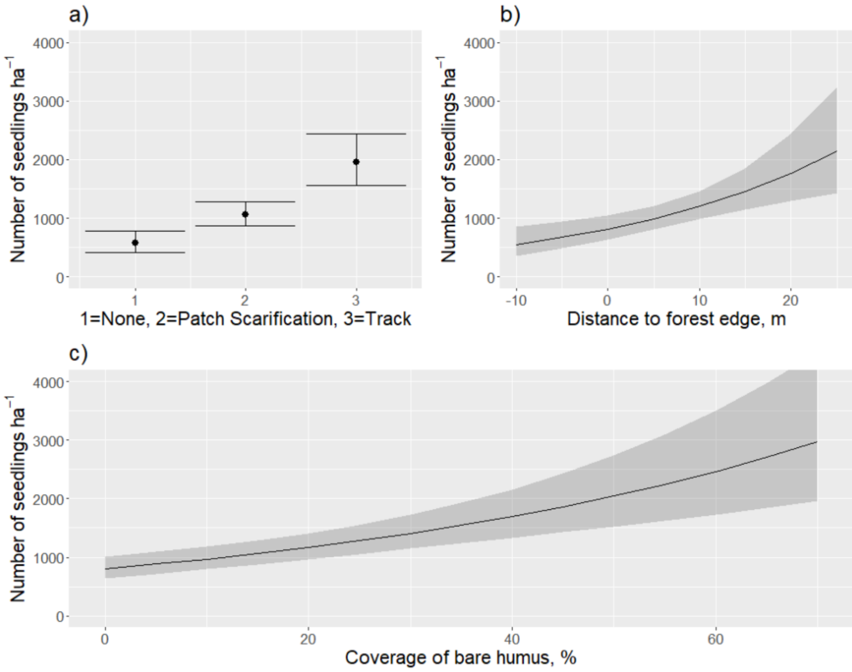

Figure 7. Model 4 (smallest RMSE) predictions for the number of naturally established Scots pine seedlings after small gap cuttings, with point estimates and 68% CIs: (a) site preparation (1 = no preparation, 2 = patch scarification, 3 = track preparation); (b) distance from forest edge; and (c) bare humus coverage.

Table 8. Study III model and parameter estimates for the number of Scots pine seedlings established after selection and shelterwood cuttings (using a NB1 parametrization distribution assumption).

Variable	**Estimate**	**Std. error**	**Chi-/z-value**	**p-value**
Model 4: R^2 (marginal) = 15.5, R^2 (conditional) = 29.2, AIC = 481.7, RMSE = 3.5				
Fixed effects				
Intercept	2.082452	0.449	4.641	<0.01
Coverage of mosses, %	–0.013778	0.005	–2.728	0.006
Coverage of bilberry, %	–0.021967	0.010	–2.245	0.025
Stoniness (ref. 0–30 cm)	—	—	—	0.038
– 30–60 cm	–0.481822	0.307	–1.569	0.117
– >60 cm	–0.957193	0.429	–2.231	0.026
Site preparation (ref. Unprepared)	—	—	—	0.905
– Patch scarification	0.078128	0.365	0.214	0.830
– Track preparation	0.146359	0.334	0.438	0.661
Random effects, dispersal				
Seedling plot, variance	0.3508			
Theta	0.6			

