Effects of release cutting and soil scarification on natural regeneration in *Pinus sylvestris* shelterwoods

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Abstract

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The objective of this thesis was to evaluate different methods of improving seed production, seed germination, seedling survival and seedling growth when using natural regeneration with Scots pine (*Pinus sylvestris* L.) seed trees and shelterwoods. Two experiments and a survey study were used to evaluate effects of (i) shelterwood density and seedling height at release on survival, damage and height growth of advance growth seedlings of Norway spruce (*Picea abies* (L.) Karst.), (ii) release cutting on seed production, seed quality and needle nutrient contents in seed trees, (iii) weather and seed tree size on seed production, (iv) correlation between needle nutrient contents and seed production and seed weight, and (v) scarification in relation to seed fall.

For all advance growth seedling sizes, growth was highest at shelterwood densities of 80-160 stems ha^{-1}, whereas the optimum density for survival was about 160 stems ha^{-1}. Height, top-shoot length and top-shoot diameter in seedlings the year before release cutting showed significant positive correlations with both survival and height growth. A majority of the small seedlings (<20 cm) wilted the spring after overstorey release cutting, probably as a combined effect of drought in the humus and "light shock". The only identified damaging agent causing significant mortality was pine weevil *(Hylobius abietis* L.).

Cone and seed production were about five times higher in seed trees that had been released for 4-5 years, compared to control trees in the unreleased forest. Seed trees released for less than three years had about the same level of cone production as the controls. After release, the number of cones increased more in the lower part of the tree crowns than in the uppermost two metres. The concentration of nitrogen, potassium, and phosphorus in needles and mean needle dry weight was significantly higher in released trees compared to unreleased control trees. N, P and K concentrations in needles were significantly positively correlated to numbers of conelets as well as to mean 1000-seed weight.

In 1996, there were about eight times more cones than in 1995, probably because summer temperatures were higher in 1994 than in 1993, the years when the respective flower buds were initiated. Trees with a diameter at breast height of 400 mm produced twice as many cones as trees with a diameter of 300 mm.

By timing soil scarification in relation to a rich seed fall twice as many seedlings were established compared to scarification immediately after release cutting. Unscarified plots showed poorest result according number of seedlings, and number of plots without seedlings (0-plots). Height growth was significantly improved by scarification.

Key words: Advance-growth seedlings, cone production, conelet production, frost injury, Hylobius abietis, nitrogen, phosphorus, potassium, seed production, seed quality, seedling establishment, seedling growth, seedling mortality, soil preparation

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Appendix

Papers 1-4

The thesis is based on the following four papers, which will be referred to by their roman numerals.

I. Örlander, G. & Karlsson, C. 1999. Influence of shelterwood density on survival and height increment of *Picea abies* advance growth. In print. Scand. J. For. Res. 15: 20-29.

II. Karlsson, C. & Örlander G: 1999. Soil scarification shortly before a rich seed fall improves seedling establishment in seed tree stands of Pinus sylvestris. In print. Scand. J. For. Res. XX: XXX-XXX

III. Karlsson, C. Seed production of *Pinus sylvestris* after release cutting. Submitted to Can. J. For. Res.

IV. Karlsson, C. & Örlander, G. Mineral nutrients in needles of *Pinus sylvestris* seed trees after release cutting and their correlations with cone production and seed weight. Manuscript.

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Introduction

Definitions

Shelterwood and seed tree stand

The terms shelterwood and seed tree stand are frequently used in the literature. However, they are defined in different ways in different countries. In most definitions, the aim of a seed-tree stand is to produce and distribute seeds, while a shelterwood often is expected to have some sheltering function (Smith 1996). Hagner (1962) emphasised the multiple purposes of a shelterwood (*i*) utilise wood production capacity of the site, (*ii*) serve as seed trees, (*iii*) protect seedlings from climatic damages, and (*iv*) reduce growth of field vegetation. The difference between a seed tree stand and a shelterwood stand is often defined at a certain number of trees ha^{-1}, e.g. seed tree stand when 50-150 trees ha^{-1} and shelterwood when more than 150 ha^{-1} (Anon. 1995, Anon. 1996). In the papers presented in these thesis the term seed trees is used when the main interest is focused on seed production (paper II-IV). In the title of the thesis I have used the term shelterwood since I consider this term more general than seed tree stand.

Natural regeneration using seed trees/sheltertrees involves three different kinds of cutting (*i*) preparatory cutting, which set the stage for regeneration, (*ii*) establishment or seeding cutting, which induce the actual establishment of seedlings, and (*iii*) removal cutting, which release the established seedlings (Smith 1996). The term release cutting is used for all these three kinds of cutting. Both sheltertrees/seedtrees and seedlings are released. Shelterwoods can be arranged in different patterns. The uniform system, which means that trees are evenly distributed over the entire stand, is usually used in Sweden.

Conelets and cones

A pollinated flower is called a conelet, or 1-year-old cone, in the autumn of the second year of the reproductive cycle, when its diameter is 5-10 mm. A ripened cone in the autumn of the third year is called a 2-year-old cone, and its length normally varies between 25 and 50 mm.

