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The effects of planting practices and growing environment on the early performance of boreal tree seedlings

Laura Pikkarainen

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

Academic dissertation

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Author: Laura Pikkarainen

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Thesis supervisors:
Professor Heli Peltola
School of Forest Sciences, University of Eastern Finland, Finland

Senior Scientist Jaana Luoranen
Natural Resources Institute Finland, Finland

Pre-examiners:
Professor Urban Nilsson
Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, Sweden

Professor Bjarni D. Sigurdsson
Faculty of Environmental Sciences, Agricultural University of Iceland, Iceland

Opponent:
Professor Pasi Puttonen
Department of Forest Sciences, University of Helsinki, Finland

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ABSTRACT

In Finland, there is a desire to extend the planting season from spring and early summer to autumn, and to use the closed cardboard box storage method for both dormant and non-dormant seedlings. This thesis examined the effects of planting practices and the growing environment on the early performance of boreal container seedlings, and specifically: i) What are safe durations for the field storage of non-dormant Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) seedlings in closed cardboard boxes and open tray storage for different planting seasons (I); ii) How planting success differs in one-year-old spring, summer, and autumn plantings of Norway spruce and Scots pine in practical forestry (II); iii) How the planting depth and/or planting season affect the early field performance of small-sized silver birch (*Betula pendula* Roth) and Scots pine container seedlings (III) and iv) How warmer growing conditions affect the growth and emissions of biogenic volatile organic compounds in boreal seedlings in a controlled field experiment (IV). Non-dormant conifer seedlings can be stored in closed boxes for three days in August and a week in May, September, and October, whereas for open-stored seedlings the duration is a couple of days longer (I). Norway spruce plantings can be successful from spring to autumn if seedling storage, duration, and planting instructions are followed carefully. In Scots pine, it is still recommended to plant seedlings only in spring and early summer due to the higher failure risk (II). Deeper planting (60-80 % of shoot underground) may also enhance the early field performance of small-sized seedlings (III). Silver birch might benefit more from climate warming compared to conifer seedlings (IV). To ensure forest regeneration success with boreal tree species, recommendations for seedling materials, storage, and planting practices in different planting seasons should be carefully followed.

Keywords: boreal forest, field performance, container seedling, planting depth, climate change, planting season

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In Joensuu, April 19, 2022

Laura Pikkarainen

LIST OF ORIGINAL ARTICLES

This thesis is based on data presented in the following articles, referred to by the Roman Numerals I-IV.

I Luoranen J, Pikkarainen L, Poteri M, Peltola H, Riikonen J (2019) Duration Limits on Field Storage in Closed Cardboard Boxes before Planting of Norway Spruce and Scots Pine Container Seedlings in Different Planting Seasons. Forests 10(12):1126. https://doi.org/10.3390/f10121126

II Pikkarainen L, Luoranen J, Kilpeläinen A, Oijala T, Peltola H (2020) Comparison of planting success in one-year-old spring, summer, and autumn plantings of Norway spruce and Scots pine under boreal conditions. Silva Fennica 54(1):10243. https://doi.org/10.14214/sf.10243

III Pikkarainen L, Luoranen J, Peltola H (2021) Early Field Performance of Small-Sized Silver Birch and Scots Pine Container Seedlings at Different Planting Depths. Forests 12(5):519. https://doi.org/10.3390/f12050519

IV Pikkarainen L, Nissinen K, Prasad Ghimire R, Kivimäenpää M, Ikonen V-P, Kilpeläinen A, Virjamo V, Yu H, Kirsikka-Aho S, Salminen T, Hirvonen J, Vahimaa T, Luoranen J, Peltola H (2022) Responses in growth and emissions of biogenic volatile organic compounds in Scots pine, Norway spruce, and silver birch seedlings to different warming treatments in a controlled field experiment. The Science of the Total Environment 821: 153277. https://doi.org/10.1016/j.scitotenv.2022.153277

Laura Pikkarainen has the primary responsibility for the data analyses, interpretation of the results, and writing of articles II, III, and IV, whereas in article I the primary responsibility was shared by Jaana Luoranen and Laura Pikkarainen. Laura Pikkarainen participated in designing experiments and measurements of data for all articles. Co-authors helped to improve the manuscripts by commenting on them, and by providing valuable support for the implementation of the research in other ways.

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1 INTRODUCTION

1.1 Background of the study

In 2020, Finnish nurseries produced about 168 million container seedlings for forest regeneration areas. About 72% were Norway spruce (*Picea abies* (L.) Karst.), 25% Scots pine (*Pinus sylvestris* L.), and the rest (3%) were silver birch (*Betula pendula* Roth) container seedlings (Seed and Seedling Statistics 2020). Majority of seedlings in Finland and other Nordic countries are planted during a relatively short planting season, from spring to early summer, which causes work pressure, shortage of labour, and a rush for nurseries, planting organizers, and manual and machine planters (Nilsson et al. 2010; Luoranen et al. 2018). For these reasons, there has been much interest in extending the planting season from spring to late autumn.

Based on some previous studies, the planting season can be extended, especially for Norway spruce container seedlings in Nordic countries, from spring to summer and autumn without decreasing the field performance of the seedlings (Luoranen et al. 2005; 2006; Luoranen and Rikala 2015; Wallertz et al. 2016). This also applies to mechanized plantings of Norway spruce container seedlings (Luoranen et al. 2011). The growth of Norway spruce container seedlings has been observed to even increase under the warmer growing conditions during summer plantings (Helenius et al. 2005; Luoranen et al. 2006). On the other hand, the risk for different stress factors, such as drought periods, is higher during warmer summers, and especially on drier sites with low water holding capacity (Grossnickle et al. 2000; 2005; Grossnickle and Folk 2003; Helenius et al. 2005; Luoranen et al. 2006). In Finland, the risk for winter damage is observed to be higher for autumn planted seedlings (Luoranen et al. 2021).

In Scots pine seedlings, the success has been more variable in summer and autumn plantings compared to Norway spruce seedlings in northern forests. This result may be partially related to the fact that Scots pine container seedlings are usually planted on dryer sites, where the risk for drought damage is higher in general. Even short drought periods can weaken the regeneration results in Scots pine plantings (Huuri 1973; Luoranen et al. 2018). In Northern Idaho, Adams et al. (1991) reported that Douglas-fir (*Pseudotsuga menziesii* var. *glauca* Beissn. Franco), western white pine (*Pinus monticola* Dougl.) and ponderosa pine (*Pinus ponderosa* Laws.) seedlings can be planted early in the autumn if there is enough soil moisture. In Finalnd, Scots pine summer and autumn plantings have succeeded well in geographical regions with mild winter weather conditions if seedlings have been stored and transferred in open trays and quickly and properly planted (Luoranen and Rikala 2013; Luoranen 2018). In regions with harsh winter conditions, the situation has been the opposite (Luoranen et al. 2018). In the studies of Repác et al. (2011; 2021) the spring and autumn planted Scots pine seedlings had equal survival rate in Slovakia.

Previous studies of extended planting seasons in boreal conditions mostly represent carefully established experiments and limited geographical regions. Therefore, to provide recommendations for extending the planting season in practical forestry, the early performance of seedlings in actual forest regeneration sites must be studied, because many factors synergistically affect the regeneration success. These factors include, e.g., seedling material (tree species, origin, and size), seedling storage method, as well as duration, planting practices, and environmental conditions (Helenius et al. 2002a; Grossnickle and Folk 2003; Luoranen et al. 2018; Wallertz et al. 2018; Luoranen et al. 2021).

In Finland, seedlings intended for spring plantings are usually packed into cardboard boxes and overwintered in freezer storage. This method was originally designed and found suitable for dormant and freezer-stored seedlings (Landis et al. 2010). At present, some operators use cardboard boxes for all seedlings, regardless of planting seasons, because boxes are logistically efficient in the storage and transportation of seedlings. However, the physiological state of seedlings intended for spring, summer, and autumn plantings differ from each other at the time of their packing (Grossnickle 2000). During the summer, seedlings are in an actively growing phase and their photosynthetic levels are high, which makes them sensitive to drought and a lack of light (Grossnickle 2000; Helenius et al. 2002a). Therefore, increased temperature and the lack of light inside closed cardboard boxes could cause direct damage and stress to the seedlings (Colombo and Timmer 1992; Helenius et al. 2002b). The shortening of the photoperiod in late summer, with decreasing temperature in autumn, induces the start of frost hardening of seedlings (FH) (Weiser 1970; Li et al. 2004; Søgaard and Granhus 2009). With a limited photoperiod and restricted diurnal temperature variation, the frost hardening inside closed boxes can be disturbed in seedlings intended for autumn plantings. Therefore, there is a need for a better understanding of how storage in closed cardboard boxes, and its duration, may affect root growth and early field performance of seedlings planted in different planting seasons.