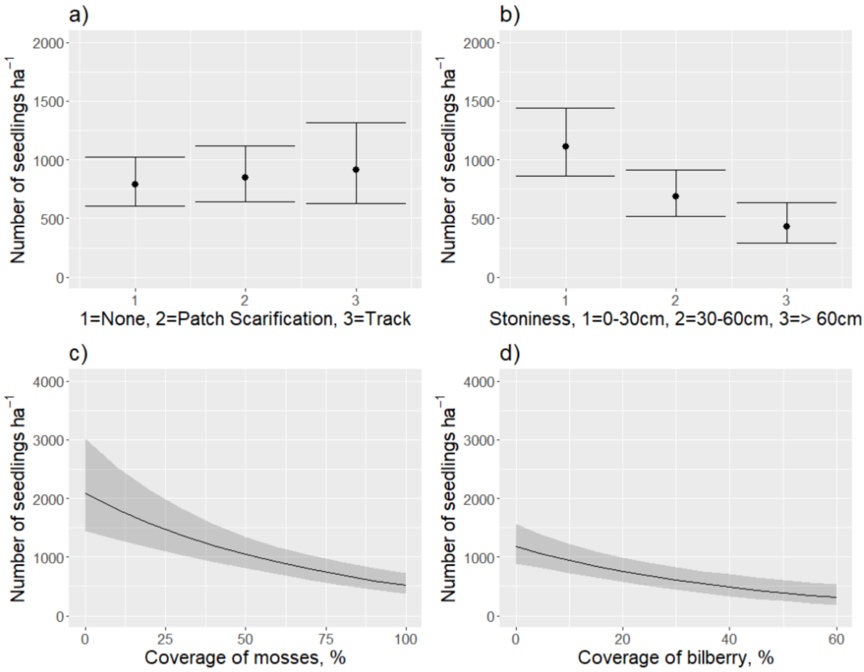

Figure 8. Model 4 (smallest RMSE) predictions for the number of naturally established Scots pine seedlings after selection and shelterwood cuttings, with point estimates and 68% CIs: (a) site preparation (1 = no preparation, 2 = patch scarification, 3 = track preparation); (b) stoniness, defined here as the soil depth to the first stone (1 = 0–30 cm, 2 = 30–60 cm, 3 = >60 cm); (c) moss coverage; and (d) bilberry coverage.

4 DISCUSSION

4.1 Evaluation of materials and methods

The natural regeneration success and the factors affecting it were evaluated for Scots pine seedlings in northern Finland 12–34 years after selection cutting (Study I), and for Norway spruce seedlings in southern Finland 25 years after selection cutting (Study II), with no mechanical site preparation. In Study III, the natural regeneration of Scots pine seedlings was evaluated 3–4 years after small gap, selection and shelterwood cuttings in northern Finland, using different site preparation intensities (i.e. no preparation, track and patch scarification). The findings from Studies I and II showed a more stabilised regeneration result, whereas the results from Study III represented the very early stage of regeneration. In Studies I and II, a minimum height of 10 cm was used in counting the seedlings, whereas in Study III, more than 1-year-old naturally established Scots pine seedlings were counted. Due to differences in the study designs (e.g. seedling plot size) and length of the observation periods after CCF cuttings, the findings between Studies I–III could only be compared to a limited extent.

Because seedling establishment and growth are driven by many factors, and their interactions can be complex, statistical modelling was used to identify the contributing factors and the direction of their effects. In all three studies, the observed and modelled numbers of seedlings described the regeneration potential, but not the number of viable seedlings in the long run because no minimum distance between the seedlings was required in the studies. The between-plot variation in the seedling numbers was very high in all three studies because all the seedlings in the plot were counted. This resulted in a greater number of extreme values, especially in the small (4 m^2) seedling plots in Study II, compared to the larger plot sizes (50 and 20 m^2) in Studies I and III, respectively. The small plot size amplified this variability because a small plot can capture either a dense cluster of seedlings or none at all, whereas a larger plot will likely include both patterns.

Linear mixed models also tend to shrink individual estimates towards the overall mean, and this did lead to an underestimation of the seedling numbers due to extreme values, particularly in Study II, with its small seedling plot size. More-accurate seedling number estimates were obtained in Studies I and III, which had larger seedling plot sizes. Consequently, in Study II, the model estimated the median number of seedlings more accurately than the mean. In Studies I and III, the overall seedling densities were lower, making mean prediction feasible. Study II lacked variables describing the ground and field layers, which were present in Studies I and III. In Study III, the much lower variation in overstory tree characteristics also improved the predictive accuracy.

In Study III, the use of remote sensing showed potential for predicting the number of seedlings established after the cuttings. The model with the smallest AIC value for small gap cutting stands (Model 1) used LiDAR and aerial image features as explanatory variables. These features were able to capture favourable combinations of the different ground and field layers in the small gaps. It was expected that this model would perform better for the small gap cutting stands because there were no overstory trees visible in the aerial images from above the seedling plots, and the laser pulses were able to reach the forest floor more effectively for the same reason. The minimum NDVI value, minimum red band value and red band variance described mixtures of vegetation (e.g. seedlings) and exposed soil surfaces, such as humus or mineral soil. The 95th percentile of the last echo density indicated sparser vegetation. However, the built model described the conditions favourable for seedling establishment rather than detecting individual seedlings. Stand attribute estimation using the ABA appeared also to be accurate. When field-measured stand attributes were replaced with ABA-based estimates, and vice versa, the prediction accuracy was similar.

