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Recruitment dynamics of naturally regenerated Scots pine under different overstorey densities in southern Sweden

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ABSTRACT

In Sweden, the majority of the area regenerated with Scots pine (*Pinus sylvestris* L.) is planted, whereas natural regeneration and direct seeding are less common. As the need for site adaptation grows, some alternative regeneration methods may become more important. Therefore, this study aimed to evaluate how mechanical site preparation (MSP) and its timing, along with overstorey density treatments, affect the recruitment of naturally regenerated Scots pine. The study was based on empirical data from three adjacent stands in southern Sweden (57.06°N, 14.39°E). The replicates in time of overstorey treatment were installed to capture annual weather variations. Both MSP and shelterwood positively affected seedling recruitment. However, these effects varied among years and tested stands. In addition, increased overstorey density enabled seedling cohorts from several years to contribute to the seedling population by the end of the observation period. Release cuttings (referred to as harvest in the text) enhanced seed production, leading to a substantial increase in seedfall in the fourth year following the harvest. Finally, conducting MSP three years after the harvest significantly improved seedling recruitment compared to MSP immediately after the harvest in 2020. However, this effect was not seen again in the second inventory three years later.

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Introduction

Despite Sweden's extensive history of silvicultural research and practical experience, seed-based regeneration of Scots pine (*Pinus sylvestris* L.) remains a challenge. Currently, only 7% of the total regeneration area in Sweden is managed through natural regeneration (Skogsstyrelsen 2024). Nonetheless, when done correctly, natural regeneration can result in very dense stands (exceeding 10,000 seedlings per hectare) at relatively low costs (Hyytiäinen et al. 2006; Lula et al. 2021). These dense stands, characterized by competitive growing conditions and significant selection potential, can produce high-quality timber (Agestam et al. 1998). Moreover, natural regeneration, which is typically achieved through partial overstorey retention using seed or shelter trees, is often favored over clearcutting due to its higher recreational and aesthetic value. Koivula et al. (2020) found that increasing logging intensity decreased the attractiveness of pine forests. Retaining an overstorey (seed or shelter trees) is also expected to dampen changes in light, temperature, water, and soil conditions that occur on a regeneration site, helping maintain forest ecosystem stability.

Spatiotemporal variation in seed production is a key driver of Scots pine population dynamics. The success of seed-based

regeneration therefore primarily relies on seed source and dispersal efficiency. It is constrained by the availability of resources such as light, microsite conditions, and nutrients, as well as damage levels (Karlsson 2001; Holmström et al. 2017). Pine seed crops can vary significantly over years (Pukkala et al. 2010), individual trees (Hagner 1965), and site fertilities (Sarvas 1962), and can be affected by seed-damaging agents such as insects and fungi. The periodicity of seed production is mainly influenced by climatic conditions and the reproductive ecology of Scots pine. High temperatures, low precipitation, and abundant sunlight during the preceding summer promote flowering in the following year (Sarvas 1962; Leikola et al. 1982; Pukkala 1987; Pukkala et al. 2010). Cone production tends to increase following manipulation of the overstorey, with the effect most pronounced in the fourth year after the release, which aligns with the three-year seed-development cycle of Scots pine (Karlsson 2006).

Seed dispersal in Scots pine stands occurs in the fourth year after flower initiation, primarily between April and June (Hannerz et al. 2002). The number of dispersed seeds per square meter decreases sharply beyond 30 meters from the parent tree (Miles and Kinnaird 1979). The main objective

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of overstory retention is to provide sufficient seeds and reduce damage to seedlings. However, overstory trees compete with the new seedlings for water, nutrients, and light, resulting in reduced seedling growth compared to clearcuts (Löf et al. 1998; Nilsson et al. 2002; Agestam et al. 2003). Manipulating the overstory influences light transmittance, soil insolation, and the understory microclimate (Lofvenius 1995). The composition, abundance, and succession rate of understory plant communities are therefore largely dictated by canopy closure and retention levels (Atlegrim and Sjöberg 1996; Hannerz and Hånell 1997; Johnson et al. 2014; Eldegard et al. 2019).