Seed viability

The percentage of mature seeds that germinates at a standardised germination test.

Germination percent

In paper II the term germination percent is used to describe the proportion of viable seeds that had germinated in autumn. Another term to describe this is seedling emergence.

Seedling establishment

In this thesis (paper II) the term seedling establishment is used to describe the period from seed germination until the end of the period that was monitored (1-7 years). The seedling heights at the end of the period were 2-50 cm.

Advance growth seedlings

Seedlings that are already in the stand at the time of the final cutting and the start of the active regeneration phase (Sundkvist 1993). Forest managers are often faced with the question of whether it is feasible to carefully harvest the overstorey and base the new tree generation on advance growth instead of cleaning and scarifying the area in order to establish a new generation by planting, sowing or natural regeneration. A group of advance growth seedlings is called advance growth.

Natural regeneration of pines

Scots pine (*Pinus sylvestris* L.) forests are often naturally regenerated using seed trees (Anon. 1998 a). In Sweden, natural regeneration was the dominating regeneration method in Scots pine until 1950. After 1950 the interest for natural regeneration decreased. During the last 50 years it has been used on 15- 30 % (30 000 – 60 000 ha yr^{-1}) of the regenerated forest area in Sweden, predominantly in Scots pine forests (Jeansson 1985, Anon. 1998 b). Seedling stocking-level requirements, given by the National Board of Forestry in Sweden 1990-1997, were met only on about 70% of the naturally regenerated area, whereas ca 85% of the planted area was in compliance (Anon. 1998 a). Scarification improved regeneration, and 87 % of the scarified area complied with stocking-level requirements, compared with 65 % for unprepared areas. In Sweden, a seed tree density of 50 - 150 seed trees ha^{-1} evenly distributed is usually recommended when regenerating Scots pine (Anon. 1996). Although there has been a long tradition of natural regeneration, failures are common. Failures are ascribed to harsh climate in the northern interior parts of the country and to vegetation, insect and browsing problems in the south. One main problem, especially in the northern parts is that too few seeds germinate, due to low seed production.

In Finland, natural regeneration using seed trees was used on 20 000 - 40 000 ha yr^{-1} during the period 1970-1990 (Niemistö et al 1993). The national forest survey of Norway classified about 50 % of forests lower than 1.3 m in height as naturally regenerated during the period 1964 to 1976 (Skoklefald 1985). Natural regeneration of Scots pine is a common method within the entire range of its distribution, which is from Spain to Siberia.

In north America the shelterwood and the seed tree methods are used in e.g. white pine (*Pinus strobus,* Corbett 1994) and red pine (*Pinus resinosa,* Corbett 1994) in the northeast of USA and southeast of Canada; loblolly pine (*Pinus taeda,* Langdon 1981), shortleaf pine (*Pinus echinata,* Shelton & Wittwer 1992), slash pine (*Pinus elliottii,* Matthews 1991), and longleaf pine (*Pinus palustris,* Boyer 1993) in the east-southeast of USA; and Ponderosa pine (*Pinus ponderosa,* Matthews 1991) in the west of USA and southwest of Canada. In the north of India and Pakistan the seed tree method is used in Chir pine regeneration (*Pinus roxburghi*, Matthews 1991).

A common characteristic for pine species where seed trees are used is that seed dispersal occurs within one year from that the seeds become ripen, and most of their seeds are only vital the first year after seed dispersal. However, the two most spread pine species in Canada, lodgepole pine (*Pinus contorta*), and Jack pine (*Pinus banksiana*), are possible to regenerate naturally without leaving seed trees. The reason is that their cones are serotinous, which means that the cones open late, often after they have been exposed to higher temperature than normal. This can happen also after the cones have fallen down to the ground. The seeds in such cones can be viable for several years (Smith 1996).

The reproductive cycle of Scots pine

Seed production is influenced by weather conditions over four years (Owens & Blake 1985). High summer temperatures and high levels of global radiation (sunlight) in year 1 initiate rich flowering in year 2 (Jackson & Sweet 1972). Dry and windy weather in May-June of year 2 enhances pollination (Sarvas 1962). Fertilisation and seed ripening occur in year 3, during which period a high air temperature, especially in early summer, improves seed viability and increases seed weight (Sarvas 1962, Sahlén 1992). Seed is dispersed in April-June of year 4, when dispersal is improved by dry and windy weather (Heikinheimo 1937). Scots pine seeds in central Sweden normally germinate in June-July, and seeds that do not germinate the year that they are dispersed have only a small chance of germinating later on (Granström 1986).

Factors affecting seed production and seed dispersal of Scots pine

The variation in seed production between years is especially pronounced in areas with a harsh climate (Hagner 1965). Differences in seed production between trees are caused largely by variation in site conditions and genetic factors (Sarvas 1962, Koski & Tallqvist 1978), and also by tree size. Trees with large diameter produce more seeds than small trees (Pomeroy 1949 a, Hagner 1958). The number of cones produced by seed trees increases a few years after release cutting (Heikinheimo 1948, Wenger 1954, Skoklefald 1985), probably because the cutting reduces shading of the tree crown (Jackson & Sweet 1972). Moreover, available water and nutrients increase as a result of the removal of competitive trees nearby, and increased nutrient mineralisation following release cutting.