4.2 Number and height growth of seedlings

In Studies I and II, the dense overstory reduced the number of Scots pine (I) and Norway spruce (II) seedlings after the selection cuttings. Also, in previous studies, larger stocking (e.g. basal area, volume and number of mature trees) has been reported to decrease the availability of water and sunlight for the seedlings and increase belowground competition (Lehto 1956; Béland et al. 2000; Nygren 2003). In Study I, the number of new established pine seedlings after the selection cuttings was greater when the overstory consisted of trees with larger diameters, meaning fewer trees for a given stand volume. The same result was observed in Study II for smaller basal areas. According to the seedling number model from Study II, at the beginning of the inventory period, there were 50% more living spruce seedlings under a basal area of 10 m^2 ha^{-1} than under a basal area of 20 m^2 ha^{-1}. Similarly, Nilsson et al. (2002) found a basal area of 10 m^2 ha^{-1} to be the most favourable for the natural regeneration of spruce. Fewer, but larger, trees and smaller basal areas create more canopy gaps, which are essential for regeneration and can also reduce belowground competition. In Study II, the proportion of empty plots was the largest for the smaller basal areas due to the greater area of canopy gaps, as illustrated in Figure 3. A large number of empty plots combined with quite a large average number of seedlings indicate the clumped regeneration result from Study II (i.e. the seedlings grew close to each other, competing for the same growing resources, which restricted their growth). Additional selection cutting in 2009 also temporarily increased both the seedling mortality and the number of empty plots in Study II.

According to Studies I and II, maintaining sparser overstory density will improve natural regeneration, but timber production per unit land area and further economic benefits may suffer (Lundqvist 2017; Ekholm et al. 2023). In Study II, the number of seedlings was higher at the beginning of the inventory period under all target basal areas but declined more rapidly under smaller basal areas during the inventory period because the seedlings either died or grew into the tree class ($h > 130$ cm) (i.e. ingrowth occurred). Consequently, the observed ingrowth was higher under smaller basal areas. However, neither target basal area nor inventory year had statistical significance in modelling ingrowth. Although Zell et al. (2019) and Lappi and Pukkala (2020) found a negative relationship between basal area and ingrowth, several other studies have not found basal area to be a significant explanatory variable for higher ingrowth (Eerikäinen et al. 2014; Lundqvist 2017).

In Study I, a thick humus layer reduced the number of established pine seedlings after the selection cuttings. This may be because the seedlings struggled to grow roots down into the mineral soil through the thick humus layer and were therefore sensitive to drought (Winsa 1995; Oleskog and Sahlén 2000). In stands with no site preparation, in particular, a thick humus layer can lower the number of naturally established seedlings, as was found in Study I and also several previous studies (Lehto 1956; Örlander et al. 1998; Hyppönen et al. 2013; Rautio et al. 2023). The number of seedlings reported in Study I could also have been increased had site preparation been used.

In Study III, the greater coverage of bare humus observed especially in plots with site preparation resulted in higher numbers of seedlings in small gaps, presumably due to reduced competition with other species, especially mosses. Previous studies have also found bare humus to be a favourable seedbed for seedling establishment (Yli-Vakkuri 1961; Miettinen et al. 2022). In the selection and shelterwood cutting stands in Study III, the number of seedlings decreased with an increase in moss and bilberry coverage, the growing conditions corresponding to plots with no site preparation. Mosses tend to occur as dry seedbeds and, like bilberry, may compete with seedlings (Yli-Vakkuri 1961; Jäderlund et al. 1997; Kyrö et al. 2022). This is why site preparation improves natural regeneration (Rautio et al. 2023). In Study III, the highest seedling numbers were found in small gap cutting stands with track preparation.

In Study III, in small gap cutting stands, the number of pine seedlings also increased with distance from the forest edge and coverage of bare humus and lichen. The gap diameter in Study III was, on average, 52 m, and therefore seed dispersal was assumed not to have been affected by the gap size. Belowground competition is also lower farther from the forest edge (Aaltonen 1919; Axelsson et al. 2014). By contrast, Hallikainen et al. (2019) found that the number of seedlings was lower farther from the forest edge. Similarly to the findings from Study III, Aaltonen (1919) and Axelsson et al. (2014) found the forest edge to restrict regeneration for up to 10 m from the edge, inside the gap.

