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Efficacy of Scots pine forest stand renewal using mechanised direct seeding: Genetic and growth parameter analysis of seedlings

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Abstract

Scots pine (*Pinus sylvestris* L.) is one of the most ecologically and economically important forest tree species in Latvia. In forest restoration, planting has traditionally predominated. However, in recent years, mechanised direct seeding has attracted increasing interest as a closer-to-nature, cost- and labour-efficient alternative. This interest is further enhanced by the improved availability of reproductive material from seed orchards. At the same time, an important practical problem is uncertainty about the origin of seedlings after direct sowing because Scots pine seeds are wind-dispersed and reforestation sites are frequently surrounded by mature pine stands. This aspect is particularly significant when improved seed material is used, because it directly affects the expected genetic gain. This study aimed to evaluate the effectiveness of mechanised direct seeding in the Scots pine stand regeneration using improved reproductive material from the Salaca pine seed orchard. Four forest stands in eastern Latvia, regenerated by mechanised seeding in spring 2014, were analysed. Seeding was carried out at an approximate sowing rate of 300 g ha^{-1} after soil preparation with a disc trencher equipped with a seeder. Stand development was assessed in the seventh growing season after sowing by measuring seedling height and root collar diameter, and by conducting genetic analyses to determine seedling origin. In total, 367 seedlings were genotyped using 16 microsatellite (SSR) markers. Maternal assignment was performed to determine the proportion of seedlings originating from the Salaca seed orchard. On average, 87% of the analysed seedlings were assigned to maternal genotypes from the Salaca seed orchard; this proportion was similar across all four forest stands. The assignment results were further supported by higher relatedness and lower genetic differentiation (*Fst*) between the assigned seedlings and the seed orchard clones compared with background (unassigned) seedlings. Allelic richness in the assigned seedlings was slightly lower than in the background group; however, no statistically significant differences were detected. Seedlings originating from improved reproductive material tended to show greater height growth, particularly with increasing age, and a higher height-to-diameter ratio, but these differences were not statistically significant. The results demonstrate that mechanised direct seeding using improved Scots pine seed material is an effective forest regeneration method that ensures a high contribution of sown seeds to stand formation, enabling the transfer of genetic gains achieved in breeding programmes and reducing regeneration costs and labour requirements.

Keywords: *Pinus sylvestris*; forest management; genetic diversity; seed orchards; bio-based solutions; close-to-nature forestry

Introduction

Scots pine (*Pinus sylvestris* L.) is one of the most ecologically and economically important forest tree species in Latvia. Scots pine is the dominant species in approximately 25% of forest stands covering over 825,000 hectares, the majority of which are located in state-managed areas (approximately 600,000 ha; Šņepsts et al. 2026). In the period 1948 to 1959, direct seeding was a widely used practice; approximately half of the stands anthropogenically regenerated at that time were established by sowing (Kundziņš 1956, Gailis and Gasiņš 1961). At present, the age of these stands is 66–77 years, but, unfortunately, no information regarding the seed material used in the stands regenerated during those years has been preserved. Direct seeding was discontinued mainly for economic reasons, since pine seeds became expensive, a seeding rate of 1 kg of seed per hectare was considered uncompetitive compared to planting, and the practice was seen as a waste of seed. Interest in direct seeding revived when seeding machines were introduced into practice, with a sowing rate of approximately 300 g of seed per hectare (Liepiņš et al. 2011).

Every year, 8,000–10,000 hectares of pine stands are regenerated in Latvia, 93% of which through sowing or planting (Official statistics portal 2025). Regeneration of forest stands with Scots pine is usually done by planting of improved material sourced from forest nurseries. However, interest in using direct seeding for stand renewal is increasing as it offers several advantages over seedling planting. Direct seeding requires less financial and logistical resources: namely forest nursery costs, transportation of seedlings from the nursery, and labour costs. In addition, root systems can develop naturally rather than being constrained, as for containerised seedlings, and there is a lower risk of spreading root diseases (Gonçalves and Fonseca 2023). However, there are also several disadvantages of direct seeding compared to planting. Seed quality and quantity are very important factors. Seed germination can be influenced by many factors, including seed quality, environmental conditions, and site preparation factors (Wennström et al. 1999). In addition, site characteristics can have a greater effect on restoration success than planting (Huth et al. 2017).

