



Birch establishes anywhere! So, what is there to know about natural regeneration and direct seeding of birch?

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Abstract

We tested three soil scarification approaches of varying intensity (intensive preparation exposing bare mineral soil, medium intensity with a mixture of organic material and mineral soil, and control without site preparation) on six clear-felled sites in two localities in northern and central Sweden between 2018 and 2021. The effect of soil scarification intensity and soil moisture on the occurrence of naturally regenerated birch seedlings was tested one, two and three years after soil scarification, and the density of direct-seeded birch seedlings one year after seeding. In addition, we tested the effect of the annual seed rain, and differences between the two birch species, on the density of direct-seeded seedlings. Soil scarification and its interaction with soil moisture had a significant positive effect on both the occurrence of naturally regenerated birch seedlings and the density of direct-seeded birch seedlings. There was no significant effect of neither annual natural seed rain nor species choice on direct-seeded seedling density. Time since soil scarification had a significant effect on the occurrence of naturally regenerated birch seedlings. In moist soils with high volumetric water content ($\geq 28\%$), birch seeds germinate at high rates and seedlings survive without soil scarification. In mesic soils, birch seeds germinate with higher rates after soil scarification. In dry soils, birch seeds rarely germinate regardless of any disturbance of the humus layer.

Keywords *Betula pendula* · *Betula pubescens* · Natural regeneration · Direct seeding · Soil moisture · Soil scarification

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Introduction

In northern Europe, the presence of naturally regenerated broadleaves in conifer plantations is an important aspect of sustainable forestry, and is emphasised in the relevant certification standards (FSC 2010, 2020). The most common broadleaves in Sweden are silver birch (*Betula pendula* Roth) and downy birch (*Betula pubescens* Ehr)¹ (Skogsdata 2021), which are shade-intolerant pioneer species (Hynynen et al. 2009). Birch is known to establish abundantly after disturbances like fire (Ascoli and Bovio 2010; Dzwonko et al. 2015), storms (Ilisson et al. 2007; Vodde et al. 2010) or clearfellings (Holgén and Hånell 2000; Götmark et al. 2005; Karlsson and Nilsson 2005). Birch in the boreal forest is important for several ecosystem services, in example provisioning wood for pulp, timber and bioenergy (Rytter 2004; Woxblom and Nylinder 2010; Felton et al. 2021; Lidman et al. 2021) or as fodder for ungulate foraging (Cederlund et al. 1980; Hörnberg 2001). In Sweden, it is common to find birch growing in mixtures with other species, particularly Norway spruce (*Picea abies* H. Karst.) (Holmström et al. 2021; Skogsdata 2021). There are many potential benefits of mixing birch into a conifer stand, higher biodiversity in the form of increased bird species richness and abundance (Felton et al. 2011, 2021; Lindbladh et al. 2017), and improved risk management (Felton et al. 2016; Huuskonen et al. 2021) are a few examples.

Sweden has 28.1 million hectares of forestland, 65% is actively managed with a rotation forestry method (Bergqvist et al. 2022). Of the one million hectares clear-felled between 2015–2020, 86% was regenerated by planting, usually with a conifer species (Skogsdata 2021; Skogsstyrelsen 2021). However, forest owners must strive for a proportion of 10 percent of broadleaf stems within conifer plantations, and manage five percent of their stands located on mesic and moist soils toward broadleaf dominance over the rotation period, to be certified according to FSC (2020). Accordingly, in Sweden today most young forests are mixtures (Ara et al. 2022), as are 30% of the older forests that are available for wood supply (Daesung et al. in prep.).

Birch is a prolific producer of small seeds, varying in quantity and quality from year-to-year, which are readily dispersed by wind over large areas (Koski and Tallqvist 1978; Holm 1994; Wagner et al. 2004; Ashburner and McAllister 2016). Birch readily regenerates naturally in Sweden (Götmark et al. 2005; Skogsdata 2021; Skogsstyrelsen 2021) at no cost to land managers (Karlsson and Nilsson 2005; Holmström et al. 2017). An even and not too low soil moisture is key for birch seeds to germinate (Sarvas 1948; Frivold 1986; Palo 1986). Silver birch grows best in dry, fine sandy and silty soils, and is more sensitive to flooding than downy birch. The less sensitive downy birch is more common on moist and compact soils, including peatlands (Raulo 1987; Sutinen et al. 2002; Mossberg and Stenberg 2018).

Even though birch establishes widely, certain conditions make some sites more suitable for natural regeneration of birch. In addition to soil moisture conditions, seed availability is crucial (Karlsson 2001; Holmström et al. 2016). Soil scarification can increase natural regeneration of birch by decreasing competition for water from other vegetation (Örlander et al. 1990; Johansson et al. 2013) and by exposing bare mineral soil which usually has higher and more constant moisture (Sarvas 1948; Marquis et al. 1964). On the other hand, soil scarification increases the cost of the regeneration with approximately 220 € per hectare (Skogsstyrelsen 2021). The choice of soil scarification must be adapted to the site,

¹ Unless specified, the term 'birch' in this paper refers to both species.

Table 1 Site characteristics. Soil moisture class (SMC) was assessed on site using the classification system by Hägglund and Lundmark (1981)

Site (locality and SMC)	Soil type	Dominating ground vegetation	Dominating tree species in the surrounding stands
Tierp Dry	Sorted sandy soil	Vaccinium shrubs	<i>Pinus sylvestris</i>
Vindeln Dry	Unsorted sandy soil	Vaccinium shrubs	<i>Pinus sylvestris</i>
Tierp Mesic	Unsorted sandy soil	Vaccinium shrubs and Grasses	<i>Pinus sylvestris</i>
Vindeln Mesic	Unsorted sandy soil	Vaccinium shrubs and Grasses	<i>Pinus sylvestris</i>
Tierp Moist	Unsorted sandy soil	Grasses and herbs	<i>Pinus sylvestris</i> & <i>Picea abies</i>
Vindeln Moist	Unsorted sandy soil	Grasses and herbs	<i>Pinus sylvestris</i> & <i>Picea abies</i>

otherwise the site preparation can instead increase the risk of seedling mortality (Örlander et al. 1990; Sutton 1993; Löf et al. 2012). It is therefore important to know when soil scarification is helpful to natural regeneration of birch.