Fertilisation with N or NPK as a method of increasing seed production is often practised in seed orchards (Giertych 1973, Sweet and Hong 1978, Lee 1979, Mikola 1987, Saarsalmi et al. 1994). However, fertilisation of seed trees/sheltertrees is seldom or never recommended. The number of dispersed seeds ha^{-1} and seed weight decreases when the distance to the seed tree is more than 30 m (Hesselman 1938).

Factors affecting establishment, growth and mortality of seedlings in shelterwoods

The germination environment can be improved by using prescribed burning (Schimmel 1993) or mechanical soil scarification (Pomeroy 1949 b, Lehto 1956, Hagner 1965, Örlander et al 1990). Compared with unprepared areas, scarified areas provide a more favourable growth environment (Örlander et al 1990), e.g. higher soil temperature, availability of soil moisture (Winsa 1995, Oleskog 1999), reduced competition from vegetation, and decreased risks for seedling damage and mortality caused by e.g. pine weevils (Örlander & Nilsson 1999) and slugs (Nystrand & Granström 1997). Leaving a shelterwood can reduce the risk for frost injury compared with a clear-cut area, since minimum air temperatures are increased by the presence of shelter trees (e.g. Ottosson-Löfvenius 1993, Örlander & Langvall 1993, Groot & Carlson 1996). Furthermore, shading by shelter trees might reduce the risk of frost damage by reducing the exposure of seedlings to light of high intensity on the days after a cold night (Lundmark & Hällgren 1987, Örlander 1993).

Silvicultural management methods affecting seed production and seedling establishment

Choosing stand and seed trees

By choosing stands (e.g. tree species, soil type) and seed trees (e.g. tree size, tree distribution, spacing) at establishment cutting the forester affects seed production but also the distribution and species of seeds. Choosing stands and trees with great resistance against windthrow is very important for the success of natural regeneration. By leaving un-cut forest shelters around the whole regeneration area, or parts of it, the risk for wind damage can also be reduced (Persson 1975, Karlsson 1995, Örlander 1995). Hagner (1958) recommended choosing seed trees with large diameter to increase seed production. Pomeroy (1949 a), Lehto (1956) and Hagner (1965) found that the best method of selecting trees for rich future seed production was to monitor the number of cones they produced in the preceding years, and select trees with rich production. This can be made by choosing the trees with large amounts of old cones under them (Lehto 1956).

Establishment cuttings in years with rich cone setting

Some silvicultural manuals recommend that establishment cuttings should be made in years with rich cone setting as a method of increasing seedling establishment (Wahlgren 1922, Anon. 1996).

Soil preparation

The most significant method to affect seedling establishment is probably soil scarification. Since the positive effects of scarification decreases with time (Hagner 1962) and seeds of Scots pine have only a small chance to germinate later than the first summer after dispersal, it would probably be preferable to make soil preparation shortly before a seed fall that is abundant and contains seeds of high germination capacity. This method is sometimes recommended (Anon.1995), but seldom practised. One reason for this might be the difficulty of estimating seed production in seed trees.

Earlier investigations in central Fennoscandia

There have been several studies on natural regeneration of Scots pine in Fennoscandia. Four large and often cited investigations are mentioned below.

Sarvas (1949) studied 30 Scots pine stands that were established 1910-1942 in southern Finland. Since soil scarification or prescribed burning was not mentioned, it is probable that no soil preparation was made. Sarvas (1949) concluded the seed-tree method to be an uncertain regeneration method.

Lehto (1956) studied 186 Scots pine stands in southern Finland. The study dealt with soil prepared stands (scarification and prescribed burning) contra un-prepared stands, seed-tree density, seed dispersal, seedling growth and mortality. The conclusion of Lehto (1956) was that natural regeneration in Scots pine forests was a successful method on sandy and gravely soils when soil preparation was made.

Hagner (1962) made a broad investigation on natural regeneration in 70 shelterwoods of Scots pine and Norway spruce in central Sweden. Ten of the 70 stands were pure Scots pine stands, 6 were Norway spruce stands and 54 stands were mixed shelterwoods. The investigation dealt with e.g. seed tree growth, storm felling of seed trees, and effect of scarification on seedling establishment. Hagner (1962) concluded that natural regeneration of Scots pine might give sufficient number of seedlings on mesic soils when soil scarification was made.

Skoklefald (1995) made a detailed study in an experiment on dry soil in central Norway, altitude 640 m. He studied seed and cone production, seed maturity and seedling establishment in stands of three different densities. Skoklefald (1995) concluded that scarification on dry Scots pine sites improved seed germination and seedling establishment. The seed tree density (40-120 stems ha^{-1}) was of minor importance.

Altogether these studies show that natural regeneration of Scots pine often is successful if scarification is made, but uncertain otherwise.

Objectives

The objectives were to determine (*i*) the optimal shelterwood density, considering damage, mortality and height growth when advanced growth is used at regeneration, (*ii*) the optimal size of advance growth seedlings at the time of release cutting, (*iii*) when scarification should be done in relation to seed fall, (*iv*) if seed production, seed quality, needle weight and mineral nutrients in needles changes the years after release cutting, (*v*) how weather and tree size affects seed production and (*vi*) if mineral nutrients in needles and needle weight are correlated to cone production and seed quality.