Only a negligible proportion of directly seeded Scots pine areas are sown manually; the majority are carried out by mechanised seeding. JSC 'Latvia's State Forests' (LVM) plans to regenerate 2,400 ha of pine forest stands through mechanised seeding in 2025–2029 (Latvijas valsts meži 2024). LVM introduced mechanised seeding into forestry practice in the spring of 2022, renewing 336 ha, then 627 ha in 2023, 601 ha in 2024, and 448 ha in 2025. Before a wider introduction of direct seeding into practice, an analysis of seeding practices in other Baltic and Nordic countries was performed. In the spring of 2014, the first trials were conducted with promising results, which allowed the achievement of 7,000–9,000 seedlings per hectare three years after mechanised seeding (Dobelis 2016). A study conducted in Finland, in which forest stands regenerated by direct seeding were surveyed over several years, concluded that with a sowing rate of 300 g of seed per hectare, mechanised sowing in furrows prepared with a disc trencher results in an initial average establishment of about 3,000 seedlings in the future stand, which is sufficient for successful forest stand regeneration (Kankaanhuhta et al. 2009).

The efficiency of direct seeding has been examined from a range of perspectives, including the effects of seed origin, and seed orchard seedlings have been shown to have higher emergence, survival, and growth rates than seedlings in areas seeded with stand seed lots (Wennström et al. 2007). However, there is a lack of studies using genetic approaches to analyse the origin of seedlings in stands regenerated by direct sowing. This is particularly crucial for Scots pine, which is shade-intolerant, so it is seeded in more open areas, and has small, wind-dispersed seeds. Scots pine seeds can generally disperse 50–100 metres, but further distances are also reported (Mukassabi et al. 2012). The survival and germinability of pine seeds in soil (soil seed banks) have mainly been investigated in the context of wildfires (Izhaki et al. 2000, Maia et al. 2012); however, one study of direct seeding in maritime pine (*Pinus pinaster*) indicated that direct seeding significantly increased the number of germinated seedlings, but only in the first year after sowing (Guignabert et al. 2020). This suggests that maritime pine seeds do not maintain viability for prolonged periods (several years) in soil.

However, the survival and germinability of Scots pine seeds in hemiboreal forest soil seed banks have not been investigated. Nevertheless, given the wide distribution and high density of Scots pine in Latvia, as well as the distance of seed dispersal, the soil bank may contain a significant number of Scots pine seeds. Therefore, not only the overall success of direct seeding is important for assessing the efficacy of restoration, but also the proportion of seedlings derived from the seed lot used for direct seeding. This is particularly significant if improved reproductive material is used, as this implies a higher investment in the seeds.

Mechanised direct seeding of Scots pine can reduce establishment costs relative to planting in boreal and hemiboreal regeneration, when target stocking is achieved without corrective treatments. In boreal Sweden, mechanised microsite preparation combined with direct seeding was projected to cost less than one third of planting by achieving the desired spacing through targeted placement on exposed mineral-soil microsites (Wennström et al. 1999). Cost savings are primarily realised by avoiding nursery seedling production and subsequent handling and transport, and direct seeding has been reported to reduce regeneration costs by roughly 30–50% relative to planting under favourable conditions (Grossnickle and Ivetić 2017).

The economic performance of direct seeding is, however, sensitive to establishment probability and the stocking threshold used to define success. If regeneration falls below target levels, remedial measures such as fill planting can offset initial savings; establishment outcomes are therefore strongly influenced by microsite quality, site preparation intensity, seed lot quality, and risks related to predation, competition, and abiotic stress (Ahtikoski et al. 2010, Grossnickle and Ivetić 2017). In northern Finland, comparisons of alternative establishment chains showed that sowing was competitive only under specific combinations of site preparation and success criteria, with results strongly affected by uncertainty in regeneration success (Ahtikoski et al. 2010). Rotation-scale modelling in southern Sweden further suggests that planting can provide higher long-term returns in productive sites when stronger early growth offsets higher establishment costs, although ratings remain sensitive to the discount rate and cost assumptions (Lula et al. 2021). Seed material also affects expected costs and returns in direct seeding systems. Finnish cost-benefit analyses indicate that the higher purchase cost of genetically improved orchard seed can be offset by improved survival and genetic gain under standard discounting assumptions (Ahtikoski and Pulkkinen 2003, Ahtikoski et al. 2012). Experimental evidence further shows that seed origin and seed type influence early establishment and subsequent performance after direct seeding (Wennström et al. 2007).

The use of DNA markers in forest tree species has allowed for the assessment of genetic diversity (Porth and El-Kassaby 2014), the development of genetic monitoring programmes (Kavaliauskas et al. 2018), and the acquisition of information on genetic processes in forest tree seed orchards (Funda and El-Kassaby 2012). The use of highly polymorphic, multi-allelic and codominant markers such as microsatellites or Simple Sequence Repeats (SSRs) considers pedigree reconstruction in open-pollinated forest tree species progeny (El-Kassaby and Lstibůrek 2009).