In Study II, the number of dead seedlings increased over the inventory period. It is known that an abundance of seedlings emerges after cuttings, but the majority die within the first few years (Leemans 1991; Valkonen and Maguire 2005). Emergence and mortality typically stabilise after 5–10 years, when seedlings reach a height of 10 cm and a stable seedling crop phase is achieved. Germination can also be delayed under northern growing conditions, where regeneration happens more slowly because germination can be delayed or limited and may continue for up to 10 years after cuttings (Kellomäki 2022). Therefore, the Study II inventory should be repeated in the future.

The height growth of the Scots pine (I) and Norway spruce (II) seedlings was slow after the selection cuttings, albeit, on average, it was better with smaller overstory densities, in contrast to the establishment of new seedlings after selection cuttings. A greater tree stock volume and basal area decreased seedling height growth by limiting the availability of growing resources. The Scots pine seedlings also grew more slowly in the northern than in the southern and western study regions in Study I due to the shorter growing season. In Study II, the Norway spruce seedlings were consistently the tallest under smaller basal areas over the inventory period. Seedlings being the tallest under smaller basal areas was associated with increased ingrowth under smaller basal areas. Thus, more seedlings exceeded the 1.3 m height threshold during the inventory period. Lower height growth under a denser overstory has also been reported in previous studies (Eerikäinen et al. 2014; Lula et al. 2025). The ground and field layers influenced seedling growth in Study I, in addition to the harsh growing conditions that are typical of the northern boreal region. Abundant moss and herb layers indicate more-fertile sites, which can lead to taller seedlings, as observed in Study I and also reported in previous studies (Hallikainen et al. 2019; Miettinen et al. 2024).

4.3 Future research needs

The results from Studies I–III mainly described the number of established new seedlings ($h < 1.3$ m) after CCF cuttings. However, an even more important outcome may be ingrowth (i.e. seedlings reaching a height of 1.3 m). Ingrowth was examined only in Study II, and further research is needed to determine the level of ingrowth needed to replace harvested trees. Also, to ensure sufficient ingrowth for future harvests, data on the number of new seedlings needed to emerge over a certain time span is required. This would require large-scale inventories, with repeated harvesting over longer periods. Based on the findings of the three studies, lower overstory density supports natural regeneration and ingrowth. However, with longer inventory periods, it would be possible to better assess how individual seedlings develop and eventually grow into trees, and how maintaining lower overstory density affects volume production. The studies excluded small gap cuttings (and shelterwood cuttings under RF) in Norway spruce stands. Also, site preparation was excluded in Norway spruce stands, where it should be avoided due to the risk of root rot. In the future, the natural regeneration success of Scots pine-dominated stands treated with selection cuttings and different site preparation intensities, and of Norway spruce-dominated stands treated with shelterwood cuttings, should also be investigated.

In Study III, LiDAR data were used to create ABA stand estimates and to directly predict the number of seedlings, although the quality of the data would have also allowed individual tree detection (ITD). With ITD, large and old trees could be characterised and preserved to support natural regeneration. It would also be useful to know whether, when the seedlings grow taller, they can be detected individually using LiDAR and ITD instead of only the seedbeds that support natural regeneration in open areas, as was examined in Study III. In Study III, drone LiDAR was used with a reduced point density to replace the ALS LiDAR. However, with drone LiDAR, seedling detection and the prediction of natural regeneration, as in Study III, could be performed in closed canopy stands because drones can fly inside the canopy, whereas prediction was limited to open areas only in Study III. Also in Study III, the prediction of natural regeneration was not determined by species because the stands were dominated by Scots pine. Such information may, however, be of interest, for example, because deciduous seedlings are often not economically important and may compete with the seedlings of other species that are.