This study aims to increase our understanding of soil scarification as a strategy for managing natural regeneration of birch in clear-felled areas, and how soil moisture conditions affect its outcomes. To pursue this aim we established a field trial to evaluate the performance of natural regeneration with birch seed from the surrounding forest, and direct seeding of birch, on freshly clear-felled areas. To account for variation in seed rain between years and time since soil scarification, the field trial was conducted for four years with new soil scarifications made every year the first three years. We evaluated the impact of scarification intensity and its interaction with soil moisture by measuring the occurrence of naturally regenerated birch seedlings and density of direct seeded birch seedlings.

Material and method

The field trial took place during 2018–2021, in two study localities representing different parts of Sweden. The first study locality was located outside Tierp in east central Sweden, at 60.34° N 17.51° E, and the second outside Vindeln in north eastern Sweden, at 64.22° N 19.64° E. Each study locality included three sites (Table 1) that had been clear-felled the previous year, and which offered the necessary range of soil moisture conditions: dry, mesic and moist. Specific definitions of the soil moisture classes are made by Hägglund and Lundmark (1981). The clear-felled sites varied between 7 and 44 hectares in size and the distance between clear-felled sites within a locality was maximum 20 km.

On each of the six sites, four blocks (10×10 m) of nine plots (1×1.5 m) were established, giving 36 plots per site, and 108 per locality. The blocks were sited between 10 and 70 m apart. There was at least five birches (old enough to produce seeds) within 200 m of each block. Each block was subjected to three soil scarification treatments: three plots per treatment, with the plots for each treatment selected randomly. The three soil scarification treatments tested were: “Mineral” which was patches of bare mineral soil where the humus layer was completely removed, “Mix” which was a mixture of mineral soil and organic material from the humus layer and “Control” which was plots of the same size as

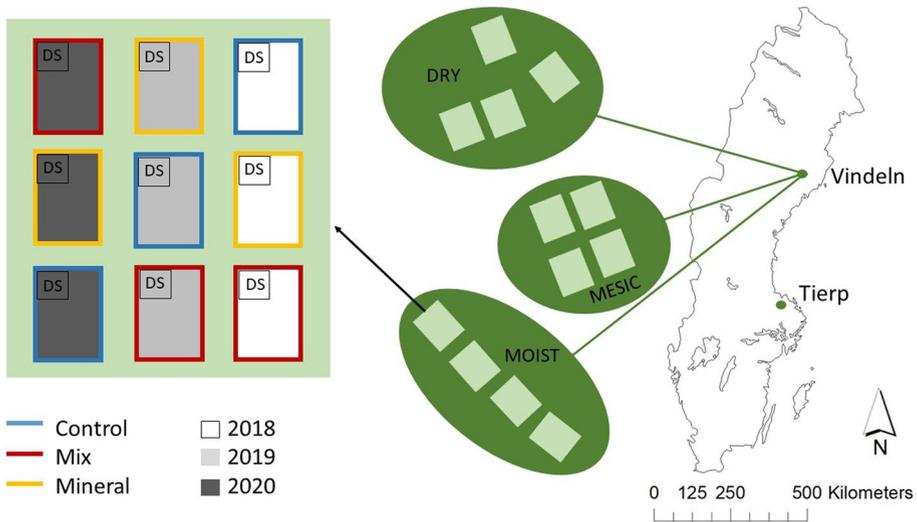


Fig. 1 Structure of the field trial with the two study localities Vindeln and Tierp, three sites within each locality, four blocks per site, nine plots per block including soil scarification treatments and location of the direct seeding (DS) subplots. The years indicate when scarification and direct seeding took place. Each plot is $1.5 \text{ m} \times 1 \text{ m}$, and the DS subplots are $0.5 \text{ m} \times 0.5 \text{ m}$. The soil scarification treatments were a control (Control), a mixture of organic material from the humus layer and mineral soil (Mix) and bare mineral soil (Mineral)

the treatments but without any soil scarification. At the start of the study in July 2018 all plots (except the control plots) were subject to soil scarification using an excavator. The Mineral and Mix treatments were repeated in one third of the plots in August 2019 and 2020 respectively, using a soil scarification spade. This was done in order to test the effect of time since soil scarification and to catch the annual variation in seed rain over the plots. To cover for years with low seed rain, a small area of each plot (referred to as a sub-plot, $0.5 \times 0.5 \text{ m}$) was directly seeded with 25 (in 2018) or 50 (in 2019 and 2020) silver and downy birch seeds on separate halves of the sub-plot. The seeding took place over the three years, with one third of all sub-plots being seeded each year, after the soil scarification (Fig. 1). No fencing or warding in order to prevent browsing of seedlings or predating of seeds were conducted.

Volumetric water content (VWC) was used as a continuous soil moisture variable. Soil moisture and temperature were constantly measured with a TEROS 11 sensor located in each combination of soil type and scarification during the growth season starting in the Summer of 2019. The soil sensors were placed 3 cm below the mineral soil surface and an electromagnetic field around the sensor measures the dielectric permittivity of the surrounding medium (in this case the soil). The dielectric permittivity was converted to volumetric water content (VWC) using the basic calibration equation provided by METER group. ZL6 loggers were used to record the data. All sensors and loggers were produced by METER group WA, USA (METER 2021). Twice a year during the vegetation period (in the end of June and in the beginning of september), an inventory of naturally regenerated (NR) and direct-seeded (DS) birch seedlings was carried out on each plot. The inventory measured seedlings originating from seeds only, excluding any which had clearly developed from root sprouts.