In this study, the efficacy of mechanised direct seeding for the renewal of Scots pine stands using improved reproductive material was assessed. We hypothesise that Scots pine forest stand renewal by mechanised direct seeding using forest reproductive material originating from seed orchards is an effective method of its stand regeneration, and (i) does not reduce genetic diversity, and (ii) growth parameters of pine trees grown from seeds from a seed orchard are comparable with those grown from locally sourced seeds. The proportion of seedlings obtained from the seed orchard was estimated, and genetic diversity parameters were compared between seedlings assigned as clones from the seed orchard and background (unassigned) seedlings. In addition, growth parameters of both assigned and unassigned seedlings were measured and compared over five years.

Materials and methods

Seed material, site preparation and sowing

The seeded forest stands were located in north-eastern Latvia: Stand A – forest compartment no. 101- 361- 5 (57.800, 25.949), Stand B – forest compartment no. 101- 362-7 (57.799, 25.957), Stand C – forest compartment no. 101-361-12 (57.798, 25.942), and Stand D – forest compartment no. 101-360-6 (57.796, 25.936; Figure 1). Stand A was the *Vacciniosa* forest site type, which represents dry, well-drained mineral-soil conditions. This site type is typically associated with sandy parent material and podzolization, resulting in nutrient-poor podzolic soils and a thin organic (humus) layer. Stands B–D were the *Myrtillosa* forest site type, also belonging to the dry mineral-soil group, but generally characterised by better moisture and nutrient conditions than *Vacciniosa*. *Myrtillosa* is commonly described on well-aerated mineral soils: on sands to loamy sands, with an organic layer typically around 4–5 cm (Zālītis and Jansons 2013, Liepa et al. 2014).

The analysed Scots pine stands were seeded in May 2014 using seeds from the Salaca Scots pine seed orchard. The seed lot was combined from seeds collected between 2002 and 2012, with a germination rate of 72%.

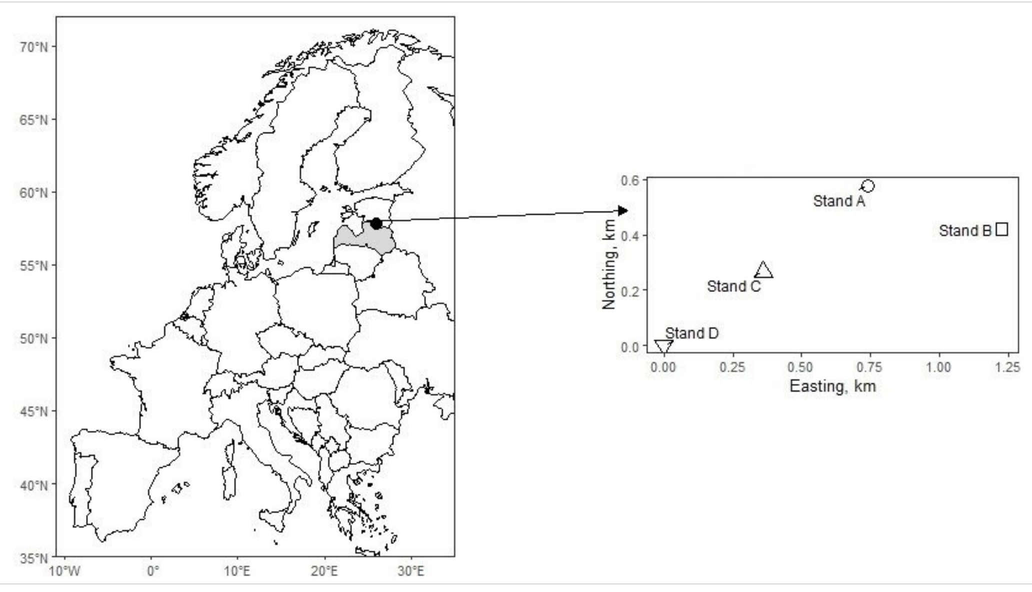

Figure 1. Location of the analysed seeded forest stands

Figure 2. Mechanically seeded Scots pine seedlings one and three years after stand renewal

The seeding rate was approximately 300 g ha^{-1}. Soil preparation was done using a disc trencher that was equipped with a TTS-SIGMA seeder. As a result, 7,000–9,000 seedlings emerged in the seeded areas, some of which were tightly clustered (Figure 2). Five years after direct seeding of the forest stands, the clustered seedlings were thinned.

Seedling measurements

Seedlings were measured in June of 2020, the sixth growing season after mechanised seeding (Figure 3), and two years after the first agrotechnical tending, during which thinning of the seeded tree groups was also carried out. In each location, five 10-metre-long sample plots were established, where the first ten trees were measured both in the right and the left furrow created by the disc plough – a total of 20 trees per plot and 100 trees per location. Tree age was determined by counting branch whorls. Sample plots were positioned at approximately equal intervals along a transect aligned with the longest diagonal of the stand, ensuring that the first and fifth plots remained unaffected by edge effects.