5 CONCLUSIONS

The sustainability of continuous cover forestry (CCF) depends on the success of natural regeneration and the ingrowth of seedlings. The aim of this thesis was to examine how different factors affect the success of natural regeneration of Scots pine in the northern boreal zone and Norway spruce in the southern boreal zone. The results of the three studies showed that seedling regeneration and growth were generally slow. In Studies I and II, lower overstory density (i.e., stand basal area) following selection cuttings promoted the regeneration of Scots pine (I) and Norway spruce (II), likely due to reduced competition for resources. In Study I, seedling establishment was limited by a thick humus layer, which increased exposure to drought. In contrast, Study III showed that seedling establishment was enhanced by exposed humus and site preparation, particularly track preparation, through e.g. improved soil moisture conditions. Height growth increased with greater herb and moss cover and in more southerly and westerly regions of Finland, indicating more fertile growing conditions (I). Small gap cuttings, compared with selection and shelterwood cuttings, and increasing distance from the forest edge improved the regeneration of light-demanding Scots pine (III). In selection and shelterwood stands, lower cover of moss and bilberry further enhanced pine regeneration, likely due to reduced above- and belowground competition (III). In addition, less stony soils improved regeneration by providing more favourable seedbed conditions (III). The number of naturally regenerated seedlings in small gaps could be reliably detected using LiDAR and aerial image features, with aerial image features being particularly strong predictors (III). Overall, the results indicate that lower overstory density in both Scots pine- and Norway spruce-dominated stands, as well as small gap cuttings and site preparation in Scots pine stands, can enhance natural regeneration and seedling ingrowth. The number of naturally regenerated Scots pine seedlings reported in Study III may increase over time, as the inventory was conducted only 3–4 years after harvesting. Further research is needed to include both species across northern and southern boreal zones. For more reliable estimates, regeneration inventories should be repeated, as the seedlings have not yet reached a stable developmental stage. In addition, the number of seedlings required for sufficient ingrowth, and the threshold needed to ensure the sustainability of CCF, should be determined in future studies. Remote sensing methods should also be applied at larger spatial scales to assess regeneration success more comprehensively. Because CCF relies heavily on natural regeneration and seedling ingrowth, understanding the factors controlling these processes is essential for its sustainable management.

REFERENCES

Aaltonen VT (1919) *Kangasmetsien luonnollisesta uudistumisesta Suomen Lapissa*. [On the natural regeneration of dry heath forests in Finnish Lapland]. Communicationes ex Instituto Quaestionum Forestalium Finlandiae 1: 1–319.

Ahtikoski A, Gong P, Rørstad PK, Viitala E-J, Repola J (2025) Financial performance. In: Rautio P, Routa J, Huuskonen S, Holmström E, Cedergren J, Kuehne C (eds) Continuous cover forestry in boreal Nordic countries. Managing forest ecosystems, vol. 45. Springer, Cham, pp 135–148. https://doi.org/10.1007/978-3-031-70484-0_8.

Äijälä O, Koistinen A, Sved J, Vanhatalo K, Väisänen P (2019) Metsänhoidon suositukset. [Forest management practices]. Tapio Oy, Finland. https://metsanhoidonsuositukset.fi/fi

Appelroth E, Heikinheimo O, Kalela EK, Laitakari E, Lindfors J, Sarvas R (1948) *Julkilausuma.* [Statement]. Metsätaloudellinen Aikakausilehti 11: 315–316.

Axelsson E, 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 (2025) MuMIn: Multi-model inference. (version 1.48.11). https://cran.r-project.org/web/packages/MuMIn/index.html. Accessed 9 February 2026.

Béland M, Agestam E, Ekö PM, 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.

Bollandsås OM, Hanssen KH, Marthiniussen S, Næsset E (2008) Measures of spatial forest structure derived from airborne laser data are associated with natural regeneration patterns in an uneven-aged spruce forest. For Ecol Manage 255: 953–961. https://doi.org/10.1016/j.foreco.2007.10.017.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM (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.

Brunner A, Valkonen S, Goude M, Hanssen KH, Erefur C (2025) Definitions and terminology: What is continuous cover forestry in Fennoscandia? In: Rautio P, Routa J, Huuskonen S, Holmström E, Cedergren J, Kuehne C (eds) Continuous cover forestry in boreal Nordic countries. Managing forest ecosystems, vol. 45. Springer, Cham, pp 11–43. https://doi.org/10.1007/978-3-031-70484-0_2.

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.

Eerikäinen K, Valkonen S, Saksa T (2014) Ingrowth, survival and height growth of small trees in uneven-aged *Picea abies* stands in southern Finland. For Ecosyst 1, article id 5. https://doi.org/10.1186/2197-5620-1-5.

Ekholm A, Lundqvist L, Petter Axelsson E, Egnell G, Hjältén J, Lundmark T, Sjögren J (2023) Long-term yield and biodiversity in stands managed with the selection system and the rotation forestry system: A qualitative review. For Ecol Manage 537, article id 120920. https://doi.org/10.1016/j.foreco.2023.120920.

Finnish Forest Centre (2020) Jatkuvan kasvatuksen hakkuut ovat hieman lisääntyneet. [Continuous growth cuttings have slightly increased]. Metsäkeskus. https://www.metsakeskus.fi/fi/ajankohtaista/jatkuvan-kasvatuksen-hakkuut-ovat-hieman-lisaantyneet. Accessed 6 February 2026.

