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Regeneration methods and long-term production for Scots pine on medium fertile and fertile sites

Mikolaj Lula

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Mikolaj Lula
Faculty of Forest Science
Southern Swedish Forest Research Centre
Alnarp

SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES

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Abstract

Tree species choice is a central issue for forest management, and survey studies show that urgent improvements in regeneration practices are needed in Sweden. Most Swedish forest is regenerated with Scots pine (*Pinus sylvestris* L.) or Norway spruce (*Picea abies* (L.) H. Karst). However, direct yield comparisons of the two species are rare. The first objective of this thesis was to compare productivity of Scots pine and Norway spruce stands across latitude and fertility gradients in Sweden. To do so, long-term field experiments were combined with modelling in Heureka. In contrast to general perceptions and a majority of previous findings, Scots pine was more productive not only on poor sites but also on medium-fertile to fertile sites (Paper I). The second objective of this thesis (Papers II-IV) was to investigate the potential for cultivating Scots pine on medium-fertile to fertile sites. Effects of planting, natural regeneration and direct seeding were compared in terms of short-term regeneration outcomes, long-term volume production and financial revenue. This was done using empirical field experiments and simulations in Heureka. Results indicated that Scots pine may be successfully regenerated even on medium- to fertile sites. However, regeneration via planting was more reliable than natural regeneration or direct seeding. Natural regeneration and direct seeding generally had less certain outcomes, mainly because key processes such as seed production and germination depend on weather conditions. Experimental results confirm earlier findings that mechanical site preparation (MSP) increases both survival and growth of planted seedlings. For natural regeneration and direct seeding, MSP improves seeds' germination and seedlings' survival and growth. For planted seedlings, reduced pine weevil damage probably helped increased survival whereas reduced competition from ground vegetation helped natural regeneration and direct seeding. Dense shelterwoods had slower seedling growth. However, inexpensive regeneration and income from shelter trees made profit from natural regeneration in shelterwoods only slightly lower than planting on clearcuts.

Keywords: *Pinus sulvestris*, *Picea abies*, growth and yield, planting, natural regeneration, direct seeding, pine shelterwood, growth simulation, profitability of regeneration method

Föryngringsmetoder och långsiktig tillväxt för tall på medelgoda och goda ståndorter

Sammanfattning

Valet av trädslag vid föryngring av svenska hyggen står oftast mellan gran och tall. Det är dock ont om vetenskapliga studier där produktionen av de två trädslagen jämförs på samma lokaler. Det första syftet var därför att jämföra produktion hos gran och tall i latitud- och bördighetsgradienter. För detta kombinerades data från långsiktiga försök med produktionsprognoser i Heureka. Till skillnad mot många tidigare studier visade resultaten att tall hävdar sig produktionsmässigt väl mot gran på relativt bördiga lokaler. Avhandlingens andra syfte var därför att studera föryngring av tall på bördiga marker. Med hjälp av data från föryngringsförsök och simulering med Heureka jämfördes föryngringsmetoderna plantering, naturlig föryngring och sådd både med avseende på kortsiktiga effekter på plantöverlevnad och tidig tillväxt och långsiktiga effekter på produktion och ekonomi. Resultaten indikerade att tall kan föryngras på relativt bördiga ståndorter. Plantering var dock en mer robust metod jämfört med sådd och naturlig föryngring. De två sistnämnda metoderna var mindre förutsägbara eftersom groning och etablering av groddplantor är beroende av årsmån. Resultat från studierna verifierade tidigare resultat att markberedning både ökar överlevnad och tidig tillväxt för planterade plantor och är positiv för groning och etablering av naturlig föryngring och sådd. För de planterade plantorna var troligen minskade skador av snytbagge en viktig anledning till högre överlevnad efter markberedning medan minskad konkurrens från markvegetation också var viktigt för naturlig föryngring och sådd. Plantornas tillväxt påverkades negativt av täta skärmar men på grund av låga föryngringskostnader och inkomster vid avverkning av skärmträden var det ekonomiska utfallet under hela omloppstiden obetydligt lägre för naturlig föryngring under skärm jämfört med plantering.

Keywords: *Pinus sulvestris*, *Picea abies*, tillväxt, plantering, naturlig föryngring, sådd, tallskärm, tillväxt simulering, föryngringsmetoders ekonomi

Dedication

To my Mother and Father

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Lula, M., Zvirgzdins, A., Trubins, R., Johansson, U., Liziniewicz, M., Nilsson, O., Nilsson, U. Productivity of Norway spruce and Scots pine in Sweden (manuscript)

II. Lula, M., Andersson, M., Hjelm, K., Johansson, U., Wallertz, K., Nilsson, U. Recruitment, survival and early development of naturally-regenerated and direct -seeded Scots pine under varying shelterwood densities (manuscript)

III. Lula, M., Andersson, M., Hjelm, K., Johansson, U., Wallertz, K., Nilsson, U. Survival and early growth of planted seedlings under varying shelterwood densities (manuscript)

IV. Lula, M., Trubins, R., Ekö, PM., Johansson, U., Nilsson, U. (2021). Modelling effects of regeneration method on the growth and profitability of Scots pine stands. Scandinavian Journal of Forestry Research, 36 (4),263-274.

Paper IV is reproduced with the permission of the publishers.

The contribution of Mikolaj Lula to the papers included in this thesis was as follows:

I. Developed the research idea together with co-authors and performed parts of the fieldwork. Compiled and analysed the data. Wrote the manuscript in collaboration with the co-authors.

II. Developed the research idea together with co-authors and collected all the field data. Compiled and analysed the data. Wrote the manuscript in collaboration with the co-authors.

III. Developed the research idea together with co-authors and collected all the field data. Compiled and analysed the data. Wrote the manuscript in collaboration with the co-authors.

IV. Developed the research idea together with co-authors. Compiled and analysed the data. Wrote the manuscript in collaboration with the co-authors.

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Abbreviations

DBH	Diameter at breast height
DSSs	Decision support system
LEV	Land expectation value (euro ha^{-1})
MAI	Mean annual increment (m^{-3} ha^{-1} $year^{-1}$)
MAI_{max}	Culmination of mean annual increment (m^{-3} ha^{-1} $year^{-1}$)
MSP	Mechanical site preparation
SI_H	Site index estimated from height (m)
SI_S	Site index estimated from site properties (m)

1. Introduction

Scots pine (*Pinus sylvestris* L.) is the most widely -distributed coniferous in the world (Mirov, 1967) and the second most important commercial tree species in Sweden after Norway spruce (*Picea Aabies* L.). However, the share of Scots pine in regenerations in Sweden has changed alarmingly during the last two decades. Currently, Scots pine is a dominant regeneration tree species in the north, whereas use of Norway spruce in the south (Götaland) far exceeds other tree species (SFA, 2021). Forest owners' perceptions of the uncertainty of regeneration outcomes have been identified as one of the main factors behind this trend (Lodin et al., 2017). Recent survey studies have shown that regardless of geographical region, Scots pine is rarely the species of future crop trees in young stands in Sweden (Ara et al., 2021). In addition, the use of natural regeneration has substantially decreased from approximately 40% down to 10% of the total regeneration area in Sweden since the year 2000, whereas the use of direct seeding has remained limited (<5%) (SFA, 2018). In Sweden, both methods are primarily used in Scots pine regenerations.

1.1 Tree species choice

The optimal tree species choice in relation to site properties is fundamental for sustainable forest management. In Sweden, the issues of wrong or suboptimal tree species choice has received considerable attention (Lodin, 2020; Nilsson, 2020; Petersson, 2019). In a study of southern Sweden, Lodin et al. (2017) investigated drivers underlying forest owners' choice of species. They concluded that Norway spruce was the preferred regeneration tree species mainly due to its perceived superior profitability and documented lower browsing rates compared to Scots pine or broadleaved trees. The same study indicated that Scots pine is perceived as well-suited to low fertility sites. In spite of this, Norway spruce is prevalent in regenerations of low fertility sites in southern Sweden (Figure 1).

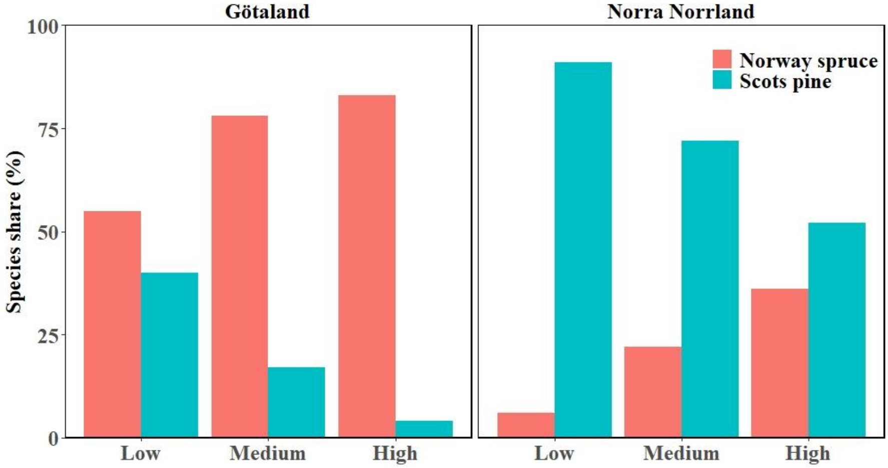

Figure 1. Species share (Norway spruce and Scots pine) of the total regeneration area in Götaland (southern Sweden) and Norra Norrland (northern Sweden) on low-, medium- and high-fertility sites (SFA, 2021).

The use of Norway spruce on low-fertility sites may contribute to reduced stand-level growth and yield (Holmström et al., 2018; Nilsson et al., 2012). This in turn may lead to substantial financial losses. However, there have been only a few experimental studies which compare these two species growing on the same sites (Drössler et al., 2018; Holmström et al., 2018; Nilsson et al., 2012). Furthermore, based on practical experience, the risk of damage is believed to increase for Norway spruce when growing on dry, nutrient-poor sites. Norway spruce suffers from storm damage, drought, frost, root rot (*Heterobasidion annosum)* and bark beetle (*Ips typographus*) (Honkaniemi et al., 2017; Laurent et al., 2003; Langvall et al., 2001; Peltola et al., 2000; Christiansen & Bakke, 1988). This may be especially important in the context of ongoing climate change, which is likely to exacerbate the impacts of these damage agents (Netherer et al., 2019; Marini et al., 2017; Schlyter et al., 2006).

Rapidly-homogenising species composition in regenerations in Sweden (i.e. dominance of Norway spruce in the south and Scots pine in the north), has already had dramatic environmental and economic impacts. For example, in the four northern-most counties in Sweden (Norrbotten, Västerbotten, Västernorrland and Jämtland), the term *multi-damage forest* refers to young Scots pine forests that are severely affected by browsing and several fungal diseases, primarily Scots pine blister rust (*Cronartium flaccidum*), snow needle blight (*Phacidium infestans*), and *Gremmeniella abietina* (Normark, 2019). Moreover, several adverse effects of increased homogeneity of Swedish forests are foreseen to arise in the future. Norway spruce and Scots pine stands support different vascular plant, cryptogam and bird communities (Petersson et al., 2021; Felton et al., 2020; Lindbladh et al., 2019; Petersson et al., 2019). Thus, a decrease in the share of one of these two tree species may negatively affect species-specific biodiversity at both stand and landscape levels. Reduced species richness is also likely to limit the production of other ecosystem goods and services. Furthermore, it may increase exposure of a given species (either Norway spruce or Scots pine) to various damaging agents (Felton et al., 2016). For instance, further expansion of Norway spruce at the landscape level may contribute to increased browsing pressure on remaining Scots pine stands (Bergqvist et al., 2014; Wallgren et al., 2013). Finally, relying on a single tree species is risky considering future uncertainties in the wood market, timber prices and climate (Jonsson, 2011).

Given existing uncertainties in regeneration species choice, it is extremely difficult to ignore the importance of mixed forests for future forest management. The use of mixed-forest stands has been widely recognized as a risk-spreading strategy (Bauhus et al., 2017; Pretzsch et al., 2015; Felton et al., 2010; Pretzsch, 2009). In a study from central Sweden, Holmström et al. (2018) compared a mixture of Scots pine and Norway spruce with their respective monocultures at an age of 53 years on a medium-fertility site. The study showed that the mixture had almost the same standing volume (m^3 ha^{-1}) as the best-yielding monoculture (Scots pine). Furthermore, mixed forests are also regarded as an effective tool for balancing production and environmental goals (Felton et al., 2010), which are demanded by the Swedish Forestry Act.

1.2 Regeneration methods for Scots pine

Planting, natural regeneration and direct seeding are conventional regeneration methods for Scots pine in Sweden. However, over the last two decades, the use of natural regeneration has gradually declined from around

40% down to around 10% of the total regeneration area in Sweden. At the same time, the use of direct seeding has remained rare (Figure 2). In Sweden, natural regeneration and direct seeding are mainly used for Scots pine. Regeneration with seeds is generally regarded as well suited to low- to medium-fertility sites (Karlsson & Örlander, 2004), whereas planting can be conducted on almost all site types (Hallsby *et al.*, 2013). This is primarily due to abundant ground vegetation, which outcompetes naturally-regenerated and direct seeded seedlings on richer sites.

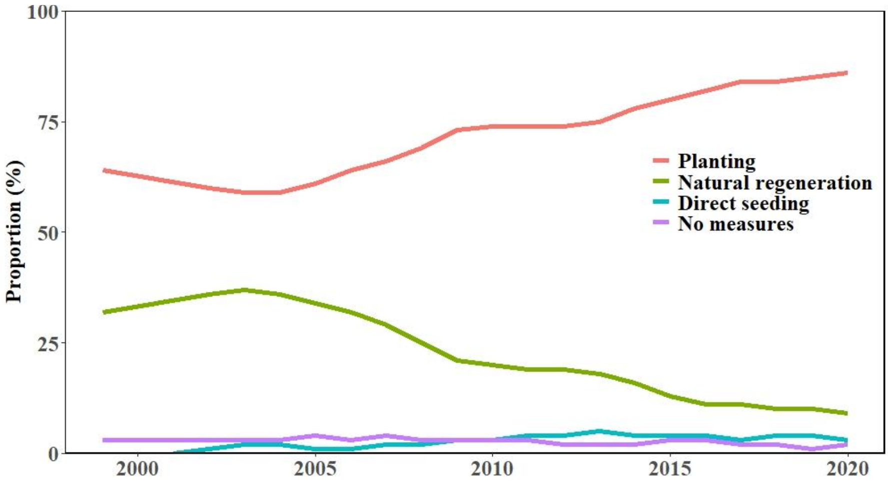

Figure 2. The share of different regeneration methods (planting, natural regeneration and direct seeding) for all species in Sweden (SFA, 2018).