To correct for the possible occurrence of NR seedlings on the DS subplots, and to avoid over-estimating seed germination, the average number of NR seedlings per m² for each site and treatment type was subtracted from the average number of DS seedlings per m². Birch seed rain was monitored by placing 25 seed traps on each site, within 2–3 m around the blocks in July and emptying them in the autumn after seed fall. Each trap was circular, with a diameter of 61 cm and placed on poles approximately 1 m above the ground.

Data analysis

Naturally regenerated seedlings

The effects of soil scarification, VWC, and their interaction on the occurrence of NR seedlings in all plots were tested using a generalised linear model with a binomial error distribution (Eq. 1, Fig. 3):

$$Y_{NR} = treatment * VWC_s \quad (1)$$

Here $Y_{NR} = 1$ if the inventory in September 2021 noted one or more NR seedlings in the plot, and 0 if there were no NR seedlings. VWC_s , the average volumetric water content for each soil type in each site between 2019 and 2021, was used as a covariate, and the fixed factor *treatment* was one of three soil scarification treatments. Average seed rain per site was not included in the model since the variation in seed rain was larger within sites between years, than between sites within years (Fig. 4).

A second generalised linear model with a binomial distribution was used to test the effect of soil scarification, VWC, the interaction between the two, and the effect of time since soil scarification on the occurrence of NR seedlings in the scarified plots (Eq. 2.)

$$Y_{NR} = treatment * VWC_s + T \quad (2)$$

Here $Y_{NR} = 1$ if the inventory in September 2021 noted one or more NR seedlings in the plot, and 0 if there were no NR seedlings. VWC_s , the average volumetric water content for each soil type in each site between 2019 and 2021, was used as a covariate, and the fixed factor *treatment* was either the bare mineral soil treatment or the mixture of mineral soil and humus layer treatment. T was time in number of years, since soil scarification.

Direct-seeded seedlings

The effects of soil scarification, VWC, interaction between soil scarification and VWC, birch species, and annual seed rain on the density of DS seedlings were tested using a generalised linear mixed model with a zero-inflated Poisson distribution (Eq. 3), using the R package *glmmTMB* (Brooks et al. 2017).

$$Y_{DS} = treatment * VWC_y + species + seedrain + (1|block) \quad (3)$$

where Z_{i} formula = Site, Y_{DS} is the number of DS seedlings on a plot in September, one year after soil scarification and direct seeding. VWC_y is the average annual volumetric water content for each site. The four blocks within each site were a random factor, and the fixed factor *treatment* was one of three soil scarification treatments. The fixed factor *species* was either silver or downy birch, and the covariate *seed rain* was the average annual seed rain at the same site the year the inventory was carried out. The average annual seed rain from the

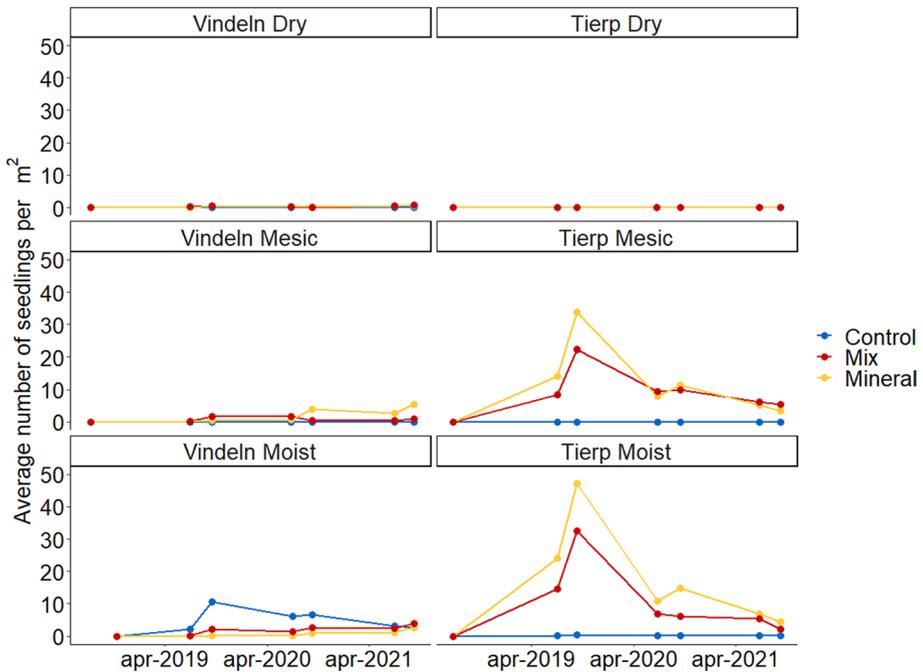


Fig. 2 Average number of naturally regenerated (NR) birch seedlings (*Betula pendula* and *Betula pubescens*) at each inventory, per square meter for three different soil scarification treatments on dry, mesic and moist sites in northern (Vindelns) and central (Tierps) Sweden, between 2018 and 2021 for plots that were soil scarified in 2018. The soil scarification treatments were a control (Control), a mixture of organic material from the humus layer and mineral soil (Mix) and bare mineral soil (Mineral)

year before the inventory was also tested in Eq. (3) but was excluded since it did not have a significant effect on the response variable. In addition, study area and site were tested as factors in Eq. (3), but were excluded to limit the number of parameters in the model, and because their inclusion did not improve the model's performance. Statistical tests were performed in R version 4.1.2. (R Core Team 2021). The packages *car* (Fox and Weisberg 2019) and *emmeans* (Lenth 2021) were used to perform variance analyses and statistical assessments of the differences between means.