Material and methods

Sites of experiments and surveys

Paper I and II origins from two different experiments, while paper III and IV origins from surveys (Fig 1). All stands had been regularly thinned, although all thinnings were made more than ten years before the start of the experiments and surveys. No preparatory cutting was made. Sheltertrees/seedtrees were evenly distributed over the regeneration areas at the establishment cuttings.

Weather data were collected from measurements in Asa (paper I), Siljansfors (paper II), and Jädraås (paper III) Experimental Forests. The length of the growing season was defined as the number of days on which the daily mean temperature exceeded 5 °C. Temperature sums were calculated as the accumulated daily mean temperature during the growing season, exceeding a threshold value of 5 °C (Morén & Perttu 1994). Site properties were estimated according to definitions by Hägglund & Lundmark (1977) and H100 site index (dominant height at 100 years total age) was measured according to definitions by Hägglund & Lundmark (1981).

The shelterwood experiment (paper I) was established in Asa Experimental Forest in southern Sweden (lat. 57º 10´ N, long. 14º 47´ E, alt. 180 m). Advance growth seedlings of Norway spruce (*Picea abies* (L.) Karst.) in different shelterwood densities were the focus of this study in which damage, mortality and height growth were registered. The experiment was performed in a forest that was relatively dense before treatment, and in which damage to the seedlings after cutting could, consequently, be expected. Mortality caused by logging operations and remaining slash, which is important in practical forestry was not investigated (Skoklefald 1967, Andersson & Fries 1979, Youngblood 1990, Westerberg & Berg 1994). The ground was fairly flat on the experimental site, and the H100 site index was estimated to be 30 m, corresponding to a mean annual stem volume growth of ca 10 m^3 ha^{-1} $year^{-1}$. The stand was a mixture of Norway spruce and Scots pine, 70-90 years old. The soil was fine sand covered with 10-20 cm of well-humified peat. The temperature sums varied between 1189 to 1397 degree-days (> 5 ºC) during the eight years of seedling monitoring.

The scarification experiment (II) was located in two Scots pine seed tree stands in Siljansfors Experimental Forest in central Sweden (lat. 60° 53´ N, long. 14° 24´ E, alt. 240-275 m). The number of seed trees was 61 and 84 ha^{-1}, respectively, for the two stands. The H100 site index was estimated to be 18 m, corresponding to a mean annual stem volume growth of ca 4 m^3 ha^{-1} $year^{-1}$. Seedling establishment, mortality and height growth were monitored for seven years from the start of the experiment. The field layer was dominated by *Vaccinium myrtillus* and *Vaccinium vitis-idea*, while the bottom layer was of moss type and dominated by *Hylocomium splendens*, *Pleurozium schreberi*, *Dicranum sp*., *Sphagnum sp* and

Cladina sp. The soil was deep (> 70 cm), and the dominating soil type was sandy till. The dominating soil moisture class was mesic, and surface/subsurface water flow occurred occasionally on most plots. The mean thickness of the humus layer was 9.5 ± 3.5 (SD) cm. The temperature sums varied between 851 to 1193 degree-days (>5 ºC) during the seven years of seedling monitoring

The effects of release (establishment) cutting on cones, seeds, and needles (III-IV) were investigated in 1995 - 1996 among Scots pine seed trees in central Sweden (lat. 60° 18´ - 60° 20´ N, long. 16° 10´ - 16° 20´ E, alt 170 - 200 m). The effects of between year variation in weather and tree size on cone production were also examined. Trees in seed tree stands that had been released for 1 - 11 years (growing seasons) were compared with control trees in uncut forest stands. Correlation between contents of 14 needle elements and seed weight and number of conelets were analysed. The field layer was dominated by *Vaccinium myrtillus*, *Vaccinium vitis-idea* and *Deschampsia flexuosa.* The bottom layer was moss type, dominated by *Hylocomium splendens*, *Pleurozium schreberi*, *Dicranum spp*. and *Sphagnum spp*. The soil was 'deep' (> 70 cm), and the major soil type was sandy till. The soil moisture class was mostly mesic and the dominant surface/subsurface water flow class was 'seldom'. Site index (H100) varied between 21 m and 26 m, corresponding to a mean annual stem volume growth of ca 5 - 7 m^3 ha^{-1} $year^{-1}$.

Design of experiments and surveys

In paper I eight different shelterwood densities (treatments) was established. One replication was used. Treatment 1 was "no cutting", and treatment 8 was clear-cutting. Treatments 2-7 were shelterwoods with densities ranging from 320 to 10 stems ha^{-1}. Pine was favoured when choosing shelterwood trees. The plot size in treatments 1-7 was ca 50 x 100 m, while treatment 8 (clear-cut) was about 100 x 100 m. The seedlings were annually monitored in 2 plots per treatment plot.