An increase in the number of seedlings was observed during inventories carried out immediately after seeding and surveys of the stands two years later. In the seedling measurements, it was not possible to identify six annual growth increments for all measured individuals, and some trees belonging to the Salaca pine orchard had only five annual increments. This indicates very slow growth in the first years, or that some seeds germinated in the following year. Direct seeding was done four months later than when pine naturally regenerates by seed; therefore, in the mineralised strip, the sown seeds mainly remained unburied, while naturally self-sown seeds were displaced sideways or buried by the disc plough.

Root collar diameter and all annual growth increments contributing to total tree height were measured. Needle samples were collected from all trees measured in the sample plots for genetic analyses (20 trees from each sample plot). In total, samples from 100 individuals from each forest stand were collected for genetic analysis.

DNA extraction and genotyping

DNA was extracted from needles using a modified CTAB method (Porebski et al. 1997). Genotyping was done with 16 microsatellite markers: psyl2, psyl16, psyl18, psyl25, psyl42, psyl44, psyl57, psyl17, psyl19, and psyl36 (Sebastiani et al. 2012), SPAC12.5 and SPAC11.6 (Soranzo et al. 1998), PtTX2146, PtTX4011, PtTX4001, and PtTX3107 (Aukland et al. 2002). PCR reactions were done in four multiplex bins: Bin1 (PtTX4011, PtTX4001, PtTX3107, psyl17, psyl19, psyl36), and Bin2 (PtTX2146, SPAC12.5, SPAC 11.6), Bin3 (psyl16, psyl25, psyl44), Bin4 (psyl18, psyl2, psyl57, psyl42).

PCR reactions were performed in a volume of 10 µL containing approximately 50 ng DNA, 2 µL HOT FIREPol® Blend Master Mix (Solis BioDyne; containing 10 mM $MgCl_2$), and 0.3 µM forward and reverse primers. PCR was carried out in a thermocycler (Eppendorf Mastercycler Epgradient) using the following protocol: initial pre-denaturation step at 95°C for 15 min, followed by 35 cycles of 95°C for 30 s, annealing for 30 s, and 72°C for 45 s, and a final extension step of 72°C for 10 min. Annealing temperatures were 53°C for Bin1 and Bin2, and 55°C for Bin3 and Bin4. Forward primers were labelled with 6-FAM, HEX or TMR fluorescent dyes to facilitate visualisation on a capillary sequencer. All PCR reaction products were diluted 1 : 10 with de-ionised water, and visualised on an Applied Biosystems ABI Prism 3100xl Genetic Analyzer. Genotyping was performed using GeneMapper 4.0 (Applied Biosystems 2005). Individuals with more than 25% missing genotypes were removed from further analysis to increase the accuracy of pedigree analysis. After quality filtering, 92 individuals were analysed from Stand A, 94 individuals from Stand B, 91 individuals from Stand C, and 90 individuals from Stand D.

Sample collection from the Salaca pine seed orchard

The Salaca Scots pine seed orchard is located in north-eastern Latvia (57.808, 24.472). It has a total area of 13.2 ha and contains 114 grafted Scots pine clones.

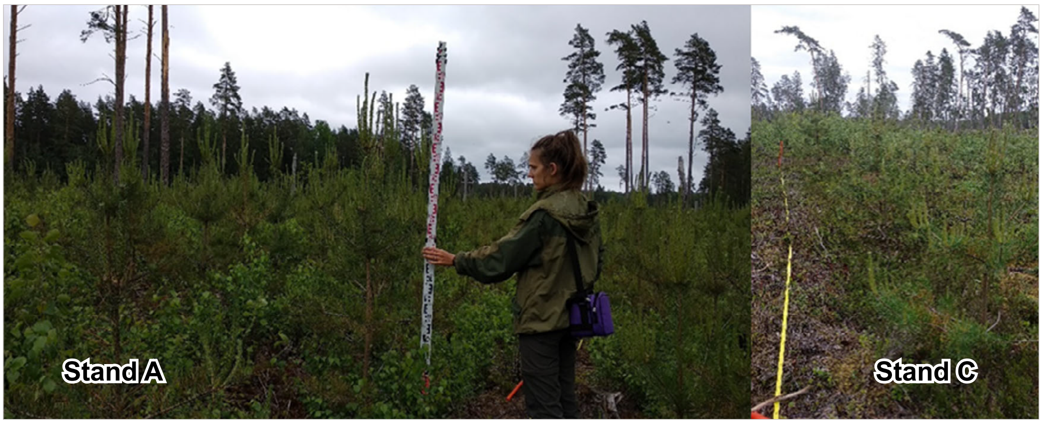

Figure 3. Measurement of seedlings in summer 2020, six years after seeding

The number of ramets per clone ranges from 1 to 111 (average 22.2). Representative ramets of four clones were not able to be located at the time of sample collection based on the seed orchard scheme. In addition, the multilocus genotypes of two pairs of individuals collected from the Salaca seed orchard were identical, which was probably due to errors during sample collection or in the seed orchard scheme, leading to the collection of two ramets from one clone. Therefore, 109 maternal genotypes were used for further analysis.