Results

Naturally regenerated seedlings

The average occurrence of naturally regenerated birch seedlings was significantly higher in treated plots than in control plots three years after soil scarification, and the occurrence of seedlings significantly increased with soil moisture. There was also a significant positive effect on seedling occurrence from the interaction between soil moisture and soil scarification (Figs. 2, 3 Tables 2, 3, 4). On average the plots that were scarified in 2018 displayed higher seedling density than the control plots. The one exception to this was the moist site outside Vindelns in northern Sweden, which had the highest

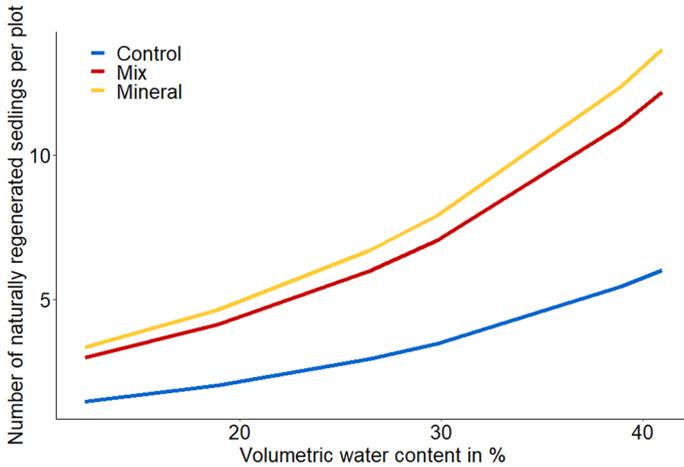


Fig. 3 Model predictions (Eq. 1) of number of naturally regenerated (NR) birch seedlings (*Betula pendula* and *Betula pubescens*) per plot, over the volumetric water content gradient, for each soil scarification treatment. The soil scarification treatments used were a control (Control), a mixture of organic material from the humus layer and mineral soil (Mix), and bare mineral soil (Mineral)

Table 2 Average number of naturally regenerated birch seedlings per m², locality, soil scarification treatment and soil moisture class (SMC), in 2021, one, two and three years after soil scarification

Site (locality and SMC)	Soil scarification	Number of naturally regenerated birch seedlings		
		1 year after Soil scarification	2 years after soil scarification	3 years after soil scarification
Tierp Dry	Control	0	0	0
	Mix	0	0	0
	Mineral	0	0	0
Vindeln Dry	Control	0	0	0
	Mix	0.2	7.1	2.2
	Mineral	0.4	3	1.7
Tierp Mesic	Control	0	0	0
	Mix	5.6	3.9	17.6
	Mineral	1.7	10.2	9.2
Vindeln Mesic	Control	0	0.2	0.2
	Mix	6.5	8.3	3.3
	Mineral	1.3	11.6	17.6
Tierp Moist	Control	0	0	0.3
	Mix	2.8	13	9.6
	Mineral	5.6	11.7	9.6
Vindeln Moist	Control	1.7	11.1	8.5
	Mix	7.2	17	12.8
	Mineral	0.2	19	8.7

The soil scarification treatments were a control (Control), a mixture of organic material from the humus layer and mineral soil (Mix) and bare mineral soil (Mineral)

Table 3 Analysis of variance (type II Wald χ^2 test) for occurrence of naturally regenerated birch (NR) seedlings per plot in September 2021, and density of direct-seeded (DS) birch seedlings per plot in September the year after soil scarification, with modelled estimates

Response variable	Predictor variables	Estimate	χ^2	df	p-value
NR seedling occurrence in all plots	VWC _s	0.311	41.87	1	<0.001
	Treatment	9.738 (Mix) 11.415 (Mineral)	52.11	2	<0.001
	VWC _s * Treatment	-0.176 (VWC _s *Mix) -0.254 (VWC _s *Mineral)	10.82	2	0.004
NR seedling occurrence in plots with Mix or Mineral treatment	VWC _s	0.064	26.98	1	<0.001
	Treatment	-1.704 (Mix)	1.24	1	0.265
	VWC _s * Treatment	0.082 (VWC _s *Mix)	3.81	1	0.051
	Time	0.762	10.12	2	0.001
DS seedling density in all plots	VWC _y	1.438e ⁻⁰¹	4.43	1	0.035341
	Treatment	7.201e ⁺⁰⁰ (Mix) 6.166e ⁺⁰⁰ (Mineral)	91.54	2	<0.001
	VWC _y * Treatment	-1.274e ⁻⁰¹ (VWC _y *Mix) -1.034e ⁻⁰¹ (VWC _y *Mineral)	12.34	2	0.002
	Birch species	-7.130e ⁻⁰² (<i>B.pendula</i>)	0.77	1	0.379
	Seed rain	9.855e ⁻⁰⁵	2.81	1	0.094

VWC_s = average growing season volumetric water content per site between 2019 and 2021. VWC_y = average growing season volumetric water content per year, for each site. Time = number of years since soil scarification. Birch species = *B. pendula* or *B. pubescens*. The soil scarification treatments were a control (Control), a mixture of organic material from the humus layer and mineral soil (Mix) and bare mineral soil (Mineral)

Table 4 Occurrence of naturally regenerated (NR) birch seedlings per plot in September 2021, and density of direct-seeded birch (DS) seedlings per plot in September the year after soil scarification

Response variable	Soil scarification treatment	EMMs	Significance
NR seedling occurrence	Control	-4.02	A
	Mix	0.30	B
	Mineral	0.80	B
DS seedling density	Control	-2.21	A
	Mix	1.44	B
	Mineral	1.07	C

Letters in the final column indicate significant differences among soil scarification treatments using estimated marginal means (EMM) within response variables at $p=0.05$. The soil scarification treatments were a control (Control), a mixture of organic material from the humus layer and mineral soil (Mix), and bare mineral soil (Mineral)

density of naturally regenerated seedlings until 2021. The dry sites displayed the lowest average seedling density, followed by the mesic and moist sites (Fig. 2). In addition, there was a significant positive effect of time since soil scarification on seedling occurrence, in the plots where soil scarification had taken place (Table 5).