In paper II a complete randomised block design was used, with two blocks and three treatments in each block. The treatments were (*i*) scarification the autumn following cutting and before a seed-fall expected to be poor, (*ii*) scarification in autumn two years after release, before a seed-fall expected to be rich, and (*iii*) no soil preparation (control). Scarification was made with a disc trencher and ca 30 % of the mineral soil was laid bare. The treatment plots were 80 x 100 m in size. The seedlings were annually monitored in 20 plots per treatment plot. The seedling monitoring plots were 3.14 m^2 circular plots (radius 100 cm). Each year during the monitoring period 5 trees from each stand was felled from the seed tree population just outside the treatment plots to estimate number of cones and measure seed variables.

In paper III and IV ten randomly sampled trees from each stand was felled to estimate cones, conelets, seeds and needles. In 1995 four seed tree stands and four forest stands were studied and in 1996 ten seed tree stands and five forest stands were studied (paper III). The investigations in paper IV was made in six seed tree stands and four forest stands. The stands in paper III and IV were partly the same stands.

Methods of cone and seed inventory and seed analysis (Paper II - IV)

Sampled trees were felled, whereupon the total number of cones per tree was counted. Cones in the uppermost 2 metres were picked separately in the survey studies. The cones from each stand were divided into two sets; those from the uppermost 2 metres of the tree crown, and those from lower down (paper III and IV). In paper II one sample from each stand and year was analysed. Samples of cones were analysed regarding seed viability, 1000-seed weight and number of viable seeds per cone. The percentage of viable seeds was analysed in a 14-day germination test using a Jacobsen apparatus, with temperature set at 20 °C for 16 hours and at 30 °C for 8 hours a day. Light was constant at 1000 lux (Lestander 1984). In paper II, a second method of determining seed production was used. In each treatment, ten seed traps were placed in 1996 and 1997. The collecting area of each seed traps was 0.25 m^2, and the traps were emptied in May and August both years.

Methods of sampling and nutrient analysis in needles (Paper IV)

From each felled tree, one branch was randomly sampled from the whorl nearest 2 m from the treetop. From each sampled branch, 25 needle pairs (current year needles) were sampled from the tip of the branch. The needles from pairs of trees in each of the stands were pooled, providing five samples per stand. Carbon and nitrogen were analysed with a PE 2400 Elemental Analyser (Perkin Elmer, Norwalk, Connecticut, USA). The other macronutrients were analysed by ICP/AES, using a PE Plasma 2000 system, and micronutrients were analysed by ICP/MS, using a PE Elan 5000.

Statistical analysis

Before the statistical analysis, homogeneity of variance was checked for all groups using Levene's, Bartlett's, or F-tests. Variances were assumed to be equal when tests for normal homogeneity showed $P > 0.05$. One-way ANOVA was used to analyse differences between groups, and multiple comparison was performed using Tukey's or Dunnett's test. Results were considered significant when $P < 0.10$. Analysis of variance (ANOVA) was not possible to perform in paper I, since there were no true replications of treatments. Linear regression analysis was used to analyse correlations. Residuals from ANOVA and regression analysis were checked using the Ryan-Joiner normality test and accepted when $P > 0.10$. Logistic regression and a chi-square test were used to analyse probability of survival (Table 5 and Fig 6 in paper I). Square-root and log 10 transformations of response variables were tested in the analyses. In some of the analyses transformation improved the homogeneity of variance, normality of residuals and *P*-value. In cases where a transformation was not mentioned in the results, it was not used. Statistical analyses were conducted using SAS release 6.12 (Paper I, Cody & Smith 1997), and Minitab release 12 (Paper II-IV, Anon. 1998 c)

Results

Paper I: Influence of shelterwood density on survival and height increment of *Picea abies* advance growth

Mortality was generally high, especially on clear-cuts and in low-density shelterwoods (≤ 80 stems ha^{-1}). Seedlings with a small initial size showed higher mortality compared with larger ones (>50 cm, Fig 1). Mortality was caused by "release effects" (25%), pine weevils (*Hylobius abietis L.*, 28 %), and undetermined factors (47%). Mortality was attributed to "release effects" in cases where seedlings wilted the first spring following cutting, and no other damaging agent could be detected. This damage was most frequent among seedlings shorter than 20 cm on clear-cuts or in shelterwoods of low density. The most severe damage by pine weevils was found in the same plots and was especially pronounced for seedlings 20-50 cm high. Although frost frequently damaged seedlings (treatments ≤ 80 stems ha^{-1}), no seedling mortality was ascribed directly to frost. The mean annual height growth for 1989-1996 was greatest for seedlings that were largest at the start of the experiment. For all seedling sizes, growth was highest at densities of 80-160 stems ha^{-1}, whereas the optimum density for survival was about 160 stems ha^{-1}. Height, top-shoot length and top-shoot diameter the year before release cutting showed significant positive correlations with both survival and height growth for 1989-1996.