1.2.1 Planting

Currently, approximately 84% of the total regeneration area in Sweden is managed using clearcutting followed by mechanical site preparation and planting (Figure 2). The wide application of this method is associated mainly with well-established and clear management regimes. Clearcutting allows for single-machine operation, effective reforestation of relatively big areas and is considered to be economically efficient (Nilsson *et al.*, 2010). It is also suitable for regeneration of light-demanding species such as Scots pine. In Sweden, planting of Scots pine is currently almost exclusively done with containerized, nursery-grown seedlings (Skogsstyrelsen, 2020). Bare-rooted seedlings are used occasionally, mainly at vegetation-rich sites, frost prone sites or sites where damage by pine weevil (*Hylobius abietis*) is high.

Planting usually results in shorter rotations compared to regeneration with seeds. In addition, faster growth of planted seedlings is likely to shorten their exposure to different growth-limiting factors like pine weevil, browsing, and *Lophodermium* needle cast primarily caused by *Lophodermium seditiosum*.

1.2.2 Natural regeneration

Fire is a major disturbance in natural Scots pine forests. Natural regeneration with seed and shelter trees combined with mechanical site preparation (MSP) is regarded as an approximation of natural dynamics in Scots pine stands. MSP replaces burned forest floor and a retained overstorey mimics surviving trees (Hille & Den Ouden, 2004; Beland *et al.*, 2000). Formation of shelterwood stands requires at least two machinery interventions, whose timing, intensity and manner of execution are important (Karlsson, 2000; Matthews, 1991; Smith, 1986). Furthermore, decisions about stocking levels, spatial distributions and duration of retained overstorey are critical (Valkonen, 2000b). Regeneration under seed/shelter trees is associated with high wind-throw risk (Nilsson *et al.*, 2006; Örlander, 1995) and is likely to result in more heterogeneous height and spatial structure (patchiness) compared to planting (Agestam *et al.*, 1998). Natural regeneration is generally associated with higher complexity and requires more knowledge compared to conventional clearcutting with planting. On the other hand, it avoids high initial investments in planting material as it relies on natural seed fall. It is sometimes possible to achieve high-density stands with acceptable cost. Importantly, seed and shelter tree retention is also an effective way to reduce competition from ground vegetation (Beland *et al.*, 2000; Kuuluvainen & Pukkala, 1989a; Hagner, 1962), risk of pine weevil (Petersson & Örlander, 2003; von Sydow & Örlander, 1994) and frost damage (Langvall & Örlander, 2001; Lofvenius, 1995) to the new generation. In addition, partial overstorey retention in the form of seed/shelter trees reduces changes to the forest ecosystems (light, water, soil, and micro-climate conditions) compared to clearcutting.

1.2.3 Direct seeding

Direct seeding (especially when mechanized) is associated with more simplified silvicultural management and lower initial investments than planting. This is mainly because it avoids complicated and expensive nursery seedling production, handling and planting (Grossnickle & Ivetić, 2017;

Wennström *et al.*, 1999). The risk of root and stem deformation is more of a concern for container-grown or transplanted seedlings and less for direct-seeded seedlings. In addition, direct-seeded seedlings may be less affected by pine weevils as they are too small to feed on. When successful, direct seeding yields very dense stands, which can constitute a solid foundation for production of high-quality wood. The main disadvantage of direct seeding, and a hypothetical reason for its infrequent use (Figure 2), is the high variability in seed quality, which reduces the predictability of this method. Usually, less than 50% of viable planted seeds emerge as seedlings in field conditions (Wennstrom *et al.*, 2007; Wennström *et al.*, 1999). This is due to low germination rates, high seed predation, and a wide range of other biotic and abiotic factors. In addition, germination rates are highly variable due to variable climatic conditions and site properties (Nystrand & Granström, 1997). This makes direct seeding less predictable than planting. Use of genetically-improved seeds improves germination rates, seedling survival and growth (Grossnickle & Ivetić, 2017; Wennstrom et al., 2007; Wennström et al., 1999; Winsa & Bergsten, 1994). In addition, unlike natural regeneration, direct seeding allows the use of different provenances.

1.2.4 Clearcut-free forestry

Although Swedish law (1993) requires a balance between production and conservation goals, current management practices are often perceived as very intense, at least in relation to forest management in other European countries (Lodin, 2020). Growing demands to decrease logging intensity and increase a wide range of other ecosystem services in Sweden have led to renewed interest in alternative silviculture approaches (Lodin, 2020). The Swedish forest agency (Skogsstyrelsen) has recently formulated new rules and definitions of clearcut-free forestry, which includes regeneration under shelterwoods. This allows the possibility to avoid clearcutting and introduce more diversity in structure and age. However, overstorey trees retained after the regeneration phase have an adverse effect on the growth of the new generation (Erefur *et al.*, 2011; Erefur *et al.*, 2008; Valkonen *et al.*, 2002; Valkonen, 2000a). This practical concern poses important challenges to artificial or natural regeneration of Scots pine under dense shelterwoods, especially when the shelterwood is retained for long periods. Traditionally, high stocking levels of overstorey trees are combined with their early removal, immediately after successful regeneration (Valkonen, 2000b). The interest in regenerating Scots pine under shelter is not new (Möller, 2013; Wiedemann, 2013) and a considerable amount of literature has been published on different selective cutting regimes (from single trees to gaps) across its natural range. However, this thesis focuses on the seed and shelterwood systems which have consistently got the most attention in Sweden.

Shelterwoods are generally appreciated for their higher aesthetic and recreational value compared to conventional clearcutting regimes. Ericsson (1993) found that forest attractiveness (combined aesthetic and recreational value) decreases with increasing logging intensity. The same authors recommended use of clearcut-free methods around settlements and in recreational areas. In addition, considerably higher plant biomass and production of blueberries (*Vaccinium myrtillus* L.) are reported under Scots pine shelterwoods compared to clearcuts. Blueberries are highly valued non-wood products (Hansen & Malmaeus, 2016; Kovalčík, 2014), an important source of fodder for ungulates, and a keystone species for biodiversity (Petersson, 2019). Finally, overstorey trees supply the forest floor with the dead wood in the form of branches and woody debris, which is a key factor for biodiversity (Valkonen, 2000b).

2. Thesis aim

There are two overall objectives of this thesis. The first is, to assess differences in productivity of Scots pine and Norway spruce stands across latitudinal and fertility gradients in Sweden. The second, is to investigate short- and long-term effects of different Scots pine regeneration methods on medium-fertile and fertile sites in southern Sweden. The thesis was divided into three parts:

In the first part (**Paper I**), simulated long-term yields of Scots pine and Norway spruce were compared across latitudinal and fertility gradients in Sweden. The study contributed to the debate regarding optimal tree species choice in relation to site properties.

The second part (**Papers II-III**) investigated short-term regeneration outcomes of three different Scots pine regeneration methods i.e. planting, natural regeneration and direct seeding. It determined the potential of these methods on medium-fertility sites. These studies focus on southern Sweden.

The third part (**Paper IV**) examined effects of three regeneration methods (planting, direct seeding and natural regeneration) on the production and profitability of Scots pine stands in southern Sweden. Like part II, the focus was on medium fertile to fertile sites.

The following objectives were addressed in this thesis:

- To determine productivity of Norway spruce and Scots pine across latitudinal and fertility gradients in Sweden (**Paper I**);
- to determine (short-term) effects of regeneration methods on seedling recruitment, survival and early growth in Scots pine stands (**Papers II-III**); and
- to determine (long-term) effects of regeneration methods on growth and profitability of Scots Pine stands (**Paper IV**).

3. Material and methods

Short-term field experiments (Papers II-III), as well as a combination of long-term field experiments with and modelling in a computerized decision support system (DSS) (Papers I and IV), were used to address the objectives outlined in this thesis. This section has attempted to provide a summary of these methods. Further details can be found in the individual papers.

3.1 Part I

The material used in Paper I originated from 102 tree species comparisons, where Norway spruce and Scots pine were randomly assigned to plots in the same stand and where it was possible to track their age, removals in thinnings and mortality. The locations were distributed across the whole of Sweden (Figure 3) and the site index ranged between 22-35 m and 15-38 m at the reference age (100 years), for Scots pine and Norway spruce, respectively. As most of the stands used in the study had not reached the culmination of MAI, stand development until culmination of mean annual increment (MAI_{max}) was modelled in Heureka, a computerized decision support system (Wikström et al., 2011). The measured single-tree data (height, DBH and age) from each stand were used as starting values for the simulations of the volume development. The outcome from Heureka was evaluated using full-rotation-length analyses and based on the culmination of mean annual increment (MAI_{max}). Originally, the stands were established as experimental silvicultural or genetic trials. Planting material and study design differed across locations but was consistent within locations; each site was either a silvicultural or genetic trial.

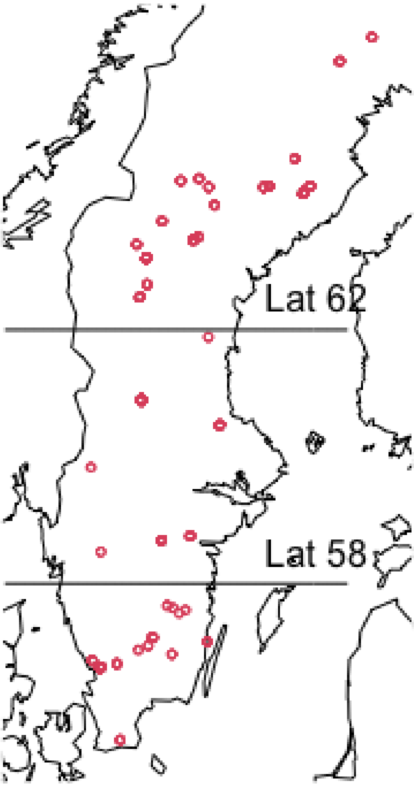

Figure 3. The geographical distribution of the stands used for the simulations. Dots represent sites of experimental trials with one or more tree species comparisons.

3.2 Part II

Regeneration studies (Papers II-III) were based on an experiment carried out in two Scots pine-dominated stands located in southern Sweden at Tagel estate (57.06°N, 14.39°E, 200 m.a.s.l). The experiments were established in 2017 (Site I) and 2020 (Site II). Each stand was divided into three shelterwood densities (0, 100 and 200 stems ha^{-1}). The experiment used a split-plot design with three or four blocks in each shelterwood density. Individual blocks consisted of one plot (8 x 16 m), with natural regeneration and direct seeding and one (16 x 16 m) with planting.

For natural regeneration and direct seeding, mechanical site preparation (MSP) was done with an excavator to create four intermittent rows of mineral soil in each plot. The soil in between the rows was left undisturbed. Natural regeneration was evaluated on both soil with and without site preparation. Direct seeding and effects of genetically-improved seeds were tested only in rows with site preparation.

For planted seedlings, one plot received MSP and one was left untouched. Furthermore, half of each scarified and non-scarified plot was treated with herbicides and half was a control. Finally, a total of eight small (two-year old containerized) and sixteen big (Plug+1) seedlings were planted in each of the four sub-plots. Big seedlings were two-year old hybrids grown in containers in the first year and bare rooted during the second year.

Natural regeneration and direct-seeded seedlings (Paper II) were mapped and monitored annually over a period of five (2017-2021) and two (2020-2021) years, at sites I and II, respectively. In addition, height from the ground (cm), root collar diameter (mm) and length of the leading shoot (mm) of the tallest seedling in each sampling plot were measured after four growing seasons at site I. Seedling survival, damage, height from ground level (cm), length of the leading shoot (mm) and diameter at ground level (mm) of all planted seedlings were measured annually in the late autumn of 2017-2021 (site I).

3.3 Part III

The material examined in this study consisted of two experiments and one demonstration trial from three locations in southern Sweden: Linnebjörke (Site I, 57.00°N, 15.10°E, 225 m a.s.l.), Tagel (Site II, 57.10°N, 14.36°E, 200 m a.s.l.), and Tönnersjöheden (Site III, 56.41°N, 13.05°E, 70 m a.s.l.). The primary objective of the experiments was to compare effects of different Scots pine regeneration methods (planting, natural regeneration and direct seeding) on long-term production and profit. Tested treatments and experimental set ups varied across the locations. Since the three experiments varied in experimental design and treatments, they cannot be considered as replicates but should be regarded as three case studies. However, the experiments constitute valuable material for the study as comparisons of different Scots pine regeneration methods on long-term production and profit are very rare.

Data describing the stand growth, as well as both thinning and harvesting operations at the three sites, were imported into Heureka as tree lists and then subjected to two kinds of simulations. First, the development of the overstorey (seed and shelter trees) was simulated during the period from the first release cutting until its full removal. Second, the new stand's development was simulated from the latest inventory in which it was measured until final felling by clearcut. Separate simulations of stands with overstorey retention were needed to assess its direct financial effects, relative to a clearcut. The concept of the financial result of overstorey retention is explained in Paper IV. Figure 4 illustrates graphically how the two simulations fit together. Financial and production results of each approach were assessed in terms of land expectation value (LEV) and mean annual increment (MAI) for the whole rotations.