Data analysis

Pedigree analysis was done using the software program Cervus 3.0.3 (Kalinowski et al. 2007). Null allele frequencies were estimated, and only one locus (SPAC11.6) had an estimated null allele frequency of over 0.2. Null allele frequencies of < 0.2 do not greatly affect parental assignment, and higher frequencies can increase false parentage exclusions (Dakin and Avise 2004). As the inclusion of the locus SPAC11.6 would not lead to incorrect maternal assignments, all 16 loci were included in the analysis. The maternal simulation generated simulated genotypes for 500,000 offspring and 110 candidate mothers, proportion sampled 0.95, proportion of mistyped loci 0.05, minimum typed loci 8. Confidence levels were set at 80%. Based on this analysis, seedlings were divided into two groups. Seedlings maternally assigned to one of the Salaca seed orchard clones with confidence > 80% were classified as 'Salaca offspring', while those with no maternal assignment or below the 80% confidence limit were classified as 'background'. The use of an 80% confidence limit is relatively accurate and useful for population-level studies where maximising the number of assignments is more important than avoiding every possible error (e.g. estimating overall reproductive success; Slate et al. 2000).

Pairwise relatedness was calculated using the Queller and Goodnight (1989) estimator, and 95% confidence intervals and limits of population means were determined by bootstrapping (9999) and permutation (9999) using the GenAlEx 6.5 software package (Peakall and Smouse 2012). Pairwise *Fst* values for each stand (999 permutations) were calculated using GenAlEx 6.5. Estimation of allelic richness (Ar) using a rarefaction approach to enable comparisons between groups of different sizes was done using the FSTAT 2.9.3.2 computer program with 1000 permutations to determine the significance of differences (Goudet 1995, 2002).

Statistical analyses of seedling measurements were performed in R (R Core Team 2025). Root-collar diameter and height development were analysed using linear mixed-effects models to account for the hierarchical sampling structure. Height was evaluated separately for each measurement year (2016–2020), representing the tree height recorded in the respective year. Models included origin class, stand, within-stand position, and plot density as fixed effects, with sample plot included as a random effect. Model assumptions were assessed through inspection of residual distribution and homoscedasticity. Fixed effects were evaluated using Wald tests, and estimated marginal means were calculated for categorical predictors, with differences among factor levels summarised using compact letter displays. Statistical significance was assigned at $p < 0.05$.

Results

Genetic analyses

Overall, 87% of analysed seedlings in the seeded regeneration areas were assigned to the Salaca seed orchard, and the proportion was similar when analysing each stand separately. When the parentage of seedlings from all areas was analysed over the entire data set, 92 of the 109 Salaca clones were maternally assigned to seedlings. When analysing each area separately, between 42 and 52 of the 109 Salaca clones were identified as mothers of the seedlings determined to be derived from the Salaca seed orchard (Table 1). This indicates that in a larger number of sampled seed orchard progeny (> 300 individuals), the Salaca seed orchard clones are well represented. However, when a smaller number of seed orchard progeny are sampled (approximately 80 seedlings in each seeded area were identified as Salaca seed orchard progeny), the number of clones represented decreases due to stochastic sampling effects.

Table 1. Proportion of individuals assigned to Salaca clones and number of unique Salaca clones with maternal assignment

	Stand A	Stand B	Stand C	Stand D	Overall
No. of individuals	92	94	91	90	367
Proportion of individuals assigned to Salaca clones	0.88	0.85	0.87	0.87	0.87
Number of unique Salaca clones with maternal assignment	44	42	52	51	92

The pairwise relatedness was significantly higher between the seedlings assigned to the Salaca seed orchard clones compared to the mother tree clones in all analysed stands except Stand D (Figure 4). The pairwise relatedness of the background seedlings (not assigned to the Salaca seed orchard) was lower in all stands except Stand B. This supports the maternal assignment analysis, as seedlings derived from the seed orchard seeds would be expected to have higher relatedness compared to both the seed orchard clones as well as the background (unassigned) seedlings.

