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# Regeneration methods for Scots pine and lodgepole pine: a comparison in Central Sweden

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**ABSTRACT**

The experiment was conducted in a mature Scots pine (*Pinus sylvestris* L.) stand at the Jädraås Experimental Forest, Central Sweden (60.82° N, 16.50° E, elevation 185 m). The site index (H100), which represents the mean height of the 100 largest-diameter trees per hectare at age 100, was estimated to be 18 m, corresponding to a mean annual increment (MAI) of approximately 3.5 $m^3$ $ha^{-1}$ $y^{-1}$. A fully randomised design with nine treatments and four replicates was applied. The study evaluated regeneration methods (planting, direct seeding, natural regeneration), site preparation techniques (disc trenching, wheel tracks), seed sources (seed orchard vs. local seed), and seed tree fertilisation on regeneration success (tree density) and growth of Scots pine and lodgepole pine (*Pinus contorta* Douglas ex Loudon). Planting resulted in significantly greater height growth compared to direct seeding or natural regeneration. Disc trenching improved natural regeneration, yielding higher tree density, taller trees, and reduced patchiness, whereas wheel tracks provided insufficient soil disturbance to expose mineral soil. Fertilisation of seed trees did not significantly affect tree density. Scots pine and lodgepole pine exhibited comparable height growth and tree density for planted and sown trees, respectively.

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Direct seeding; Loggepole pine; natural regeneration; planting; regeneration methods; Scots pine

## Introduction

Choice of regeneration method is arguably one of the most important management decisions during a forest stand's rotation. Scots pine (*Pinus sylvestris* L.) can be regenerated naturally by various reproduction-cutting methods or artificially by planting or direct seeding. Each regeneration method has advantages and disadvantages. The optimal choice depends on management objectives, site and stand characteristics. Silvicultural treatment programmes and planning time horizons differ between the specific regeneration methods.

Clearcuts in Central and Northern Sweden are commonly planted or seeded one or two years after felling and mechanical site preparation (MSP). One-year-old containerised nursery-grown seedlings are the preferred regeneration material for planting. Seeds used for seedling production or direct seeding are collected either from local stands or seed orchards. Currently, seed orchards supply 97% of nursery-grown Scots pine seedlings in Sweden (SFA 2020b). The expected additional production over a full rotation of trees planted from orchard seeds is between 10% and 25%, depending on the breeding cycle, with additional gains arising from improved stem quality. However, seed shortages during poor seed years and/or due to extensive pest damage may limit the use of orchard-produced seeds (Gull et al. 2017).

Inadequate seed production and consequently low seedling recruitment limit natural regeneration, especially in northern Sweden's harsh climate at high latitudes or altitudes (Hagner 1958). There are two known strategies to improve seed production in Scots pine stands. The first is fertilisation with nitrogen (N), or nitrogen, phosphorus and potassium (NPK) fertilisers. Fertilisation is a standard procedure in seed orchards, whereas fertilising seed trees in operational forestry is rare and not recommended because it increases windthrow risk (Laiho 1987; Hirvelä and Hynynen 1990; Valinger and Lundqvist 1992). The second strategy is release cutting which increases cone production of seed trees for several years (Karlsson 2000, 2006). This is likely because light-reaching crowns (Jackson 1972) and water and nutrient availability (Sheriff 1996; Karlsson and Örlander 2002) all increase. However, as pine cones take three years to develop (Heikinheimo 1937, 1948; Hagner 1958; Sarvas 1962; Koski and Tallqvist 1978), the fertilisation or release effects on seed supply cannot be realised earlier than during the fourth spring after treatment application, when cones open and seeds disperse.

Natural regeneration usually involves leaving seed trees uncut followed by MSP. Once the regeneration cut is planned, forest managers need to decide whether it is feasible to conduct MSP immediately after cutting or waiting to do MSP in a good seed year. Currently, the first approach is

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more common, especially in southern Sweden where competition from ground vegetation is a major concern. However, Karlsson and Örlander (2000) showed that MSP shortly before a rich seedfall improves Scots pine seedling establishment in Central Sweden. A practically applicable regeneration method has emerged from this and several other studies of natural regeneration and seed production in Scots pine stands (Karlsson 2000; Karlsson and Örlander 2002), together with years of silvicultural experience from Central Sweden (Karlsson 2022, 2022b). This silviculture programme involves (i) preparatory cutting, (ii) clearcutting all but seed trees, (iii) MSP the third autumn after clearcutting, and (iv) harvest of seed trees three years after MSP. Waiting three years between clearcutting and MSP was found to increase seed production fivefold (Karlsson 2000). The seed trees are stimulated to flower the year after the clearcutting, and the process from the first stimulation to increased seed dispersal takes four years for Scots pine. Early harvest of seed trees is intended to favour rapid growth of the new regeneration.

MSP, primarily by disc trenching or mounding, is applied on 92% of regeneration areas in Sweden (SFA 2020a). The use of MSP brings a range of positive effects, such as reduced pine weevil (*Hylobius abietis*) damage risk (Petersson et al. 2005; Wallertz et al. 2018), decreased competition for water and nutrients from ground vegetation (Thiffault et al. 2005; Johansson et al. 2013), lower frost damage risk (Langvall et al. 2001; Simard et al. 2003), improved soil temperature (Nilsson and Örlander 1999; Thiffault et al. 2013) and enhanced soil aeration (Ritari and Lähde 1978; Kabrick et al. 2005). On the other hand, in some cases MSP may harm seedling growth and survival, for instance by increasing frost heaving risk (Sahlén and Goulet 2002; Heiskanen et al. 2013). MSP generally has a long-term positive effect on stand growth. Gains achieved in the regeneration phase are maintained, but do not usually continue to increase later in the forest stand cycle (Sutton 1995; Nilsson and Örlander 1999; Nilsson et al. 2010).