A majority of planted seedlings in Finland are 1–2-year-old (80–125 cm^3 cell volume) Norway spruce, 1-year old (40–80-cm^3 cell volume) Scots pine, and 1-year old (80-120 cm^3 cell volume) silver birch seedlings. Lately, there has been a growing inclination to increase the use of < 1-year old, small (mini) seedlings for forest regeneration, particularly in Scots pine (15–40-cm^3 cell volume) (Lindström et al. 2005; 2010). These mini-seedlings are already commonly used in the northern parts of Sweden and Finland. There, due to the humid climate, the risk for drought damage is lower compared to southern regions (Lindström et al. 2010; Kumpare 1998). Also, silver birch can be grown in smaller volume containers (80-120 cm^3) for a short growth time (Luoranen et al. 2003). The advantages of the mini-seedlings are their lower production and transport costs. On the other hand, the mini-seedlings have a small root plug volume, and thus lower water storage capacity, which may make them more prone to environmental stress factors than larger seedlings (see e.g., Rosner and Rose 2006; Johansson et al. 2007). Consequently, mini-seedlings may be more prone to damage during prolonged storage and post-planting drought (Lindström et al. 2010). However, the growth height has not differed in small-sized Scots pine seedlings, compared to larger ones, which also suffered more damage from pine weevils (*Hylobius abietis*) (Kumpare 1998; Lindström et al. 2005; Danielsson et al. 2008). Based on these findings, the use of small-sized Scots pine seedlings in forest regeneration may also be an interesting option in Finland.

On planting sites, the early performance of the seedlings can also be improved with appropriate site preparation and careful planting practices. Site preparation, for instance, mounding, improves the soil temperature, water, and nutrient availability for seedlings at the planting site (Johansson 1994; Örlander et al. 1990). Vegetation competition for water and nutrients is also lower in the mounds (Nilsson and Örlander 1999). Proper site preparation can also reduce damage caused by pine weevils, drought, and frost (Örlander et al. 1990; Örlander and Nilsson 1999). Planting in freshly prepared soil will improve the early performance of seedlings (Nilsson and Örlander et al. 1995; Luoranen et al. 2021). However, timing all site preparations and plantings soon after the clear cut is difficult in practice, especially in a relatively short planting season from spring to early summer. Also, the logging residues left for drying on regeneration sites delays plantings. These factors increase the pressure to extend the planting season from spring to late autumn.

Seedlings should be planted deep enough so that the peat plug reaches the humus layer below the mound (Örlander et al. 1986; Smolander and Heiskanen 2007). In general, the recommendation for planting depth for conventional container seedlings is 5 cm when seedlings are planted in the spot or inverted mound. This would mean that, for small-sized seedlings, the entire shoot might be below ground. Concern has arisen that deep planting of the silver birch could increase stem spot fungi and disrupt seedling development. On the other hand, the growth of conifer and broadleaved species have been observed to benefit, or at least not to suffer, from deep planting (Buitrago et al. 2015; Gemmel et al. 1996; Paquette et al. 2011; Tarroux et al. 2014). Deep planting has also been shown to increase the growth and survival rate of 1–2 -year-old conventional conifer seedlings by protecting the seedlings from drought and pine weevil feeding damage (Örlander et al. 1991; Luoranen and Viiri 2016; Viiri and Luoranen 2017). Yet, we do not know if deep planting would also be a protective planting practice for small-sized seedlings. Furthermore, we need an advanced understanding of the field performance of small-sized conifer and birch container seedlings using different planting practices (e.g., planting season and depths).

As a consequence of climate change, the mean temperature is expected to increase about 1–5°C and precipitation about 5–11% in Finland during a potential growing season (April–September) by the 2080s (Ruosteenoja et al. 2016). In general, birch can continue to increase in height until late summer (Viherä-Aarnio et al. 2005), whereas the mainly pre-determined growth pattern of boreal conifers limits their height growth period to a few weeks (Thompson 1976; von Wühlich and Muhs 1986; Kilpeläinen et al. 2006). On the other hand, the period of diameter growth in boreal conifers typically lasts from mid-May to mid-August and about 80–90% of it occurs during June and July (Henttonen et al. 2009; Nissinen et al. 2020; Peltola et al. 2002). When subjected to climate warming, the height growth of boreal conifers, e.g., Scots pine, may start and complete slightly earlier, but its duration is not expected to change greatly (Bergh et al. 2003; Kilpeläinen et al. 2006). However, the duration of diameter growth, e.g., in Scots pine, may lengthen by a few weeks (Peltola et al. 2002).

The growth of boreal tree species is, in general, predicted to increase under climate change (Kellomäki et al. 2008; 2018). However, the growing environment is predicted to become suboptimal and the amount of growth decrease for some boreal tree species like Norway spruce in southern regions. This may also occur in middle boreal conditions and especially on sites with low water holding capacity. On the other hand, especially the silver birch, but also the Scots pine, are expected to benefit from climate change (Ruosteenoja et al. 2016; Kellomäki et al. 2008; 2018; Nissinen et al. 2020). Despite this, the Norway spruce plantings dominate in southern and central Finland, and Norway spruce is nowadays planted also on less fertile sites with low water holding capacity. This is due to large problems with moose browsing in Scots pine plantings. To adapt to the changing climate, and to increase the resilience of forests to increasing multiple abiotic and biotic damage factors, there is a need to increase the cultivation of other tree species, especially Scots pine and silver birch in Finnish forests. This is because Norway spruce is expected to be the most vulnerable to increasing abiotic and biotic damage risks under a changing climate (Venäläinen et al. 2020).

In addition to the growth of trees, climate change (e.g., warming) can also affect the emissions of secondary compounds such as biogenic volatile organic compounds (BVOC) (Holopainen et al. 2018; Holopainen et al. 2018), because plant BVOC emissions are interlinked with growth. They perform eco-physiological functions and increase the resilience of plants to different abiotic stress factors by improving their stress tolerance, and furthering their survival in, and fitness for, the environment (Niinemets 2010; Peñuelas and Staudt 2010; Vickers et al. 2009; Holopainen et al. 2018). However, in nutrient-poor sites, the allocation of carbon into secondary compounds may happen at the expense of growth, unlike in nutrient-rich soils (Bryant et al. 1983; Herms and Mattson 1992; Ormeño and Fernandez 2012). BVOC emissions (and their profiles) are strongly influenced by temperature (Kesselmeier and Staudt 1999; Peñuelas and Staudt 2010), and therefore they are also expected to increase from boreal trees under a warming climate. However, the emissions are tree species-specific (Hartikainen et al. 2012; Kivimäenpää et al. 2013; 2016; Holopainen et al. 2018). To get a deeper understanding of the differences in the responses of growth and BVOC emissions for different boreal tree species to warmer growing conditions, we need to simultaneously study their performance under the same growth environment.

1.2 Aims and hypotheses of the study

The primary goal of this work was to study the effects of planting practices and the growth environment on the early field performance of boreal container seedlings. Specific research questions in the individual research articles were as follows:

i) What are safe duration periods for the field storage of non-dormant Norway spruce and Scots pine seedlings in closed cardboard boxes at different planting seasons (Study I)
ii) How the planting success differs in one-year-old spring, summer, and autumn plantings of Norway spruce and Scots pine in practical forestry (Study II)
iii) How does the planting depth and/or planting season affect the early field performance of small-sized silver birch and Scots pine container seedlings (Study III)
iv) How does warmer growing conditions affect the growth and emissions of biogenic volatile organic compounds in boreal seedlings in a controlled field experiment (Study IV)?

The following hypotheses were tested in different studies:

i) Non-dormant conifer seedlings should be stored in closed boxes for a shorter duration in early autumn, and in spring, compared to later autumn.
ii) The mortality of spring-planted seedlings is lower compared to summer- or autumn-planted seedlings.
iii) Deeper planting does not decrease the field performance of seedlings in terms of growth, vitality, and risk of damages, compared to shallower planting.
iv) Warmer growing conditions increase seedling growth and emissions of biogenic volatile organic compounds more in silver birch seedlings than in Scots pine and Norway spruce seedlings.

2 MATERIALS AND METHODS

2.1 Study on the safe field storage duration for non-dormant Norway spruce and Scots pine seedlings in closed cardboard boxes (Study I)

The study on the safe field storage duration for non-dormant Norway spruce and Scots pine seedlings in closed cardboard boxes at different planting seasons consisted of three different experiments. For experiments 1 and 2, Norway spruce seeds (seed orchard SV 374) were sown in containers (Plantek 81F, hard plastic cell, volume 85 cm^3, BCC, Landskrona, Sweden) on 7 June 2016. Seedlings were grown in a greenhouse until October 2016 and then transferred to an outdoor growing area, where they were overwintered and grown in the following growing season as well. Seedlings were also treated with a three-week-long short-day treatment, which started on 10 July 2017. For experiment 3, Scots pine seeds (seed orchard no. 323) were sown in containers (Airblock 196F, hard plastic cell, volume 30 cm^3, BCC, Landskrona, Sweden) between 13 and 14 June 2017. Seedlings were overwintered outdoors. Fertilizing, irrigation, and growth media are discussed in detail for all experiments in study **III**.