Also supporting the maternal assignment analysis, pairwise *Fst* values were higher between seedlings assigned to the Salaca seed orchard clones and the background (unassigned) seedlings in each stand, compared to the pairwise *Fst* values between the mother clones and

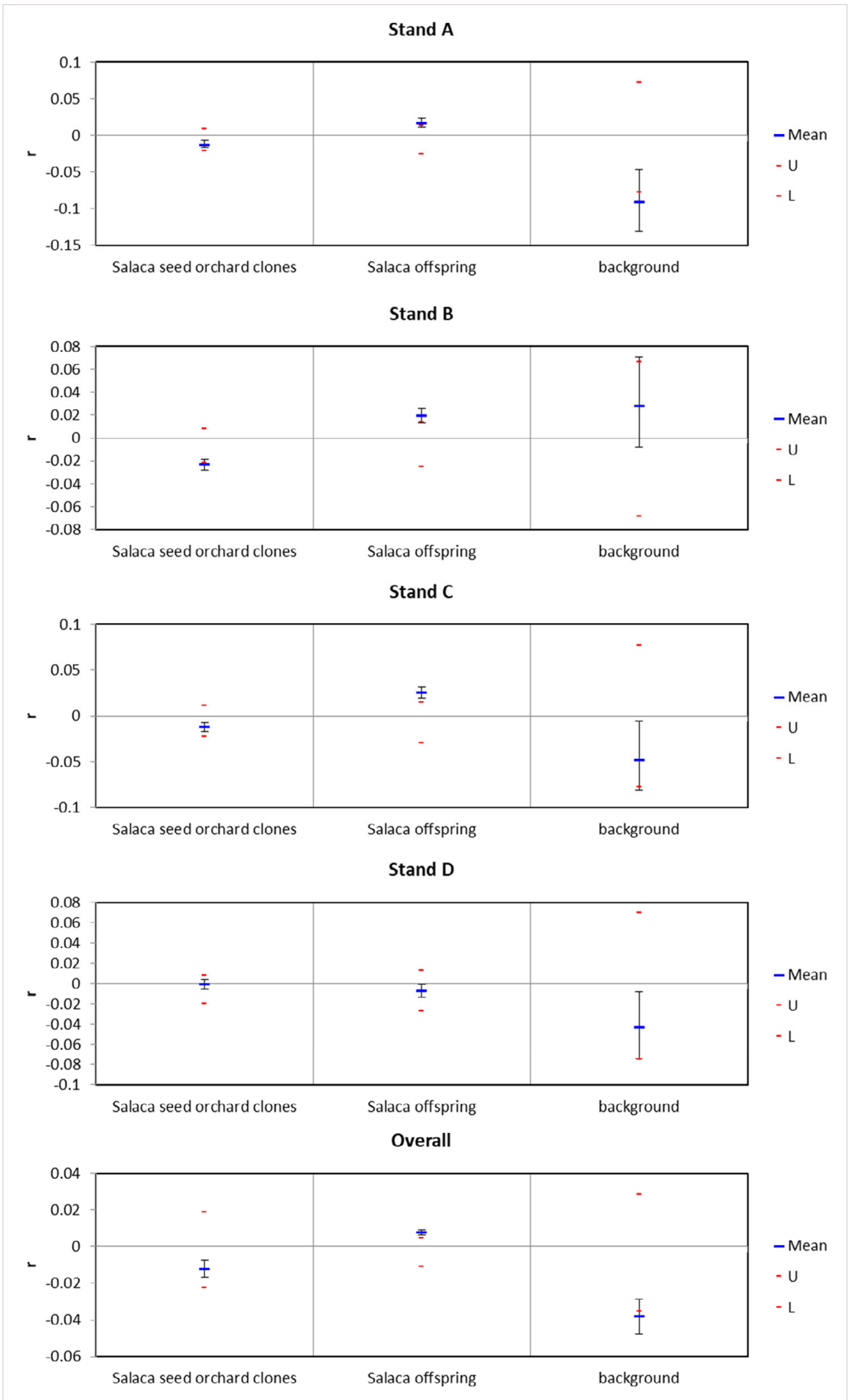

Figure 4. Mean within population pair-wise values

Upper and lower error bars bound the 95% confidence interval about the mean values as determined by bootstrap resampling. Upper (U) and lower (L) confidence limits bound the 95% confidence interval about the null hypothesis of no difference across the populations.

the individuals assigned to the Salaca seed orchard clones in all analysed seeded regeneration areas (Table 2).

Allelic richness was lower in the individuals assigned to the Salaca clones in each seeded regeneration area (4.828) compared to the unassigned individuals (5.138), but this difference was not statistically significant.

Table 2. Pairwise *Fst* values between seedlings assigned to the Salaca orchard, the mother clones and background (unassigned seedlings)

	Salaca offspring			
	Stand A	Stand B	Stand C	Stand D
Salaca seed orchard clones	0.004	0.004	0.005	0.004
Background	0.018	0.019*	0.026*	0.014

Note: * $p < 0.05$.