Organic soil horizons, which are highly sensitive to changes in air humidity, can reduce germination and increase the risk of root desiccation (Oleskog and Sahlén 2000b; Hille and Den Ouden 2004). Mechanical site preparation (MSP) removes the soil organic layer and improves contact between newly emerged seedling roots and the mineral soil, which has a more stable water content. Additionally, higher soil surface temperatures on bare mineral soils enhance root growth and water and nutrient uptake compared to undisturbed soil (Nilsson and Örlander 1999b). MSP also improves soil drainage and aeration (Örlander et al. 1990) and reduces competition from ground vegetation (Norberg et al. 1997; Johansson et al. 2013), which is a significant growth-limiting factor in southern Sweden (Nilsson and Örlander 1995; Nilsson et al. 1996; Örlander et al. 1996; Nilsson and Örlander 1999a). However, MSP could potentially hinder seedling growth and survival. For example, it may lead to decreased nutrient concentrations (Munson et al. 1993; Hallsby 1995) and increase the likelihood of frost heaving (Sahlén and Goulet 2002; Heiskanen et al. 2013). The benefits of MSP diminish over time, however, this process is delayed under seed and shelter trees compared to clearcuts, primarily due to the slower ingrowth of understory vegetation on prepared ground (Beland et al. 2000). Moreover, weather variables significantly influence establishment and growth of naturally regenerated seedlings. Drought, in particular, poses a substantial threat to successful seedling establishment as constant moisture is required for successful germination and early seedling survival (Oleskog et al. 2000). Prolonged drought can lead to desiccation and increased seedling mortality. MSP, which exposes mineral soil with more stable moisture levels, is crucial in mitigating the negative effects of drought. Additionally, drought conditions can increase competition for water resources between shelterwood trees and seedlings, further stressing seedlings.

Another major constraint on natural regeneration, especially in northern Sweden, is inadequate seed production, which leads to insufficient seedling recruitment. Combining seed or shelter trees with MSP is an effective method for establishing naturally regenerated Scots pine stands (Hagner 1962; Beland et al. 2000; Karlsson and Nilsson 2005). Different types of damage to emerging Scots pine seedlings, such as from pine weevils, desiccation, frost damage, and frost heaving, are important constraints on seedling establishment and early growth. The combination of shelterwood and MSP can reduce these damage types. In central Sweden, extensive practical and scientific efforts

(Karlsson 2000; Karlsson and Örlander 2000; Karlsson and Örlander 2002; Karlsson 2006) resulted in the development of a practically applicable regeneration method (Karlsson and Örlander 2000) to address the challenge of insufficient seed production. Its primary objective is to synchronize MSP with increased cone production three years after overstory manipulation. The method has never been experimentally tested in southern Sweden for two main reasons. First, a belief prevails that seed production in the region is consistently sufficient to ensure the satisfactory seedling recruitment, and second, there is concern about the potentially rapid invasion of ground vegetation on prepared ground.

The primary objective of this study was to investigate the effects of overstory density and MSP on seedling recruitment in naturally regenerated Scots pine stands in southern Sweden. Additionally, differences in overstory density treatments were investigated in the context of environmental variables, mainly drought, focusing on recruitment of different seedling cohorts. Lastly, the effect of delayed MSP (three years after the harvest) was investigated and compared to MSP directly following harvest.

Materials and methods

Three Scots pine-dominated stands located in the hemiboreal zone of southern Sweden at Tagel estate (57.06°N, 14.39°E) were used in this study (Figure 1). The stands were situated within ~1 km of each other and their ages varied between 100 and 122 years. The 30-year mean monthly air temperatures in the area range from -1°C during winter (December-February) to 15.4°C in the summer (June-August), with an annual mean of 6.9°C. The mean annual precipitation is about 719 mm and the average growing season (referred to as the number of days with an average temperature exceeding 5°C) between 200 and 230 days (SMHI 2024). The soil type was gravel till and its moisture mesic. The estimated site index (H100, i.e. the mean height of the 100 by diameter largest trees per ha at 100 years total age) was 23–24 m (Elfving and Kiviste 1997), which corresponds to a mean annual increment (MAI) of about 5.5 m³ ha/year.

The experiments were established in February of 2017, 2020, and 2023, following release cuttings and mechanical site preparation (MSP) in each stand. We used “harvest” to denote release cutting, hence the stands were later referred to as Harvest 2017 (H17), Harvest 2020 (H20), and Harvest 2023 (H23). Each stand was divided into three density treatments: clearcut, seed-trees, and shelterwood (Figure 1 and Table 1). The treatments were replicated to capture interannual weather variations. The area of each density treatment was consistent within harvest years but varied between harvest years, with each density treatment covering approximately 2 ha in H17, and 1 ha in H20 and H23, respectively. All areas were cleared of woody understory vegetation and fenced to prevent browsing by ungulates.

Seedfall was collected using circular seed traps (9.4 cm radius) emptied twice per year (June and November) from 2018 to 2020 at H17, from 2020 to 2023 at H20, and in