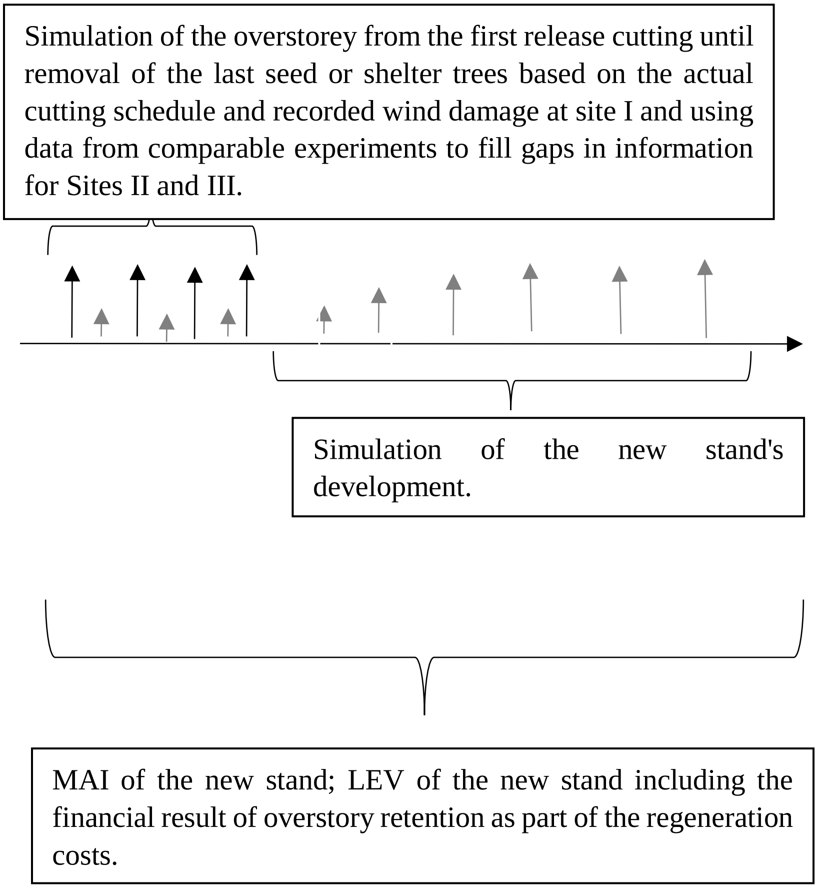

Figure 4. Schematic representation of two kinds of simulations used in the study. First, simulation of overstorey development (seed and shelter trees) during the period from the first release cutting until its full removal. Second, simulation of the new stand’s development from the latest inventory in which it was measured until final felling by clearcutting.

4. Main results and discussion

4.1 Scots pine and Norway spruce productivity (Part I)

Results from Paper I of the thesis indicated that from a production point of view, Norway spruce should be established only on the most fertile sites. At low- and intermediate-fertility sites, Scots pine yielded on average a 35.4% and 26.4% higher MAI_{max} than Norway spruce, whereas on high-fertility sites, Norway spruce produced on average 13.4% more than Scots pine (Figure 5). Most previous survey studies from both Sweden (Ekö et al., 2008; Leijon, 1979) and Norway (Öyen & Tveite, 1979) find similar results on high fertility sites, but generally also show Norway spruce outperforming Scots pine on intermediate sites. On the other hand, experimental studies by Holmström et al. (2018) and Nilsson et al. (2012) showed that Scots pine outperforms Norway spruce on intermediate sites in central and northern Sweden, respectively. In addition, empirical studies conducted by Drössler et al. (2018) indicated that both species grow comparably well on high-fertility sites (SI_H up to 32 m for Norway spruce) at ages between 26-57 years. However, data from the sites used in the three studies cited above were also included in the large database used in this study.

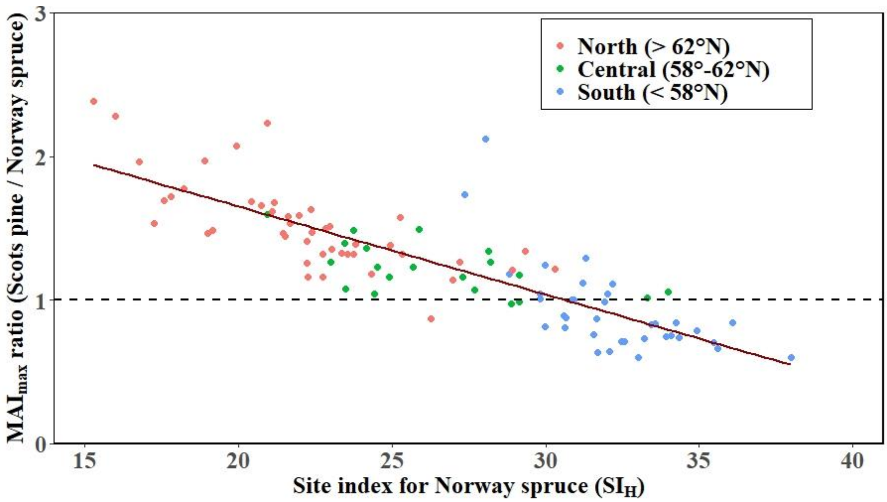

Figure 5. The ratio of simulated maximum mean annual increment (MAI_{max}, $m^3\ ha^{-1}\ yr^{-1}$) between Scots pine and Norway spruce as a function of site index estimated from dominant height (SI_H) for Norway spruce as calculated based on net volume production at the last inventory. Each point is a species comparison within an individual comparison (n=102). The solid lines indicate the relationship between relative Scots pine production and site index for Norway spruce. The horizontal dashed line represents a Scots pine:Norway spruce ratio of 1 where the two species have an equal MAI_{max}. The locations at latitudes below 58°N, between 58°-62°N and above 62°N are referred to as southern, central and northern Sweden, respectively.

The causes of the discrepancy between results obtained in this study and most prior investigations (Ekö et al., 2008; Öyen & Tveite, 1998; Leijon, 1979) are not totally clear. However, the use of experimental data in Paper I versus survey data in previous studies was identified as one important possible explanation. There are several reasons why survey-based yield comparisons between species may be questioned. First, species- and site-selection in survey studies are not independent. Second, management histories in such stands are often unknown. Third, species-specific silvicultural regimes (e.g. initial planting densities, thinnings) may bias comparisons between the two species. Finally, survey studies assume either similar site conditions when comparing neighbouring stands or rely on a rather inaccurate site index conversion system for both species if the comparisons cannot be arranged in pairs. Furthermore, many of the experiments used in this study were fenced to reduce browsing by ungulates. Browsing damage is a major concern for both productivity and profitability of Scots pine plantations (Nilsson et al., 2016; Wallgren et al., 2013; Bergquist et al., 2003), and to a lesser degree for Norway spruce (Månsson et al., 2007; Cederlund, 1980). In addition, seedling mortality rates are expected to be lower in the experimental areas compared to operational plantations due to more careful seedling handling and selection of planting spots.

The method of site index estimation may be an important problem in the survey studies. In the modelling study by Ekö et al. (2008), site index was estimated by site properties (SI_S) using functions developed by Hägglund and Lundmark (1977), which is generally considered to be a less accurate and reliable way of quantifying production potential of forestland compared to estimates from height development curves (SI_H) (Mason et al., 2018; Nilsson et al., 2012; Elfving & Nyström, 1996). Site index from height development curves (SI_H) relies on well-established correlations between the top height (tree bio-data) and volume production (Skovsgaard & Vanclay, 2008; Eichhorn, 1902), whereas SI_S is estimated indirectly from various site property measures.

Approximately 78% of the total regeneration area in southern Sweden (Götaland) is made up of poor- and medium-fertility sites (SFA, 2021). However, current tree species composition in regenerations in southern Sweden is characterized by the predominance of Norway spruce (Figure 1). Although this study focuses on volume production and disregards other factors that should be taken into consideration when choosing a species for regeneration, it may still be concluded that the share of Scots pine forests in southern Sweden could be increased. Against this background, it is of great interest to evaluate the potential for regenerating and managing Scots pine on medium- and high-fertility sites in the region. Therefore, the next papers of this thesis (Papers II-IV) move on to discuss different Scots pine regenerations strategies on medium- and high-fertility sites in southern Sweden.

4.2 Planting, natural regeneration and direct seeding of Scots pine (Parts II-III)

4.2.1 Planting

Planting results (Papers III-IV) varied across shelterwood densities and tested treatments. MSP was crucial for avoiding high mortality and sustaining fast early growth of planted seedlings (Paper III; Figures 6-7). In this study, damage by pine weevils was identified as the most important cause of seedling mortality. The positive effects of MSP on survival and growth are likely due to: (i) reduced pine weevil damage (Petersson *et al.*, 2005); (ii) reduced competition from ground vegetation (Nilsson & Örlander, 1999); (iii) increased soil temperature, aeration, water and nutrient availability (Löf *et al.*, 2012; Örlander *et al.*, 1990), and (iv) reduced risk of frost (Langvall *et al.*, 2001).

Although the use of either MSP or insecticides *per se* was sufficient to reduce seedling mortality to acceptable levels for big seedlings, insecticide alone was not enough to protect small seedlings on untreated soil (Figure 6). This may be primarily attributed to lower susceptibility to pine weevil damage of big compared to small seedlings (Örlander & Nilsson, 1999). Seedling basal diameters of at least 12 mm are needed to avoid lethal damage by pine weevils (Wallertz *et al.*, 2005). Regardless of the seedling size and insecticide treatment, planting on intact soils resulted in considerably lower early seedling growth. Overall, it may therefore be concluded that insecticide-treated and untreated big seedlings can be successfully planted after MSP, whereas use of small seedlings should always be combined with both insecticides and MSP.

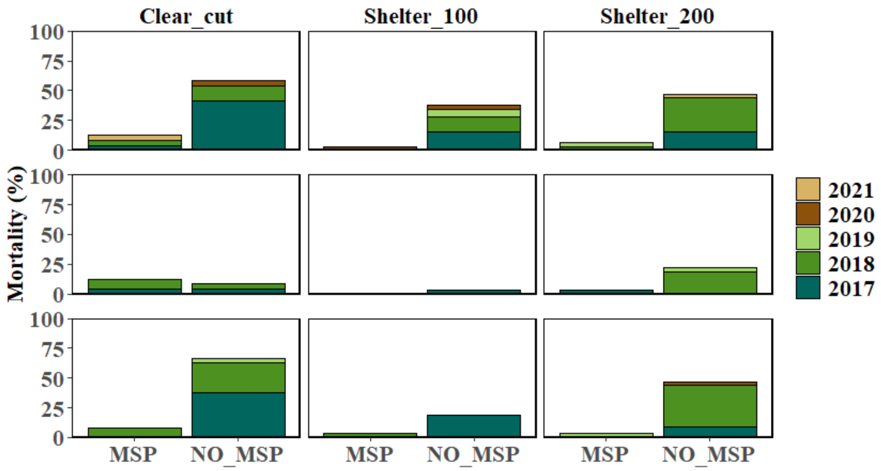

Figure 6. Total mortality (%) from 2017 to 2021. The top, middle and bottom panels represent small seedlings with insecticide, big seedlings with insecticide and big untreated seedlings, respectively. Shelterwood density: clearcut (Clear_cut), shelterwood with 100 stems ha^{-1} (Shelter_100), shelterwood with 200 stems ha^{-1} (Shelter_200). Site preparation treatments: mechanical site preparation (MSP), no site preparation (NO_MSP).

Planting under shelterwoods (100-200 stems ha^{-1}) resulted in lower mortality rates compared to open clearcut areas. This is consistent with a study by von Sydow and Örlander (1994), who found that shelterwood densities between 80-160 trees ha^{-1} reduce pine weevil damage and sustain satisfactory early seedling growth. The actual mechanisms behind lower pine weevil damage under shelterwoods are not yet fully understood (Wallertz *et al.*, 2006; Nordlander *et al.*, 2003; Oerlander *et al.*, 2000). However, environmental conditions in combination with alternative feeding sources, primarily ground vegetation, may constitute part of the explanation (Wallertz *et al.*, 2006; Örlander *et al.*, 2001).

Consistent with previous literature (Nilsson *et al.*, 2006; Beland *et al.*, 2000; Oerlander & Karlsson, 2000; Gemmel *et al.*, 1996; von Sydow & Örlander, 1994), this research, Papers III-IV found that although shelterwood retention may be beneficial for seedling survival, it has an adverse effect on seedling growth. Regardless of the regeneration method, seedling growth (length of leading shoot, height, and stem volume) decreased with increasing shelterwood density (Figure 7). The poorer seedling growth under shelterwoods is most likely due to belowground rather than aboveground competition from the shelter trees (Strand *et al.*, 2006; Valkonen, 2000b; Kuuluvainen & Pukkala, 1989b). After five growing seasons, growth reduction of planted seedlings under dense and sparse shelterwood compared to the clearcut corresponds to approximately one year of growth (Paper III).

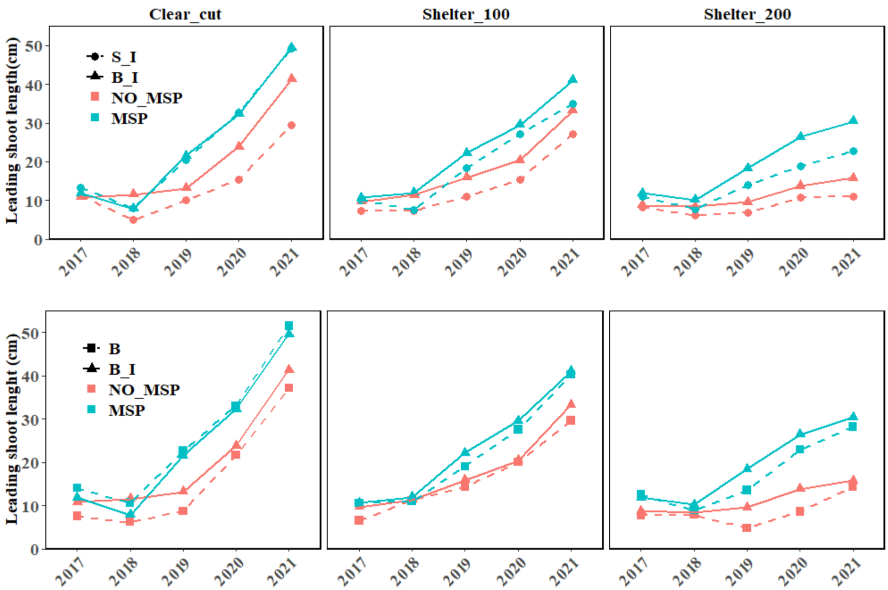

Figure 7. Leading shoot length (cm) 2017-2021. Small and big insecticide-treated seedlings (upper panels). Big untreated and insecticide-treated seedlings (lower panels). Shelterwood density: clearcut (Clear_cut), shelterwood 100 stems ha^{-1} (Shelter_100), shelterwood 200 stems ha^{-1} (Shelter_200). Abbreviations: S and B refer to small and big seedlings, respectively; I indicates insecticide treatment; MSP and NO_MSP refer to mechanical site preparation and no mechanical site preparation.