Seedling measurements

In general, plant height was higher in the individuals assigned to the Salaca seed orchard, compared to the background (unassigned individuals). However, there also may be a site effect, as the height of individuals in Stand D assigned to the Salaca seed orchard was lower than that of unassigned individuals. This tendency was more pronounced with increasing seedling age; however, the differences were not statistically significant ($p > 0.05$; Figure 5). This increase in height is also associated with a smaller root collar diameter; however, this correlation was not statistically significantly different between the seedlings assigned to the 'Salaca offspring' and the 'background' groups ($p > 0.05$; Figure 6). A higher height-diameter ratio in Scots pine plus-tree progenies compared to genetically unimproved trees has been previously reported (Egbäck et al. 2018).

Discussion

Direct seeding can be a cost- and time-saving method of renewing oligotrophic forest stands. Numerous studies have investigated direct seeding for a range of tree species and climactic regions, both for ecosystem restoration (Palma and Laurance 2015), as well as for silvicultural applications (Grossnickle and Ivetić 2017). However, there is a lack of studies of direct seeding that incorporate genetic analyses to investigate the origin of the seedlings that establish in the renewed areas. This is particularly important when using improved reproductive material for renewing forest stands, in order to maximise the genetic gain via the use of seeds from advanced generation seed orchards. In addition, Scots pine seeds are wind-dispersed, and areas renewed using direct seeding are often surrounded by Scots pine stands, thus increasing the likelihood of seeds from surrounding stands falling on the renewed areas.

In this study, a high proportion (87%) of seedlings in the renewed stands were assigned to mother clones from the Salaca Scots pine seed orchard, indicating that direct mechanised seeding using improved reproductive material is a viable option for forest management. This maternal assignment analysis was supported by the higher pairwise relatedness among individuals assigned to the seed orchard, as well as the lower *Fst* values between the seed orchard clones and the assigned seedlings, compared to the background (unassigned) seedlings. In addition, the height increments tended to be larger in the individuals assigned to

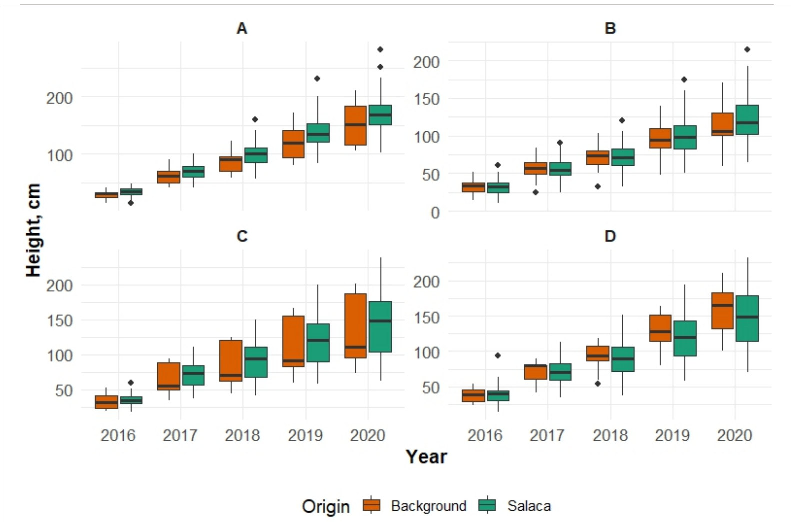

Figure 5. Comparison of seedling height in each stand (A, B, C, D) between individuals assigned to the Salaca seed orchard and background (unassigned) individuals

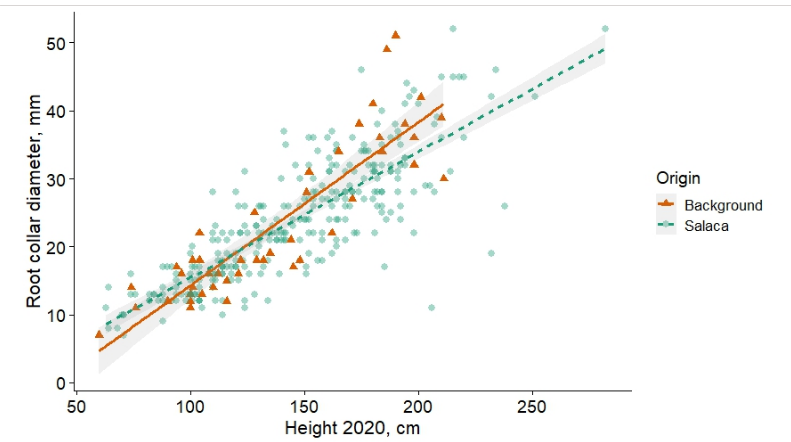

Figure 6. Comparison of seedling height and root collar diameter in 2020 between individuals assigned to the Salaca seed orchard and background (unassigned) individuals

the seed orchard, as expected from improved material that is selected for increased growth indices.