In experiment 1, a total of 2100 Norway spruce seedlings were packed in cardboard boxes in August, September, or October. The height growth of Norway spruce had already ceased before August packing whereas the diameter growth was still ongoing. In experiments 2 and 3, a total of 375 of both Norway spruce and Scots pine seedlings were packed in the middle of May (Figure 1). As controls in experiments 1 and 2, 2025 Norway spruce seedlings and 980 Scots pine seedlings were stored in an outdoor growing area in the nursery in each packing month until planting. All seedlings were watered a day before packing and, if needed, also before planting. Only healthy seedlings with undamaged peat plugs were chosen for packing into boxes. Temperature inside boxes were measured with data loggers (HOBO Pendant UA-001-64; Onset Computer Corp., Bourne, MA, USA) which were placed in each box at the time of packing in September, October, and May.

In each experiment, the seedlings were stored in closed cardboard boxes under a shading roof for 1, 3, 7, 14, and 21 days. In experiment 1, a freezing test was also performed for the seedlings (see Figure 1). Seedlings from each treatment combination were randomly selected for the measurement of chlorophyll fluorescence (an indicator of plant photosynthetic performance), height (an accuracy of 0.1 cm), and diameter (1 cm above the root collar, accuracy 0.1 mm) at the end of each storage period. After storage, the seedlings were planted in a former nursery field in the Suonenjoki Research Nursery.

In the planting experiments, the vitality of the seedlings (healthy, minor damage, weakened, dead), the cause of any damage (gray mold, drought, lack of light, other reason), and multiple leaders were visually evaluated at the time of planting, and again in August 2018 and 2019. Root growth of the seedlings was assessed (numbers of roots grown out from peat plugs) after three weeks from planting (Figure 1).

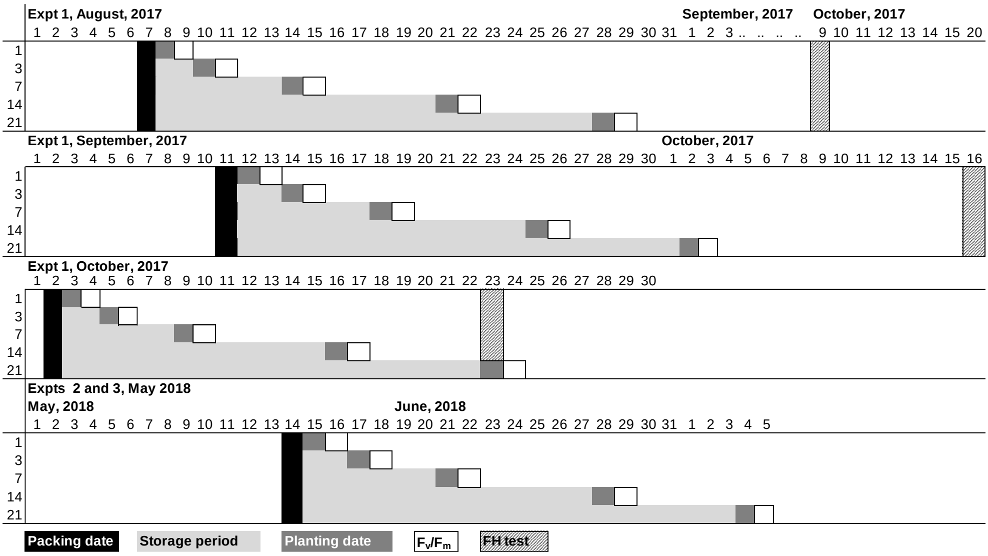

Figure 1. Timetable of packing, planting, chlorophyll fluorescence (Fv/Fm) measurements, frost hardiness (FH) tests, and storage durations in experiments in autumn 2017 (Expt 1) and spring 2018 (Expt 2 and 3). Experiments 1 and 2 were implemented with Norway spruce and experiment 3 with Scots pine seedlings (Study III)

The statistical differences in root growth, height, and current-year height increase of seedlings in both measuring years, probability of mortality (combining the classes “weakened” and ”dead” as dead), and seedlings with multiple leaders were analyzed in each experiment separately, using IPM SPSS Statistics Version 25.0. The probabilities for mortality or yellowish color were analyzed while using the general linear mixed model (GENLINMIXED). In the analysis, the storage method, storage period, and packing month were used as fixed effects. The random effects consisted of the block, month within a block, period within a month, block and method within a period, and month and block. In experiment 1, the heights and numbers of roots were analyzed with a linear mixed model (MIXED). Differences between treatments in experiments 2 and 3, in terms of chlorophyll fluorescence, shoot height, and diameter of seedlings after storage treatment were analyzed with ANOVA, separately, for each packing month in each experiment. The damage from frost hardiness (FH) treatments was visually assessed based on the buds and needles. The FH was analyzed for each packing month while using a generalized linear mixed model (GLMM) in PROC GLIMMIX in SAS (SAS Institute Inc., Cary, NC, USA).

2.2 Study on the regeneration success in spring, summer, and autumn plantings of Scots pine and Norway spruce in practical forestry (Study II)

The study on forest regeneration success in spring, summer, and autumn plantings of Scots pine and Norway spruce in practical forestry was based on a field inventory of one-year-old spring, summer, and autumn plantings of Norway spruce and Scots pine in the operating area of the Metsä Group company. It included a total of 1270 regeneration areas planted between

Table 1. Range of viable seedling density per hectare for the corresponding grade based on target density (Study II).

Tree species	Target, seedlings/ha	Grade, seedling/ha Excellent	Good	Moderate	Weak
Scots pine	2500	≥ 2375	2374–2125	2124–1300	1299 ≥
Scots pine	2200	≥ 2090	2089–1870	1869–1300	1299 ≥
Scots pine	2000	≥ 1900	1899–1700	1699–1300	1299 ≥
Norway spruce	2000	≥ 1900	1899–1700	1699–1200	1199 ≥
Norway spruce	1800	≥ 1710	1709–1530	1529–1200	1199 ≥
Norway spruce	1600	≥ 1520	1519–1360	1359–1200	1199 ≥

the spring and autumn seasons in central and southern Finland in 2016. The field inventory was done using systematic, circular 50-m^2 sample plots, between spring and autumn in 2017, by trainees and local forest managers working for the Metsä Group company. Plantings were classified as spring (by the end of week 25, i.e., 26 June), summer (weeks 26–34, i.e., 27 June to 28 August), and autumn (from week 35, i.e., 29 August onward) plantings based on the planting season.

Planting results of each planting area were evaluated based on the average density of viable seedlings, versus a target density per hectare, using the following grading classes: excellent > 95% of the target density, good 85-95% of the target density, moderate < 85% of the target density, but ≥ 1300 or 1200 viable seedlings/ha for Scots pine or Norway spruce, and weak < 1300 viable seedlings/ha (Table 1). The excellent and good planting results were considered as successful and the moderate and weak results as poor. Possible reasons for failure (poor planting results) were recorded and classified into the two main groups of poor work quality and natural damage. Possible reasons for poor work quality included reasons such as planting mistakes, poor site preparation, and poor seedling material. Natural damage could be the result of mammals such as deer, moose, voles, and hares, or by birds, fungus, frost, drought, or by other agents (e.g terrain-related difficulties, excessive vegetation) and by unclear reasons for poor planting.

The statistical analyses were done with IBM SPSS Statistic 24. The probability of a successful planting was modeled using a logistic regression with a forced entry method. The independent variables were selected for the model based on a preliminary data analysis. The final model included tree species, planting season, region, and the interaction between tree species and the planting season. The significance level was $p<0.05$. The possible reasons for poor planting results in different tree species and/or planting seasons could not be studied using statistical data analyses due to a limited number of observations.

2.3 Study on the effects of planting depth on field performance of small-sized spring-planted silver birch and spring- and autumn-planted Scots pine seedlings (Study III)

The study of the effects of planting depth on early field performance of small-sized spring-planted silver birch and spring- and autumn-planted Scots pine seedlings was based on separate planting experiments. Experiment 1 was located in Rautalampi, and experiment 2 in Pieksämäki, both located in central Finland. All seedlings used in the study were grown at the Suonenjoki Research Nursery of the Natural Resources Institute Finland. For experiment 1, seed-orchard–coated silver birch seeds (seed orchard SV 424) were sown in containers (Plantek PL81F, hard-walled plastic cell, volume 85 cm^3, BCC, Iso-Vimma, Finland) on 22 June 2015. Seedlings were grown in a greenhouse until they were transferred to the outdoor growing area on 27 July 2015. Further, 480 silver birch seedlings were packed into cardboard boxes and transferred to freezer storage on 28 October 2015 and lifted from the freezer storage on 29 April 2016. For experiment 2, Scots pine seeds (seed orchard SV323) were sown in containers (Airblock 196F, hard, plastic cell, volume 30 cm^3, BCC, Landskrona, Sweden) on 6 June 2018. Scots pine seedlings were grown in a greenhouse until they were transferred on 2 August 2018 to the outdoor growing area. Further, 600 Scots pine seedlings were packed into cardboard boxes and transferred to freezer storage on 6 November 2018. They were lifted from the freezer storage on 2 May 2019. Fertilizing, irrigation, and growth media are discussed in detail for both experiments in study **II**.