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.

Hantula J, Elfstrand M, Hekkala A-M, Hietala AM, Honkaniemi J, Klapwijk M, Koivula M, Matala J, Rönnberg J, Siitonen J, Widemo F (2025) Forest damage. In: Rautio P, Routa J, Huuskonen S, Holmström E, Cedergren J, Kuehne C (eds) Continuous cover forestry in boreal Nordic countries. Managing forest ecosystems, vol. 45. Springer, Cham, pp 221–241. https://doi.org/10.1007/978-3-031-70484-0_12.

Hartig F, Lohse L, de Souza leite M (2024) DHARMa: Residual diagnostics for hierarchical (multi-level / mixed) regression models. (version 0.4.7). https://cran.r-project.org/web/packages/DHARMa/index.html. Accessed 6 February 2026.

Hertz M (1932) *Tutkimuksia aluskasvillisuuden merkityksestä kuusen uudistumiselle Etelä-Suomen kangasmailla*. [Studies on the importance of undergrowth for spruce regeneration in the heaths of southern Finland]. Commun Inst For Fenn 17: 206.

Hertz M (1935) *Tutkimuksia kasvualustan merkityksestä männyn uudistumiselle*. [Studies on the importance of the seedbed for pine regeneration]. Commun Inst For Fenn 20: 98.

Hyppönen M (2002) Männyn luontainen uudistaminen siemenpuumenetelmällä Lapissa. [Natural regeneration of Scots pine using the seed-tree method in Finnish Lapland]. Rovaniemen tutkimusasema, Metsäntutkimuslaitoksen tiedonantoja 844. https://urn.fi/URN:ISBN:951-40-1824-9.

Hyppönen M, Hallikainen V, Niemelä J, Rautio P (2013) The contradictory role of understory vegetation on the success of Scots pine regeneration. Silva Fenn 47, article id 903. https://doi.org/10.14214/sf.903.

Imangholiloo M, Saarinen N, Markelin L, Rosnell T, Näsi R, Hakala T, Honkavaara E, Holopainen M, Hyyppä J, Vastaranta M (2019) Characterizing seedling stands using leaf-off and leaf-on photogrammetric point clouds and hyperspectral imagery acquired from unmanned aerial vehicle. Forests 10: 415. https://doi.org/10.3390/f10050415.

Jäderlund A, Zackrisson O, Dahlberg A, Nilsson M-C (1997) Interference of *Vaccinium myrtillus* on establishment, growth, and nutrition of *Picea abies* seedlings in a northern boreal site. Can J For Res 27: 2017–2025. https://doi.org/10.1139/x97-185.

Kellomäki S (2022) Regeneration biology of selected tree species. In: Kellomäki S (ed) Management of boreal forests: Theories and applications for ecosystem services. Springer, Cham, pp 111–137. https://link.springer.com/10.1007/978-3-030-88024-8.

Korhonen KT, Räty M, Haakana H, Heikkinen J, Hotanen J-P, Kuronen M, Pitkänen J (2024) Forests of Finland 2019–2023 and their development 1921–2023. Silva Fenn 58, article id 24045. https://doi.org/10.14214/sf.24045.

Korhonen L, Pippuri I, Packalén P, Heikkinen V, Maltamo M, Heikkilä J (2013) Detection of the need for seedling stand tending using high-resolution remote sensing data. Silva Fenn 47, article id 952. https://doi.org/10.14214/sf.952.

Kostensalo J, Mehtätalo L, Tuominen S, Packalen P, Myllymäki M (2023) Recreating structurally realistic tree maps with airborne laser scanning and ground measurements. Remote Sens Environ 298, article id 113782. https://doi.org/10.1016/j.rse.2023.113782.

Kuuluvainen T, Ylläsjärvi I (2011) On the natural regeneration of dry heath forests in Finnish Lapland: A review of V. T. Aaltonen (1919). Scand J For Res 26: 34–44. https://doi.org/10.1080/02827581.2011.517951.

Kyrö MJ, Hallikainen V, Valkonen S, Hyppönen M, Puttonen P, Bergsten U, Winsa H, Rautio P (2022) Effects of overstory 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.

Lappi J, Pukkala T (2020) Analyzing ingrowth using zero-inflated negative binomial models. Silva Fenn 54, article id 10370. https://doi.org/10.14214/sf.10370.