Paper II: Soil scarification shortly before a rich seed-fall improves seedling establishment in seed tree stands of *Pinus sylvestris*

After seven years, the seedling density was highest (ca 69 000 ha^{-1}) in the area where soil scarification preceded a rich seed-fall, whereas scarification immediately after cutting resulted in 34 000 seedlings ha^{-1} (Fig 2). The frequency of plots (size 3.14 m^2) without seedlings was 5 and 7.5 % where scarification was made before the rich seed fall and before the poor seed fall, respectively. Unscarified plots showed poorest result according number of seedlings (6000 ha^{-1}), and number of plots without seedlings (52.5 %). There was no significant difference in mortality of germinated seedlings between treatments. Height growth was significantly improved by scarification. The time elapsed since scarification clearly affected seed germination: The germination percentage of viable seeds dispersed on exposed mineral soil varied from 28.6 % the first year following scarification to 0.8 % the seventh year. The mean germination percentage in unprepared humus (control) was only 0.9 % during the monitored period.

Paper III: Seed production of *Pinus sylvestris* after release cutting

Cone and seed production were about five times higher in seed trees that had been released for 4-5 years, compared to control trees in the unreleased forest (Fig 3). Seed trees released for less than three years had about the same level of cone production as the controls. After release, the number of cones increased more in the lower part of the tree crowns than in the uppermost two metres. The mean 1000 - seed weight, percentage of viable seeds, and number of viable seeds per cone were not significantly different between released and unreleased trees.

In 1996, there were about eight times more cones than in 1995, probably because summer temperatures were higher in 1994 than in 1993, the years when the respective flower buds were initiated. Trees with a diameter at breast height of 400 mm produced twice as many cones as trees with a diameter of 300 mm. Tree height, length of green crown, and tree age showed no significant correlation with cone production.

Paper IV: Mineral nutrients in needles of *Pinus sylvestris* seed trees after release cutting and their correlations with cone production and seed weight

The mean number of conelets was 65 % higher in released seed trees than in control trees in unreleased stands. The mean 1000-seed weight was about 15 % higher in the released trees, while the mean percentage of viable seeds was lower in released trees (94 %) compared to control trees (98 %). However, the number of viable seeds per cone was not significantly different between released and unreleased trees.

The concentration of nitrogen, potassium, and phosphorus in needles was 23 %, 10 %, and 19 % higher, respectively, in released trees. The mean needle dry weight was 20 % higher. Nitrogen, potassium and phosphorus concentrations in needles were significantly positively correlated to numbers of conelets as well as to mean 1000-seed weight (Fig 4). None of the other analysed mineral nutrients were significantly correlated to seed production. The mean needle dry weight was significantly positively correlated to the number of conelets, but not to the mean 1000-seed weight.

Discussion and management implications

Is it possible to use advance growth at regeneration?

Paper I focuses on two factors of great importance, which must be taken into consideration when advance growth in shelterwoods is planned to be used; *(i)* are the seedlings high enough too survive release cutting and *(ii)* which shelterwood density should be used?

The forest managers probably also asks if the seedlings are of the desired species. Although the shelterwoods in the present experiment were dominated by Scots pine, the advance growth nearly solely consisted of Norway spruce. This is natural in dense forests on fertile soils since Norway spruce is more shade tolerant than Scots pine. Effects of release cutting have been similar to Scots pine seedlings in other studies (Vaartaja 1952, Sundkvist 1993) as it was to Norway spruce in the present study. Consequently, it is probable that the same silvicultural measurements could be used in Scots pine seedlings as in Norway spruce seedlings, the two most commonly used tree species in Sweden. Other species as advance growth in Swedish forest cannot be evaluated with present silvicultural knowledge.

Paper I showed that seedling height before release should be at least 50 cm to secure seedling survival. The seedling height at which release cutting could be recommended probably varies with humus thickness, since root contact with the mineral soil might increase seedling survival, and small seedlings have most of their roots in the humus layer (Fig X). Taller seedlings, whose roots are spread into the mineral soil, can be attributed to the fact that production is delayed while the needles adapt to the higher amounts of radiation after release from overstorey (Tucker & Emmingham 1977). Small seedlings probably have problems with both needle adaptation and the soil water deficit in the humus layer.

Seedling mortality caused by pine weevil was also high in small seedlings, and survival seems to be secured at about 50 cm height (Paper I, Lekander & Söderström 1969). All mortality cannot be explained as effects of the release cutting, since ca 40 % of seedlings < 20 cm died in the control (forest). However, that mortality might be affected by other reasons, e.g. low levels of light.

A question of interest is what to do if there are lots of advance growth seedlings but most seedlings are less than 50 cm in height. The pre-released forest might for example be too dense and not allow enough seedlings to reach 50 cm in height, or it may take to long time. The answer is probably to make release cutting into desired shelterwood density in two steps. The first release cutting is then called "preparatory cut" and the number of stems ha^{-1} is in the range of 200-400. This silvicultural management system has been used earlier in Swedish forestry (Näslund 1955, Hagner 1962).

Later on, in connection with the removal cutting, the response of the established seedlings is once again a factor of importance (Skoklefald 1967). However, at which seedling height the removal cutting of shelterwood trees should be done is not in the focus of the present thesis.