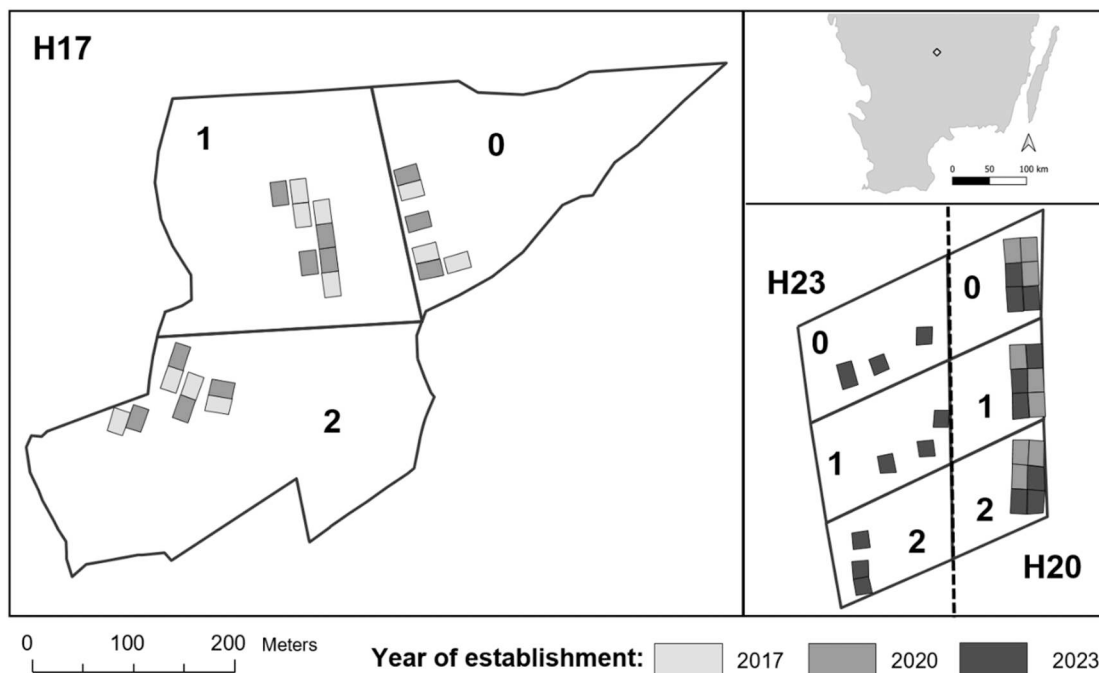


Figure 1. Spatial layout of the experiments. Rectangles indicate blocks. The colors of the blocks correspond to the establishment year according to the legend. The top right corner shows the location of the site in southern Sweden (57.06°N, 14.39°E). H17, H20 and H23 refer to Harvest 2017, Harvest 2020, and Harvest 2023, respectively.

2023 at H23. There were 20, 10 and 6 traps in each density treatment at H17, H20 and H23, respectively. All seeds without wings were counted as Scots pine due to difficulty of differentiating Scots pine and Norway spruce seeds without their wings. Due to a sampling error, seedfall of 2017 was not collected.

The experiment employed a split plot design with three or four blocks, each measuring 8 × 16 meters, in each overstory density treatment (Figure 1). The proximity of the clearcut blocks to the forest edge was a result of other experiment occupying the remaining space. MSP was performed using an excavator to create four continuous rows of mineral soil (~0.5 m wide) in each block, leaving the

soil between the rows undisturbed. Natural regeneration was assessed on both prepared and unprepared soil. Sampling plots were systematically distributed within each block. There were 16 and 8 sampling plots per block, with and without MSP, respectively. The center of each sampling plot was marked with a plastic stick (Figure 2). If the plastic stick was displaced, compromising measurement accuracy, or missing during the observation period, the plot was excluded from the analysis. Seedling recruitment was monitored annually in late autumn at the sampling plot level over three years at H17 (2017–2019) and H20 (2020–2022) and one year at H23 (2023). Each sampling plot had either a small (15 × 15 cm) or large (30 × 30 cm) plastic cross

Table 1. Top height (m), stem density (trees ha⁻¹), quadratic mean diameter at breast height (DBH, cm), basal area (m² ha⁻¹) and standing volume (m³ ha⁻¹) of all tree species in the clearcut, seed-trees and shelterwood treatments. “Before” refers to the inventory before harvest, and “after” refers to the inventory following harvest.

	Overstory density treatment	Time of inventory	Top height (m)	Stem density (trees/ha)	DBH (cm)	Basal area (m ² /ha)	Volume (m ³ /ha)
Harvest 2017	Clearcut	before	25.2	350	32.0	28.2	287
		after		0.0	0.0	0.0	0.0
	Seed-trees	before	25.0	376	31.9	30	325
		after		96	34.5	9.0	96
	Shelterwood	before	24.6	346	31.0	26.1	267
		after		205	34.0	18.6	189
Harvest 2020	Clearcut	before	22.0	350	28.7	22.7	216
		after		0.0	0.0	0.0	0.0
	Seed-trees	before	23.0	297	30.6	21.9	223
		after		99	32.9	8.4	83
	Shelterwood	before	24.2	403	30.4	29.2	302
		after		240	31.8	19.1	194
Harvest 2023	Clearcut	before	23.2	340	29.9	23.9	224
		after		0.0	0.0	0.0	0.0
	Seed-trees	before	23.4	276	31.1	20.9	204
		after		99	33.8	8.9	89
	Shelterwood	before	24.6	332	29.8	23.2	244
		after		156	33.6	13.8	145