Table 5 Amount of seedlings in the directly-seeded (DS) area as a percentage of the number of seeds sown, in September one year after seeding with *Betula pubescens* and *Betula pendula*, by site, soil scarification treatment, and year. All values above zero in bold to highlight the results

Site	Soil scarification			2020			2021		
	2019	2020	2021	Germination (%) <i>B. pubescens</i> / <i>B. pendula</i>	VWC (%)	Germination (%) <i>B. pubescens</i> / <i>B. pendula</i>	VWC (%)	Germination (%) <i>B. pubescens</i> / <i>B. pendula</i>	VWC (%)
Tierp dry	Control	15	0/0	0/0	12	0/0	10	0/0	10
Tierp dry	Mineral	15	0/4	2/0	12	2/0	10	0/0	10
Tierp dry	Mix	15	0/0	0/0	12	0/0	10	4/2	10
Tierp mesic	Control	21	0/0	0/0	17	0/0	18	0/0	18
Tierp mesic	Mineral	21	79/179	2/14	17	2/14	18	2/0	18
Tierp mesic	Mix	21	49/52	16/8	17	16/8	18	10/0	18
Vindel'n dry	Control	27	0/0	0/0	26	0/0	27	0/0	27
Vindel'n dry	Mineral	27	0/16	8/20	26	8/20	27	8/0	27
Vindel'n dry	Mix	27	20/67	30/16	26	30/16	27	1/0	27
Tierp moist	Control	28	12/4	0/2	29	0/2	32	4/0	32
Tierp moist	Mineral	28	81/64	9/21	29	9/21	32	12/11	32
Tierp moist	Mix	28	104/76	47/37	29	47/37	32	2/8	32
Vindel'n mesic	Control	41	8/0	0/0	38	0/0	37	0/2	37
Vindel'n mesic	Mineral	41	52/28	38/26	38	38/26	37	0/0	37
Vindel'n mesic	Mix	41	0/7	66/38	38	66/38	37	23/13	37
Vindel'n moist	Control	42	0/11	0/1	41	0/1	40	1/0	40
Vindel'n moist	Mineral	42	8/16	57/41	41	57/41	40	4/0	40
Vindel'n moist	Mix	42	43/47	5/15	41	5/15	40	40/16	40

The amount of DS seedlings was adjusted for the average NR seedling density per m and year, to avoid over-estimating seed germination. VWC =average growing season volumetric water content per site and year. The soil scarification treatments were a control (Control), a mixture of organicmaterial from the humus layer and mineral soil (Mix) and bare mineral soil (Mineral). The sites are listed in order of increasing VWC

The bold numbers are all %- values above 0, to make the table easier to read and to give the reader a clue of what the results in the table are

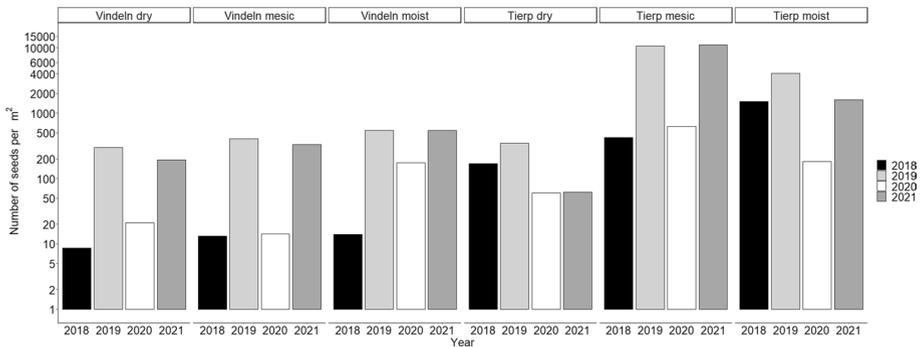


Fig. 4 Birch seed rain per m² for each site and year, with a logarithmic scale on the y-axis

Direct-seeded seedlings

Scarification creating patches with bare mineral soil resulted in a significantly higher average density of direct-seeded birch seedlings than the scarification with the mixed mineral and organic soil, which in turn produced a significantly higher seedling density than no scarification (Tables 3, 4). Soil moisture also had a significant effect on seedling density one year after seeding. As with naturally regenerated seedlings, there was a significant interaction between soil moisture and soil scarification on direct-seeded seedling density one year after seeding (Table 5). All direct-seeded seedlings found in the control plots one year after seeding were on sites with an average VWC of 28% or higher (Table 5). Birch species' densities did not differ significantly in the subplots by September one year after seeding (Tables 3, 5).

Seed rain varied between years and sites. For most sites the largest seed rain was recorded in 2019, but for a few sites the peak was in 2021 (Fig. 4). The annual seed rain did not have a significant effect on the seedling density in the subplots that were direct-seeded (Table 5).

Discussion

Soil scarification had a significant positive effect on both naturally regenerated (NR) seedling occurrence and direct-seeded (DS) seedling density (Table 5), which corresponds with the findings of previous studies (Raulo and Mälkonen 1976; Fries 1984; Perala and Alm 1990; Karlsson et al. 1998; Nilsson et al. 2002). DS seedling density increased significantly with increasing soil disturbance (Table 4), as found by Holmström et al. (2016) and Saurasunet et al. (2018). Likewise, the significantly positive effect of soil moisture on NR seedling occurrence and DS seedling density (Fig. 2, Tables 1, 3), aligns with the results of previous studies (Fries 1984; Frivold 1986). Further, there was a significant effect on NR seedling occurrence and DS seedling density from the interaction between soil scarification and soil moisture (Table 5). This is probably because the soil scarification itself decreases competition from other vegetation (Löf et al. 2012; Johansson et al. 2013), making water and other resources more available to new seedlings.