For natural regeneration of Scots pine, MSP aims to improve site and soil properties for the benefit of seed germination, seedling growth and survival. However, MSP effects vary among the specific methods and sites. MSP creates different seedbed types, among which bare mineral soil is the most favourable for germination, but not necessary for seedling survival (Marquis et al. 1964; Oleskog and Sahlén 2000; Karlsson 2001; Pardos et al. 2006). Abundant germination usually outweighs increased mortality rates on mineral soil, resulting in greater seedling density for a few years following MSP (Kyrö et al. 2022). A mixture of mineral soil and humus is often perceived as the most favourable seedbed for natural regeneration as it balances satisfactory seedling emergence, survival and growth (Winsa 1995). However, this perception was not supported by the findings of Beland et al. (2000) who found no significant difference in mortality rates between different seedbed types.

In naturally regenerated stands, seeds are spread all over the regeneration area, meaning that dispersed seeds may land on various seedbed types. In contrast, planting and direct seeding are done exclusively on prepared ground, usually mineral soil or a mixture of mineral soil and humus. Another important difference is that both planting and direct seeding rely on a single year's seedling cohort (pine seeds are usually viable for one year), whereas several seedling cohort years may form a naturally regenerated stand (Beland et al. 2000; Kyrö et al. 2022). Should regeneration fail, for instance, due to unfavourable weather in a given year, planting or direct seeding must be repeated.

In northern Sweden, the non-native lodgepole pine (*Pinus contorta* Douglas ex Loudon) is sometimes recommended as an alternative to native Scots pine, primarily on nutrient-poor and dry soils (Elfving et al. 2001). Lodgepole pine is mainly chosen for its higher establishment phase survival, and faster initial growth and volume production compared to Scots pine (Elfving and Norgren 1993). In Sweden, lodgepole pine can only be regenerated by planting or direct seeding. So far, natural regeneration has not been used in Sweden on a significant scale.

Information about which regeneration method to use, how to apply it, and what results to expect (both short- and long-term) is essential for forest management and planning. This information is obtained from analysing experiments comparing different regeneration methods within individual sites. However, such experiments are rare as they are spatially and temporally complex to configure, expensive, and involve long-term monitoring and planning horizons. Contemporary knowledge of different regeneration methods' performance derives mostly from: (i) comparative studies of planted, direct-seeded and naturally regenerated stands, assuming similar or same site conditions (Agestam et al. 1998), (ii) modelling studies predicting seedling establishment depending on the regeneration method (Miina and Saksa 2008), and (iii) modelling studies where both production and economic performance of different regeneration methods is evaluated through an entire rotation (Hyytiäinen et al. 2006; Simonsen 2013; Lula et al. 2021). Although these and other studies have provided significant insights and understanding, there is still a need for controlled experiments comparing different regeneration methods.

This study aimed to evaluate the effect of different genetic material, fertilisation and mechanical site preparation options on the establishment and growth of planted, direct-seeded and naturally regenerated Scots pine. In addition, planting and direct seeding of lodgepole pine was compared with Scots pine.

## Materials and methods

### *Experimental site*

The experiment was established in a mature Scots pine (*Pinus silvestris* L.) stand at the Jädraås Experimental Forest in Central Sweden (60.82° N, 16.50° E, elevation 185 m). The estimated site index (H100, i.e. the mean height of the 100 largest-diameter trees per hectare at an age of 100 years) was 18 m, which corresponds to a mean annual increment (MAI) of about 3.5 $m^3$ $ha^{-1}$ $y^{-1}$ (Elfving and Kiviste 1997). The soil type was a deep glacifluvial sand sediment, and the textural composition varied from fine to coarse sand (0.125–1 mm, Axelsson and Bråkenhielm 1980). The forest stand was about 170 years old and had not been thinned during the preceding 20 years or fertilised before the start of the experiment.

### Weather conditions

Meteorological data were collected at a weather station in the experimental forest (elevation 185 m) in an open area about 500 m from the study site. Air temperature was measured 1.7 m above ground, and precipitation 25 cm above the ground. Measurements were collected automatically every minute. Temperature was measured year-round, while precipitation was only measured during the growing season. Growing season length was defined as the number of days with a daily mean temperature persistently >+5°C. Temperature sums were calculated as the accumulated daily mean temperature during the growing season exceeding a threshold value of +5°C.

For the 30-year reference climate period 1991–2020, the mean air temperature was 4.4°C and total annual precipitation was 723 mm (estimate based on joint data from this station and the nearby national weather station in Åmot). The mean temperature sum was 1155 degree days (DD) and the mean precipitation 395 mm during the growing season (Karlsson et al. 2024).

During the experiment temperature sums varied from 1006 to 1516 DD and precipitation during the vegetation period from 227 to 654 mm. Snowpack has not been recorded at site during the experimental period, but images from a webcamera are available from 2017 and forward. Previous recordings in the area show that it has been mostly covered by a layer of snow between November and April. The snow is often gone before the pine seeds are dispersed during the period from late April–early June (Hannerz et al. 2002). Scots pine and lodgepole pine seedlings in general can benefit from a dense snowpack during winter, independent of the regeneration method, by reducing frost heaving and winter browsing by ungulates.