4.2.2 Natural regeneration

Overall, results from Paper II showed that seedling densities (at the last inventory) were positively affected by MSP and shelterwood density (0-200 stems ha^{-1}; Figure 8). These observations agree with previous research from southern Sweden (Karlsson & Nilsson, 2005; Beland et al., 2000) but also from other parts of Scots pine's natural range (Rosenvald et al., 2020; Aleksandrowicz-Trzcińska et al., 2017; Barbeito et al., 2011; Karlsson, 2000). Considering the very large differences between regeneration results obtained on intact soils and MSP-treated soils, it could be concluded that MSP is needed when regenerating with seeds (Karlsson & Nilsson, 2005; Hille & Den Ouden, 2004; Beland *et al.*, 2000). High seedling densities obtained under shelterwoods (100-200 stems ha^{-1}) compared to clearcut areas (Figure 8) are likely due to: (i) increased seedfall, (ii) delayed ageing of MSP (primarily reduced ground vegetation ingrowth; Paper II), (iii) reduced pine weevil damage (Paper III), and (iv) abiotic factors such as temperature and plant water availability. However, as expected, the variation in the results between the sites and growing seasons was considerable (Figure 9). For instance, the effect of shelterwood density was less pronounced at Site II compared to Site I. This was mainly due to poor regeneration under dense shelterwood (200 stems ha^{-1}) but also very successful seedling recruitment in the clearcut. Poor regeneration under dense shelterwood was unexpected and not possible to explain with the available data. However, it could be speculated that quality of mechanical soil preparation and/or variation is soil properties may constitute a part of the explanation (Paper II). Abundant regeneration on the clearcuts, especially in the first years after experiment establishment at both sites, may result from proximity of the clearcut to the adjacent shelterwoods which could have served as seed source. Natural regeneration on larger clearcuts with greater distance to seed sources is expected to be less successful because of limited seed dispersal (Ackzell, 1994; Hagner, 1962; Hesselman, 1938).

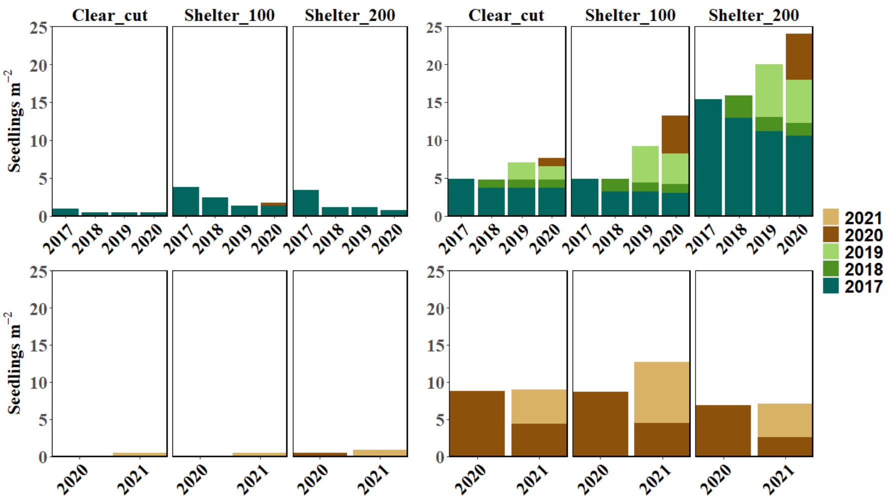

Figure 8. The density of seedlings (m^{-2}) in rows without (left panels) and with (right panels) site preparation. The upper and lower panels represent site I and site II, respectively. Seedling cohorts originating from different years are represented by the respective bar segments according to the legend. Clear_cut, Shelter_100, and Shelter_200 refer to the clearcut, shelterwood 100 stems ha^{-1}, and shelterwood 200 stems ha^{-1} treatments, respectively.

4.2.3 Direct seeding

Results from Papers II and IV showed a very large inconsistency in the regeneration outcomes obtained after direct seeding. Germination rates reported in Paper II ranged between approximately 4-32%, depending on the study sites and seeds' genetic origin (Figure 9). These findings are in line with the range of earlier field studies indicating that usually no more than 50% of all viable, sowed seeds ultimately germinates (Wennstrom *et al.*, 2007; Wennström *et al.*, 1999; Winsa & Bergsten, 1994). The actual reasons underlying the observed variation could not be assessed with the data collected in this study. In fact, such evaluations are difficult to obtain in outdoor field experiments due to the large number of biotic and abiotic factors that require frequent monitoring. In Papers II and IV, it is likely that observed differences in germination rates arose from differences in site properties, year-to-year weather conditions, levels of seed predation and germination capacity of seeds.

Contrary to expectations and several earlier investigations (Grossnickle & Ivetić, 2017; Wennstrom et al., 2007; Wennström et al., 1999; Winsa & Bergsten, 1994), no significant differences (in germination rates, survival or early seedling growth) between genetically-improved and unimproved seeds were found in Paper II (Figure 8). Improved performance of genetically-improved seeds is mainly associated with their higher weight (Wennström *et al.*, 2002) which results in higher germination rates. However realized gains from the use of genetically-improved seeds compared to unimproved seeds are believed to be greater for direct seeding than for planting and it was expected that growth would also be positively affected by the use of improved seeds from direct seeding (Karlsson, 2001;Wennström *et al.*, 2002; Wennström *et al.*, 1999; Ackzell & Lindgren, 1994). It is possible that the observed high variation in growing conditions (for more details see Paper II) was the probable reason for relatively poor performance of genetically-improved seeds. Unfortunately, the data collected in this study do not allow a thorough investigation of this hypothesis. However, the hypothesis is supported by a study by Wennstrom *et al.* (2007), who found little or no effect of genetically-improved seeds on seedling emergence in years when conditions for germination were judged as poor. On the other hand, Wennström *et al.* (1999) observed better performance of genetically-improved seeds compared to stand seeds on unfavourable seedbed substrates.

Figure 9. Germination and survival rates of unimproved (left panels) and genetically-improved (right panels) seeds. The upper and lower rows represent site I and site II respectively. Clear_cut, Shelter_100, and Shelter_200 refer to the clearcut, shelterwood 100 stems ha^{-1}, and shelterwood 200 stems ha^{-1} treatments, respectively.

4.3 Long-term comparison of different regeneration methods

Results showed (Paper IV) that planting 1600–3265 seedlings ha^{-1} provided good financial returns (at a 2.5% interest rate) and ensured consistency between sites (Table 1). It should be noted, however, that financial results were sensitive to initial planting densities and interest rates. Accordingly, initial densities above 3256 seedlings ha^{-1} resulted in considerably poorer financial outcomes, whereas planting of 10,000 seedlings ha^{-1} was not economically justified. This was primarily due to high initial investments (regeneration material and planting costs), which were not compensated by increased harvesting revenues. This result agrees well with the previous study by Hyytiäinen *et al.* (2006).

Generally, natural regeneration yielded inferior economic outcomes compared to conventional planting (with 1600–3265 seedlings ha^{-1}) on the clearcuts. On the other hand, natural regeneration produced high seedling densities (>10,000 seedlings ha^{-1}), which would not be economically rational if obtained by planting (Paper IV). Narrow spacing (obtained either by planting, natural regeneration or direct seeding) is regarded as an effective strategy for high-quality timber production. This is mainly due to highly competitive growing conditions and large selection possibilities (Agestam *et al.*, 1998; Johansson & Persson, 1996). The effects of initial spacing on wood quality are probably larger at high-fertility sites, as Persson (1977) found that quality at a given spacing is lower at more fertile sites compared to more infertile sites. This is because growth rates are generally positively correlated with juvenile wood content, wider annual rings and branch diameter, which are important quality traits (Liziniewicz, 2014; Pfister, 2009). In addition, high-quality timber can also be produced under Scots pine seed and shelter trees (Agestam *et al.*, 1998; Niemisto *et al.*, 1993; Junack, 1980) which reduce ring width and branch diameter of the new regeneration. However, growth models used in Heureka do not account for effects of initial spacing density, or pre-commercial and commercial thinnings, on wood quality, except their effects on diameter growth. Thus, our analyses may underestimate the financial results for naturally-regenerated, seeded and densely-planted stands if high-quality timber attracts higher premiums in the future.

Table 1. LEV ha^{-1} with indicated stand establishment procedures at 2.5% and 4% interest rates at all study sites (I-III). Regeneration methods: PL - planting; NR - natural regeneration; DS - direct seeding. PCT refers to pre-commercial thinning.

Site I	Density (seedlings ha^{-1})	Interest rate 2.5%			Interest rate 4%		
		Clear-cut	Seed-trees	Shelter-trees	Clear-cut	Seed-trees	Shelter-trees
PL	1600	2638		3357	450	-1049	186
PL	3000	2502	1208	2525	31		-552
PL	10000	-3277	-4006	-2871	-4631	-5323	-4120
NR	1600		1649	2732		-15	281
NR	4444		1758	2957		-14	431
Site II		**Interest rate 2.5%**			**Interest rate 4%**		
		Clear-cut	Seed-trees	Shelter-trees	Clear-cut	Seed-trees	Shelter-trees
PL	2000	2412			768		
DS			4396			1302	
NR			3555			45	
Site III		**Interest rate 2.5%**			**Interest rate 4%**		
		Clear-cut	Seed-trees	Shelter-trees	Clear-cut	Seed-trees	Shelter-trees
PL	1600	3717			967		
PL	2500	3642			665		
PL	3265	3621			485		
PL	4444	2059			-580		
PL	6400	731			-1793		
NR	No PCT		1839			148	

Direct seeding at site I failed at the establishment and was excluded from the study.

Results from Paper IV indicated that direct seeding could be a competitive alternative compared to planting, even on medium-fertility sites (Table 1). When done right, direct seeding can yield high stand densities and consequently high volume production and possibilities for production of high-quality timber at a relatively low cost. This finding is supported by several earlier studies (Hyytiäinen et al., 2006; Glöde et al., 2003). On the other hand, our findings also show that direct seeding sometimes resulted in very low germination and/or survival of germinated seedlings. This contributes to the low predictability of this method. Results from Papers II and IV showed very high variation in the regeneration outcomes of direct seeding among studied sites. One of the largest constraints (along with seed predation and low germination capacity) of direct seeding on medium- and high-fertility sites is the risk of severe competition from abundant ground vegetation for small seedlings, especially on clearcuts. Thus, the use of genetically-improved seeds is recommended to increase establishment rates in seeded Scots pine stands. However, results from study II did not support the hypothesis that improved seeds result in higher germination, survival and growth.

4.4 Regeneration under shelterwoods

Results from Paper IV indicated that conventional seed tree retention adds additional costs compared to clearfelling that are, in many cases, roughly equal to or larger than the savings obtained by avoiding planting. In contrast, shelter trees with longer retention periods can have good economic results (at 0% and 2.5% interest rates), although it varies depending on site index and average tree size. Furthermore, the sensitivity analyses indicated a strong effect of wind damage on the cost of overstorey retention. The potential severity of naturally-regenerated stands' increased susceptibility to wind damage after release cuttings has been previously highlighted (Örlander, 1995), and the increased frequencies of windthrows resulted in additional financial losses.

Higher harvesting revenues together with avoiding additional costs related to overstorey management were identified as a possible explanation for higher financial performance of conventional planting compared to regeneration (natural and artificial) under shelterwoods. On the other hand, despite relatively low volume production, regeneration under shelterwoods with extended retention periods yielded good financial results (Table 1, Paper IV). The present results are especially noteworthy with respect to the recent increasing interest in continuous-cover forestry. Regeneration of light-demanding tree species (such as Scots pine) under shelterwoods of high initial densities, which are meant to be subsequently thinned and retained over longer periods, is considered to be a clearcut-free method according to current regulations from the Forest Agency.

4.5 *Lophodermium* needle cast

A common view among forest practitioners is that damage by *Lophodermium* needle cast to seedlings is higher under shelterwoods compared to open clearcut areas. This view is supported by the ecological requirements of the fungus (Manka, 2005). Development of *Lophodermium* needle cast positively correlates with high summer precipitation and air humidity. Thus, low air circulation and increased air humidity under shelterwoods compared to clearcuts (Lofvenius, 1995) is likely to promote fungal growth. It is also in agreement with results from Paper III, which indicated higher infection rates of *Lophodermium* needle cast under shelterwoods (100-200 stems ha^{-1}) compared to the clearcut. However, at least to our knowledge, there is a lack of scientific evidence showing a correlation between infection intensity and overstorey density.

4.6 Drought

The anticipated climate changes for Scandinavia include, among others, more frequent and extended droughts during late spring and summer (Chen *et al.*, 2015). Therefore, increased drought during the regeneration phase is a key question for future adaptive forest management. It is especially important as the majority of regeneration efforts, for instance planting, occur during that time. Although potential effects of climate change on regeneration outcomes were not studied in this thesis, the extreme spring and summer drought of 2018 may provide a glimpse into future growing conditions.

The drought during 2018 negatively affected seed germination, and seedling survival and growth (Papers II-III). Results from Paper II showed low recruitment of naturally-regenerated seedlings in 2018, despite abundant seed fall observed during the same year (Paper II). It may be assumed that seeds' germination was inhibited by low water availability. In contrast, seedling recruitment in the subsequent growing season (2019) was high, although seed fall was low (Figure 9). This finding was unexpected and suggests that overwintering seeds might have contributed to the increased recruitment in the subsequent year. Thus, it can be hypothesized that delayed seed germination may reduce the negative effects of drought years as some of the seeds will germinate a year later. On the other hand, delayed seedling germination will result in a growth lag, increased competition from ground vegetation and prolonged rotations. However, these possibilities are just hypotheses and lower recruitment in 2018 could have been caused by other factors, for instance, lower germination rates or increased predation.