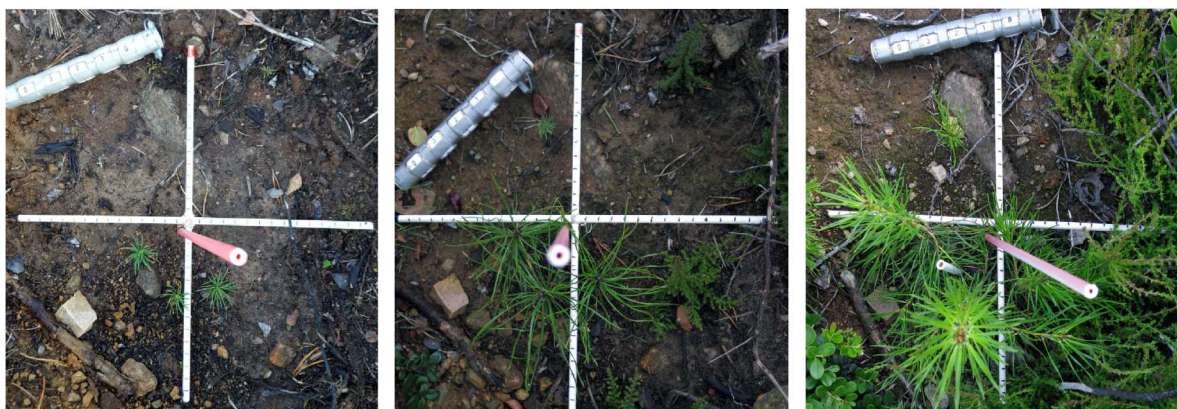


Figure 2. Monitoring of seedling recruitment. Photos show the same clearcut sampling plot after mechanical site preparation in the stand harvested in 2017 (H17) over time, starting with the 2017 inventory (left), followed by 2018 (center), and 2019 (right).

scale placed at its center and oriented toward magnetic north for measurement accuracy (Figure 2). The small cross was used where terrain obstacles prevented the use of the large cross. Scales accurate to 1 cm were used to record the positions of individual seedlings for identification and tracking over time, allowing all newly emerged seedlings to be mapped to unique positions and assigned to germination year cohorts. A total of 4,440 seedlings were mapped and monitored over a period ranging from 1 to 3 years after overstory harvest between 2017 and 2023. The number of seedlings per square meter in respective cohorts was calculated by summing the areas and seedling numbers observed in the individual plots for each treatment and block. Seedlings that did not survive to the stage where species identification was possible were registered as Scots pine.

R was used for all statistical analysis (R Core Team 2023). Seedling recruitment (seedlings/m²) was compared across stands and overstory density treatments by fitting a linear mixed-effects model using logarithmic distribution in the *lmer* package, where overstory density treatment was a fixed factor and block within a stand was a random factor. To interpret model results, we used estimated marginal means from the *emmeans* R package (Lenth 2023) which included contrast analysis, enabling comparisons between different treatments. Variation in seedfall between years and stands was analyzed using a two-sample t-test assuming equal variances. If the assumption of equal variances was not met, we instead used the non-parametric Wilcoxon rank-sum test. We used $p = 0.05$ to determine statistical significance throughout this study.

Additionally, data was collected daily from a climate station 5 km from the experiments throughout the study period (2017–2023). Climate conditions varied across the observation period from 2017 to 2023. There was one year of abundant precipitation (2019) and two drought years (2018 and 2023). Notably, 2018 was an extreme drought year with comparatively low precipitation until late summer. The other drought event in 2023 took place from May to late June, although after that the accumulated precipitation increased (Figure 3). Similarly, data on vapor pressure deficit (VPD) highlight 2018 and 2023 as dry years, with both maximum and mean VPD above average (Table 2).

Results

Seedfall varied across stands, overstory density treatments, and years. In 2020, seedfall at H17 (the fourth year after harvest) was significantly higher compared to H20 (first year after harvest; $p < 0.001$; Figure 4). Similarly, in 2023, seedfall at H20 (fourth year after harvest) was significantly higher compared to H23 (first year after harvest; $p = 0.029$; Figure 4).

Mechanical site preparation (MSP) had a strong positive effect on seedling recruitment during the first year after harvest ($p < 0.0001$). On undisturbed ground, the majority of seedling recruitment occurred within the first year following harvest (Table 3). In the subsequent years, there was minimal recruitment of new seedling cohorts, so only MSP treatments were investigated further.