### Experimental design and treatments

This study used a complete randomised experimental design, with nine treatments and four replicates of each treatment (Figure 1). Treatments were applied to 30 ×

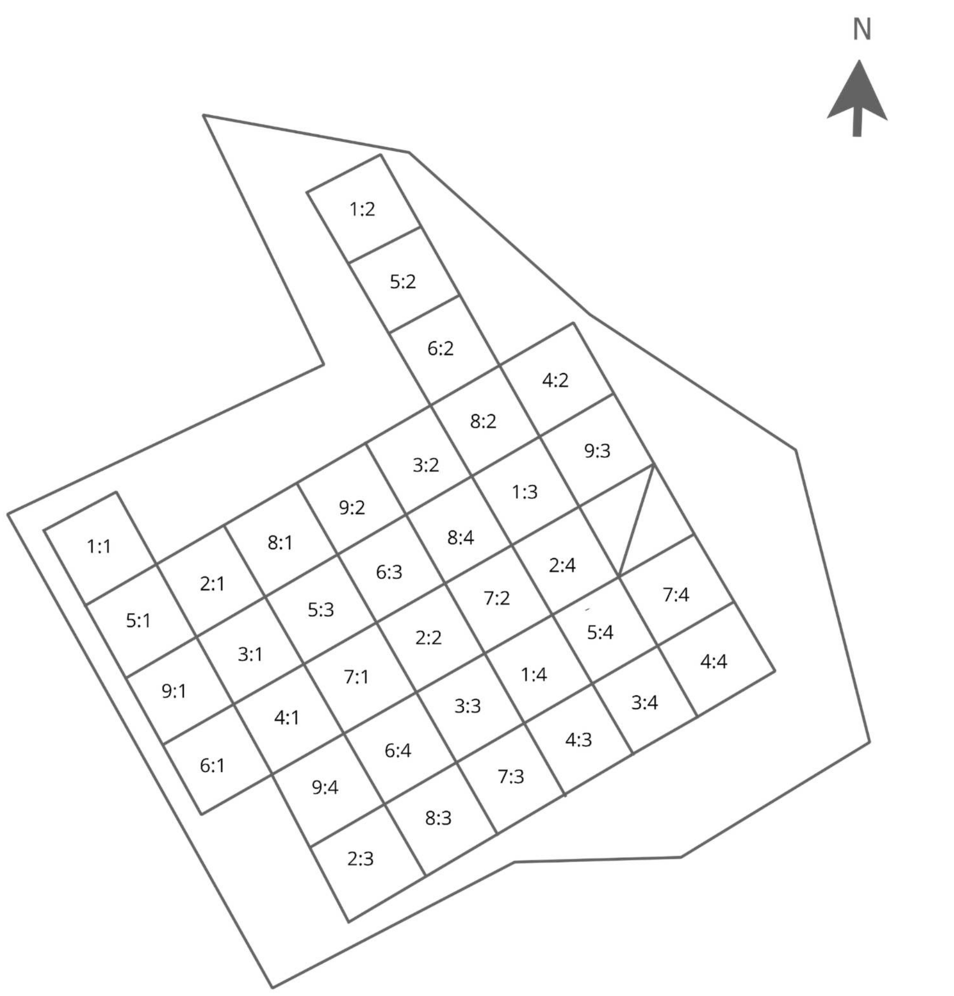


**Figure 1.** Spatial layout of the experiment. The grid represents plots (30 × 30 meters). Each plot is labelled with two digits: the first digit denotes the treatment number (1–9 according to Table 1), and the second digit (1–4) specifies the replicate number. The solid line around the experimental area shows a fence for protection against ungulates.

**Table 1.** Treatment descriptions.

| Treatment | Regeneration cuttings in 2011 | Trees species | Mechanical site preparation and timing | | Regeneration method and timing | | Seed source | Fertilisation of seed trees, timing |
|---|---|---|---|---|---|---|---|---|
| 1 | Clearcut | Scots pine | Disc trenching | 2011 autumn | Planting | 2012 spring | Seed orchard (Sollerön 442, S09/036) | – |
| 2 | Clearcut | Scots pine | Disc trenching | 2012 spring | Direct seeding | 2012 spring | Seed orchard (Sollerön 442, S09/036) | – |
| 3 | Clearcut | Lodgepole pine | Disc trenching | 2011 autumn | Planting | 2012 spring | Seed orchard (Skörserum 713, S10/065) | – |
| 4 | Clearcut | Lodgepole pine | Disc trenching | 2012 spring | Direct seeding | 2012 spring | Seed orchard (Skörserum 713, S10/065) | – |
| 5 | Clearcut | Scots pine | Disc trenching | 2015 spring | Planting | 2016 spring | Local stock seeds from fertilised trees | – |
| 6 | Clearcut | Scots pine | Disc trenching | 2015 spring | Direct seeding | 2015 spring | Local stock seeds from fertilised trees | – |
| 7 | Seed trees | Scots pine | Disc trenching | 2014 autumn | Natural regeneration | – | – | 2011 spring |
| 8 | Seed trees | Scots pine | Wheel tracks | 2014 autumn | Natural regeneration | – | – | 2011 spring |
| 9 | Seed trees | Scots pine | Wheel tracks | 2014 autumn | Natural regeneration | – | – | No |

30 m plots, with data collected from 20 × 20 m net plots to minimise edge effects. The plots were either clearcut or subjected to regeneration cuts, with seed trees retained. Both the cutting treatments and the fertilisation of seed trees were performed in 2011 (Table 1). Planting or direct seeding of genetically improved Scots pine and lodgepole pine were done in spring 2012. The initial planting density was 2800 seedlings ha$^{-1}$ for all treatments. In the spring of 2015, direct seeding was done with local Scots pine seeds and MSP was done in one of the natural regeneration treatments. In 2016, additional plots were planted with Scots pine seedlings grown from seeds from the same site (Table 1).