Paper I demonstrated that ca 150 sheltertrees ha^{-1} was optimal according to survival and height growth of the advance growth seedlings. The corresponding basal area is ca 10 m^2 ha^{-1}, and the relative amount of light is about 60 % of that impinging on clear-cut areas. The result is in accordance with the conclusions of Leinonen et al. (1989) who found that the best regeneration was achieved at shelterwood densities of 100-200 stems ha^{-1}. Is our knowledge thereby enough to proclaim general recommendations to Swedish forestry? The answer is no! The experiment must be repeated in other sites to proof its reliability. However, the knowledge about shelterwood densities achieved from this experiment in Asa Experimental Forest is probably the best in Sweden at present.

Structure and function of Scots pine seed trees

Paper III and IV shows that trees with large diameters and trees with heavy needles containing high proportions of nitrogen, phosphorus and potassium are good seed producers. The result about diameter is in accordance with Pomeroy (1949 a, loblolly pine) and Hagner (1958, Scots pine). However, the variation in cone production between individual trees is great (Fig. 2, Paper III). In poor seed years the variation between individuals are even greater than in rich years (Hagner 1958). In paper III, no effect of crown length, tree age and tree height could be seen on seed production. Pomeroy (1949 a) studied loblolly pine and reported similar results concerning crown size and tree height. The result about crown size is opposite to recommendations given in some Swedish silvicultural manuals (Anon. 1996). Choosing the trees according to the amount of old cones under them is also a method that has been recommended (Lehto 1956), although not investigated in this thesis.

After the establishment cutting, seed trees significantly increased their number of ripened (2-year old) cones from the third growing season after release. This was expected because of the flowering biology of Scots pine (Owens & Blake 1985). Although cones increased in the whole tree crown, the increase in the lower parts (> 2 m from tree top) was much heavier.

The reason why number of cones increased more in the lower parts of the crown compared to the uppermost two meters might be explained by difference in light radiation. The tendency for trees that had been released for 1-2 years to have a higher proportion of cones in the topmost 2 metres than corresponding trees in the forest is harder to explain. The reason could be that conelets (1-year old) and cones, which had been initiated in the unreleased forest, aborted to a greater degree in lower parts of the tree crowns than in upper parts during the first two years after release. The distribution of cones in the crown for trees with different length of release is illustrated in Fig. X.

The higher concentrations of nitrogen, potassium and phosphorus found in the needles of released trees can be explained as a direct effect of removing competitive trees nearby, and by increased nutrient mineralisation due to factors such as increased global radiation reaching the forest floor (Lundmark 1986). Furthermore, slash from removed trees might have released mineral nutrients. However, even though the concentrations of N, P, and K were higher in released stands, they were still below optimum levels, according to limits suggested by Brække (1994), and revised by Brække et al (1998).

The significant positive correlations between nitrogen, potassium, and phosphorus concentrations in needles and the number of conelets and the seed weight indicates that the increase of the three mineral nutrients might be one possible explanation of the improved seed production after release.

When should scarification be made?

Mechanical soil scarification has in several experiments and survey studies been demonstrated to be the most significant silvicultural measure that can be made when regeneration is focused on establishment of new seedlings (Pomeroy 1949 b, Lehto 1956, Hagner 1965, Örlander et al 1990). As expected, scarification in the present experiment (paper II) improved regeneration success in several ways: *(i)* by increasing the germination percentage, *(ii)* by decreasing the proportion of 0-plots, and *(iii)* by increasing seedling growth. The experiment supports the idea of postponing scarification until a certain amount of seed-fall with a minimum level of seed viability can be expected. Two main reasons of large between-year variations in seed fall are identified in paper III, namely weather and length of release period after cutting. By using temperature data it might be possible to predict seed production ca 2.5 years in advance of seed fall. However, no reliable prognosis function exists today for Scots pine. Reliable prognosis of seed viability can be made ca 0.5 years before seed fall with existing functions using temperature data as predicting variable (Almqvist et al 1999).

Paper III indicates that length of release period should be considered at the planning of when scarification should be conducted. Always making scarification the third autumn following release cutting instead of first autumn would be an easy way, and probably result in a higher proportion of stands where stocking-level requirements are met. The price of this is the loss of 1-2 years of production in stands that have enough seeds the first or second year after release. The question for a silvicultural manager is then how the risk of loosing production is valued in relation to the possibility of increasing chances to reach a successful regeneration result. Dense regeneration stands can be both positive and negative also from other point of views. From the positive view dense stands of Scots pine are needed to create high quality saw timber with small branches (Persson 1977). From the negative view dense stands means a lot of work to reduce stem number in cleanings and thinnings. The effect of scarification is also dependent on which proportion of mineral soil that gets uncovered. In paper II ca 30 % of the mineral soil was laid bare, and this might be controversial for other interest groups than forest managers. Therefore, if scarification is used, it is important to optimise the use of it. Scarification before a rich seed fall means that less mineral soil has to be laid bare compared to scarification before a poor seed fall.

In more fertile forest types, e.g. in the southern parts of Sweden, the general consensus today is that soil preparation should be carried out as quickly as possible after seed tree release (Anon 1995). This recommendation is based mainly on the argument that the new stand should be established as quickly as possible to avoid competition from field vegetation. Such advice might be correct if seed-fall in southern Sweden is generally more abundant and less variable over time compared with the situation in our study area. However, the literature contains little data on variation in seed- fall between years in southern Sweden

(Hagner 1965, Koski & Tallqvist 1978); thus the value of such recommendations cannot be assessed at present.