A striking result to emerge from Paper III is the stalled growth of planted seedlings observed in the second and third years after planting (2018-2019; Figure 7). This pattern was true for all seedlings, regardless of treatments and shelterwood densities. Stalled growth in years 1-3 following planting is common in Norway spruce plantations and has also been observed in several other coniferous tree species (Grossnickle & Blake, 1987; Sutton & Tinus, 1983; Armson, 1958). It is usually attributed to post-planting stress (mainly water stress) and high below-ground investments that seedlings need to take in the preceding growing season (Nilsson et al., 2019; Grossnickle, 2005; Burdett et al., 1984). However, this phenomenon is less common in Scots pine (Nilsson et al., 2019). Therefore, it is likely that the observed growth reduction was partly due to the severe drought during June and July 2018.

Finally, drought could have contributed to the relatively high mortality rates observed on intact soils (Paper III) under the dense shelterwood in 2018 (Figure 6). It could be hypothesised that severe water stress under the dense shelterwood may have increased the probability of seedling mortality through decreased vigour. However, this could not be validated with the data collected in this study.

5. Major limitations of each paper

(I) The major limitation of this study was a lack of equal representation of different fertility classes across northern, central and southern Sweden. The majority of the species comparisons on low- and high -fertility sites were clustered in the northern and southern latitudes, respectively.

(II-III) This study had only two replicates in time and space, which represented very similar site conditions. Thus, caution must be applied as findings might not be applicable for other sites.

(IV) It is important to bear in mind that this study was based on three case studies, with different experimental designs and different treatments. These results therefore need to be interpreted with caution and cannot be extrapolated.

In addition, most of the experiments included in this thesis were fenced to minimize browsing by ungulates. Browsing damage is a major concern in Scots pine forests in Sweden. Therefore, these studies represent a rather idealized scenario where browsing was kept to a negligible level. However, because browsing often is so extensive in Scots pine regenerations in southern Sweden, it would not have been possible to study effect of regeneration treatments without excluding browsing.

6. Conclusions and implications

The first part of this thesis was undertaken to evaluate production in Scots pine and Norway spruce stands across wide fertility and geographical gradients. Contrary to a general believe and the majority of earlier investigations research (Ekö et al., 2008; Öyen & Tveite, 1998; Leijon, 1979), the results from this part indicated that from a production point of view, Scots pine should be established not only on low but also on relatively fertile sites. Given that approximately 78% of the total regeneration area in southern Sweden (Götealand) represents has either poor and or medium fertilitye sites, the present results (part I) opens up a vast potential for increasing the use of Scots pine in the region. However, regeneration of Scots pine (especially with seeds) on fertile sites is difficult. This is primarily due to risk of wood quality deterioration and regenerations failures, caused by severe competition from ground vegetation to the small seedlings. Therefore, to further understand if Scots pine can be successfully regenerated on medium-fertile and fertile sites, the next parts of this thesis (II-III), investigated the effects of three Scots pine regeneration methods (planting, natural regeneration and direct seeding) on short- and long-term regeneration outcomes, on such sites.

The choice of an optimal regeneration strategy is a well-known forest-management dilemma. Probably the most important aspect of this decision is the risk-of-failure assessment. In this regard the results from the second part of this thesis indicated that compared with natural regeneration and direct seeding, planting is probably a more reliable and effective regeneration method for Scots pine on fertile sites. This was seen in short-term regeneration outcomes, long-term volume production and in financial revenues. Regeneration with seeds was generally associated with a high degree of uncertainty, mainly as its key processes such as seed production and germination are largely dependent on climatic conditions. In addition, effects of natural regeneration and direct seeding seem to be more site specific compared to conventional planting. Therefore, there is a need for more frequent monitoring of seedling germination and development in such stands. Furthermore, natural regeneration under seed/shelter trees is associated with higher management complexity due to the need of overstorey management. Shelter/seed trees need to be removed in one or several steps to ensure sustained growth of the new generation. Overall, greater efforts and knowledge are needed to ensure good results when regenerating with seeds.

Taken together, these results suggest that Scots pine may be successfully regenerated even on medium-fertility sites. However, the choice of a particular regeneration method should be based on knowledge of local conditions and be suited to different management objectives. The findings obtained in this thesis will be of interest to a wide range of forest actors in southern Sweden, especially concerning increasing demands for more extensive use of Scots pine in this region. In addition, shelter trees provide an opportunity for clearcut-free forestry according to current definitions by the Swedish Forest Agency. However, these results may also be relevant for professionals in other regions within the entire Scots pine natural range. In addition, this thesis has provided a glimpse into potential future impacts of climate change on the regeneration of Scots pine.

7. Future research

This thesis has raised several interesting questions that might be worth addressing in the future research. The following section has attempted to provide a brief summary of the identified knowledge gaps. Some of the most important issues are listed below:

(I) Fully coherent hybrid physiological/mensurational growth and yield models should be built for Swedish foresters in the future. This is to make accurate predictions of the effects of climate change on volume production and consequently provide needed support for taking the most optimal management decisions.

(II) Further empirical studies with greater site replication are probably needed to draw stronger conclusions about the performance of different regeneration methods on medium-fertile and fertile sites.

(III) Regeneration of light-demanding tree species (such as Scots pine) under shelterwoods of high initial densities, which are meant to be subsequently thinned and retained over longer periods is considered to be a clearcut free method according to current regulations from the Forest Agency. Therefore, developing appropriate strategies allowing for secure establishment and sustained fast growth of Scots pine in such conditions is an important consideration. The optimal way to manage shelterwoods remains to be determined. For instance, a question remaining unsolved is whether shelterwood removal should be performed in one or several steps. In addition, the right timing of shelterwood removal needs to be decided. Ideally, such investigations should be done across wide latitude and fertility gradients.

(IV) The effects of different regeneration methods should continue to be evaluated in the form of long-term field experiments across latitude and fertility gradients. Such studies should include comparisons of volume production, wood quality and other ecosystem services.

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IV

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Modelling effects of regeneration method on the growth and profitability of Scots pine stands

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Modelling effects of regeneration method on the growth and profitability of Scots pine stands

Mikolaj Lula[a], Renats Trubins[a], Per Magnus Ekö[a], Ulf Johansson[b] and Urban Nilsson[a]

[a]Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre, Alnarp, Sweden; [b]Unit of Field-based Forest Research, Swedish University of Agricultural Sciences (SLU), Simlångsdalen, Sweden

ABSTRACT

Despite numerous studies there are still uncertainties regarding regeneration strategies that are optimal for productivity and profitability. Thus the aim of this study was to establish effects of three regeneration methods (planting, direct seeding and natural regeneration) on the production and profitability of Scots pine (*Pinus sylvestris* L.) stands in southern Sweden. Long-term stand development was simulated, with the StandWise application of the Heureka decision support system, starting from short-term regeneration outcomes observed in several field experiments at sites with relatively high productivity (H100 site indices, i.e. heights of dominant pines at 100 years: 27–30 m). Financial and production results of each approach were assessed in terms of Land Expectation Value (LEV) and Mean Annual Increment (MAI), respectively, across a whole rotation. Planting on clear-cuts with 1600–3265 seedlings per hectare resulted in the highest profitability and production, whereas high-density planting (10,000 seedlings per hectare) resulted in negative LEV. However, sensitivity analysis showed that the results depended on the interest rate. Retention of seed-trees incurred additional costs relative to single-operation clear felling. In contrast, retention of shelter-trees had good financial results (at 0% and 2.5% interest rate), although they depended on the site index and average tree size.

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Introduction

Scots pine (*Pinus sylvestris* L.) is the most widely distributed coniferous tree species in the world (Mirov 1967) and the second most important commercial tree species in Sweden after Norway spruce (*Picea abies* (L.) *Karst.*). In 2018, the growing stock of Scots pine in Sweden amounted to 1352 million m^3, corresponding to ca. 39% of the total national stock (SLU 2018). Clear-cutting regimes have been generally applied in commercial Swedish forestry, and conventional methods for regenerating Scots pine stands are planting, direct seeding and natural regeneration with seed trees or under shelterwood. However, the naturally regenerated area of Scots pine forest decreased from about 40% of the total regeneration area in 2000 to about 10% in 2018 (SFA 2018).

Active stand establishment involves a series of silvicultural operations, such as site preparation, planting, seeding or natural regeneration, cleaning and pre-commercial thinning (PCT) (Hyytiäinen et al. 2006). In combination with site conditions, these management practices are major determinants of the new stands' growth, quality and hence subsequent management requirements. The qualities and quantities of initial inputs are often related to substantial financial investments that must be compensated for long periods. To be economically rational, the investments need to pay off in terms of increases in revenues from harvesting, income from other uses, and/or reductions in rotation periods. In commercial forestry, the regeneration method providing maximum financial returns from growing timber and retaining high aesthetic and biodiversity values is desired.

For a long time, forest researchers and companies in northern Europe have intensively sought ways to increase the cost-effectiveness of regeneration, particularly methods that could improve seedling survival and establishment (Nilsson et al. 2010b). Hence, short-term effects of various regeneration treatments have been reported in numerous empirical studies (Karlsson 2000; Örlander and Nilsson 1999; Örlander et al. 1990; Davies 1985). The results have provided valuable guidance for forest management. However, knowledge of regeneration success and juvenile growth *per se* is not sufficient for comparing the financial results of different regeneration methods. Information about revenues from harvests, and non-wood benefits over the entire period from regeneration to final felling (or a period of comparable duration if uneven-aged management is applied) is also required for robust assessment and selection of management options (Hyytiäinen et al. 2006).

Unsurprisingly, given the commercial importance of Scots pine (and predominance of clear-cutting regimes), there have been several attempts to evaluate the long-term financial consequences of applying different regeneration methods in even-aged Scots pine plantations in Scandinavia, as

CONTACT Mikolaj Lula mikolaj.lula@slu.se Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre, P.O. Box 49, SE-230 53 Alnarp, Sweden

briefly reviewed here. Hyytiäinen et al. (2006) combined experimental data, process-based forest growth models and stand-level economic optimization to investigate effects of several regeneration and soil preparation methods. Their results showed that planting and sowing yielded the highest stand value at 1% interest rate, but natural regeneration was the optimal regeneration method at 3% interest rate, and sowing provided comparable results to natural regeneration at 5% interest rate. Simonsen (2013) assessed the profitability of planting and natural regeneration with seed trees across sites with a range of site indices in northern Sweden. Their results indicated that planting was only the optimal regeneration method for highly productive sites, e.g. with H100 site indices (heights of dominant pines at 100 years) of at least 26 m for sites at latitude 60°N. Glöde et al. (2003) compared natural regeneration, direct seeding and planting on four study sites, two in northern and two in southern Sweden, and concluded that natural regeneration provided the best financial outcomes at all locations. However, they only investigated sites with relatively low fertility (H100: 24 and 20 m in southern and northern Sweden, respectively). Zhou (1998) investigated the optimal management and rotation length following natural regeneration with seed trees in northern Sweden. In addition, Zhou (1999) developed an optimization model for choosing planting or seed-tree regeneration methods, considering uncertainties in stocking levels, based on a case study in northern Sweden. Gong (1998) considered theoretical aspects of selecting decision support models for determining financially optimal planting densities in pine plantations, particularly in northern Sweden. The optimal investments in stand management and its intensity have also been studied by several authors (Tahvonen et al. 2013; Uotila et al. 2010; Hyytiäinen et al. 2005). Nevertheless, although all these studies provided valuable information or indications of important factors to consider, substantial uncertainties remain. This is at least partly because of "the necessity of optimizing all of the management variables simultaneously", so (for example) "previous results concerning sensitivity to timber price and the relationship between maximum sustainable yield and economic solutions do not hold true in models that provide a more realistic description of forest management" (Tahvonen et al. 2013). Moreover, there is particularly limited information (and correspondingly high uncertainty) regarding the profitability of different methods for regenerating Scots pine stands in Sweden, particularly on high-fertility sites in southern Sweden, south of latitude 60°N.

Forest growth simulators are useful tools for both research and practical forestry. They are often used to evaluate long-term effects of various silvicultural measures, and address gaps in knowledge and uncertainties such as those outlined above. One that is widely used in Sweden is the Heureka decision support system (Heureka DSS), which projects the growth of stands during whole rotation periods in two stages (Wikström et al. 2011). First, growth in the young stands is modelled based on functions presented by (Nyström 2000) and height-diameter relations developed by Nyström and Söderberg (1987). Further development, after the stands reach an average height of approximately 7 m, is simulated using basal-area growth functions developed for mature forests (Fahlvik et al. 2015; Elfving and Nyström 2010). Clearly, under- or overestimation of the stand growth in the first stage will lead to bias in the second stage (Fahlvik et al. 2015). Therefore, use of empirically validated starting values after the initial young phase from controlled experiments is highly advantageous for long-term simulations.

The objective of this study was to reduce some of the uncertainties outlined in this Introduction by using the Heureka StandWise application to assess effects of three establishment methods (planting, direct seeding and natural regeneration) on the long-term production and profitability of Scots pine stands in southern Sweden. In contrast to some earlier studies, effects of variations associated with differences in young forest models were eliminated by initializing the simulations with empirical data from stands at stages within the range covered by mature forest growth models. Furthermore, the data used were obtained from experiments in which two or more regeneration methods were applied to plots at the same sites, while earlier reports refer mostly to differences between neighbouring stands that were assumed to have similar growing conditions. The management implications of the choice of regeneration method were assessed in terms of Land Expectation Value (LEV) and Mean Annual increment (MAI) under financially optimal (maximum LEV) rotation lengths.

Materials and methods

The simulations presented in this paper are largely based on material observed in three field experiments located at the following sites in southern Sweden: Linnebjörke (57°00′N, 15°10′E, 225 m a.s.l.), Tagel (57°1′N, 14°36′E, 200 m a.s.l.), and Tönnersjöheden (56°41′N, 13°05′E, 70 m a.s.l.). Henceforth, these sites (described in the following sections) are referred to as Sites I, II and III, respectively. Observations of material in selected plots included in a nationwide thinning experiment were also used to provide estimates of missing data for Sites II and III, as described below.