## *Seeds and seedlings*

The containerised seedlings planted in 2012 were grown in Sjögränd Nursery (Stora Enso) and those planted in 2016 were grown in Tallhed Nursery (Orsa besparingsskog). Seedlings were grown for one year in the nursery and treated with Merit Forest WG80 for pine weevil protection (Bayer Environmental Science 2011).

The seed sources were:

- Scots pine in 2012 (direct seeding and planting): Sollerön 442, S09/036. FP-616 Sollerön T14:2. Year of seed maturity: 2008. Seeds were treated with the Prevac method and then seeds on the surface were chosen. The seeds were then sieved into three different size classes, and the largest third of the seeds was chosen (>2.45 mm). The viability of the chosen seeds was 99.8% and the weight per 1000 seeds was 7.08 g.
- Lodgepole pine in 2012 (direct seeding and planting): Skörserum 713, S10/065. FP-713 Skörserum. Year of seed maturity: 2009. Seed viability was 95.8% and the weight per 1000 seeds was 4.31 g.
- Scots pine in 2015 (direct seeding) and 2016 (planting): Seed from fertilised pine seed trees in this experiment (exp. no. 9807). Year of seed maturity: 2014. Seed viability was 96.6% and the weight per 1000 seeds was 4.82 g. The cones were picked on 27 October 2014. The cone samples were analysed at Skogforsk in Sävar with respect to seed viability and mean 1000-seed weight (g). Seed viability was analysed in a 14-day germination test using a Jacobsen apparatus, with a diurnal temperature regime of 20°C for 16 h and 30°C for 8 h. Light was kept constant at 1000 lux (Lestander 1984).

The disc trencher did the direct seeding, and the machine counted the number of seeds sown. The mean number of seeds per metre was 14.2 for Scots pine in 2012 and 15.0 in 2015. The mean number of seeds per metre was 12.6 for lodgepole pine in 2012.

## *Seed trees*

In treatments with natural regeneration, five to seven seed trees were left in each plot (corresponding to 56–78 trees ha$^{-1}$) during the release cutting in spring 2011. The mean volume of the seed trees was about 1.0 m$^3$ tree$^{-1}$ in 2018. All seed trees were felled in March 2019.

Seed trees were assessed in October 2014 and November 2018. In 2014, only diameter at breast height (DBH) was measured, and in 2018 DBH and tree height were measured (Table 2).

**Table 2.** Average diameter at breast height (DBH), tree height, stem density and basal area of the seed trees four and eight years after release cuttings, respectively.

| Treatments | Year | DBH (cm) | Height (m) | Seed tree density (stems ha$^{-1}$) | Basal area (m$^2$ ha$^{-1}$) |
|---|---|---|---|---|---|
| Disc trenching + | 2014 | 33.1 | | 56 | 6.3 ± 0.3 |
| fertilisation | 2018 | 35.0 | 23.0 | 56 | 6.8 ± 0.3 |
| Wheel tracks + | 2014 | 35.2 | | 78 | 7.6 ± 0.1 |
| fertilisation | 2018 | 36.5 | – | 78 | 8.1 ± 0.2 |
| Wheel tracks | 2014 | 35.3 | | 78 | 7.6 ± 0.1 |
| No fertilisation | 2018 | 36.6 | 23.7 | 78 | 8.2 ± 0.9 |

Note: Data are shown as treatment means ± SE ($n$ = 4).

## Measurements and selection of main stems

### Planting and direct seeding

All plots were assessed in autumn 2022. For planted plots, tree height of all living trees within the $20 \times 20$ m measurement area was recorded. In direct-seeded plots, up to 2800 main stems ha$^{-1}$ were selected. The minimum spacing between the selected stems was 1 m and no more than 14 seedlings per row were selected to ensure even spatial distribution of the trees. The largest and most vital trees were selected as the main stems. Tree height was measured for all selected stems. Trees shortened by damage were not considered for sampling. No pre-commercial thinning to the main crop was done prior to the measurements.

Planting and direct seeding with orchard seeds were compared at the same age by also assessing the second-last year height (by excluding the current-year leading shoot) of the planted seedlings for both tree species.

### Natural regeneration

Natural regeneration was measured in autumn 2022. Five circular subplots of 1.78 m radius (10 m$^2$) were distributed systematically on the measurement area diagonals. Within each subplot, up to 3000 main stems ha$^{-1}$ were selected (3 seedlings per subplot). Tree height was measured for all selected stems. The minimum distance between selected stems was 60 cm. In the plots treated with a disc trencher, only trees found in mineral soil or in mineral soil mixed with humus were selected for the analyses. On plots prepared with wheel tracks, differentiation between the seedbed types was not possible. In addition, the total number of Scots pine seedlings was recorded for each subplot, regardless of the seedbed type (mineral soil, mineral soil mixed with humus or undisturbed).