The seedlings were planted at three different planting depths, using 3, 6, and 8 cm depths for silver birch in experiment 1, and 2, 5, and 8 cm depths for Scots pine in experiment 2 (planting depth = the part of shoot below ground). In experiment 1, silver birch seedlings were planted on 4 May 2016, and in experiment 2 Scots pine seedlings were planted on 25 September 2018 and on 16 May 2019.

At the time of planting, and again at the end of each growing season, the height of each seedling was measured (accuracy of 0.5 mm), and the possible causes and degree of damage (healthy, slightly damaged, dying, dead) were recorded. In experiment 1, the stem base diameter of seedlings (accuracy of 0.1 mm) was measured at planting, and at the end of the first and third growing seasons. In experiment 1, the site preparation was done with spot mounding, and in experiment 2 with soil inversion.

All statistical analyses were performed using IBM SPSS Statistics v.27.0 software. In the data analyses, the fixed effects included planting season (S) and planting depth (D) for Scots pine, but only planting depth (D) for birch. Block was used as a random effect in both experiments. A repeated linear mixed model (MIXED) was used to analyze the differences in seedling height (both species) and diameter (only in silver birch). The probability of mortality, multiple leaders, the occurrence of damage, and damage from stem spot fungus and moose, were tested with binary data, using a binomial distribution with a log-link function in the generalized linear model (GENLIN) model.

2.4 Study on the responses in growth and emissions of biogenic volatile organic compounds in boreal seedlings to warmer growing conditions (Study IV)

The responses in growth and emissions of biogenic volatile organic compounds (BVOCs) in Scots pine, Norway spruce, and silver birch seedlings were studied under different warming conditions in a controlled field experiment in Botania garden, Joensuu, Finland (details in Nybakken et al. 2012; Nissinen et al. 2020). The study consisted of 12 plots that were divided into four replicate plots of each treatment: control (ambient, T0), elevated temperature of +2 °C (T2), and +4°C (T4) above ambient (total of 12 experimental plots size of 0.8 x 2.4 m). The plots were divided into three sub-plots (size of 0.8 x 0.8 m), one for each tree species. One-year-old silver birch and Scots pine and two-year-old Norway spruce container seedlings were planted in the sub-plots on 13 May in 2019 (96 seedlings per species). The fast-growing silver birch seedlings were planted on the northern side, and Scots pine seedlings on the southern side, of the plot. Norway spruce was planted in the middle of the plot because it tolerates shadiness best among these tree species.

In the T2 treatment, two heaters were attached in the middle of the aluminum frame, and in the T4 treatment four heaters in two rows were attached to an aluminium frame. In the control plots (T0), pieces of wood the same size as the heaters were attached to the aluminum frame to mimic the shading effect of the heaters. In the heated plots, warming was on from 17 May to 21 August in 2019 and from 15 May to 20 August in 2020. Soil moisture was monitored for each species and treatment combination. The plots were watered if the soil moisture dropped below 30%. At the start of the experiment, the heaters were set 145 cm above the ground level and were raised to keep pace with the fast-growing silver birch during the experiment, so that the heaters were kept 60 cm above the highest shoot tip.

The BVOC samples were collected from the current-year uppermost whorl (conifers) or shoot (silver birch) from the T0, T2, and T4 plots between 10 and 11 August 2020. The BVOC analyses were conducted with gas chromatography mass spectrometry (GC−MS, Hewlett Packard GC type 6890, Waldbronn, Germany; MSD 5973, Beaconsfield, UK) with thermal desorption, as described by Ghimire et al. (2016). Different BVOCs were identified by comparison with pure standards. The BVOC emission rates were calculated in ng g^{-1} (foliage dry mass) h^{-1}. The compounds were classed or summed as isoprene, nMTs (non-oxygenated monoterpenes), oMTs (oxygenated monoterpenes), HTs (homoterpenes), SQTs (sesquiterpenes), GLVs (green-leaf volatiles), and MeSA (methyl salicylate).

The height of the seedlings was measured once a week from 15 May to 20 August in 2019 and from 15 May to 17 August in 2020. A wireless solar-energy-powered sensor system measured, at 15-min intervals, the basal diameter growth of the seedlings, the intensity of photosynthetically active radiation (PAR), air temperature, air humidity, soil temperature, and soil moisture. Before the heaters were turned on in May, the diameters of the seedlings were measured with a digital Vernier caliper. The growth in diameter during the growing seasons was monitored with dendrometers till the end of each inventory period. Four seedlings per species per plot were sampled for biomass measurements on 27 August 2019 and 18 August 2020. All the biomass parts were dried in the study bags at +60 °C over one week. For carbon and nitrogen analysis, 2 g of current-year needles from the conifers, and full-grown leaves from silver birch, were collected into study bags and dried in the same way. Dried needle and leaf samples were homogenised using a Planetary Mono Mill Pulverisette 6 ball mill (Fritsch, Idar-Oberstein, Germany).

All statistical analyses were performed using IBM SPSS Statistics (version 27.0, IBM Corp., Armonk, N.Y., USA) for each tree species separately. The effects of the warming treatments on the total height and diameter, plant biomass (including shoot, foliage/needles, branches, stems, and roots), root:shoot ratio, the average day (Day(H/D90%)), and average Tsum (Tsum(H/D90%)) on and at which 90% of the annual growth of height and diameter were reached for seedlings harvested in years 2019 and 2020 were tested with ANOVA. The fixed part of the model was treatment, while treatment(block) was used as a random factor. There were no statistical differences observed in initial seedling height or diameter prior to treatment. A repeated function of the linear mixed model was used to test the effects of the warming treatment on the annual height and diameter growth of the same seedlings harvested in 2020. The fixed parts of the model were treatment and year, while plant was used as a random factor. All the main effects were statistically significant when $p<0.05$. For BVOCs, a linear contrast test (LCT) for one-way ANOVA was used to test the effects of the warming treatments. To reduce the risk of committing a type-II error, due to the low degree of replication, the main effects and contrasts were considered statistically significant when $p < 0.1$ (see e.g., Filion et al. 2000).

3 RESULTS

3.1 Duration limits on field storage and storage in closed cardboard boxes before planting in different planting seasons (Study I)

In all of the experiments (1, 2, and 3) the temperature variation was higher in open storage compared to closed boxes. In experiment 1, the accumulated temperature sums (T ≥ +5 °C, degree-days (d.d.)) inside boxes in August, September, and October were 8 d.d., 9 d.d. and 2 d.d. greater compared to open storage. In experiment 2, for Norway spruce spring plantings, the average and maximum temperature were almost on the same level in both storage methods, excluding the minimum temperature in closed boxes which was 3.5 °C higher compared to the open storage. In experiment 3, for Scots pine spring plantings, the temperatures in open storage were, on average, slightly (1 °C) higher, and the minimum temperatures slightly (2.4 °C) lower, and the maximum temperatures slightly (2 °C) higher than inside the boxes. In experiments 2 and 3, the accumulated temperature sums inside boxes in May were 5 d.d smaller for Norway spruce and 23 d.d. smaller for Scots pine compared to open storage.

In experiment 1, for autumn plantings of Norway spruce, the growth in height had already ceased in all seedlings at the time of packing. The average seedling heights were in a range of 26-28 cm and the average stem base diameters were in a range of 3.1-3.8 mm in August, September, and October plantings. The duration of seedling storage in closed boxes affected their diameter growth, and the final diameter of the seedlings was smaller the longer they were stored inside boxes ($p<0.05$). The average diameter of Norway spruce seedlings was also slightly larger in open storage than in closed boxes ($p<0.05$).

In August, developing apical buds were not visible in the seedlings with 1, 3, and 7-day closed box storage periods. At the 14- and 21-day storage periods, visible buds were observed in 11% of seedlings stored in closed boxes. The corresponding numbers were 36% and 56% in open storage seedlings for these periods. All the seedlings had visible buds at the time of packing in September and October. At the time of box opening, the color of the seedlings stored for 7 and 14 days in August and September was a lighter green compared to open storage seedlings.

Three weeks after planting, roots were actively growing in August, but root growth decreased in September and completely ceased in October. In August and September, there was a lower number of roots growing out from peat plugs in seedlings stored in closed boxes compared to open storage in all storage periods, three weeks after planting ($p<0.05$).

The photosynthetic capacity (determined by variable/maximum fluorescence ratio, Fv/Fm) of the Norway spruce seedlings stored in closed boxes started to decrease after a 3-day storage period in August, whereas it remained steady in the open stored seedlings ($p<0.05$). The length of the storage period affected photosynthetic capacity less in September and October compared to August storage. The frost hardiness of needles and buds tended to decrease in August and October as the storage period prolonged in the closed boxes ($p<0.05$, excluding buds in August).

During the next spring, June 2018, the proportion of dead and dying Norway spruce seedlings in August, September, and October packing months (in 2017) were, on average, 4%, 11%, and 12%, respectively. Shallow planting at 14-day storage (September) and frozen soil, 21-day storage (October) clearly increased the mortality of Norway spruce seedlings. After the first growing season, the average mortalities were 41%, 58%, and 76% for August, September and October packing months, respectively. High mortality was caused by extremely warm and dry weather in the spring and early summer of 2018. As a result, the differences in height increases between storage methods or periods could not be compared.