In the first year following harvest, seedling recruitment on all three stands was significantly higher under the shelterwood treatment ($p = 0.039$) compared to clearcut areas (mean values 2.7 and 5.1 seedlings per m² for the clearcut and shelterwood, respectively). For seed trees there was a trend of higher recruitment (mean value 3.3 seedlings per m², $p = 0.069$) compared to clearcuts. However, three years after harvest for H17 and H20 there was no significant effect on recruitment under seed trees ($p = 0.364$) compared to clearcuts (Figure 5), while there was a trend for the shelterwood treatment ($p = 0.070$).

Recruitment of the third-year cohort under shelterwoods of both H17 and H20 was higher compared to clearcut areas ($p = 0.032$; Figure 5). In comparison, the third-year cohort under seed trees had only a tendency toward higher recruitment ($p = 0.051$). Moreover, comparing immediate and delayed MSP, we used 2020 and 2023 as pair years (H17 delayed compared with H20 immediate and H20 delayed with H23 immediate). MSP three years after harvest had a significant positive effect on the recruitment of seedlings under shelterwoods in 2020 ($p = 0.005$), compared to immediate MSP (Figure 6). However, this was not statistically significant effect under seed trees in 2020 ($p = 0.332$) or for any of the treatments in 2023 (Figure 6).

Discussion

In our study, seedfall varied greatly among overstory density treatments, years, and tested stands. For H17, the most

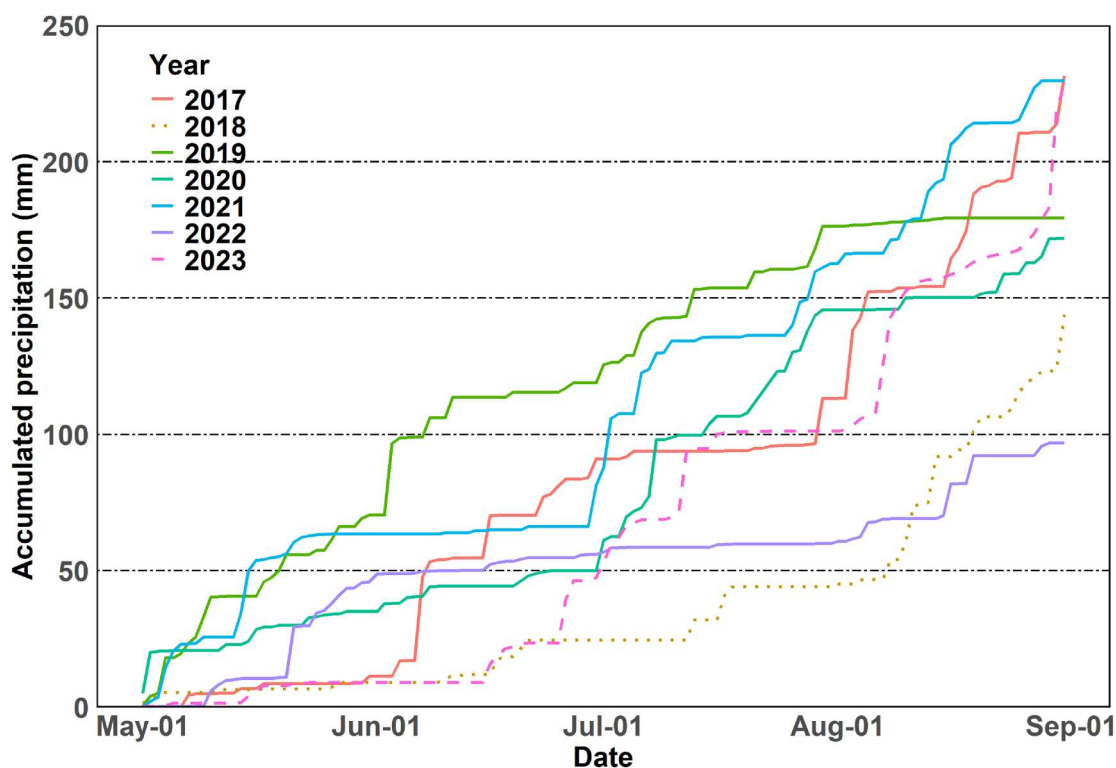


Figure 3. Accumulated precipitation (mm) from May to September for the study years 2017–2023. The drought years, 2018 and 2023, are indicated with dotted and dashed lines, respectively.

abundant seedfall occurred in the fourth year after harvest (Figure 4), in line with previous studies (Karlsson 2000; Karlsson 2006). This was likely due to increased sunlight intercepted by the crowns and reduced competition from neighboring trees. While we also see this release effect in H20, the highest seedfall overall occurred in the third year after release, 2022, reported as an abundant seed year in southern Sweden (NFI 2023).