## Statistical analyses

R was used for all statistical analysis (R Core Team 2023). We chose a linear mixed effects model (lme package) to evaluate the effect of the regeneration method on stem density and height. Replicate was used as a random effect and regeneration method as an independent factor. To further explore pairwise differences among tested treatments, post-hoc comparisons were performed (using the emmeans package) with Tukey's adjustment for multiple comparisons. We used $p = .05$ to determine statistical significance throughout this study.

## Results

The different regeneration method treatments yielded plants in different development stages and size thresholds, i.e. seedlings, saplings and trees, which are hereafter simply referred to as trees.

## Stem density

At the end of the study, planting and direct seeding resulted in stem densities ranging from 2269 (SE ± 80) to 2781 (SE ± 19) stems per hectare (Table 3). In contrast, stem densities in naturally regenerated plots varied from 13,050 (SE ± 3426) to 30,650 (SE ± 2917) among the tested treatments. Stems were densest on disc-trenched plots (Table 3). Wheel-tracked plots had less than half to the stem density of disc-trenched plots and were minimally affected by fertilisation. No empty subplots were recorded after disc trenching, whereas 40% and 35% of the subplots were treeless in wheel-tracked plots with and without fertilisation, respectively (Table 3).

## Main tree height

### Regeneration with orchard seeds

At the end of the observation period, lodgepole pine closely matched the mean height of Scots pine whether planted or directly seeded. However, mean height was significantly higher by 1.38 m for planted trees of both species ($p = .002$ on Scots pine and $p = .001$ on lodgepole pine), compared to direct-seeded trees (Figure 2). Notably, this comparison includes the difference in age, as planted trees were measured at 12 years (accounting for one year of seedling age at planting) and direct-seeded trees were measured at 11 years. When compared at the same age (i.e. after 11 growing seasons) the pattern remained the same, as planted trees were still significantly higher by 0.93 m (Scots pine: $p = .017$; lodgepole pine: $p = .008$), compared to direct-seeded trees (Figure 3).

### Regeneration with local seeds

At the end of the observation period, planting yielded the greatest mean tree height of all tested treatments, followed by direct seeding and natural regeneration after mechanical site preparation. Planting yielded on average 0.64 m ($p < .001$) and 0.74 m ($p < .001$) taller trees compared to direct seeding and natural regeneration, respectively. No statistically significant differences ($p = .586$) were observed

**Table 3.** Main and total stems per hectare in November 2022.

| Species | Regen. method | Origin | MSP | Fertilisation | Main stems ha$^{-1}$ | | Total stems ha$^{-1}$ | | Empty subplots (%) |
|---|---|---|---|---|---|---|---|---|---|
| SP | Planting | Orchard | DT | | 2519 | ±77 | | | |
| SP | Seeding | Orchard | DT | | 2644 | ±33 | | | |
| LP | Planting | Orchard | DT | | 2594 | ±24 | | | |
| LP | Seeding | Orchard | DT | | 2269 | ±80 | | | |
| SP | Planting | Local | DT | | 2725 | ±10 | | | |
| SP | Seeding | Local | DT | | 2781 | ±19 | | | |
| SP | Nat. gen. | Local | DT | Yes | 2900 | ±69 | 30,650 | ±2917 | 0 |
| SP | Nat. gen. | Local | WT | Yes | 2579 | ±192 | 13,050 | ±3426 | 40 |
| SP | Nat. gen. | Local | WT | No | 2667 | ±214 | 13,050 | ±3153 | 35 |

Note: For naturally generated plots, number of empty subplots are also shown. Data are shown as replicate means ± SE. Species are Scots pine (SP) and lodgepole pine (LP) and mechanical soil prepration (MSP) are disc trenching (DT) and wheel tracks (WT).