At the time of box opening in experiment 2 (Norway spruce spring plantings), 16% of the current year's growth was etiolated (pale growth due to lack of light) in the Norway spruce seedlings in 7-day storage in closed boxes. The proportion increased rapidly as the storage duration increased (76% at 14-day and 100% at 21-day storage). In comparison, the seedlings in open storage remained healthy and little damage was observed. At the time of box opening, the average seedling height and stem base diameter were 29.3 cm and 4.0 mm. Seedlings were actively growing during storage periods but there were no differences in lengths of the current year leader between storage methods.

In the spring plantings of Norway spruce, the root growth decreased with an increasing storage period ($p<0.05$). However, the decrease was more severe in the box-stored than in open-stored seedlings ($p<0.05$). The photosynthetic capacity of the seedlings stored in closed boxes started to decrease strongly at the 14-day storage period, whereas in open-stored seedlings there was a small drop at the 21-day storage period ($p<0.05$).

After the second growing season in the spring experiment, the mortality of box-stored Norway spruce seedlings increased after a one-week storage period, whereas in open-stored seedlings it increased after a two-week storage period (Study **I**: Figure 7) ($p<0.05$). Norway spruce seedlings stored for 14- and 21- days grew less regardless of the storage method, and the growth reduction was greater in the seedlings stored in boxes ($p<0.05$).

At the end of each storage period in experiment 3 (Scots pine spring plantings), all the seedlings were in good condition, regardless of the storage method. Yet, there were still small signs of etiolation from the 14-day period onward in the seedlings that were stored in boxes. At the time of box opening, the average seedling height and stem base diameter were 11.6 cm and 2.2 mm. Seedlings were actively growing during storage periods but there were no differences in seedling heights between storage methods. Root growth decreased with increasing storage periods, being more severe in the box-stored than in open-stored seedlings ($p<0.05$). The photosynthetic capacity of Scots pine seedlings decreased equally in both storage methods. However, because of errors in measurements, there were no data for 1- and 3- day storage periods.

After the second growing season, there were no differences in mortality between storage methods for the one-week storage duration, but after that, the mortality increased with prolonged storage being higher in the box-stored seedlings (Study **I**: Figure 7) ($p<0.05$). The increase in height of Scots pine seedlings started to decrease at 14- and 21- days storage, regardless of the storage method, but the reduction was greater for box-stored seedlings ($p<0.05$).

3.2 Planting success in one-year-old spring, summer, and autumn plantings of Norway spruce and Scots pine seedlings (Study II)

Overall, 84% of Norway spruce plantings were successful. The spring and autumn plantings succeeded equally well (85% and 84%, respectively). In comparison with those, planting success in the summer planted sites was more uncertain and only 69% of sites were successful. The number of viable seedlings in spring, summer, and autumn plantings was, on average, 1707, 1581, 1694 seedlings/ha respectively. In spring, there were no differences in planting success between the southern and central regions. The summer plantings succeeded slightly more in southern (71%) than in central (68%) Finland. However, the autumn plantings succeeded slightly less in southern (82%) than in central Finland (87%) (Figure 2). In Norway spruce plantings, a low density of appropriate planting spots, and planting mistakes, were among the major reasons for poor planting results, regardless of the planting season. Also, the proportion of other and unknown reasons was relatively high. Biotic factors were not as prevalent in Norway spruce plantings. A small amount of individual insect and mammal damage in the spring and summer plantings was observed.

Overall, only 52% of Scots pine plantings were successful. The Scots pine spring plantings were slightly (53%) poorer compared to the summer plantings (55%). Only 40% of Scots pine autumn plantings were successful. The numbers of viable seedlings in spring, summer, and autumn plantings were 1686, 1705, 1731 seedlings/ha, respectively. The Scots pine spring plantings in southern Finland succeeded less well (49%) compared to central Finland (58%). Summer plantings in southern Finland were more successful (60%) than in central (50%) Finland. The Scots pine autumn plantings clearly succeeded more in southern (47%) than in central (30%) Finland (Figure 2). In Scots pine spring plantings, almost half

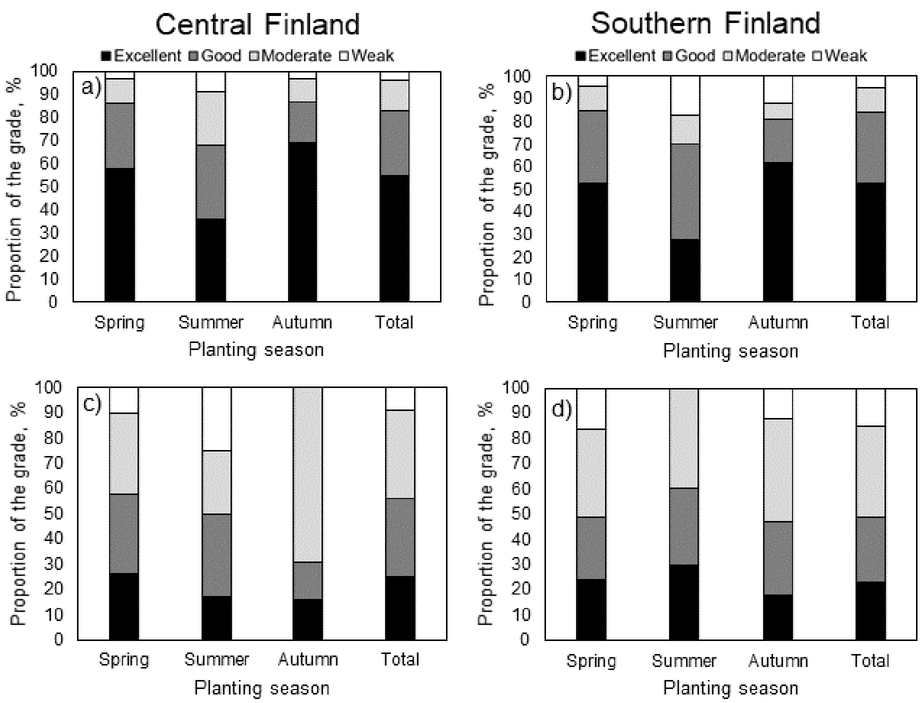

Figure 2. Proportion of sites belonging to each grade in Norway spruce (a, b) and Scots pine seedlings (c, d) separately, for different planting seasons, and in total in central (a, c) and southern (b, d) Finland (data based on Study II).

of the poor planting results were due to damage by mammals. The share of low-density planting spots, planting mistakes, and other and unknown causes were also high, regardless of the planting season. Damages from other biotic factors were not noteworthy.

The accuracy of logistic regression model was 75%. The model correctly predicted 99% of the sites with successful planting results, but only 6% of the sites with poor planting results. The model interpreted about 16% of the variance (R^2).

3.3 Field performance of small-sized silver birch and Scots pine seedlings at different planting depths (Study III)

Average planting depths (i.e., the part of the shoot below ground) for silver birch seedlings were 3, 6, and 8 cm. These planting depths corresponded to 19, 35 and 49 % of the total below ground shoot heights, respectively. After the first growing season, the average height of silver birch seedlings was highest for the deepest planting depth. However, the height differences between the planting depths disappeared during the second and third growing seasons (Figure 3a). After the third growing season, the mortality of silver birch seedlings was low (4%) and mainly caused by moose. The planting depth did not affect the seedling mortality, the moose damage, the probability of the drying of the current-year shoot, the occurrence of stem spot fungus, or the presence of multiple leaders.

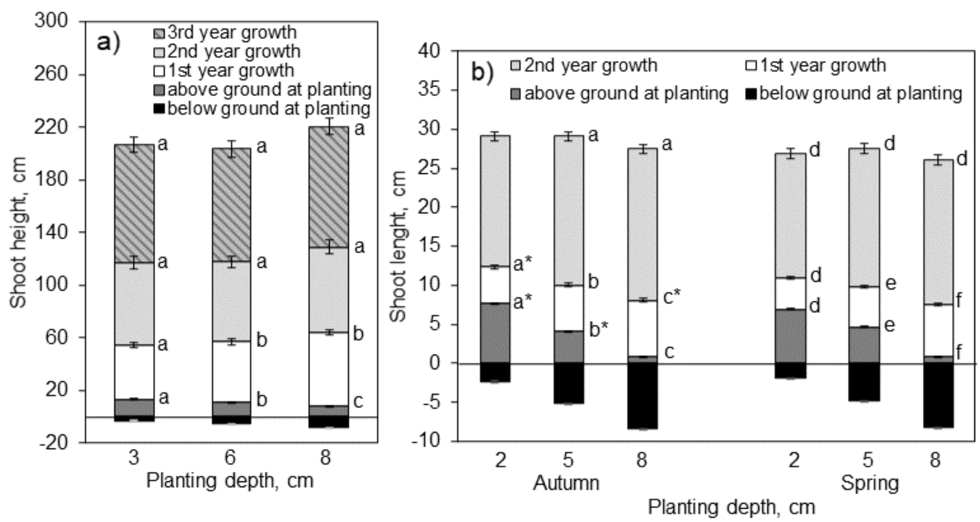

Figure 3. Height development in a) silver birch seedlings in 2016–2018 at the planting depths of 3, 6, and 8 cm (length of the belowground shoot) and height development of b) autumn- and spring-planted Scots pine seedlings in 2019–2020 at the planting depths of 2, 5, and 8 cm. The seedlings were measured at the time of planting and at the end of each growing season. Vertical bars indicate the standard error of the means (n = 73–80 for silver birch, n = 90–98 for Scots pine). The different letters indicate statistically significant differences among planting depths in the inventory year. Asterisks (*) indicate statistically significant differences between the planting seasons at certain planting depths and years (Study III).