Some contrasting results emerged from the moist site in Vindeln. There, soil scarification was negatively associated with the density of NR birch seedlings (Fig. 2). Similar results were found by Karlsson et al. (1998), who showed that soil scarification on mesic soil produced a higher density of birch seedlings than soil scarification on moist soil. One explanation for why soil scarification on the moist site in Vindeln (Fig. 2.) had a negative effect on NR seedling density, in contrast to the plots without soil scarification, is most likely that the site was too wet, depriving the seedlings of sufficient oxygen (Örlander et al. 1990). This suggests that the type of soil scarification used in this instance only is beneficial up to a certain level of soil moisture. At the same time, DS seedlings only seemed to establish on sites without soil scarification that had an average VWC of 28% or higher (Table 5). The modelled predictions of NR seedling occurrence showed a clear increase at around the same VWC percentage (Fig. 3). This implies that in order to obtain a substantial NR seedling occurrence, there is no need for soil scarification on moist sites, whereas soil scarification can be recommended on mesic sites, although soil scarification will not ensure NR seedling occurrence on dry sites. Time since soil scarification did have a significant positive effect on naturally regenerated birch seedling occurrence (Table 5), contradicting the results of Saurasunet et al. (2018), where no such effect was found with respect to birch, although they did find a significant positive effect on naturally regenerated seedling density of Scots pine. A possible explanation for this is given by Saurasunet et al. (2018), who suggests that more years of seed rain has been able to fall and establish, on the sites that were first scarified, than on those which were scarified more recently.

In this study, no differences in DS seedling germination were found between the two species of birch. There was no significant effect of seed rain from the birches in the surrounding stands, on seedling density in the subplots that were directly seeded (Table 5). However, there was considerable variation in seed rain between sites and years (Fig. 4). The heavy seed rain in 2019 was expected because of a warm summer in 2018 (SMHI 2018), which is known to favour birch seed production the following year (Gallego Zamorano et al. 2018). Large variations in seed rain within sites between years are common (Koski and Tallqvist 1978; Karlsson 2003).

This study offers several useful pointers for forest management and natural regeneration of birch. How many seedlings one needs to have a successful natural regeneration differs depending on the goals of the forest owner, i.e. if the wish is to increase the amount of birch in a conifer stand for biodiversity purposes or to create a birch monoculture. According to the Swedish Forestry Act a clear-felled area needs at least 1000–1500 seedlings per hectare (depending on the site conditions), to be approved as a successful regeneration (Skogsstyrelsen 2019). Although, if a forest owner wants to produce quality timber of naturally regenerated birch, the double amount of seedlings would be a more suitable goal in order to increase the selection of stems (Yrjölä 2002; Hynynen et al. 2009). Even though there is a significant effect of soil moisture and soil scarification on NR seedling occurrence and DS seedling density, the effect on the future stand might not be significant in the end. To have more than one seedling per square meter might not be significantly better than to have one seedling per square meter when the seedlings outcompete each other anyway in a few years, due to that the birch is shade intolerant (Nygren and Kellomäki 1983; Hynynen et al. 2009).

In terms of predicting the natural regeneration of birch the most useful starting point is perhaps to consider the seed rain from the surrounding landscape (Holmström et al. 2017). Then, when choosing if to carry out soil scarification and which type, soil moisture conditions should be taken into consideration as there is an interaction between the two

(Table 5). On dry sites birch seedlings may not establish at all, even if soil scarification is carried out (Fig. 2, Table 2). At the same time, planting conifer seedlings in moist or wet soil risks seedling mortality because of oxygen deficiency in standing water (Örlander et al. 1990; Holmström et al. 2019). Based on our detailed insight into when soil scarification is effective or not, and our findings that birch seeds both germinate and survive well without soil scarification when soil moisture is high (VWC > 28%), we suggest that natural regeneration of birch can replace costly planting on moist sites, while also minimizing soil disturbance. If natural birch regeneration is desired also on mesic sites, soil scarification is recommended. However, it should be taken into consideration that natural regeneration increases the uncertainty in the outcome (Jonsson et al. 2022), and there is no improvement of the genetic material, which is something that you can expect from nursery seedlings (Stener and Jansson 2005).

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Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article. The datasets generated during the current study are available from the corresponding author on reasonable request.

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References

- Sarvas R (1948) Tutkimuksia koivun uudistumisesta Etelä-Suomessa [A research on the regeneration of birch in South Finland]. *Commun Inst Forestalis Fenniae* 35:91
- Ara M, Barbeito I, Kalén C, Nilsson U (2022) Regeneration failure of Scots pine changes the species composition of young forests. *Scand J for Res* 37:14–22
- Ascoli D, Bovio G (2010) Tree encroachment dynamics in heathlands of north-west Italy: the fire regime hypothesis. *iForest-Biogeosciences and Forestry* 3:137. <https://doi.org/10.3832/ifor0548-003>
- Ashburner K, McAllister HA (2016) The genus *Betula*: a taxonomic revision of birches. Reprinted with corrections, 2016. Kew publishing
- Bergqvist J, Eriksson A, Nilsson C, Paulsson J, Pettersson J, Roberge J-M (2022). Skogens utveckling och brukande. Skogliga konsekvensanalyser: Online
- Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9:378–400
- Cederlund G, Ljungqvist H, Markgren G, Stålfelt F (1980) Foods of moose and roe-deer at Grimsö in Central Sweden - results of rumen content analysis. *Swedish Wildlife Res Viltrevy* 11:167–247