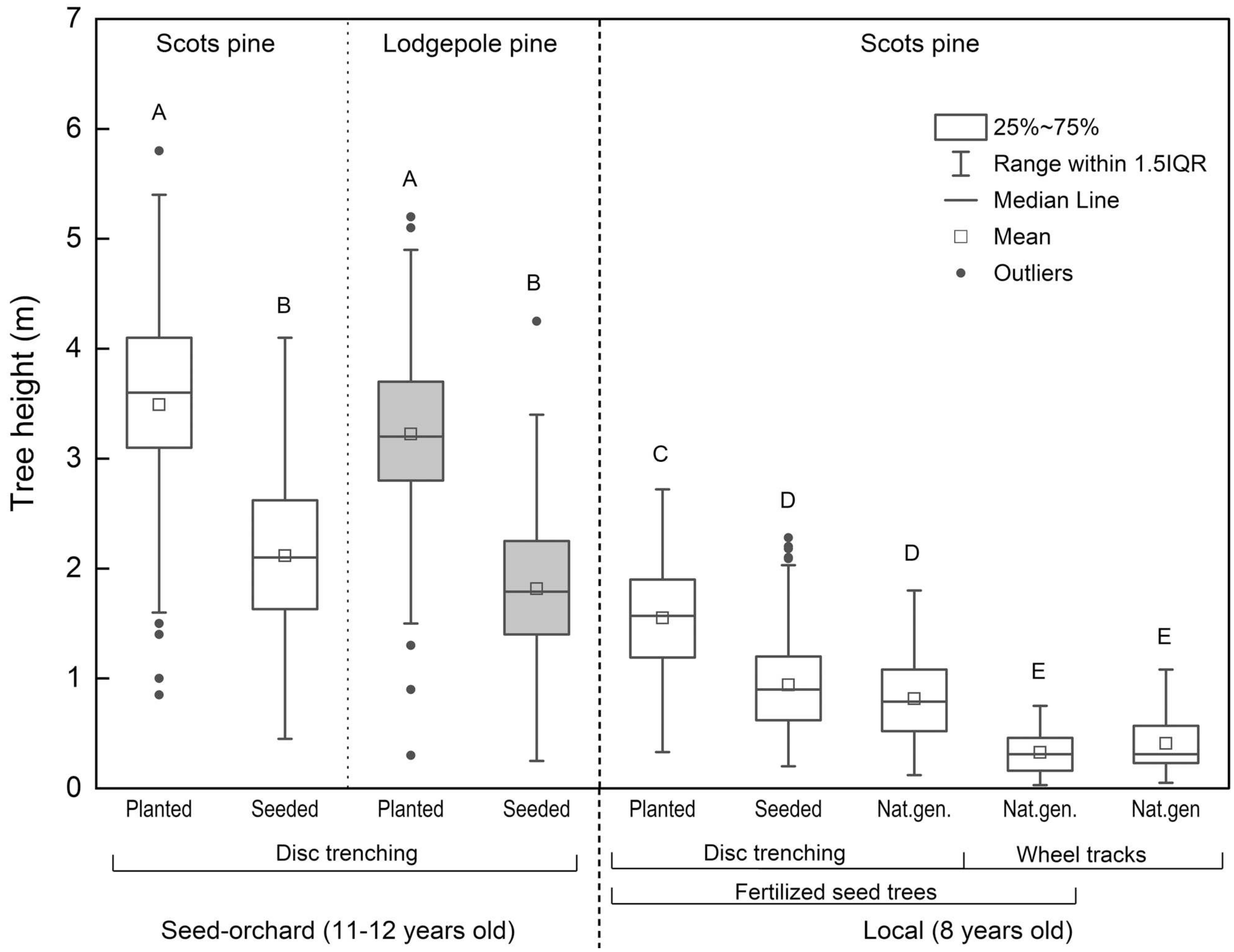


**Figure 2.** Mean tree height (m) at nine different regeneration methods for Scots pine (white boxes) and lodgepole pine (grey boxes). Data for direct seeding and natural regeneration refers to main stems. Boxes show the central 50% interquartile range. The horizontal line inside the box is the median, the open square is the mean and black dots are outliers. The upper and lower whiskers show 1.5 times the interquartile range. Different letters indicate statistically significant differences ($p \leq .001$) between tested pairwise comparisons.

between direct seeding and natural regeneration after disc trenching (Figure 2).

In naturally regenerated plots treated with disc trenching, 59% of selected main stems were found in pure mineral soils, 23% in mixed mineral soil and humus, and 18% on unprepared ground. No clear pattern in tree height was found among the different substrate types, i.e. intact soil, pure mineral soils, mixed humus-mineral soil (Figure 4). Natural regeneration after disc trenching was significantly taller ($p = .003$) than after wheel track treatment. It should be noted that in disc-trenched plots, only trees found in mineral soil or in mineral soil mixed with humus were included in the statistical analyses to make a fair comparison with the wheel track treatment. On average, the mean height difference between the two treatments was 0.45 m. Fertilisation of seed trees had no statistically significant effect ($p = .868$) on tree height (Figure 2).

## Discussion

At the end of the observation period, planted trees were significantly taller than direct-seeded seedlings (Figures 2 and 3). Planted seedlings were anticipated to grow faster which can be attributed to their initial height (approximately 10 cm at planting). This initial size advantage was likely a result of favourable nursery conditions during their first year. Furthermore, the physiological advantage of the planted seedlings, along with the protective root soil plug, likely facilitated a more successful establishment in the plantation compared to seedlings from direct seeding or natural regeneration (Mäkitalo 1999; Thiffault et al. 2003; Collet and Le Moguedec 2007). This pattern was consistent across both lodgepole pine and Scots pine.

No statistically significant differences in tree heights were observed between direct seeding and natural regeneration after disc trenching (Figure 2). Therefore, it is probably fair to assume that most naturally regenerated trees originated from the first year's seedling cohort. Direct seeding depends on the successful establishment of seedlings within the first year. In contrast, in naturally regenerated stands the second- or third-year seedling cohorts (Beland et al. 2000; Kyrö et al. 2022) may also contribute to population establishment, mitigating the risk of failure during the initial establishment phase.