Consistent with the literature (Beland et al. 2000; Karlsson et al. 2002; Karlsson and Nilsson 2005; Saurasunet et al. 2018), our study demonstrated that mechanical site preparation (MSP) significantly improved seedling recruitment regardless of overstory density treatment. On untreated ground, the majority of seedling recruitment occurred within the first year following harvest. In the subsequent years, there was minimal or no recruitment of new seedling cohorts (Table 3). Surprisingly, high seedling recruitment was observed on undisturbed ground in the first year after harvest in H17,

likely due to favorable weather conditions with particularly high precipitation in June. Moist conditions allow seedlings to colonize a broader range of seedbed substrates (Hanssen 2002). High germination rates of Scots pine seeds were previously noted on humus substrates under dense canopy cover when irrigation was applied (Oleskog and Sahlén 2000a).

Similarly, after MSP, the highest recruitment rates were observed in the first year following harvest. This result is consistent with other research which found that mineral soil enhances seed to soil contact, thus increasing accessibility to soil moisture, being the optimal substrate for seed germination (Löf et al. 2012). Observed lower recruitment rates in subsequent years were likely due to accumulation of organic matter, formation of biological soil crust (the first millimeters of topsoil), and soil surface erosion. However, an exception occurred in H20, where recruitment in the third year after harvest was higher compared to the first and second years, respectively (Figure 5). This was likely due to a combination of high seed fall in the third year and generally low recruitment in the first two years.

Further, the delayed MSP (before the growing season on the fourth year after harvest) had a significantly positive effect on seedling recruitment compared to MSP conducted immediately after the harvest in 2020, under shelterwood (Figure 6). This finding was consistent with the earlier research conducted in central Sweden (Karlsson and Örlander 2000), which indicated similar benefits of delayed MSP on seedling recruitment. These results supported the hypothesis that timing MSP to occur just before a substantial seedfall can

Table 2. Length of the growing season (referred to as the number of days with an average temperature exceeding 5°C), precipitation sum and vapor pressure deficit (VPD; May–June) for the study years 2017–2023.

Year	Length of the growing season (days)	Precipitation sum. May–June (mm)	Max VPD May–June (kPa)	Mean VPD May–June (kPa)
2017	220	84	2.22	0.61
2018	218	23	3.04	1.05
2019	201	119	2.24	0.59
2020	221	45	2.33	0.69
2021	212	66	3.03	0.78
2022	210	56	2.82	0.65
2023	218	46	3.54	1.01

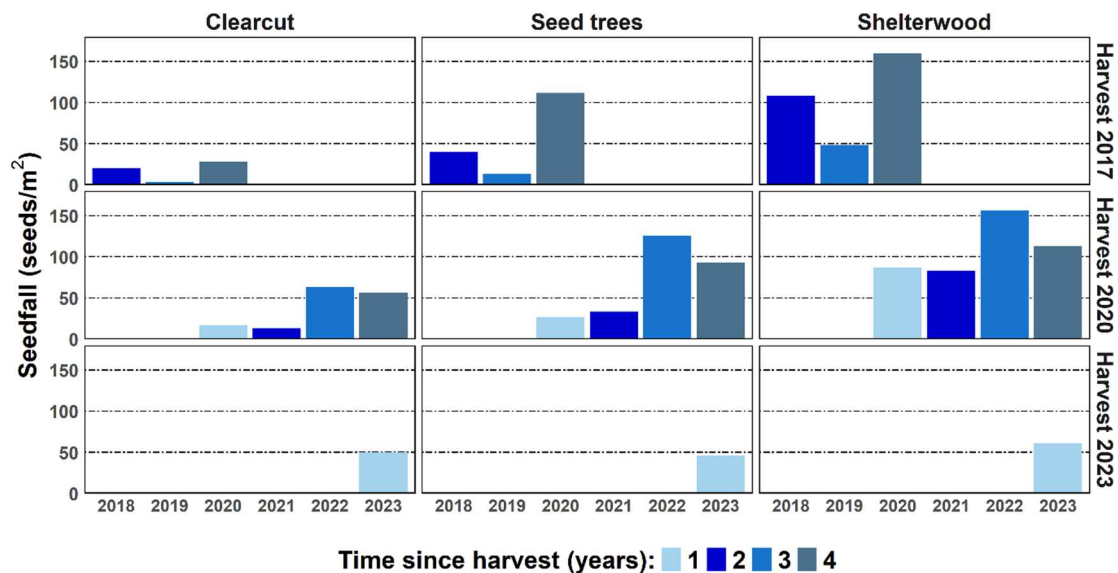


Figure 4. Seedfall (seeds/m²) during 2018–2023. The upper, middle and lower rows represent data from stands harvested in 2017, 2020 and 2023, respectively. Due to a sampling error, seedfall in 2017 was not collected.

significantly enhance seedling recruitment. However, longer monitoring of seedling survival is needed to confirm its effectiveness, as the seedlings may be outcompeted by ground vegetation over time. Moreover, results suggested that the method is sensitive to variation in environmental factors, as we did not see the effect replicated in 2023. Instead, seedling recruitment was comparatively low and not significantly increased by the delayed MSP treatment. The reason may be that the 2023 drought reduced germination in all MSP and overstory harvest treatments.