Study area and experimental design

Site I

Originally, the experiment at this site was designed to study effects of shelterwood density and the timing of its removal on Scots pine growth and wood quality (Beland et al. 2000). Site I has typical characteristics of a relatively high fertility, forested site in southern Sweden, with an estimated site index (H100 for Scots pine) of 27 m, corresponding to a MAI of about 7.2 m^3 ha^{-1} $year^{-1}$. The soil is moist podzol, the vegetation type according to (Hägglund and Lundmark 1977) is "blueberry" and "broadleaved grass", the ground is flat, and the site conditions are relatively homogenous. Before the experimental treatments, the 69-year-old stand was dominated by Scots pine, which accounted for 61% of the total standing volume. The mean standing volume and stem density was 284 m^3 ha^{-1} and 573 stems ha^{-1}, respectively. There is no documentation of stand management history prior to the experiment. However, there are indications that it was regenerated by direct seeding with seeds of a German provenance (a widely applied technique in the early twentieth century). In January 1992, the first cuttings divided the stand into three parts: one that was clear-cut, one where seed trees were retained (at ~150 stems ha^{-1}) for a standard retention period (ca. 6 years), and one where shelterwood (~200 stems ha^{-1}) was retained for a longer period (Table 1). Pine was favoured when selecting shelter or seed trees. The whole area was fenced to exclude browsing by ungulates.

The new generation of Scots pine was established by planting, natural regeneration and direct seeding. Soil scarification (disc trenching) was applied on all plots. Planting was done using seedlings originating from seeds collected from the old stand, at three initial planting densities (1600, 3000 and 10,000 seedlings ha^{-1}) in a randomized block design (Figure 1). Two blocks were established on the clear-cut and one block in shelterwood of each density. Each treatment had one repetition per block, except planting with 1600 seedlings ha^{-1}, which was not applied under the seed trees. In addition, plots for natural regeneration were established in each block under both seed and shelter trees. Plot-size varied within the blocks, ranging from 956 to 1945 m^2 (mean: 1644 m^2). Plots planted with 10,000 seedlings ha^{-1} were subjected to PCT (15 years after planting), in which naturally regenerated tree species were removed. Naturally regenerated plots were also subjected to PCT, leaving 1600 trees ha^{-1} in half of each plot and 4444 trees ha^{-1} in the other half. Direct seeding failed due to extensive frost heaving and was excluded from the study.

Seedlings were affected by needle cast caused by *Lophodermium seditiosum* and Brunchorstia disease caused by *Gremmeniella abietina* in the first years after establishment. The highest mortality was observed among naturally regenerated seedlings. In addition, parts of the fence were periodically destroyed during the observation period. Thus, some browsing damage occurred. Storm damage to the overstory occurred during the period 1993–1995 and additional losses occurred in the shelterwood in 2005 during storm Gudrun (Table 1).

Site II

The experiment at this site was a demonstration trial (Figure 1), the main objective being to study effects of the three focal regeneration methods on growth and volume production of Scots pine (Kardell 2013). The estimated H100 for Scots pine was 30 m, corresponding to a MAI of 8.8 m^3 ha^{-1} year^{-1} (Hagglund and Lundmark 1981).

The regeneration methods (direct seeding, planting and natural regeneration under the seed trees) were each applied in two plots with an average size of 900 m^2. The treatments were not randomized and there were no buffer zones between the plots. Half of the stand was clear-felled and in the other half seed-trees were retained. Soil was scarified by disc-trenching in all plots, and the entire area was subsequently fenced. In all plots, naturally regenerated trees, mostly birch, were removed in a PCT 16 years after the start of the experiment. Seed trees were harvested after six growing seasons.

Site III

The experiment at Site III included two naturally regenerated and two planted Scots pine stands (Figure 1) located within 1 km of each other (Agestam et al. 1998). Each stand had similar site conditions (estimated H100 for Scots pine 27 m on average, corresponding to an MAI of ca. 7.2 m^3 ha^{-1} yr^{-1}, with dry podzolic soil and all stands fenced). Planting was done on clear-cut areas with seedlings of a local provenance at densities ranging between 1600 and 6400 seedlings ha^{-1}. Broadleaved trees were removed in a PCT from both of these areas. The natural regeneration treatment involved retention of seed trees. Half of each naturally regenerated stand was subjected to PCT to 4500 seedlings ha^{-1}, while the other half was left as a PCT-free control. Data were collected before the first thinning. Plot sizes varied between 400 and 1000 m^2. The area was not fenced.

Data collection at the three sites (I–III)

The regeneration was inventoried 17–24 growing seasons after initiation of the experiments (Table 2). At every site, the diameter at breast height (dbh) of each tree was recorded in four 100 m^2 circular sampling plots, systematically placed in each treatment plot. Fifteen trees of each arboreal species present were also systematically selected in each of the circular sampling plots, then their height and height to the first living branch were measured. The height and diameter measurements of sample trees were used to parametrize the following diameter-height relationship model for each treatment plot (Näslund 1937):

$$H(D) = BH + \frac{D^x}{(aD + b)^x} \quad (1)$$

Here, H is the tree height (m), D is the tree diameter at breast height (cm), BH is the breast height (m), x is 3 for Norway spruce and 2 for all other tree species, a and b are parameters.

Table 1. Seed and shelter trees after cutting in 1992, and both before and after cuttings in 1998. Data concerning storm-felled (Storm f.) trees were collected after storms in 1993, 1995, 1998 and 2015. bc and ac indicate before and after cutting, respectively.

	Seed trees					Shelter trees				
Year	No. trees *ha^{-1}*	Height *m*	Basal area *m^{2}ha^{-1}*	Dbh *cm*	Volume *m^{3}ha^{-1}*	No. trees *ha^{-1}*	Height *m*	Basal area *m^{2}ha^{-1}*	Dbh *cm*	Volume *m^{3}ha^{-1}*
1992 ac	154	23.9	11.5	30.4	122	198	23.8	14.5	30.2	153
Storm f. 1993	*18*		*1.4*	*30.5*	*14*	*13*		*0.8*	*28.1*	*9*
Storm f. 1995	*3*		*0.2*	*28.4*	*2*	*2*		*0.1*	*28.0*	*2*
Storm f. 96–98	*2*		*0.2*	*31.0*	*2*	*4*		*0.3*	*28.4*	*3*
1998 bc 1998 ac	129	23.9	11.4	33.2	121	179	23.9	15.1	32.5	159
						75	24.0	6.8	33.7	73
Storm f. 99–15						*12*		*1.1*	*34.0*	*11*
2015						63	25.2	7.6	38.8	80

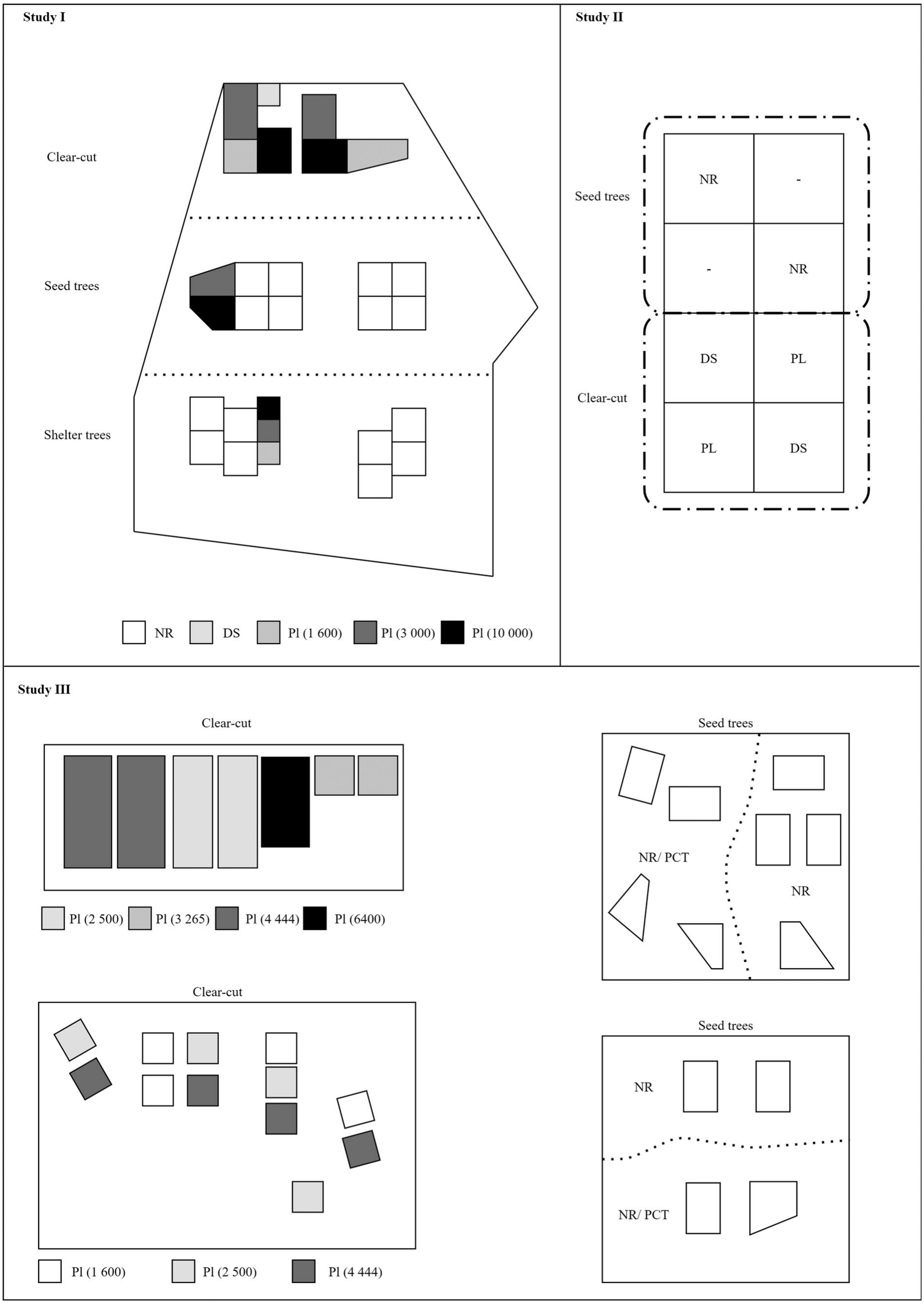

Figure 1. Schematic experimental design at all study sites (I–III). Abbreviations: NR, PL, DS, PCT refer to natural regeneration, planting, direct seeding, pre-commercial thinning, respectively. Numbers in the parenthesis refers to initial planting densities (number of seedlings per hectare).

Table 2. Parameters of stands at all three experimental sites at indicated ages, showing means of plot values, which were used for modelling. Regeneration methods: PL – planting, NR – natural regeneration, DS – direct seeding. PCT refers to pre-commercial thinning.

Regeneration method	Initial density *No. trees ha^{-1}*	Age *years*	Dominant height *m*	No trees ha^{-1}	Basal area *m^{2}ha^{-1}*	Volume *m^{3}ha^{-1}*
Site I						
PL/Clear-cut	1600	24	13.48	1537	23.20	134
PL/Clear-cut	3000	24	13.86	1867	28.14	175
PL/Clear-cut	10,000	24	13.85	3175	27.22	167
PL/Seed-trees	3000	24	11.44	2100	23.84	126
PL/Seed-trees	10,000	24	12.21	2325	19.74	109
PL/Shelter-trees	1600	24	10.54	1925	14.73	72
PL/Shelter-trees	3000	24	12.20	2237	18.28	101
PL/Shelter-trees	10,000	24	12.14	2675	16.60	90
NR/Seed-trees	1600	24	9.71	1450	13.81	64
NR/Seed-trees	4444	24	10.35	3194	17.44	82
NR/Shelter-trees	1600	24	8.96	1450	6.25	26
NR/Shelter-trees	4444	24	9.55	3700	11.56	49
Site II						
DS	–	25	13.43	2044	26.18	162
PL	2000	25	12.92	2145	23.60	136
NR/Seed-trees	–	27	13.14	1938	23.98	139
Site III						
PL	1600	17	7.14	1579	14.83	54
PL	2500	17	8.12	2307	18.49	75
PL	3265	17	9.81	3244	24.70	117
PL	4444	17	8.58	3990	23.90	101
PL	6400	17	9.66	5612	30.17	142
NR	No PCT	31	12.85	5488	33.58	194
NR	PCT	31	13.16	3350	32.13	190

Simulations

The StandWise application of the Heureka DSS was used for all modelling reported here. Data describing the stand growth, as well as both thinning and harvesting operations at the three sites described above, were imported to the software as tree lists, then subjected to two kinds of simulations. First, the development of the overstory (seed and shelter trees) was simulated during the period from the first release cutting until its full removal 6–25 years later. Second, the new stand's development was simulated from the latest inventory in which it was measured, until final felling by clear-cut. At Sites II and III the latest inventory of the young stand occurred 9–18 years after final overstory removal. At site I some of the overstory was still left at the time of the inventory (Table 1), and the overstory removal and young stand inventory were assumed to have occurred simultaneously. Separate simulations of stands with overstory retention were needed to assess its direct financial effects, relative to a clear-cut alternative. The concept of the financial result of overstory retention is explained later in the text. Figure 2 illustrates graphically how the two simulations slices fit together.

Overstory

Overstory development was modelled in Heureka from the time of the first release cutting until removal of the last seed and shelter-trees. For Site I, starting values for the simulations were drawn from the old stand data, recorded when the experiment was established. The timing and intensity of the release cuttings were applied according to the documented management in the experiment (Table 1).

Overstory data were not available for Sites II and III. Hence, overstory development was modelled using data obtained from 10 selected plots from a nationwide thinning experiment encompassing sites with similar conditions to Sites II and III (Nilsson et al. 2010a). The selected plots were located in the southern part of Sweden, south of 60° N latitude. H100 site indices for Scots pine at the plots varied between 21 and 27 m.