Average planting depths (shoot belowground) for Scots pine seedlings were 2, 5, and 8 cm, the values corresponding to 23, 53 and 91 %, respectively, of the total below ground shoot height. After the first growing season, the average seedling height was lowest for the deepest planting depth and highest for the shallowest planting depth. However, the height differences between the planting depths disappeared during the second growing season (Figure 3b). After the first growing season, there were no differences in mortality between planting depths, but the mortality was slightly higher in autumn-planted (5%) than spring-planted seedlings (2%) (p<0.05). However, the proportion of damaged and dead seedlings decreased with decreasing planting depth (p<0.05). Seedling damages were mainly caused by drought and insects, and some seedlings were missing. After the second growing season, the mortality was still low (6%) and planting depth or season did not affect it. Seedling damages in the second year, in addition to the first year, were caused by fungus and mammals.

3.4 Growth and BVOC emissions of boreal tree seedlings under different warming treatments (Study IV)

Height growth started at mid-May in Scots pine, Norway spruce, and silver birch seedlings, and ceased at the end of June in conifer species and continued until the end of the inventory period for silver birch seedlings in both growing seasons. The growth in diameter started at the same time as growth in height, but it lasted until the end of the inventory period in all tree species in both growing seasons.

In silver birch seedlings, there was a trend wherein the mean height, diameter, and biomass increased with increasing temperature (T2 and T4) compared to ambient (T0) conditions in both growing seasons (p<0.05). During the first growing season, the biomass increase in silver birch was relatively larger in shoots than in roots under T2 and T4, resulting in a lower root:shoot ratio (p<0.05). During the second growing season above- and below-ground biomasses increased equally and the root:shoot ratio remained the same in the different temperature treatments. In silver birch seedlings, the oMT emissions were three and eight times higher under T2 and T4, compared to ambient conditions (p<0.05). The total HT emissions increased twofold and fivefold under T2 and T4, respectively (p<0.05). The total SQT emission rates were three and seven times higher under T2 and T4, compared to ambient conditions (p<0.05)(Figure 4).

In Norway spruce, there were no differences in the mean height or diameter between temperature treatments (T0, T2, and T4) after the first growing season. After the second growing season, the mean height was 17% larger under both T2 and T4 and the diameter increased only under T4 compared to T0 (p<0.05). The T4 treatment increased root biomass by 20% in the first growing season, resulting in a larger root:shoot ratio under T4 (p<0.05). During the second growing season, the shoot biomass of Norway spruce seedlings increased with increasing temperature (p<0.05). The effect was same for root biomass under T4 (p<0.05). However, the increase of shoot biomass was relatively larger compared to root biomass, resulting in a decreased root:shoot ratio in higher temperatures (p<0.05). In Norway spruce seedlings the total GLV emission rates decreased by 46% under T2, but increased by 340% under T4, compared to ambient conditions (p<0.05).

In Scots pine seedlings, there were no differences in the mean height or diameter between temperature treatments (T0, T2, and T4) after the first growing season. After the second growing season, the mean height was slightly greater under T4 (p<0.05). The mean diameter increased with temperature increase (p<0.05). The T4 treatment increased both root and shoot

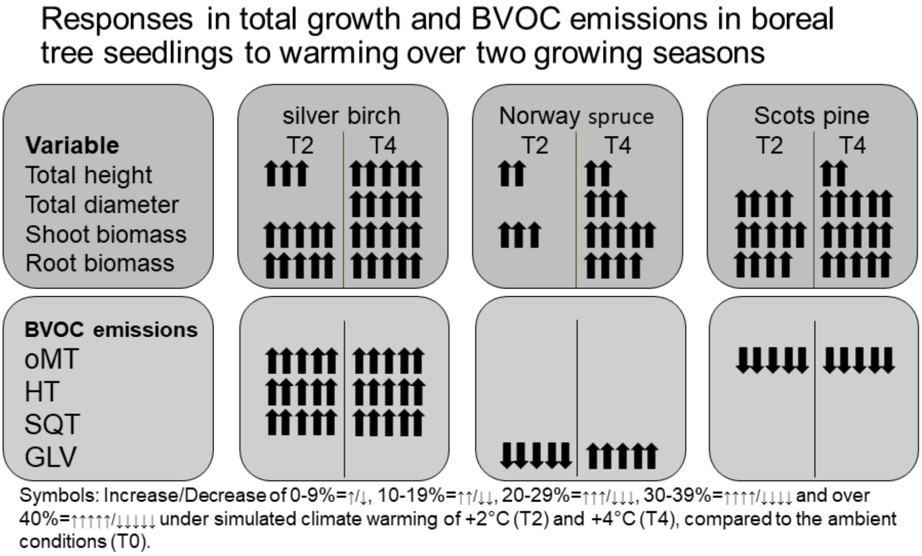

Figure 4. Pairwise comparison of warming treatments +2°C (T2) and +4°C (T4) compared to ambient (T0) conditions in total growth and BVOC emissions in 2020 for silver birch, Norway spruce, and Scots pine seedlings. The results represent only statistically significant differences. Compound group abbreviations: oMTs, oxygenated monoterpenes; HTs, homoterpenes; SQTs, sesquiterpenes; GLVs, green leaf volatiles; BVOC, total biogenic volatile organic compounds (Study IV).

biomass by 42% compared to T0 in the first growing season (p<0.05). During the second growing season, the shoot and root biomass of Scots pine seedlings increased with temperature increase (p<0.05). The root:shoot ratio remained unchanged in both growing seasons. In Scots pine, the total oMT emission rates were 25% and 59% lower under T2 and T4, respectively, compared to ambient conditions (p<0.05).

4 DISCUSSION

4.1 Duration limits of different field storage methods

In Finland, the closed cardboard box storage method was developed for dormant seedlings but it is also used for non-dormant seedlings. In study **I**, the storage period and packing method affected the vitality of the studied seedlings. In both Norway spruce and Scots pine box-stored seedlings with 21 days storage duration, the shoots were clearly longer compared to seedlings in open storage in spring. This is a typical response for plants to avoid shading and maximize their acquisition of light energy (see e.g., Smith 1982). In box-stored Norway spruce seedlings, the new shoot growth was a light green in color. This etiolated shoot growth is a result of the use of carbohydrate reserves, which leads to decreased photosynthetic capacity with prolonged storage, as shown by lowered Fv/Fm, due to a lack of light and water (Smith 1982). In box-stored Scots pine seedlings, the new shoot growth seemed to be healthy at the time of box opening (a bit lighter green colored needles compared to open stored seedlings), but the latent damages became severe after planting.

In the autumn experiment (Study **I**), the increase in height of the Norway spruce seedlings had ceased at the time of all packing months, but the buds were still initiating in August (buds were initiated in September and October packing months). To harden for winter, the growth must be stopped, and terminal buds formed (Weiser 1970). In boreal conditions seedlings start to develop frost hardiness (FH) in early September, but the rate increases as the temperature decreases (Glerum 1973; Bigras et al. 2001). In the autumn experiment, prolonged storage in closed boxes delayed the bud formation of seedlings packed in August. This may be one reason for the reduced FH in the box-stored seedlings in early August. In addition, temperatures were higher inside the boxes (Study **I**: Figure 2), which may have delayed the development of FH in Norway spruce seedlings (Levkoev et al. 2018). Also, the lowered photosynthetic capacity of the seedlings stored in boxes over a week indicates a reduction in FH since it is dependent on the current photosynthates available (van den Driessche 1970).

In August, September, and May, the seedlings stored in closed boxes had clearly reduced root growth after planting (Study **I**). Even short periods in dark conditions can be stressful for stored seedlings. Tabbush (1986) showed that mechanically stressed seedlings grew fewer roots compared to unstressed ones. Further, long storage periods in dark conditions, without watering, increases the risk of drought. Seedlings planted in late autumn did not root as well in the field as the seedlings that were planted earlier. The root growth of conifer seedlings stops in areas with low winter temperatures, which happens in boreal conditions around September or October (Lyr and Hoffmann 1967). Also, the open-stored spring-planted seedlings had signs of reduced root growth as the storage period was prolonged. Long storage durations in open trays, especially in actively growing seedlings, increases the risk of root overgrowth in plug, and root growth from plug to plug. When collecting the seedlings from trays for planting, the root system can be damaged, affecting seedling development after planting (Luoranen et al. 2005). In addition, if the root system has grown too large for their container, it can reduce plant survival and growth after planting (South and Mitchell 2006). Longer storage in open trays may also induce different environmental stresses. In this study, exceptionally warm and dry growing season of 2018 may also have affected harmfully the open stored seedlings.