My recommendation is to define a minimum level of cones per tree and a minimum percentage of seed viability and seed weight that is needed for a successful regeneration result. When these requirements are met, scarification should be conducted shortly before seed fall. Possible ways of making prognosis-not yet developed-are by measurements of pollen production ca 2 years before seed fall, conelet production ca 1.5 year in advance or cone production ca 0.5 years in advance. A possible method is to predict seed production using weather-data combined with data about length of release.

Is it possible to increase seed production before the establishment cutting?

It is somewhat strange that few efforts have been devoted to improvement of nutrient status among pine seed trees. Fertilising with nitrogen, potassium and phosphorus is regularly done in Scots pine seed orchards to improve seed production, although with wide variation in success (Mikola 1987, Saarsalmi et al. 1994). The effects of fertilisation in forests are probably greater since soils in forests probably in most cases are less fertile, and trees less widely spaced compared to seed orchards. Paper IV indicates that it might be beneficial to fertilise seed trees with N, P and K 3-4 years before the establishment cutting in order to improve seed production and seed weight. However, the present survey did not investigate the importance of other factors e.g. soil water and light Therefore, fertilisation experiments in seed trees, before and after release cutting, should be conducted in order to test this hypothesis.

If the forest not has been thinned for a long time, it is possible that a preparatory cutting before the establishment cutting stimulates seed production. A preparatory cutting can also be made for other reasons, e.g. to stimulate stem growth of shelter trees, height growth of advance growth seedlings, and stabilise shelter trees against wind-throw. However, how many years in advance a preparatory cutting should be made might vary depending on the main objective. Paper IV indicates that there was an optimum of seed production 4-5 years after the release cutting, but the decrease later on was not significant. The conclusion is that a significant effect can be expected 3-5 years after a cutting, but it is uncertain what happens after that.

Methods of inventory

The two experiments were well designed for the purpose of the studies. However, a great disadvantage - limited of cost restrictions - was that only one replication could be used in experiment I, and only two replications in experiment II. The reason for using a survey method in paper III and IV was that an experiment would have required a long time (eleven years) and more money than was available.

The strength of the two experiments was that the seedlings were checked every year from the beginning of the regeneration period. In experiment I, three inventories were made in each of the first two years, while only one inventory per year was done in experiment II. It is obvious that several inventories each year gives important information about e.g. causes of mortality (e.g. Nystrand & Granström 1997). In experiment II seedlings were monitored on plots with a radius of one m (3.14 m^2). After seven years of inventory I strongly recommend the use of smaller plots when registering seedlings that have germinated current year. Plots with areas in the range of 0.5 m^2 to 1.0 m^2 would probably be easier to use, and the risk of missing seedlings less.

The methods of estimating seed and cone production in paper II may be interpreted as expensive and complicated. However, the task of estimating cone and seed production and seed characteristics such as viability and seed weight is rather complicated. The dominating method to estimate cone production in earlier studies has been counting with binoculars (Wenger 1954, Hagner 1958, Skoklefald 1995). This is an unreliable method (Hagner 1958) since it is subjective and gives no information about number of seeds, seed viability etc. The main method to estimate seed production has been the use of seed traps (Heikinheimo 1937, Wenger 1957, Hagner 1965, Skoklefald 1995). With this method it is possible to estimate the total seed fall with great accuracy, since it is an objective method. However, the disadvantages are problems of determining seed characteristics e.g. seed viability. Furthermore, seed trapping gives no information about number of seeds per cone. My conclusion is that the use of both seed tree felling and seed-traps gave good information.

Statistical analysis

In Silvicultural research, statistical analysis often are made in a stereotypic way, e.g. often using $P < 0.05$ as cut off level for significance and Tukey's test for multiple comparisons. If the number of replications is high this might be a good strategy, but when the number of replications is low it often means "killing" probable results. This is the reason why I used $P < 0.10$ as level of significance. According to Hinkelmann & Kempthorne (1994) it sometimes even can be motivated to use $P < 0.20$. Since all P-values less than 0.10 are presented in the results, it is up to the reader to judge if the result is significant. I used Tukey's multiple comparison test when there were less than three groups to compare and Dunnett's test otherwise. Tukey's test compares all groups with one another while Dunnett's test compares each group to one control. Significance is reached at less replication when comparison only is made to a control group.

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LEGENDS TO FIGURES

Figure 1: Probability of survival for seedlings with different pre-release heights in dense (160-320 stems/ha) and sparse (0-80 stems/ha) shelterwoods.
———— shelterwoods 160-320 stems/ha
------------ clearcut and shelterwood 0-80 stems/ha

Figure 2: Mean number of living Scots pine seedlings per hectare in autumn 1997 for plots scarified before a rich (1992) and poor (1990) seedfall. Data were analysed by year of germination.

Figure 3: No. of cones per tree at different years after release cutting

Figure 4: Correlations between concentrations of N, K, and P in needles and seed weight (A-C), and number of conelets in top 2 m of the trees (D-F)