

**Direct seeding of *Pinus sylvestris* (L.) in the
boreal forest using orchard or stand seed**

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Abstract

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The overall aim was to analyse the possibilities for operational forestry of using *Pinus sylvestris* (L.) orchard seeds (OS) for direct seeding in the boreal forest.

The use of OS instead of stand seeds (SS) increased seedling establishment by 41% two years after mechanical direct seeding at four sites in northern Sweden. OS was advantageous to use in combination with microsite preparation to achieve desired spacing and different regeneration strategies, at low cost, and on an operational scale.

On average, OS had 16% and 12% higher seedling emergence than SS in a northern (Lat 64°N) and southern (Lat 60°N) field experimental series where six orchard seed lots and six stand seed lots of adequate geographical origins were analysed with up to six seeding years. The survival rate from year 1 to year 4 was 77% and 72% in the northern series and 58% and 49% in the southern series for orchard and stand seedlings respectively. On average, OS were 26% and 13% taller than SS after four years in the northern and southern series, respectively.

Effects on early seedling growth of seeding OS and SS in different mixtures (100, 75, 50, 25, and 0% of OS) at 4-cm target spacing were quantified in a nursery (optimal) and a field (harsh) experiment. SS in high competition vs. low competition (mixture 75% vs. 25%) were 11% taller, had 15% greater slender value, and 25% less root biomass after two years in the nursery. OS had 9% greater slender value in mixture 100% compared to mixture 25%. In the field experiment the influence of mixture was not significant after five years. The tallest OS in each plot compared with the tallest SS were 22% taller and had 103% larger stem volume. After thinning, leaving the tallest seedling in each plot, 79% of the seedlings in 50% mixtures would be OS. Seedlings sown in 12-cm spacing were 79% taller and had 527% larger stem volume than seedlings in 4-cm spacing. An increase of seed weight from 3 to 7 mg increased height growth by 18-65% and 10-27% in the field and nursery experiment, respectively. Seed weight explained approximately 31-56% and 75-86% of the increased growth of using OS compared to SS in the field and nursery experiment. Two-year-old OS seedlings allocated 10% more to needles and had 113% longer total needle length than SS in the field experiment. In the nursery experiment OS did not allocate more to needles than SS did.

The high cost of OS makes a mixture of OS and SS as a suitable alternative in several regeneration strategies. SS can be used complementary to OS, i.e., to increase stand density, reduce the cost of seeds, as insurance if seedling establishment is low, and to increase the total wood production and timber quality. The genetically improved orchard seedlings will be dominant after future thinnings.

Key words: biomass allocation, competition, early growth, Scots pine, seed weight, seedling emergence, seed type, seed quality, survival.

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Contents

Background, 7

Objectives, 10

Results and Discussion, 11

Direct seeding with orchard and stand seeds of Scots pine, 11

Interactions with environment, 13

Seeding density, 16

Mixing orchard and stand seed, 17

Practical implications with examples, 18

Conclusions, 19

Acknowledgements, 22

References, 23

Personal communications, 27

Appendix

The thesis is based on studies reported in the following articles, which are referred to in the text by their corresponding Roman numerals.

- I.** Wennström, U., Bergsten, U. and Nilsson, J-E. 1999. Mechanised microsite preparation and direct seeding of *Pinus sylvestris* in boreal forests - a way to create desired spacing at low cost. (New Forests 18(2): 179-198).
- II.** Wennström, U., Bergsten, U. and Nilsson, J-E. 2001. Early seedling growth of *Pinus sylvestris* (L.) after sowing with a mixture of stand and orchard seed in dense spacing. (Can. J. For. Res. 31(7): 1184-1194).
- III.** Wennström, U., Bergsten, U. and Nilsson, J-E. (In review). Effects of seed weight and seed type on early seedling growth of *Pinus sylvestris* (L.) under harsh and optimal conditions.
- IV.** Wennström, U., Bergsten, U. and Nilsson, J-E. (Manuscript). Seedling establishment and growth after direct seeding with *Pinus sylvestris* (L.): effects of seed type, seed origin, and seeding year.
- V.** Wennström, U. (Manuscript). Differences in biomass allocation for orchard and stand seedlings of *Pinus sylvestris* (L.) in harsh and optimal conditions.