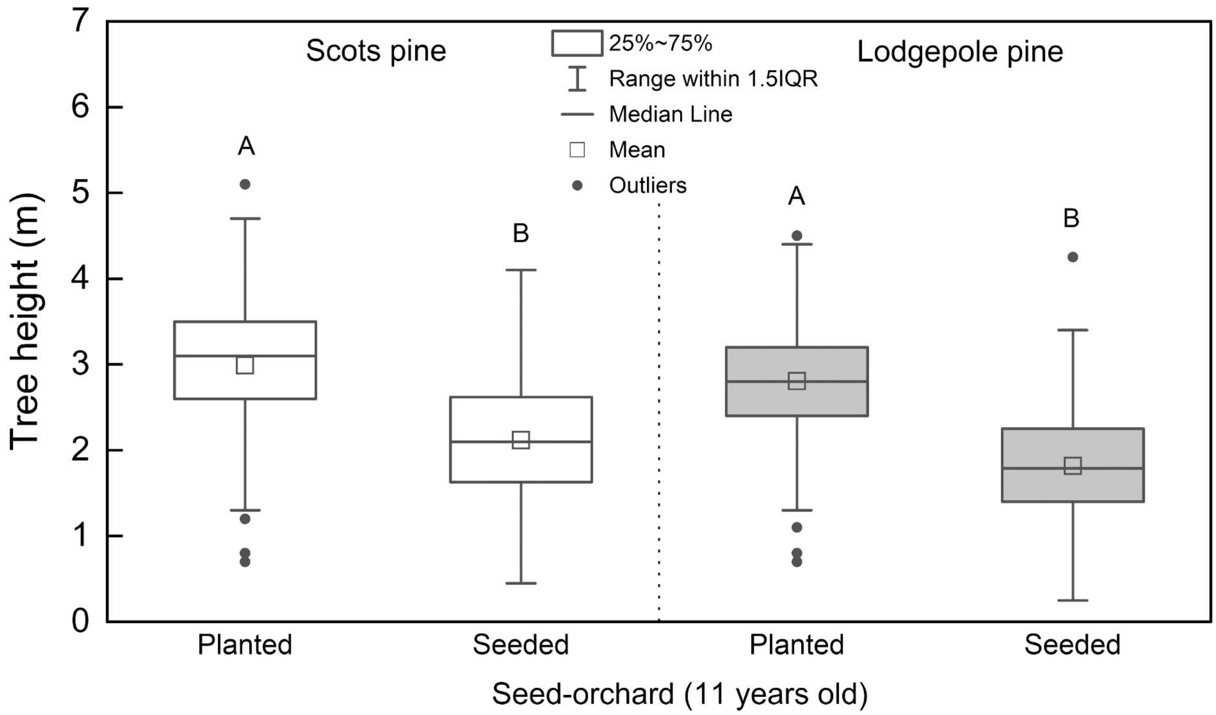


**Figure 3.** Mean tree height (m) of planted and main stems of direct-seeded Scots pine and lodgepole pine, grown from orchard seeds at the same age (i.e. after 11 growing seasons). Boxes show the central 50% interquartile range. The horizontal line inside the box is the median, the open square is the mean and black dots are outliers. The upper and lower whiskers show 1.5 times the interquartile range. Different letters indicate statistically significant differences ($p \leq .001$) between tested pairwise comparisons.

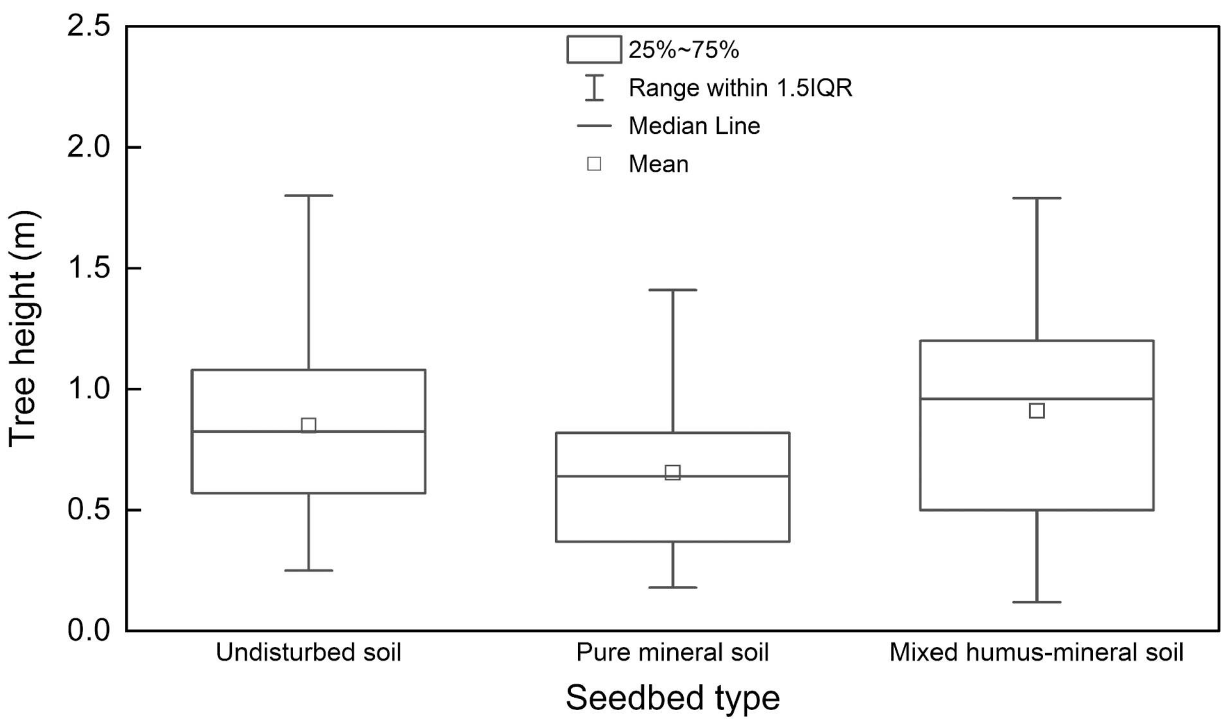


**Figure 4.** Mean tree height (m) of selected main stems of naturally regenerated Scots pine after disc trenching on different seedbed types. Boxes show the central 50% interquartile range. The horizontal line inside the box is the median, the open square is the mean. The upper and lower whiskers show 1.5 times the interquartile range.