The time of the first release cutting was chosen according to the optimal rotation, defined as the rotation that maximized the LEV. For each stand, three scenarios (representing development following regeneration with seed trees, with a shelterwood and reference clear-cut) were simulated. Wind damage levels were chosen according to previous findings that on average 9% of the overstory trees were wind-felled during the first seven years after cutting in shelter woods in

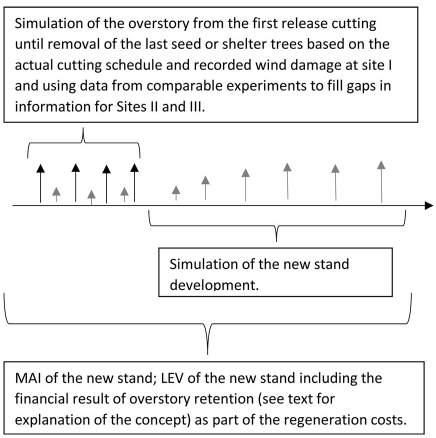

Figure 2. Schematic representation of the simulations in the study.

Table 3. Financial results of overstory retention at Site I in EUR ha^{-1}. Observed wind damage level refers to the wind damage registered during the observation period.

	Wind damage level	Seed trees Observed (~16%)	Low (4%)	Moderate (9%)*	High (14%)	Shelter trees Observed (~7%)	Low (4%)	Moderate (9%)*	High (14%)
Interest rate	0%	−73	308	149	−9.58	2478	2677	2345	2012
	2.5%	−368	−32	−172	−312	568	704	477	251
	4%	−526	−213	−343	−473	−159	−48	−233	−419

*Moderate wind damage of 9% is the observed probability of wind-throws in shelterwoods in southern Sweden, during a 7-year period after first release cutting (Nilsson et al. 2006).

southern Sweden (Nilsson et al. 2006). This ("moderate") level and two additional levels: moderate plus and minus one standard deviation ("high (+4%)" and "low (−4%)", respectively) were tested in the simulations.

Financial result of overstory retention

The financial result of overstory retention was used as an approximation of the effect of choosing natural regeneration rather than clear-cutting on the profitability of the previous rotation. When negative, it constitutes a cost that should be assigned to the new, naturally regenerated stand. In contrast, if positive it constitutes a financial "bonus" that can be assigned to the new stand. It was defined as the difference between the sum of discounted revenues from release cuttings until complete removal of the overstory and the revenue from a reference clear-cut. Calculations were done for three interest rates: 0%, 2.5% and 4% (Table 3). The timber value of the wind-felled seed/shelter trees was assumed to be equal to the variable costs of removing these trees. However, the fixed cost for starting the machinery operation was added at each occasion. Three wind damage levels were also included in sensitivity analyses, using recorded wind damage at Site I and data from comparable experiments (Nilsson et al. 2010a) to fill gaps in information for Sites II and III.

A multiple linear regression model (MLR) was used to analyse the variation of financial result of overstory retention for the 10 plots included in a nation-wide thinning experiment (the average results to be used as proxies for the financial results at sites II and II), calculated at no interest rate and with the moderate wind damage level (9%). MLR was conducted using R software, version 3.6.1 (Team 2013).

New stand

Starting values for the simulations were drawn from data obtained in the experiments presented above (Table 2). Further stand growth was simulated until final felling at the time of MAI culmination.

To account for the effect of release after removal of the last remaining shelter-trees at Site I (75 trees ha^{-1} at the time of the inventory), data on the overstory trees were included in the input. The shelter trees were then removed during the first period of the simulation. The time span between removal cuttings and the understory inventory in other naturally regenerated plots was much longer (9-18 years). Thus, the release effect was assumed to be captured by the understory data.

Thinnings were applied according to thinning guidelines obtained from the forest owners association Södra. A dominant height of 22 m was an upper limit, above which thinnings were not conducted.

Financial calculations

The financial performance of tested regeneration methods was compared in terms of LEV (Faustmann 1849) with the following formula:

$$LEV = \frac{1.0p^u}{(1.0p^u - 1)} * NPV \qquad (2)$$

where LEV is the land expectation value, u is the length of the rotation period, p is the interest rate, and NPV is net present value of the costs and revenue streams from the first rotation.

Calculations were done with two interest rates: 2.5% and 4% (Brukas et al. 2001). The economic calculations included all costs and incomes related to management activities throughout the rotation. The cost for seedlings, including planting costs, was 0.42 EUR per seedling, while costs of mechanical soil scarification and PCT were 238 and 229 EUR ha^{-1}, respectively. Costs of supplementary planting (+20%) were also added to costs for all planted parcels. Timber prices were applied according to the roadside pricelist for the region of Växjö (2019). Harvester costs for thinning and final felling operations were set at 118 and 127 EUR/hour, respectively, and corresponding forwarder costs at 71 and 75 EUR h^{-1}, respectively. In Heureka, harvester-forwarder productivity is estimated using time consumption functions presented by Wikström (2008).

Results

Financial results of overstory retention

Seed tree retention at Site I (Linnebjörke) incurred costs under all conditions except in simulations with 0% interest and either low or moderate wind damage. The financial result of shelter tree retention was positive at 0% and 2.5% interest rates, but negative at 4% interest rate (Table 3). Wind damage significantly affected the financial result of overstory retention (Tables 3 and 4). At 2.5% interest rate, the financial result of retaining seed and shelter trees was about 300 and 450 EUR ha^{-1} lower, respectively, with high wind-damage than with low wind damage.

The financial results of overstory retention at Sites II and III were estimated from simulations of overstory development for comparable plots in a nationwide thinning experiment

Table 4. Average financial results of overstory retention in EUR ha^{-1} (means with standard errors in parentheses) obtained from simulations of stand development in 10 long-term experimental plots (GG-experiment) at two interest rates and three wind damage levels.

		Seed trees			Shelter trees		
	Wind damage level	Low (4%)	Moderate (9%)*	High (14%)	Low (4%)	Moderate (9%)*	High (14%)
Interest rate	0%	−119 (27)	−247 (26)	−375 (27)	1980 (246)	1690 (228)	1399 (209)
	2.5%	−390 (27)	−503 (29)	−616 (31)	149 (133)	−38 (120)	−187 (96)
	4%	−510 (44)	−607 (52)	−745 (34)	−463 (72)	−621 (66)	−780 (60)

*Moderate wind damage of 9% is the observed probability of wind-throws in shelterwoods in southern Sweden, during a 7-year period after first release cutting (Nilsson et al. 2006).

(Table 4). For seed trees, it was negative regardless of the interest rate and wind damage level. The result of shelterwood retention was positive at 0% interest rate, and at 2.5% interest rate with low wind damage. The estimated result at 2.5% interest rate was on average 95% higher for shelterwood retention than for retaining seed trees, regardless of the wind damage level. At 4% interest rate, retention of seed and shelter trees had roughly equal financial results.

Results of the multiple regression analysis indicated that the financial result of shelter tree retention is affected by site index and average tree size (Table 5), becoming increasingly positive (or less negative) with increases in either site index or average tree size (Figure 3). However, correlations between these variables and the financial result of retaining seed trees are weak.

Overall, estimates of the financial results of overstory retention at Site I were higher than the estimates derived from the nation-wide thinning experiment.

Volume production in the new stand

At Site I, the average simulated MAI was on average 8.9% and 5.2% higher, at all planting densities, on the clear-cut (7.7 m^3 ha^{-1} year^{-1}) than in plots with retained seed and shelter trees, respectively. On average, natural regeneration yielded 18.5% lower MAI than planting, with or without shelter or seed-trees. However, natural regeneration was not tested on the clear-cut.

The highest MAI under each treatment was observed on the parcels with 3000 seedlings (or stems or remaining after PCT) ha^{-1}. Planting with 3000 seedlings ha^{-1} on a clear-cut yielded the highest overall MAI (8.3 m^3 ha^{-1} year^{-1}) of all combinations of regeneration treatment and seedling density (Figure 3).

In contrast, the MAI was lowest (5.6 m^3 ha^{-1} year^{-1}, on average) in naturally regenerated plots that were pre-commercially thinned to 1600 stems ha^{-1} with either seed or shelter trees. The differences in this respect between naturally regenerated plots with shelterwood or seed trees and the same numbers of stems after PCT were negligible (Figure 4). In naturally regenerated plots, the MAI was on average 14.71% higher when 4444 stems ha^{-1} were retained after the PCT than when 1600 stems ha^{-1} were retained (Figure 4).

At Site II, direct seeding yielded the highest MAI (8 m^3 ha^{-1} year^{-1}), which was 15.1% higher than the MAI yielded by planting. Volume production in naturally regenerated plots was slightly higher than in planted plots in the clear-cut (Figure 5).

Results for Site III indicated that the MAI in plots planted on the clear-cut increased with increasing planting density and ranged from 7 to 10 m^3 ha^{-1} year^{-1}. Natural regeneration under seed trees yielded on average 40.2% lower MAI. PCT in naturally regenerated plots had little effect on volume production (Figure 6).

Economic performance of the regeneration methods

Results from site I showed that at 2.5% interest rate, planting with 1600–3000 seedlings per hectare under shelter-trees yielded 12.6% higher LEV than planting with corresponding densities on the clear-cut. Furthermore, natural regeneration under the shelter trees resulted in 9.6% higher LEV than planting (with 1600–3000 seedlings ha^{-1}) on the clear-cut. Natural or artificial regeneration under seed trees resulted in substantially lower LEV. Planting with 10,000 seedlings per hectare resulted in negative LEV, regardless of shelterwood density (Table 6).

At the higher (4%) interest rate, all investments in stand establishment resulted in relatively low or negative LEV, according to calculations including the financial result of overstory retention with the wind damage level recorded in the actual experiment (Table 2).

At Site II, direct seeding yielded the highest LEV at both 2.5% and 4% interest rates (45.1% and 19.1% higher LEV than planting and natural regeneration, respectively, at the 2.5% interest rate), assuming a moderate level (9%) of wind damage to the seed trees (Table 3).

At site III, LEV decreased with increases in initial planting density, at 4%interest rate. However, at 2.5% interest rate, LEV remained rather stable up to an initial density of 3265 seedlings ha^{-1}. Further increase in initial planting density resulted in substantial reduction of LEV. At 2.5% interest rate,

Table 5. Results of linear regression analysis of effects of increases in site index (H100, in m) and average tree size (dbh, in cm) on the financial result (in EUR ha^{-1}) on overstory (shelter tree) retention.

	Seed trees					Shelter trees				
	Estimate	SE	t-value	*p*-value	pEta-sqr*	Estimate	SE	t- value	*p*- value	pEta-sqr*
Intercept	39,841	503.97	0.791	0.452	0.073	−5654.58	1675.04	−3.376	0.00970	0.5875
Site index (H100)	−27.47	24.33	−1.13	0.29	0.137	226.02	80.86	2.795	0.02337	0.4941
Average tree size	0.9	5.51	0.163	0.874	0.003	63.69	18.31	3.479	0.00834	0.6020

*pEta-sqr: partial determination coefficients for the relationships between SI and tree size versus financial result.

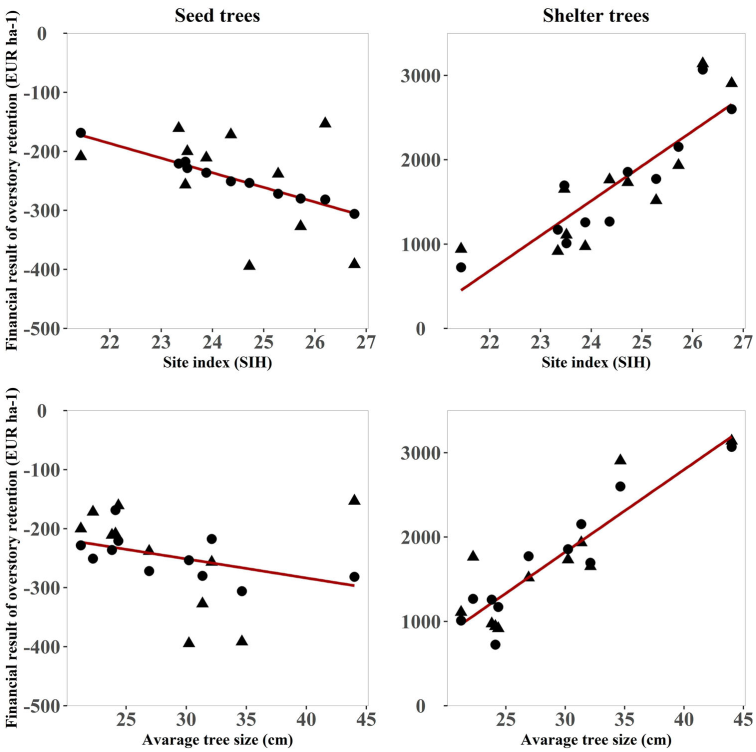

Figure 3. Dependence of financial results of seed tree (first column) and shelter tree (second column) retention on site index (H100 in m) and average tree size (dbh in cm). Circles and triangles indicate values based on fitted and observed overstorey development data.

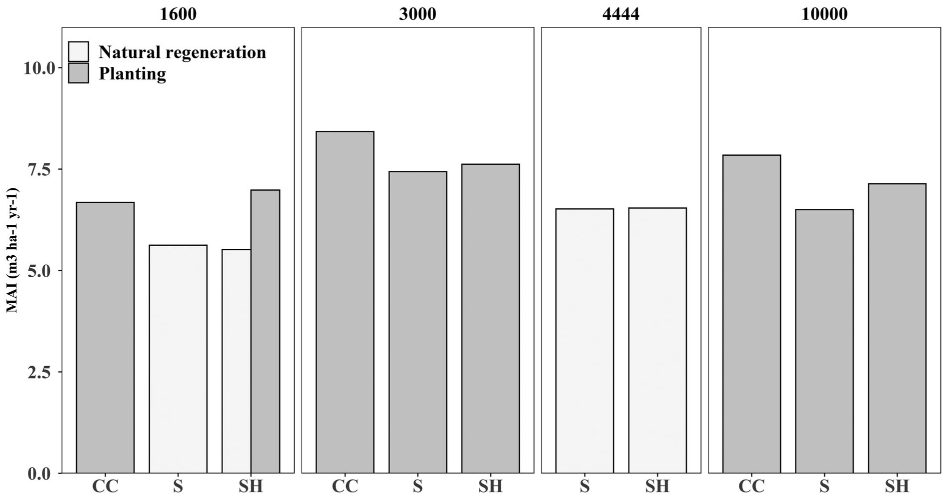

Figure 4. Estimated MAI (m^3 ha^{-1} $year^{-1}$) at Site I. Numbers in the top row are initial planting densities or numbers of stems after PCT (seedlings ha^{-1}). CC, S and SH refer to clear-cut, seed trees and shelter trees, respectively.