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Background

Scots pine (*Pinus sylvestris* L.) is a native species in Sweden with a distribution from 55°30' N in the south to 68°30' N in the north (Anon 1990). Scots pine represents 39% of the total standing volume of trees in Sweden (Anon 2001). Scots pine has traditionally been used as a raw material in the construction industry, pulp industry, and furniture industry.

Yearly, about 200,000 ha is subjected to final felling in Sweden (Anon 2001) and according to Swedish law, new forests must be established with measures carried out at latest three years after final felling (Anon 1979). New forests can be established with artificial or natural regeneration. In many cases artificial regeneration is the most reliable method. Artificial regeneration can be accomplished by planting or direct seeding. Artificial regeneration gives an opportunity to change species or genetic composition of the forest and does not rely on abundant seed fall. Kohh (1968) estimated that at 67° N 500 m.a.s.l. germination exceeding 90% can only be expected three times in a century, and the probability that high germination coincides with high cone abundance is low (cf. Hagner 1958).

A critical component of any regeneration strategy is the initial density in the new stand (e.g. Ocker-Blom et al. 1988, Väisänen et al. 1989, Houliere et al. 1995). Ocker-Blom has proposed three operationally practicable densities for Scots pine:

(i) Wide spacing (e.g., 1,000 stems ha⁻¹) with minimal silvicultural costs for regeneration, thinning, harvest etc. and high per stem wood production is desirable. However, total wood production per ha is sub-optimal, and spacing that is too wide may not be allowed according to forest legislation (Anon 1993).

(ii) Medium spacing (e.g., 2,500 stems ha⁻¹) with low silvicultural and harvesting costs and intermediate volume production and timber quality is desirable.

(iii) Close spacing (e.g., 5,000 stems ha⁻¹) with near maximum total wood production and good timber quality is also desirable, however silvicultural costs will be high.

In addition, higher densities, up to 10,000 stems ha⁻¹ or more, may be desired (Persson et al. 1995) to maximise wood production and wood quality, although silvicultural costs might be very high because one or more pre-commercial thinnings are needed (Hynynen 1993).

Artificial regeneration requires regeneration with plants or direct seeding. Planting is a reliable well-tried method. Survival of planted material is generally high. However, damage from *Hylobius abietis* can in some areas be very high during the first years. Chemical or mechanical protection or a 3 to 4 year clear-cut rest before planting is an alternative. Planted seedlings normally have high initial growth rate, especially when using genetically improved material, which add only

small extra cost compared to stand seed. However, planting is expensive. Planting with densities higher than in strategy (ii) are rare because of the high cost.

Direct seeding allow us to create very dense stands to a low cost with conditions necessary for growing trees with desirable stem and wood properties (Persson 1976, Uusavara 1989, Ståhl et al. 1990). Successful mechanisation of the technique for direct seeding has been made and development of new scarification technique, especially developed for direct seeding, is under test (Bergsten 2000). An efficient method for mechanised direct seeding that yields consistent regeneration results would make it possible to easily vary the desired spacing. Another advantage is a reduced risk of root and stem deformations caused by the container cultivation and/or transplanting (Long 1978, Hultén 1982, Rosvall 1994). Directly seeded seedlings might not be damaged in the same high extent as planted seedlings by *Hylobius abietis*, simply because directly seeded seedlings are too small to be interesting shortly after the clear-cut when the *Hylobius* population is high (von Hofsten and Weslien 2001).

The negative aspect of direct seeding has been the inconsistent seedling emergence, survival and growth (Valtanen and Engberg 1987). Increasing the number of sown seeds has been tried to solve this problem but as many environmental factors affect the result, the method cannot become reliable just by increasing seed dosage (Kinnunen 1982, Winsa and Bergsten 1994). Furthermore, seed is expensive and excessive seedling emergence could require costly pre-commercial thinnings.