Naturally regenerated seedlings germinate and grow in various substrates (Figure 4). In this study, we observed that in disc-trenched naturally regenerated plots, 59% of selected main stems were found in pure mineral soils, 23% in mixed mineral soil and humus, and 18% on unprepared ground. The observed distribution of seedlings across different substrate types indicates their capacity to adapt to a variety of environmental conditions. Consistent with our results, previous research (Beland et al. 2000; Kyrö et al. 2022) has shown that mineral soils typically offer a favourable balance between seedling survival and growth compared to other substrate types. As a result, seedlings growing in pure mineral soil were prioritised for analysis in our study. However, it is crucial to note that seed germination and seedling growth are influenced by multiple factors, such as air humidity, seed burial depth, substrate compaction, and hydraulic conductivity, with varying effects depending on moisture levels (Oleskog et al. 2000; Oleskog and Sahlén 2000).

On the other hand, directly sown seeds are typically placed in the centre of furrows on mineral soil. Small seedlings growing in mineral soils are particularly vulnerable to frost heaving, which may pose a significant challenge for direct seeding (Winsa and Bergsten 1994; Bergsten et al. 2001). While increased mortality rates on bare mineral soil may occur, the higher germination rates (compared to other substrates) (Oleskog et al. 2000; Oleskog and Sahlén 2000) typically lead to greater seedling density for several years after MSP, as observed in this and several other studies (Beland et al. 2000; Kyrö et al. 2022).

Mechanical site preparation (MSP) is an integral part of current Swedish forest regeneration (SFA 2020a), but its use may be restricted in the future to minimise harm to biodiversity, damage to historical remnants, reduction of reindeer forage, or the suitability for human activities in the forest (Löf et al. 2012). This study found twice the stem density (Table 3) and significantly taller naturally regenerated trees (Figure 2) in disc-trenched areas compared to wheel-tracked areas. These results suggest that substantial disturbance is needed to successfully establish naturally regenerated stands. In addition, no empty subplots were recorded after disc trenching, whereas 35–40% of subplots treated with wheel tracks were treeless (Table 3). Achieving uniform seedling distribution is important because patchiness is a significant feature of natural regeneration (Valkonen 2000; Zagidullina and Tikhodeyeva 2006), leading to reduced yield (Agestam et al. 1998). MSP to expose more mineral soil is an effective strategy to address this issue (Huth et al. 2022). It should be noted however, that the wheel track disturbance in this study was judged as relatively low. In large parts of the area, the humus layer remained intact and mineral soil was not exposed. Unfortunately, data on soil disturbance levels were not collected.

High seedling densities in naturally regenerated plots offer greater selection possibilities and highly competitive growing conditions (Table 3), leading to the development of less-tapered stems with denser wood and smaller-diameter branches compared to stands established with wide initial spacing (Agestam et al. 1998; Tegelmark 1998, 1999). Wood quality was not assessed in this study, but will likely be included in upcoming long-term studies.

Fertilisation of the seed trees had no significant effect on either the height or number of stems per hectare (Figure 2, Table 3). However, an earlier study by Karlsson (2006) showed a positive significant interaction between release cutting and fertilisation three years after regeneration cutting. After five years, trees that were both released and fertilised produced about 42% more cones compared to the only released trees.

This study found no significant height difference between Scots pine and lodgepole pine (Figure 3). By the end of the observation period, both species yielded a comparable number of stems per hectare (Table 3). This may be due to the relatively southerly field site. Additionally, the outcomes might have differed if the area had not been fenced. Under such conditions, Scots pine likely would have been subject to higher browsing pressure than lodgepole pine (Elfving et al. 2001).

Lodgepole pine has previously been found to grow faster than Scots pine in northern Sweden, regardless of the site index (Elfving and Norgren 1993). Lodgepole pine also survives better, both after planting and during establishment (ex. Martinsson et al. 1983; Fries 1993). This advantage increases in harsh northerly climates where mortality rates are generally higher. The superior survival of lodgepole pine is primarily due to its fast growth, resistance to abiotic and biotic stresses, greater frost hardiness, reduced susceptibility to snow blight (*Phacidium infestans*) and lower browsing rates compared to Scots pine (Elfving et al. 2001).

These results represent an idealised scenario that excludes ungulate browsing, a significant constraint for Scots pine regeneration in Sweden. Additionally, this is a case study without replicates across a range of site indexes. Finally, this study lacks replicates to capture year-to-year variation in weather and seed dispersal. These results therefore need to be interpreted and generalised with caution. Additionally, the long-term outcomes of the tested treatments remain unknown and may differ from the now observed short-term outcomes.

## Conclusions

In summary, this study found that planting resulted in significantly greater height growth than direct seeding and natural regeneration. This was likely due to the seedlings' larger initial size and favourable nursery conditions during their first year. The physiological condition of the planted seedlings, combined with the protective root soil plug, likely resulted in a better start in the plantation compared to seedlings from direct seeding or natural regeneration. After disc trenching, no significant height differences were observed between direct seeding and natural regeneration. Disc trenching enhanced natural regeneration, resulting in a higher number of trees per hectare and taller trees compared to wheel-tracked areas, which often lacked enough soil disturbance to expose mineral soil effectively. Fertilisation of seed trees had no significant effect on the number of trees per hectare. Both Scots pine and lodgepole pine yielded similar height and tree density per hectare.

This study's unique scope, testing multiple regeneration methods under identical site conditions, provides a rare opportunity to evaluate their relative effectiveness. Such comparative empirical experiments are uncommon or non-existent. The findings from this study offer valuable insights to assist forest owners and managers in the decision-making process regarding stand regeneration.

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