While overstory treatments had an effect on seedling recruitment in the first year after harvest, the effect was clearer under shelterwood than seed trees compared to clearcuts. This may be due to the varying microsite conditions established in the stand after harvest. Previous studies showed that increased overstory density positively affected seedling recruitment primarily due to increased seedfall and reduced competition from ground vegetation (Beland et al. 2000) as well as less pine weevil damage (Von Sydow and Örlander 1994). More stable conditions under shelterwoods in terms of soil moisture and temperature variations, may also contribute to higher seedling densities (Childs and Flint 1987; Blennow 1998; Langvall and Örlander 2001). Generally, results from this study align with previous investigations listed above, however, they varied greatly between the years and tested stands. For example, recruitment rates observed in the clearcuts were almost comparable with

those under the seed trees in all three harvest years (Figures 5 and 6). This was likely due to a relatively small clearcut (1 ha) and the proximity of clearcut blocks to the forest edge, which ensured a sufficient seed supply for successful germination.

While three years after harvest the effect of overstory treatment on total recruitment was not significant, we did see a significant positive effect of shelterwoods on recruitment of the 3rd year cohort. This result confirmed that slower aging of MSP under overstory allows seedling cohorts from several years to contribute to higher densities. By the end of the three-year observation period, the 2nd and 3rd year seedling cohorts constituted approximately half of the total population, irrespective of the overstory density treatment (Figure 5). However, mortality of these subsequent cohorts remains poorly studied, as is their contribution to the final stand. Previous research indicated gradual reduction of mortality of such seedlings 8 years after recruitment (Kyrö et al. 2022), but such long-term monitoring was outside the scope of this study. On the other hand, seedlings from subsequent cohorts may play an important role in the future stand, as they were expected to form high-quality stems. This is due to highly competitive growing conditions created by larger trees (Agestam et al. 1998).

Another important result of our study was the observed variation in recruitment between different stands and years. For example, there was a positive trend of increased overstory density on seedling recruitment at H17 which was not found for H20 or H23 (Figure 5 and 6). This may be due to differing stand characteristics, such as a higher proportion of rocks, contributing to poorer seedling recruitment. Similarly, in 2018, despite high seedfall, seedling recruitment was low due to a prolonged spring and summer drought. Extremely low precipitation and dry topsoil conditions hindered seed germination. In this case, overwintering seeds from 2018 may have contributed to the increased recruitment observed

Table 3. Recruitment of seedlings (seedlings per m²) originating from the first year's cohort without MSP in stands harvested in 2017 (H17), 2020 (H20), and 2023 (H23), respectively. Values shown are block means ± SE. There was no or minimal recruitment of seedlings originating from the second and third years' cohorts.

	H17	H20	H23
Clearcut	0.97 ± 0.49	0	0
Seed trees	3.82 ± 0.87	0	0.46 ± 0.46
Shelterwood	3.45 ± 2.2	0.46 ± 0.46	1.39 ± 0.8