Comparison of the effects of storage periods and storage methods was difficult in study **I** due to high mortality, especially in autumn. This was explained by an exceptionally warm and dry growing season in 2018. In the study of Krasowski et al. (1996), summer planted white spruce (*Picea glauca* (Moench) Voss) seedlings stored in open trays and directly transported from nursery to the regeneration site in the southeastern boreal forest of British Columbia were in better condition in the next growing season compared to spring-planted and freezer-stored seedlings. Also, in the study by Luoranen et al. (2021), the Norway spruce seedlings stored in open trays and planted in July recovered from winter damage better than seedlings in other planting seasons in experimental sites located in central Finland.

Based on study **I**, conifer seedlings can be stored in closed boxes for only three days in August, and about a week in September, October, and in spring. However, it would be preferable to use open storage methods for seedlings intended for summer and autumn plantings, as these duration guidelines are quite hard to follow in practice. Luoranen et al. (2021) found similar results with Norway spruce; seedlings can be packed in the closed boxes until early June, but for summer and autumn plantings it is better to use open storage methods. Also, in the study of Krasowski et al. (1996) in the British Columbia, summer planted white spruce seedlings stored in open trays and directly transported from nursery to the regeneration site recovered better from winter damage in the next growing season compared to spring-planted and freezer-stored seedlings. Overall, prolonged storage decreases field performance in open- and box-stored seedlings, but more in box-stored seedlings (Study **I**; Luoranen et al. 2021; Tikkinen et al. 2021). Therefore, the safe storage duration for open-stored, non-dormant seedlings is a couple of days longer compared to box-stored seedlings. Although the safe storage periods for freezer-stored seedlings (up to two weeks) are longer than those for the non-dormant seedlings, the storage period is the same (about a week) for freezer-stored and properly thawed seedlings under warm conditions as for non-dormant seedlings in closed boxes (Helenius et al. 2004). The boxes should be opened immediately after they have arrived from the nursery and placed in a shaded place because non-dormant seedlings can be sensitive to quick changes in radiation and temperature (Grossnickle et al. 2000). Non-dormant and dormant thawed seedlings should be planted as soon as possible.

4.2 Early performance of seedlings in different planting seasons

Studies **I** and **III** consisted of single site experiments whereas study **II** consisted of 1270 regeneration sites in practical forestry. In study **II**, Norway spruce plantings succeeded well. They were also clearly more successful compared to Scots pine plantings. In previous studies, the Norway spruce plantings were also more successful and the risk of failure was higher overall for Scots pine plantings (Kinnunen 1977; Saksa & Kankaanhuhta 2007). In study **II**, Norway spruce spring and autumn plantings were, on average, slightly more successful than summer plantings. This is contrast to other Norway spruce summer planting field studies which were successful and where the growth was observed to even increase during summer due to warmer growing conditions (Helenius et al. 2002a; Helenius et al. 2005; Luoranen et al. 2006). Scots pine autumn plantings were, on average, slightly less successful compared to other planting seasons. In contrast to study **II**, the Scots pine autumn and spring plantings, in study **III**, with small-sized seedlings, were very successful. High mortality in study **I** due to extreme weather conditions made planting success comparison very difficult. However, there was a trend in study **I** that the earlier in the autumn the Norway spruce seedlings were planted, the lower the mortality was during the first winter after the planting. Also in study **I**, the August and spring plantings had an approximately equal mortality rate. This is in accordance with previous findings that have shown equivalent survival of seedlings for autumn and spring plantings (Luoranen et al. 2006; Luoranen and Rikala 2013; Luoranen 2018). Silver birch spring plantings with small-sized seedlings were very successful in study **III**, which excluded other planting seasons. However, in previous studies, the silver birch plantings were successful from spring to late summer when using seedling material targeted to each planting season (Luoranen et al. 2003).

In study **II**, the poor work quality, and unknown reasons, mainly contributed to the poor planting result, regardless of tree species. Poor work quality was related to a difficult working environment (rocky terrain), resulting in a low density of prepared planting spots. Therefore, planting results, in many cases, could be improved by preparing a sufficient number of planting spots. Among biotic factors, the Norway spruce spring and summer plantings suffered relatively more from insect damage (exclusively pine weevil) in study **II.** Moose browsing contributed to a great proportion of the damage in the Scots pine spring plantings, regardless of region. Moose browsing was also the major damage-causing factor in study **III** for spring-planted silver birch seedlings, but its occurrence was still very low. The high amount of damage from unknown reasons might be related to seedling storage methods, and duration, as seedlings were packed in cardboard boxes regardless of the planting season. We did not study the storage duration in study **II**, but a study by Rantala et al. (2003) observed that the seedling storage duration varied between 1 and 49 days in practical forestry companies. Reflecting on the results from study **I**, Luoranen et al. (2021) and Tikkinen et al. (2021) this long storage duration could seriously reduce seedling field performance. Also, seedling watering is often neglected during field storage (Rantala et al. 2003). If the seedlings were not watered during these storage periods, the seedling performance before planting is further reduced (Mena-Petite et al. 2001; Tikkinen et al. 2021). The neglected watering during field storage could even reduce seedling field performance years after planting (Tikkinen et al. 2021).

In study **II**, low summer precipitation in southern Finland might have contributed to the poorer Scots pine summer planting results since it is usually planted on drier sites (study **II**, Table 2). Also, in some previous studies, the growth and survival of summer-planted Scots pine seedlings were poorer than in other planting seasons due to drought periods (Valtanen et al. 1986). Further, in the study by Huuri (1973), the planting results varied greatly among the plantings sites depending on soil properties. The effect of storage method and duration could have also affected the poor results from summer-planted Scots pine and slightly poorer summer-planted Norway spruce and seedlings in study **II**. Seedlings are actively growing during this phase and new leader shoots are easily damaged when exposed to radiation after dark conditions. As was observed in study **I**, even short periods in closed boxes could damage the seedlings' field performance, especially in small-sized Scots pine seedlings. This, along with possible prolonged storage duration without proper watering, may have greatly reduced the seedlings' ability to recover from field storage. Planting the Scots pine seedlings in typical dry, coarse soil could be lethal for weakened seedlings as discussed above.

In addition, some summer-planted conifer seedlings in study **II** might have been late terminated freezer-stored (dormant) seedlings. Luoranen et al. (2021) observed (similar to study **II**) that some seedlings were planted at the end of June and, thereafter, were actually freezer-stored seedlings instead of non-dormant seedlings. The planting period of freezer-stored Norway spruce seedlings should end no later than mid-June (Luoranen et al. 2005). Planting freezer-stored seedlings after that can increase mortality and autumn frost damage, and reduce growth (Luoranen et al. 2005; Hänninen et al. 2009; Luoranen et al. 2021). Overall, Norway spruce summer plantings can be successful if the recommendations regarding seedling types, storage methods, and durations are carefully followed. In Scots pine, there are large uncertainties in the success of summer plantings and, therefore, they are not recommended, based on this study. These findings are also in line with the result of Luoranen et al. (2013).

In study **II**, Norway spruce autumn plantings suffered relatively more from frost and drought damage. There was no record of pine weevil damage in the autumn plantings, probably due to the short period between planting and inventory. In study **I**, the mortality of Norway spruce was exceptionally high in autumn plantings, but this was related to the extremely warm and dry growing season. In addition, both tree species were grown on sandy soil containing some organic matter. In coarse soils, the risk of drought is high, especially for Norway spruce. In practical forestry, the Norway spruce seedlings are usually planted in mounds, with a nutrient-rich humus layer under the mound to enhance the growth and survival of seedlings (Örlander et al. 1990; Nordborg et al. 2003; Nilsson et al. 2019).

In study **II**, there were many unknown reasons for the failed autumn plantings, especially in Scots pine, that could be a result of neglected storage management. As discussed in study

I, long durations in dark conditions disturb the development of frost hardiness and reduce the root growth potential in seedlings intended for autumn plantings. This exposes seedlings to winter damage which was also observed in the study of Luoranen et al. (2021). For comparison, in the carefully established planting experiment in study **III**, there was no difference in mortality between autumn-planted and in spring-planted small-sized Scots pine seedlings after the second growing season. Also in the study of Luoranen (2018), the Scots pine autumn plantings were successful when there were no harsh winter weather conditions, the seedlings were properly planted, and there was no box storage before planting. However, in the inventory study of Luoranen et al. (2018), the conditions were reversed and resulted in poor field performance of autumn-planted Scots pine seedlings. In a literature review of Grossnickle and McDonald (2021) reasons for unsuccessful autumn plantings were associated with nursery hardening practices and stressful environmental conditions. Thus, successful autumn planting requires the use of open storage and careful planting, and not too harsh winter weather conditions. In reality, the winter weather conditions, and snow depth levels are hard to predict. Therefore, it might be wise to continue to plant Scots pine seedlings only in the spring season.