In this study, a mixed seed lot consisting of seeds collected between 2002 and 2012 was used for direct seeding. In this case, seeds were stored in conditions to maintain viability, and germination tests were carried out on the seed lots. This is in contrast to other reports about direct seeding of Scots pine in northern Europe, where only seeds collected in the previous year were used for direct seeding, as without storage in appropriate conditions, Scots pine seeds are usually viable for only one year (Lula et al. 2025). The use of mixed seed lots consisting of seeds collected over several years can be expected to increase the genetic diversity compared to seeds collected in a single year (Ivetić et al. 2016). In addition, seeds collected from seed orchards are genetically improved and can be expected to have better survival, growth and other parameters (depending on the breeding criteria), as shown in this study. In addition, the use of Scots pine seed orchard material does not lead to a decrease in genetic diversity compared to naturally regenerated stands (García Gil et al. 2015).

In a study conducted in central Sweden, planted Scots pine seedlings were found to be taller than directly seeded individuals after 11 growing seasons, and this was also observed for lodgepole pine (*Pinus contorta*) as well (Lula et al. 2025). This was attributed to the larger initial height of the planted seedlings, as well as the physiological condition of the seedlings and the protection provided by the root soil plug, thus enabling the planted seedlings to rapidly establish vigorous growth compared to directly seeded individuals. There is still a lack of data on the long-term differences between planted and directly seeded individuals (i.e. after 60 or more years, when Scots pine is harvested). The seeds used for direct seeding in this study were sourced from a seed orchard, which would be expected to have superior growth parameters compared to unselected material. However, the growth was measured at an early stage, six years after sowing, and so differences between selected and unselected material are not so pronounced. In addition, the Salaca seed orchard is a first-generation seed orchard consisting of phenotypically selected plus tree clones, and so would be expected to produce lower genetic gains compared to second-generation seed orchards, which are established using the results of progeny trials. However, the establishment costs for direct seeding are much lower compared to planting of seedlings, even if improved seed orchard reproductive material is utilised.

Studies about the viability of Scots pine seeds in the soil seed bank are scarce. However, this is probably not a significant long-term reservoir of Scots pine seeds, as they have very little or no seed dormancy, and therefore are unlikely to form a persistent seed bank (Castro et al. 2005). In addition, experimental studies have found that direct seeding of maritime pine significantly increased the number of germinated seedlings, but only in the first year after sowing (Guignabert et al. 2020), indicating that the soil seed bank is not a significant long-term source of viable Scots pine seeds. However, in this study, it was not possible to identify six annual increments for all measured pines, and some trees belonging to the Salaca pine orchard had only five annual increments, which indicates that some seeds remained viable and germinated in the following year.

In nutrient-poor soils, sown pines grow more slowly than seedlings grown in fertilised nursery fields or in substrates enriched with plant nutrients. In addition, nursery seedlings are irrigated, in contrast to field conditions, where seedlings are dependent on the amount of precipitation in the renewed areas. However, once planted in forest stands, nursery seedlings are more sensitive to drought stress. Direct seeding does not require additional labour, sowing takes place simultaneously with soil preparation, and seeds with lower germination capacity – unsuitable for container seedling production – can be used for sowing. The main benefit of direct seeding is the possibility to reduce heavy manual labour in forest regeneration by using methods that imitate natural processes (close-to-nature forestry), as well as the opportunity to renew pine stands using improved reproductive material. An additional benefit, which was not assessed in this study, is that in contrast to planting of containerised seedlings, the trees do not experience transplant shock and root systems development is not hindered or disturbed. Mechanised direct seeding provides an economically competitive method for Scots pine stand renewal, particularly if improved reproductive material is used, which results in higher silvicultural value of the mature stands, while also maintaining genetic diversity.

Conclusions

This study indicates that direct seeding of Scots pine using improved reproductive material is a viable option for renewing oligotrophic forest stands in hemiboreal regions. The main drawback of direct seeding, as mentioned by forestry practitioners, is that without genetic analyses, it is not possible to determine which trees have grown from sown seeds and which originate from the surrounding stands or the soil seed bank. This study indicated that a high proportion (> 85%) of seedlings were derived from seed orchard seeds, and that, overall, these had higher growth indices after 5 years, compared to seedlings established from seeds collected in surrounding pine stands. However, there also may be a site effect, as the height of individuals in Stand D assigned to the Salaca seed orchard was lower than that of unassigned individuals. Thus, the use of improved reproductive material favours an increase in the silvicultural value of mature stands while maintaining genetic diversity.

Data availability

Genotype data of seedlings from pine stands renewed by direct mechanised seeding using seeds from the

Salaca pine seed orchard, visit https://doi.org/10.5281/zenodo.17415692.

Height and diameter measurements of seedlings from pine stands renewed by direct mechanised seeding using seeds from the Salaca pine seed orchard, visit https://doi.org/10.5281/zenodo.17416266.

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