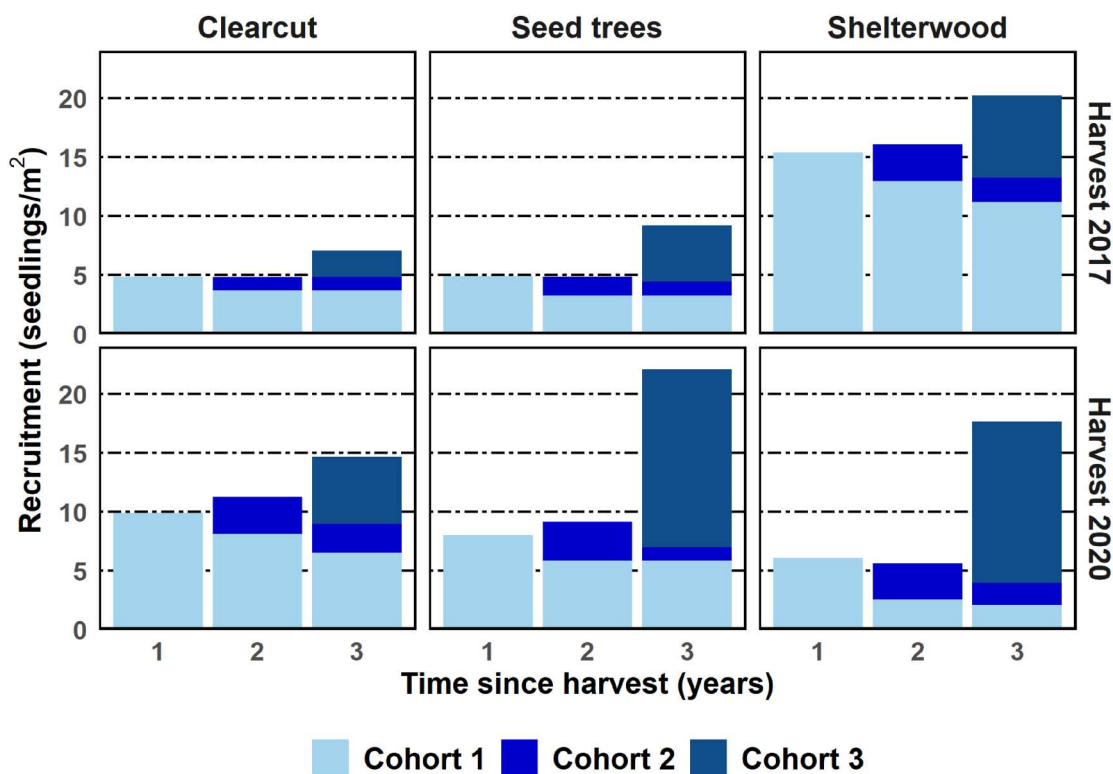


Figure 5. The number of seedlings (per m²) after mechanical site preparation. The upper and lower rows represent data from stands harvested in 2017 and 2020 (H17 & H20), respectively. Seedling cohorts originating from different years are represented by different colors according to the legend and correspond to seedfall colors in Figure 4.

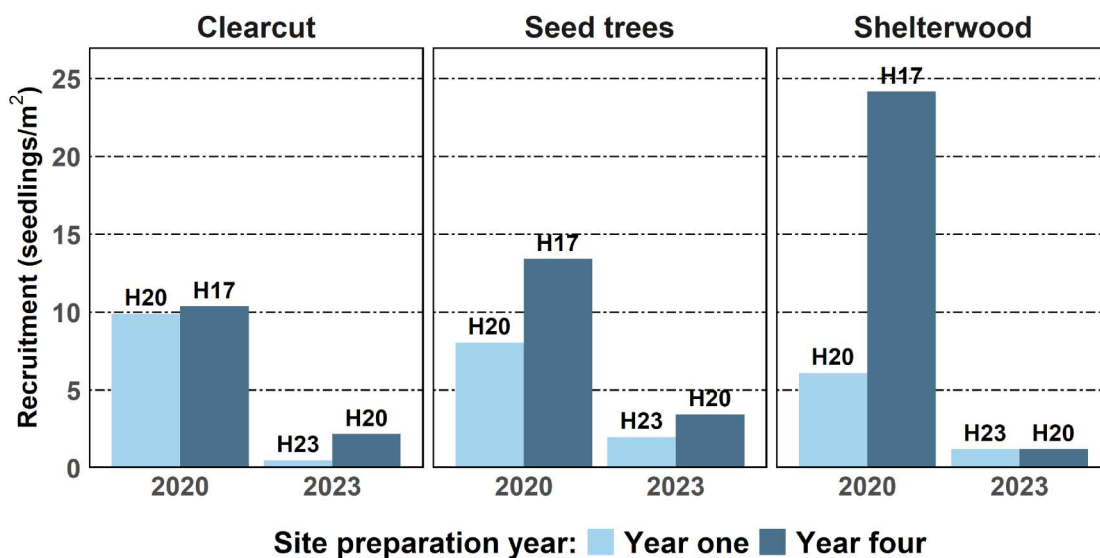


Figure 6. Recruitment of seedlings (per m²) after immediate and delayed mechanical site preparation (MSP) for clearcut, seed tree and shelterwood treatments. Years 2020 and 2023 were used as pair years (H17 delayed MSP with H20 immediate MSP and H20 delayed with H23 immediate). Immediate MSP was done in connection with harvesting and delayed MSP before the start of the growing season in the fourth year after harvest.

in 2019 despite relatively low seedfall (Figures 4 and 5). Winsa (1995) observed germination of overwintering seeds after being released from rain shelters in a study on the effects of moisture availability on Scots pine seedling emergence after direct seeding.

No damage to overstorey trees was recorded during the study, which was unexpected since wind throw is common

in seed trees stands and shelterwoods. The results represented an idealized scenario with no browsing by ungulates, a major concern for Scots pine regeneration in southern Sweden. The study's lack of statistically valid replicates and narrow range of site fertility mean the within-site response was not investigated. Therefore, we advise caution in interpreting and generalizing the results.

Conclusions

In conclusion, this study supported previous findings and practical recommendations, demonstrating that the combination of MSP with overstorey retention was an effective strategy for establishing dense, naturally regenerated Scots pine stands. However, the effectiveness of this approach was largely influenced by seasonal variation, a range of environmental factors, and site-specific characteristics. This underlined the importance of careful site selection and the application of local knowledge to mitigate possible regeneration failures.

Additionally, results from this study indicated that delaying MSP until just before the growing season in the fourth year after release harvest further enhanced seedling recruitment. However, to determine the practical viability of these methods in the region, extended monitoring is needed to assess the potential effects of competing ground vegetation on seedling survival.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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