- Dzwonko Z, Loster S, Gawroński S (2015) Impact of fire severity on soil properties and the development of tree and shrub species in a Scots pine moist forest site in southern Poland. For Ecol Manage 342:56–63. <https://doi.org/10.1016/j.foreco.2015.01.013>
- Felton A, Andersson E, Ventorp D, Lindbladh M (2011) A comparison of avian diversity in spruce monocultures and spruce-birch polycultures in Southern Sweden. Silva Fennica 45:1143–1150
- Felton A, Nilsson U, Sonesson J, Felton AM, Roberge J-M, Ranius T, Ahlström M, Bergh J, Björkman C, Boberg J (2016) Replacing monocultures with mixed-species stands: ecosystem service implications of two production forest alternatives in Sweden. Ambio 45:124–139. <https://doi.org/10.1007/s13280-015-0749-2>
- Felton A, Hedwall P-O, Trubins R, Lagerstedt J, Felton A, Lindbladh M (2021) From mixtures to monocultures: bird assemblage responses along a production forest conifer-broadleaf gradient. For Ecol Manag 494:119299. <https://doi.org/10.1016/j.foreco.2021.119299>
- Fox J, Weisberg S (2019) An R companion to applied regression. Sage, Thousand Oaks
- Fries C (1984) Den frösådda björkens invandring på hygget. Sveriges Skogsvårdsförbunds Tidskrift 82 (3/4): 35–49: Swedish
- Frivold L (1986) Natural regeneration of birch and Norway spruce on clearfelled areas in the East Norwegian lowlands in relation to vegetation type and moisture. Meddelelser fra Norsk Institutt for Skogforskning 39
- FSC (2010) FSC Standard for Finland: Finnish FSC Association
- FSC (2020) The FSC National Forest Stewardship Standard of Sweden FSC-STD-SWE-03-2019 EN. Forest Stewardship Council
- Gallego Zamorano J, Hokkanen T, Lehikoinen A (2018) Climate-driven synchrony in seed production of masting deciduous and conifer tree species. J Plant Ecol 11:180–188. <https://doi.org/10.1093/jpe/rtw117>
- Götmark F, Fridman J, Kempe G, Norden B (2005) Broadleaved tree species in conifer-dominated forestry: regeneration and limitation of saplings in southern Sweden. For Ecol Manage 214:142–157. <https://doi.org/10.1016/j.foreco.2005.04.001>
- Holgén P, Hånell B (2000) Performance of planted and naturally regenerated seedlings in *Picea abies*-dominated shelterwood stands and clearcuts in Sweden. For Ecol Manage 127:129–138. [https://doi.org/10.1016/S0378-1127\(99\)00125-5](https://doi.org/10.1016/S0378-1127(99)00125-5)
- Holm SO (1994) Reproductive patterns of *Betula pendula* and *B. pubescens* coll. along a regional altitudinal gradient in northern Sweden. Ecography 17:60–72
- Holmström E, Hjelm K, Johansson U, Karlsson M, Valkonen S, Nilsson U (2016) Pre-commercial thinning, birch admixture and sprout management in planted Norway spruce stands in South Sweden. Scand J for Res 31:56–65. <https://doi.org/10.1080/02827581.2015.1055792>
- Holmström E, Karlsson M, Nilsson U (2017) Modeling birch seed supply and seedling establishment during forest regeneration. Ecol Model 352:31–39. <https://doi.org/10.1016/j.ecolmodel.2017.02.027>
- Holmström E, Gållander H, Petersson M (2019) Within-site variation in seedling survival in Norway spruce plantations. Forests 10:181. <https://doi.org/10.3390/f10020181>
- Holmström E, Carlström T, Goude M, Lidman FD, Felton A (2021) Keeping mixtures of Norway spruce and birch in production forests: insights from survey data. Scand J For Res 1–9. <https://doi.org/10.1080/02827581.2021.1883729>
- Huuskonen S, Domisch T, Finér L, Hantula J, Hynynen J, Matala J, Miina J, Neuvonen S, Nevalainen S, Niemistö P (2021) What is the potential for replacing monocultures with mixed-species stands to enhance ecosystem services in boreal forests in Fennoscandia? For Ecol Manag 479:118558. <https://doi.org/10.1016/j.foreco.2020.118558>
- Hynynen J, Niemistö P, Viherä-Aarnio A, Brunner A, Hein S, Velling P (2009) Silviculture of birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.) in northern Europe. Forestry 83:103–119. <https://doi.org/10.1093/forestry/cpp035>
- Hägglund B, Lundmark J-E (1981) Handledning i bonitering med Skogshögskolans boniteringssystem. D. 1, Definitioner och anvisningar. Skogsstyrelsen
- Hörnberg S (2001) The relationship between moose (*Alces alces*) browsing utilisation and the occurrence of different forage species in Sweden. For Ecol Manage 149:91–102. [https://doi.org/10.1016/S0378-1127\(00\)00547-8](https://doi.org/10.1016/S0378-1127(00)00547-8)
- Ilisson T, Köster K, Vodde F, Jögiste K (2007) Regeneration development 4–5 years after a storm in Norway spruce dominated forests, Estonia. For Ecol Manage 250:17–24. <https://doi.org/10.1016/j.foreco.2007.03.022>
- Johansson K, Ring E, Hogbom L (2013) Effects of pre-harvest fertilization and subsequent soil scarification on the growth of planted *Pinus sylvestris* seedlings and ground vegetation after clear-felling. Silva Fennica 47. <https://doi.org/10.14214/sf.1016>