In study **I**, Norway spruce seedlings planted earlier in the autumn rooted better than those seedlings planted later in the autumn. Naturally, root growth decreases with decreasing temperature in September and finally ceases in October (Lyr and Hoffmann 1967). Nevertheless, the roots of conifer seedlings can grow from early spring to late autumn under favorable weather conditions (Mattson 1986). Poorly rooted seedlings are more susceptible to winter damage, and they start their root growth more slowly in the next spring than the better-rooted seedlings (Luoranen 2018; Luoranen et al. 2021). This can affect the early performance of the seedlings later in the growing season, and even in later years. However, in study **III**, in the following summer, the autumn-planted Scots pine seedlings grew better than the spring-planted seedlings. In the study of Luoranen (2018), the autumn-planted Norway spruce and Scots pine seedlings started their root growth in the following spring when the soil was just a few degrees above zero. In study **III**, the autumn-planted Scots pine seedlings may have started their growth earlier when compared to spring-planted seedlings, since soil temperatures varied between 6−25 °C on 16–31 May 2020. The roots can grow when the soil temperature is above 5 °C (Lyr and Hoffmann 1967). In comparison, spring-planted seedlings were lifted from freezer storage (−3 °C) for thawing on 29 April 2019 and planted on 16 May 2019. Thus, the longer root growth of autumn-planted Scots pine seedlings might have enhanced the shoot growth in the following year. However, we did not measure the root growth in study **III**. Overall, Norway spruce autumn plantings should be done at the latest in September and avoid periods with frozen soil.

4.3 Early performance of seedlings at different planting depths

Deep planting in study **III** did not have negative effects, or it even increased the early performance of the small-sized Scots pine and silver birch seedlings. The differences observed in seedling height among planting depths at the end of the first growing season disappeared until the end of the second growing season in both small-sized Scots pine and silver birch seedlings. This was due to the better growth of deeper-planted seedlings in the second growing season. Silver birch and Scots pine seedlings are capable of growing adventitious roots from belowground stems (Luoranen 2014; Mullin 1964; Sutton 1967), which can enhance their root (volume) and shoot growth in following years. In addition, small-sized Scots pine seedlings focus more on root than shoot growth during the first growing season (Lindström et al. 2004). This was probably the case also in study **III**, where large shoot growth differences were observed between successive growing seasons. Also, the shoot growth differences were similar in study **III**, compared to the study by Luoranen and Viiri (2016), in Norway spruce with a similar kind of growing conditions (medium-coarse and fine-textured soils). This suggests that the deeply planted seedlings can better reach the nutrient-rich humus layer compared to shallower-planted seedlings (Smolander and Heiskanen 2007). The planting depth did not significantly affect the diameter growth, although the deeply planted silver birch seedlings tended to be thicker. In a study by Luoranen and Viiri (2016), diameter growth was better in deeper than in shallower planted Norway spruce seedlings.

The different planting depths did not affect the mortality of seedlings in the studied tree species. This is in line with earlier findings in conifer and broadleaved seedlings (see, e.g., Buitrago et al. 2015; Gemmel et al. 1996; Paquette et al. 2011). The deeper planting depths have even been observed to decrease the mortality of Norway spruce seedlings (Örlander et al. 1991; Luoranen and Viiri 2016). In Scots pine, deeply planted seedlings suffered less from drought and insect damage during the first growing season, regardless of planting season. This corresponds to the Norway spruce results of Luoranen and Viiri (2016). The results of studies **III** and **I** highlight the importance of appropriate planting depth, especially in autumn plantings where the failure risk is higher. In study **I**, in autumn plantings, some planting holes were not properly filled with soil due to frozen soil, and some seedlings were accidentally planted too shallowly, resulting in high seedling mortality.

Especially for small-sized Scots pine, but also for silver birch seedlings, deep planting may also provide protection against abiotic stressors, such as drought. This is important since drought periods are expected to increase in boreal regions under a changing climate during spring and summer (Ruosteenoja et al. 2018). Deep planting has also been shown, in earlier studies, to protect the Norway spruce seedlings from drought damage (Örlander et al. 1991; Luoranen and Viiri 2016). Especially small-sized conifer seedlings are more sensitive to environmental stress factors (Johansson et al. 2007). To enhance the early performance of seedlings, small-sized Scots pine and silver birch seedlings can be planted at 6-8 cm planting depths in mounds, provided that at least 20%, and 50%, of their shoots, respectively, are above ground. In study **III,** at the deepest planting depth, a few seedlings were accidentally planted too deeply and were lost during planting. The results of study **III** may be applicable for corresponding sites with similar mechanical site preparation methods.

4.4 Early performance of seedlings under warmer growing conditions

In study **IV**, the growth increased in a warmer growing environment (T elevation of 2 °C and 4 °C), especially in silver birch, but also in Scots pine, and to a lesser extent in Norway spruce seedlings, which were planted in spring. Nissinen et al. (2020) had similar results with same tree species in same experimental field in a 3-year-study, however with temperature elevation of 1.3 °C. Kellomäki and Wang (2001) reported increased biomass and height growth in one-year-old silver birch seedlings under an elevated temperature of +3 °C in growth chamber experiment. Similar to study **IV**, in previous experimental studies Norway spruce have not benefited from minor temperature increase (Kivimäenpää et al. 2013; Sigurdsson et al. 2013). In the simulation studies of Kellomäki et al. (2008; 2018) the climate change can clearly increase the growth of silver birch and Scots pine compared to Norway spruce. However, the responses to changing growing conditions and growth patterns of different tree species can differ and further affect their productivity. Under boreal conditions growth is in general limited by short growing season, low temperatures, and short supply of nutrients. Therefore, under the climate change the growth of boreal tree species may be expected to increase. On other hand, the growing conditions may become sub-optimal for some boreal tree species (e.g., Norway spruce), especially on sites with low water holding capacity (Kellomäki et al. 2018), which must be taken account of in forest regeneration.

In study **IV**, the warmer growing conditions enhanced BVOC emissions in August, the most in faster-growing silver birch seedlings (oMT, HT, SQT) whereas in conifer seedlings it was less effective. In Scots pine seedlings, only oMT emission decreased as temperature increased. In Norway spruce there was first decrease and then increase of GLV emission under increasing temperature. However, in study **IV**, the BVOCs emissions were measured only once. Further studies are needed to generalize the findings and to better understand how climate warming affects the magnitude and direction of BVOC emissions (and their profiles) in seedlings of different boreal tree species. This is because, the magnitude and direction of BVOC emissions are affected both by tree species, phenology stage of trees (season), and growing conditions (e.g., temperature and nutrient availability) (Niinemets 2010; Kivimäenpää et al. 2016; Ghimire et al. 2017; Tiiva et al. 2018).

Based on the above, an increase of plantings in faster-growing silver birch on suitable and sufficiently fertile and moist sites might be recommended under a warming climate, at the cost of Norway spruce. Scots pine should be still favored on less fertile and moist sites. However, it should be noted that a naturally dry and coarse growing environment might also increase drought stress in Scots pine under a warming climate. On the other hand, the proper planting depth, and careful planting, can mitigate the drought-induced risks at planting, as was observed in studies **I** and **III**.

5 CONCLUSIONS

In conclusion, non-dormant conifer seedlings can be stored in closed boxes for only three days in August, and about a week in September, October, and spring. However, it would be preferable to use open storage methods for non-dormant seedlings in plantings of spring/early summer and August. The safe storage durations for open-stored seedlings are a couple of days longer compared to box-stored seedlings. The storage method and duration instructions regarding different planting seasons should be carefully followed since they have a great impact on the field performance of seedlings.

Regeneration site conditions, as well as planting and seedling storage, affected greatly planting success in studies **I−III**. In study **II** there was observed remarkable low number of successful Scots pine plantings. Planting success could be increased by higher number of planting-spots and protecting seedlings from browsing. Extending the planting season from spring to autumn may be possible for Norway spruce seedlings if instructions regarding seedling material and proper storage methods and durations for different planting seasons are followed carefully. Scots pine autumn plantings can be successful with optimal storage and planting practices and favorable weather conditions. However, due to a clearly higher risk of failure in summer and autumn plantings, it is still recommended to plant Scots pine seedlings only in spring and early summer in Finland. In the study **III,** there were no differences in field performance between different planting depths at the end of the experiments. However, the deep planting reduced the occurrence on damaging factors in the first year. To enhance the field performance, seedlings can be planted at 6–8 cm planting depths, if at least between 20−50% of their shoots, are above ground.

Especially, silver birch seedlings, but also for Scots pine, and to a lesser extent Norway spruce seedlings, benefit from a warming climate. This should be considered in forest regeneration and, if necessary, current planting practices adopted in different tree species. An increase of silver birch plantings on suitable and sufficiently fertile and moist sites might be recommended over Norway spruce. On sites with low water-holding capacity forest regeneration with Scots pine is recommended over Norway spruce and silver birch.

The results of this work (Studies **I-IV**) are from 1–2-year field experiments. To inspect the long-term effects of planting season, planting depth, and warmer growing conditions on the performance of boreal tree seedlings, a longer follow-up study will be needed than that which was possible in this study. Also, greater variety in site conditions is needed for generalization of the findings. Future studies should focus on ensuring forest regeneration success under a rapidly changing climate.

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