Leemans R (1991) Canopy gaps and establishment patterns of spruce (*Picea abies* (L.) Karst.) in two old-growth coniferous forests in central Sweden. Vegetatio 93: 157–165. https://doi.org/10.1007/BF00033209.

Lehto J (1956) Tutkimuksia männyn luontaisesta uudistumisesta Etelä-Suomen kangasmailla. [Studies on the natural regeneration of pine in the heath forests of southern Finland]. Acta For Fenn 66, article id 7472. https://doi.org/10.14214/aff.7472.

Lehto J (1969) Tutkimuksia männyn uudistamisesta Pohjois-Suomessa siemenpuu- ja suojuspuumenetelmällä. [Studies on pine regeneration in Northern Finland using the seed-tree and shletrwood method]. Commun Inst For Fenn 67: 1–140.

Leikola M (1987) Metsien hoidon aatehistoriaa. [The history of forest management ideas]. Silva Fenn 21, article id 5323. https://doi.org/10.14214/sf.a15480.

Lüdecke D (2018) ggeffects: Tidy data frames of marginal effects from regression models. J Open Source Softw 3, article id 772. https://doi.org/10.21105/joss.00772.

Lüdecke D, Ben-Shachar M, Patil I, Waggoner P, Makowski D (2021) performance: An R package for assessment, comparison and testing of statistical models. J Open Source Softw 6, article id 3139. https://doi.org/10.21105/joss.03139.

Lula M, Hanssen KH, 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, vol. 45. Springer, Cham, pp 45–72. https://doi.org/10.1007/978-3-031-70484-0_3.

Lundqvist L (1991) Some notes on the regeneration of Norway spruce on six permanent plots managed with single-tree selection. For Ecol Manage 46: 49–57. https://doi.org/10.1016/0378-1127(91)90244-P.

Lundqvist L (2017) Tamm Review: Selection system reduces long-term volume growth in Fennoscandic uneven-aged Norway spruce forests. For Ecol Manage 391: 362–375. https://doi.org/10.1016/j.foreco.2017.02.011.

Maltamo M, Jukkara H, Kosunen P, Kymäläinen H, Uhlgren V-V, Liimatainen K, Nummenmaa T, Korhonen L (2026) Mapping and verifying potential continuous cover forestry areas from LiDAR data. Trees For People 24, article id 101196. https://doi.org/10.1016/j.tfp.2026.101196.

Maltamo M, Peltola P, Packalen P, Hardenbol A, Räty J, Saksa T, Eerikäinen K, Korhonen L (2023) Can models for forest attributes based on airborne laser scanning be generalized for different silvicultural management systems? For Ecol Manage 546, article id 121312. https://doi.org/10.1016/j.foreco.2023.121312.

Miettinen J, Hallikainen V, Hyppönen M, Bergsten U, Winsa H, Välikangas P, Hiltunen A, Aatsinki P, Rautio P (2022) Effects of site preparation and reindeer grazing on the early-stage success of Scots pine regeneration from seeds in Northern Finland and Sweden. Scand J For Res 37: 338–351. https://doi.org/10.1080/02827581.2022.2136404.

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.

Närhi M, Maltamo M, Packalén P, Peltola H, Soimasuo J (2008) Kuusen taimikoiden inventointi ja taimikonhoidon kiireellisyyden määrittäminen laserkeilauksen ja metsäsuunnitelmatietojen avulla. [Inventory of spruce saplings and determination of the urgency of sapling management using laser scanning and forest planning information]. Metsätieteen Aikakauskirja 2008, article id 6419. https://doi.org/10.14214/ma.6419.

Nasset E (2014) Area-based inventory in Norway – From innovation to an operational reality. In: Maltamo M, Næsset E, Vauhkonen J (eds) Forestry applications of airborne laser scanning: Concepts and case studies. Managing forest ecosystems, vol. 27. Springer, Dordrecht, pp 215–240. https://link.springer.com/10.1007/978-94-017-8663-8.

Nilsson U, Gemmel P, Johansson U, Karlsson M, Welander T (2002) Natural regeneration of Norway spruce, Scots pine and birch under Norway spruce shelterwoods of varying densities on a mesic-dry site in southern Sweden. For Ecol Manage 161: 133–145. https://doi.org/10.1016/S0378-1127(01)00497-2.