- Jonsson A, Elfving B, Hjelm K, Lämås T, Nilsson U (2022) Will intensity of forest regeneration measures improve volume production and economy? *Scand J for Res* 37:200–212
- Karlsson A, Albrektson A, Forsgren A, Svensson L (1998) An analysis of successful natural regeneration of downy and silver birch on abandoned farmland in Sweden. *Silva Fennica* 32:229–240
- Karlsson M (2001) Natural regeneration of broadleaved tree species in Southern Sweden. Doctoral thesis, Swedish university of Agricultural Sciences, Alnarp
- Karlsson M (2003) Naturlig förnygring av björk i södra sverige. Fakta skog. Swedish Univeristu of Agricultural Sciences Umeå
- Karlsson M, Nilsson U (2005) The effects of scarification and shelterwood treatments on naturally regenerated seedlings in southern Sweden. *For Ecol Manage* 205:183–197. <https://doi.org/10.1016/j.foreco.2004.10.046>
- Koski V, Tallqvist R (1978) Results of long-time measurements of the quantity of flowering and seed crop of forest trees. *Folia Forestalia* 364:1–60
- Lenth RV (2021) Emmeans: estimated marginal means, aka least-squares means
- Lidman FD, Holmström E, Lundmark T, Fahlvik N (2021) Management of spontaneously regenerated mixed stands of birch and Norway spruce in Sweden. *Silva Fennica* 55:19. <https://doi.org/10.14214/sf.10485>
- Lindbladh M, Lindström Å, Hedwall P-O, Felton A (2017) Avian diversity in Norway spruce production forests—How variation in structure and composition reveals pathways for improving habitat quality. *For Ecol Manage* 397:48–56. <https://doi.org/10.1016/j.foreco.2017.04.029>
- Löf M, Dey DC, Navarro RM, Jacobs DF (2012) Mechanical site preparation for forest restoration. *New for* 43:825–848. <https://doi.org/10.1007/s11056-012-9332-x>
- Marquis DA, Björkbohm JC, Yelenosky G (1964) Effect of seedbed condition and light exposure on paper birch regeneration. *J Forest* 62:876–881
- METER (2021) TEROs 11/12, 18225–05. METER Group, Inc. : WA, USA
- Mossberg B, Stenberg L (2018) Nordens flora. Bonnier fakta
- Nilsson U, Gemmel P, Johansson U, Karlsson M, Welander T (2002) Natural regeneration of Norway spruce, Scots pine and birch under Norway spruce shelterwoods of varying densities on a mesic-dry site in southern Sweden. *For Ecol Manage* 161:133–145. [https://doi.org/10.1016/S0378-1127\(01\)00497-2](https://doi.org/10.1016/S0378-1127(01)00497-2)
- Nygren M, Kellomäki S (1983) Effect of shading on leaf structure and photosynthesis in young birches, *Betula pendula* Roth. and *B. pubescens* Ehrh. *For Ecol Manage* 7:119–132. [https://doi.org/10.1016/0378-1127\(83\)90024-5](https://doi.org/10.1016/0378-1127(83)90024-5)
- Örlander G, Gemmel P, Hunt J (1990) Site preparation: a Swedish overview. BC Ministry of Forests
- Palo I (1986) Björkfröets groning och björkplantors etablering - Litteraturstudie. [Birch seed germination and establishment of birch seedlings - Litterature study]. Institutionen för skogsskötsel, Sveriges Lantbruksuniversitet: Umeå
- Perala DA, Alm AA (1990) Regeneration silviculture of birch: a review. *For Ecol Manage* 32:39–77. [https://doi.org/10.1016/0378-1127\(90\)90105-K](https://doi.org/10.1016/0378-1127(90)90105-K)
- R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing. <https://www.R-project.org/>. Accessed
- Raulo J, Mälkonen E (1976). Natural regeneration of birch on tilled mineral soil. *Folia Forestalia* 252. Institutum Forestale Fenniae: Helsinki
- Raulo J (1987) Björkboken [The birch book]. Skogsstyrelsen: Jönköping
- Rytter L (2004) Produktionspotential hos asp, björk och al - en litteraturstudie över möjligheter till och konsekvenser av biomassa- och gagnvirkesuttag. [Production potentials of aspen, birch and alder: a review on possibilities and consequences of harvest of biomass and merchantable timber.]. Redogörelse. Skogforsk: Uppsala
- Saurasunet M, Mathisen KM, Skarpe C (2018) Effects of increased soil scarification intensity on natural regeneration of scots Pine *Pinus sylvestris* L. and Birch *Betula* spp. L. *Forests* 9:262. <https://doi.org/10.3390/f9050262>
- Skogsdata (2021) Skogsdata 2021: aktuella uppgifter om de svenska skogarna från SLU Riksskogstaxeringen [Forest statistics 2021: current data about the Swedish forests, from SLU, The Swedish national forest inventory] 0280–0543. SLU: Umeå, Sweden
- Skogsstyrelsen (2019) Skogsvårdslagstiftningen [The swedish Forestry Act]. Jönköping, Sweden: Skogsstyrelsen
- Skogsstyrelsen (2021) Statistikdatabas. <https://www.skogsstyrelsen.se/en/statistics/statistical-database/>. Accessed 20 June 2022

- SMHI (2018) Swedens Meterological and hydrological Institute. Månadens väder och vatten i Sverige [Monthly weather and water in Sweden]. <https://www.smhi.se/klimat/klimatet-da-och-nu/manadens-vader-och-vatten-sverige?query=2018&doSearch=&searchSortField=relevance#>
- Stener L-G, Jansson G (2005) Improvement of *Betula pendula* by clonal and progeny testing of phenotypically selected trees. *Scand J for Res* 20:292–303. <https://doi.org/10.1080/02827580510036265>
- Sutinen R, Teirilä A, Päänttjä M, Sutinen M-L (2002) Distribution and diversity of tree species with respect to soil electrical characteristics in Finnish Lapland. *Can J for Res* 32:1158–1170. <https://doi.org/10.1139/x02-076>
- Sutton R (1993) Mounding site preparation: a review of European and North American experience. *New for* 7:151–192
- Vodde F, Jogiste K, Gruson L, Ilisson T, Köster K, Stanturf JA (2010) Regeneration in windthrow areas in hemiboreal forests: the influence of microsite on the height growths of different tree species. *J for Res* 15:55–64. <https://doi.org/10.1007/s10310-009-0156-2>
- Wagner S, Wälder K, Ribbens E, Zeibig A (2004) Directionality in fruit dispersal models for anemochorous forest trees. *Ecol Model* 179:487–498. <https://doi.org/10.1016/j.ecolmodel.2004.02.020>
- Woxblom L, Nylinder M (2010) Industrial utilization of hardwood in Sweden. *Ecol Bull*, 43–50
- Yrjölä T (2002) Forest management guidelines and practices in Finland, Sweden and Norway. Internal report No. 2. European Forest Institute Sweden and Norway: Finland

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