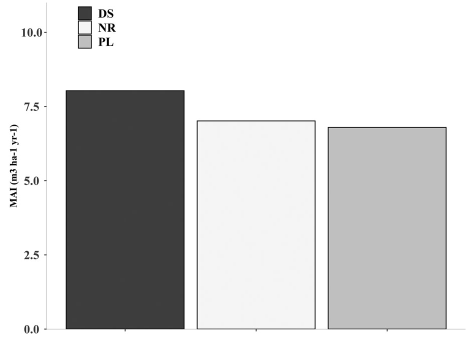

Figure 5. Estimated MAI (m^3 ha^{-1} year^{-1}) in plots subjected to direct seeding (DS), natural regeneration (NR) and planting (PL) treatments at Site II.

planting with densities of 1600–3265 seedlings ha^{-1} yielded on average 43.7% and 80.1% higher LEV than planting with 4444 and 6400 seedlings ha^{-1}, respectively. At 4% interest rate, planting with 4444 and 6400 seedlings ha^{-1} resulted in negative LEV. Naturally regenerated plots that had been pre-commercially thinned yielded 19.1% higher LEV than controls (at 2.5% interest rate). Natural regeneration with PCT resulted in 38% and 73% lower LEV than planting with 2500 seedlings ha^{-1} at 2.5 and 4% interest rates, respectively. Moderate wind damage to the seed trees was applied in the calculations.

Discussion

Volume production

Estimated MAI in the simulated rotations was higher in planted than in naturally regenerated stands at Sites I and III, but not Site II. Higher production in planted stands was also observed in a previous study by Ekö (1994), and is consistent with comparisons of yields in naturally regenerated and planted Norway spruce stands by (Klang 2000). The lower growth of naturally regenerated stands may be partly due to competition from the seed or shelter trees. This hypothesis is supported by numerous investigations of effects of retained trees on growth of Scots pine seedlings (Valkonen et al. 2002; Valkonen 2000; von Sydow and Örlander 1994; Ackzell and Lindgren 1992; Kuuluvainen and Pukkala 1989). Furthermore, planted seedlings tend to suffer less from competition from ground vegetation than naturally regenerated seedlings. This may facilitate their establishment, accelerate their juvenile growth and hence shorten their exposure to damaging biotic and abiotic factors. In contrast, Kuuluvainen and Pukkala (1989) found that proximity of seed trees impairs growth of grasses and herbs. Thus competition from ground vegetation could be weaker under seed or shelter trees than in open clear-cut areas (Karlsson and Nilsson 2005; Petersson and Örlander 2003; Nilsson et al. 2002; von Sydow and Örlander 1994). Natural regeneration also usually results in stands with a more heterogeneous structure, which may have lower volume production than otherwise similar stands with more homogeneous structure (Binkley et al. 2013; Binkley 2011). The higher production of planted stands has also been attributed to genetic improvement. However, in this study, planted seedlings had the same genetic origin as naturally regenerated seedlings.

In planted stands, the total volume production increased with increases in planting density (Figure 2), due to associated increases in basal area, as observed in several spacing experiments with Scots pine (Agestam et al. 1998; Pettersson 1992; Huuri et al. 1987; Huuri and Lahde 1985). Our results also show effects of the competition from seed and shelter

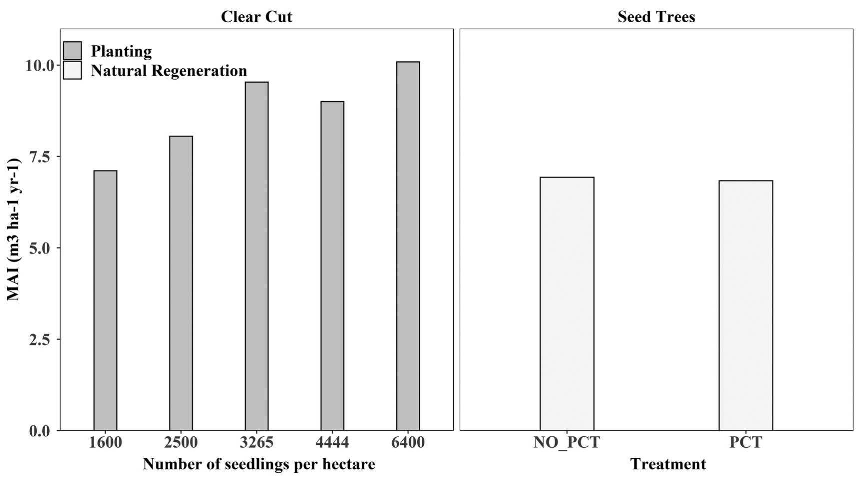

Figure 6. Estimated MAI (m^3 ha^{-1} year^{-1}) at site III in plots on the clear-cut and under seed trees. PCT refers to pre-commercial thinning.

Table 6. LEV ha^{-1} with indicated stand establishment procedures at 2.5% and 4% interest rates at all study sites (I–III). Regeneration methods: PL – planting; NR – natural regeneration; DS – direct seeding. PCT refers to pre-commercial thinning.

Site I	Density	Interest rate 2.5%			Interest rate 4%		
	(seedlings ha^{-1})	Clear-cut	Seed-trees	Shelter-trees	Clear-cut	Seed-trees	Shelter-trees
PL	1600	2638		3357	450	−1049	186
PL	3000	2502	1208	2525	31		−552
PL	10,000	−3277	−4006	−2871	−4631	−5323	−4120
NR	1600		1649	2732		−15	281
NR	4444		1758	2957		−14	431
Site II		Interest rate 2.5%			Interest rate 4%		
		Clear-cut	Seed-trees	Shelter-trees	Clear-cut	Seed-trees	Shelter-trees
PL	2000	2412			768		
DS			4396			1302	
NR			3555			45	
Site III		Interest rate 2.5%			Interest rate 4%		
		Clear-cut	Seed-trees	Shelter-trees	Clear-cut	Seed-trees	Shelter-trees
PL	1600	3717			967		
PL	2500	3642			665		
PL	3265	3621			485		
PL	4444	2059			−580		
PL	6400	731			−1793		
NR	No PCT		1839			148	
NR	PCT		2274			263	

trees on the planted seedlings. For planted seedlings, MAI was on average 8.9% and 5.2% higher in clear-cut plots than in plots with seed and shelter trees, respectively. These estimates agree well with findings by Nilsson et al. (2006).

It should be noted that damage to seedlings and trees might affect the total volume production. Extensive damage to the seedlings by *Lophodermium* needle cast and Brunchorstia disease was probably the main reason for low stems number in naturally regenerated plots at Site I (Table 2). Furthermore, strong competition from hairy grass at Site II resulted in patchy natural regeneration, which may have reduced the volume production in those stands. Browsing could have affected the result at Site III, which was not fenced. However, no data on browsing damage to the seedlings/trees was collected.

Browsing was previously found to have a substantial effect on both production and economy in Scots pine stands (Nilsson et al., 2016). Thus fencing might have led to overestimates of volume production. Costs of fencing were not included in the calculations, as they would have resulted in largely negative financial results, complicating presentation and discussion of relative differences in LEV between the studied regeneration methods. Admittedly, the financial outcomes obtained in the study represent an idealized situation where browsing is kept at a negligibly low level.

Financial outcomes

The financial outcome of the simulated Scots pine rotations depended on the regeneration method, interest rate and site. Overall, planting in clear-cut plots with 1600–3265 seedlings per hectare resulted in the smallest variation in LEV of all the tested methods, across the three study sites at 2.5% interest rate. This indicates that planting may be the most reliable regeneration method at high fertility sites (Table 4). Similarly, Simonsen (2013) found that planting was the optimal method on productive sites located in northern Sweden with site indices (H100) ranging from 16 to 28 m. Our results also indicate that initial densities higher than 3256 seedlings per hectare result in substantially poorer financial outcomes at such sites than lower densities, in accordance with results of modelling by Hyytiäinen et al. (2005). Furthermore, planting 10,000 seedlings ha^{-1} was unprofitable, due to high initial investments that were not compensated by increases in harvesting revenues. Overall, the results clearly confirm the importance of appropriate planting densities for maximizing the profitability of wood production (Coordes 2013; Tahvonen et al. 2013; Hyytiäinen et al. 2005; Gong 1998).

In accordance with findings by Glöde et al. (2003), planting under seed trees resulted in relatively poor financial outcomes, due to combined costs of planting, usually negative financial results of overstory retention and lower production than planting on clear-cuts. In contrast, planting under shelterwood resulted in higher LEV, despite anticipated reductions in volume growth (relative to planting on clear-cuts), due to the low initial costs and especially the positive financial result of overstory retention. Thus, planting under shelterwood with a long retention period could be considered a good alternative to the common clear-cutting system for fertile Scots pine sites. However, further tests with larger numbers of plots would be needed to validate these results. Natural regeneration under seed trees yielded lower LEV than planting on clear-cuts with moderate initial densities at 2.5% interest rate. However, the results indicate that under some conditions it could be competitive to planting on clear-cuts, even at high-fertility sites. The financial results of natural regeneration under shelter trees were comparable to those of planting on clear-cuts. This was partially due to relatively low initial investments and neutral or positive financial results of overstory retention, which compensated for a lower volume increment.

Our results reveal very high variation in the outcome of direct seeding among regeneration sites. *Inter alia*, it yielded the highest MAI and LEV at Site II, but totally failed at site I. Both Glöde et al. (2003) and Hyytiäinen et al. (2005) found that it outperformed natural regeneration and planting at all interest rates at medium fertility sites, due to relatively low costs of establishment and high volume production. However, sowing on medium and high fertility sites is associated with risks of abundant ground vegetation outcompeting small seedlings, especially on clear-cuts. Miina and Saksa (2008) highlighted the importance of careful site selection for good regeneration outcomes from planting, sowing and natural regeneration. Accordingly, the results from our study likely reflect both the potential and uncertainties or risks associated with direct seeding on fertile sites.

The high interest rate substantially limited the alternatives for profitable wood production. At the 4% interest rate, most of the investments became economically irrational (Table 4), suggesting that both planting and natural regeneration are difficult to justify at higher interest rates. However, these results were highly dependent on costs of management and the harvest, pulp and timber prices applied. Earlier studies showed that natural regeneration was more profitable than planting at 3–5% interest rates (Simonsen 2013; Hyytiäinen et al. 2006; Glöde et al. 2003), but results of those studies should be compared cautiously due to differences in site properties, applied growth models and timber prices. For instance, timber prices are higher in Finland than in Sweden, which may facilitate profitable wood production especially at higher interest rates, and studies by Hyytiäinen et al. (2005) confirmed the sensitivity of economic outcomes to price changes.

Natural regeneration or narrow spacing tend to promote higher quality timber than sparse planting (Liziniewicz 2014), mainly because it increases selection possibilities and leads to smaller branches through increases in competition between trees (Agestam et al. 1998). The effects of initial spacing on wood quality are probably stronger at high fertility sites, as Persson (1977) found that quality at a given spacing is inferior at more fertile sites. Regeneration under shelter trees also positively affects future wood quality, according to Ekö (1994). However, growth models used in Heureka do not account for effects of initial spacing density, or pre-commercial and commercial thinnings, on wood quality, except their effects on diameter growth. Thus, our analyses may underestimate the financial results for naturally regenerated, seeded and densely planted strands if high-quality timber attracts higher premiums in the future.

Our calculations indicate that seed-tree retention incurs additional costs compared to clear felling that are, in many cases, roughly equal to or larger than the savings obtained by avoiding planting. In contrast, retention of shelter trees can have good economic results (at 0% and 2.5% interest rates) although it varies, depending on site index and average tree size. Generally, the financial result of overstory retention declined with increases in interest rate. At 4% interest rate, costs of leaving the shelter trees were comparable to those of retaining seed trees. Furthermore, the sensitivity analyses indicated a strong effect of wind damage on the cost of overstory retention. The potential severity of naturally regenerated stands' increased susceptibility to wind damage after release cuttings has been previously highlighted (Örlander 1995), and the increased frequencies of windthrows naturally resulted in additional financial losses.

Conclusion

Planting seems to be the most suitable regeneration method on fertile sites such as those included in this study. Direct seeding can provide successful regeneration even on relatively fertile sites, but the method is rather unpredictable. Seed tree retention almost always incurs additional costs, compared to single-operation clear felling, which are often comparable to and sometimes larger than the potential savings from the avoided planting. This regeneration method is often less financially favourable than clear-cutting and planting due to the combination of lower volume production and costs associated with the seed tree removal. Regeneration under shelter-trees with a long retention period may be a competitive alternative to a conventional clear-cutting regime, mostly due to low initial investments and no additional costs related to overstory retention. However, the assessment presented here should be regarded as a case study. The lack of a statistically valid design of the original experiments and geographical limitations must be taken into account when generalizing the results.

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Disclosure statement

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

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Tree species choice is a central issue for forest management, and survey studies show that urgent improvements in regeneration practices are needed in Sweden. This thesis investigated site-specific differences in growth during the whole rotation between Scots pine and Norway spruce. Furthermore, potential for regenerating Scots pine on medium- and high fertility sites was studied. Results shows that Scots pine has a superior growth compared to Norway spruce on low- to medium fertile sites and that it can be successfully regenerated on relatively fertile sites.

Mikolaj Lula received his graduate education at Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences (SLU). He holds M.Sc. degree in Forest Management and in Forestry from SLU.

Acta Universitatis agriculturae Sueciae presents doctoral theses from the Swedish University of Agricultural Sciences (SLU).

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