Nygren M (2003) Metsäpuiden siemenopas. [Forest tree seed guide]. Metsäntutkimuslaitos, Suonenjoen tutkimusasema, Metsäntutkimuslaitoksen tiedonantoja 882. https://jukuri.luke.fi/items/7d7c13df-2e49-47c7-9d03-c6ec87fe2035.

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/10.1080/028275800750015046.

Oliver C D, Larson, B A (1996) Forest Stand Dynamics, Update Edition. FES Other Publications. 1. https://elischolar.library.yale.edu/fes_pubs/1.

Örlander G, Hallsby G, Gemmel P, Wilhelmsson C (1998) Inverting improves establishment of *Pinus contorta* and *Picea abies* — 10-year results from a site preparation trial in Northern Sweden. Scand J For Res 13: 160–168. https://doi.org/10.1080/02827589809382972.

Pinheiro J, Bates D, R Core Team (2025) nlme: Linear and nonlinear mixed effects models (version 3.1-169). https://doi.org/10.32614/CRAN.package.nlme. Accessed 9 February 2026

Rautio P, Hallikainen V, Valkonen S, Karjalainen J, Puttonen P, Bergsten U, Winsa H, Hyppönen M (2023) Manipulating overstory density and mineral soil exposure for optimal natural regeneration of Scots pine. For Ecol Manage 539, article id 120996. https://doi.org/10.1016/j.foreco.2023.120996.

Saksa T (2004) Regeneration process from seed crop to saplings – A case study in uneven-aged Norway spruce-dominated stands in southern Finland. Silva Fenn 38, article id 405. https://doi.org/10.14214/sf.405.

Sarvas R (1944) *Tukkipuun harsintojen vaikutus Etelä-Suomen yksityismetsiin*. [The impact of log selection cutting on private forests in southern Finland]. Commun Inst For Fenn 33: 1–268.

Sing T, Sander O, Beerenwinkel N, Lengauer T (2005) ROCR: Visualizing classifier performance in R. Bioinformatics 21: 3940–3941. https://doi.org/10.1093/bioinformatics/bti623.

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.

Stoddart J, Suarez J, Mason W, Valbuena R (2023) Continuous cover forestry and remote sensing: A review of knowledge gaps, challenges, and potential directions. Curr For Rep 9: 490–501. https://doi.org/10.1007/s40725-023-00206-0.

Tuulentie S, Bjärstig T, Hansen I, Lande U, McLean P, Pellikka J, Peltola R, Zhang J (2025) Multiple use of forests. 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, Cham, pp 169–193. https://doi.org/10.1007/978-3-031-70484-0_10.

Valkonen S (2019) Pienaukkojen ja osittaishakkuuaukkojen taimettuminen Häiriödynamiikka -hankkeen tutkimusalueilla. [Seedling establishment in small gaps and partial felling gaps in the study area of the Disturbance Dynamics Project]. Luonnonvara- ja biotalouden tutkimus 69/2019. Luonnonvarakeskus, Helsinki. https://jukuri.luke.fi/server/api/core/bitstreams/1f0760c7-9eb2-49e9-bff6-c2780fc68d7f/content.

Valkonen S, Maguire DA (2005) Relationship between seedbed properties and the emergence of spruce germinants in recently cut Norway spruce selection stands in southern Finland. For Ecol Manage 210: 255–266. https://doi.org/10.1016/j.foreco.2005.02.039.

Valkonen S, Koskinen K, Mäkinen J, Vanha-Majamaa I (2011) Natural regeneration in patch clear-cutting in *Picea abies* stands in southern Finland. Scand J For Res 26: 530–542. https://doi.org/10.1080/02827581.2011.611818.

Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edition. Springer, New York.

Wickham H (2016) ggplot2: Elegant graphics for data analysis. Springer, 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 seedling [sic.]. Scand J For Res 10: 167–175. https://doi.org/10.1080/02827589509382881.

Yli-Vakkuri P (1961) Kokeellisia tutkimuksia taimien syntymisestä ja ensi kehityksestä kuusikoissa ja männiköissä. [Experimental studies on the emergence and development of tree seedlings in spruce and pine stands]. Acta For Fenn 75, article id 7135. https://doi.org/10.14214/aff.7135.

Zell J, Rohner B, Thürig E, Stadelmann G (2019) Modeling ingrowth for empirical forest prediction systems. For Ecol Manage 433: 771–779. https://doi.org/10.1016/j.foreco.2018.11.052.

Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York. https://doi.org/10.1007/978-0-387-87458-6.