When direct seeding, the quality of seed is important for seedling emergence, growth, and survival. The germinable seeds from seed lots with low germination capacity (the proportion of germinable seeds analysed on germination table) have less of a chance to emerge in field conditions than germinable seed from a seed lot with high germination capacity (Wibeck 1910). For many conifer species, seed weight is positively correlated with early growth (St. Clair and Adams, Reich et al. 1994, Maltoni and Tani 1997, Castro 1999). In near optimal conditions, in greenhouses or nurseries, the influence of seed weight on height growth is generally high but often not significant after one to three years (Mikola 1985, Castro 1999).

The effect of seed weight, however, is greater in low nitrogen regimes than in high (*Pinus elliotii*: Surles et al. 1993) or in harsher field conditions than in greenhouse/nursery conditions (*Sesbania*: Marshall 1986, *Raphanus raphanistrum*: Stanton 1984). This makes seed quality an important factor in direct seeding.

In Sweden, the vegetation period and temperature sum is negatively correlated with latitude and altitude at any given location (Morén and Perttu 1994). The survival of the local provenance of Scots pine is also negatively correlated to latitude and altitude as shown by Eriksson et al. (1980) and Persson (1994). For example, the survival of the local provenance 30 years after planting at 64°00' 200 m.a.s.l. is expected to be 74%. By increasing the altitude to 400 m.a.s.l., the expected

survival of the “new” local provenance is 55% (Andersson 1996). At a given location, northern origins have higher survival than southern origins (Eiche 1966, Remröd 1976, Eriksson et al. 1980, Persson 1994). However, southern origins have higher growth rate than northern origins at the same location. The altitudinal origin is of minor importance for survival and growth (Persson and Ståhl 1993, Persson 1994). For wood volume production, the increase in survival rates from using northern origins of Scots pine outweighs the loss in height growth. Therefore, in operational forestry, Scots pine is usually southerly transferred 1-3 degrees of latitude in northern Sweden.

Seeds used for direct seeding or nursery plants can either be collected in seed orchard or stands. The first generation of seed orchards in Sweden, which today produce the main part of the collected orchard seed crop, originate from selected plus trees in natural regenerated stands. The seed from these orchards are genetically improved with approximately a 6-8% increase in height growth after 30 years when regenerated with seedlings (Danell 1993). To increase seed crop and quality, the clones in orchards are transferred from north to south, from higher to lower altitude, and to locations favourable for seed development on agricultural land (Simak and Gustafsson 1954, Hagner 1958, Almqvist et al. 1998, Hannerz et al. 2000). Trees in seed orchards are widely spaced and application of fertilizer, soil cultivation, grass mowing, heavily pruning, and the use of herbicides are routine measures. Seed from orchards have approximately 50% heavier seed weight than seed from stands (Johnsson et al. 1953, Simak and Gustafsson 1954, Hadders 1963) and better developed embryo and gametophyte, higher germination capacity, and germination rate than stand seed (Simak and Gustafsson 1954). The total area of seed orchards in Sweden was intended to satisfy the needs for seedling production in nurseries. However, in large parts of Sweden there is a surplus of Scots pine orchard seed that may be used for direct seeding (Hannerz et al. 2000).

Objectives

This thesis aims to analyse the possibilities of using *Pinus sylvestris* (L.) orchard seeds for direct seeding in operational forestry. The main hypothesis is that direct seeding with orchard seed in relation to stand seed increases seedling emergence, survival and growth. Other sub hypotheses were:

- i) the advantage of using orchard seed in relation to stand seed would be greater when direct seeding than when planting,
- ii) the higher seed weight for orchard seed largely explains the advantage of using orchard seed compared to stand seed,
- iii) higher growth of orchard seedlings would positively influence survival,
- iv) the advantage of using orchard seed would be greater in years with poor conditions for seedling emergence,
- v) the advantage of using orchard seed would be larger when seeding in substrates with poor conditions for seedling emergence.

The objectives in the different paper was to:

- Test whether mechanised microsite preparation after scarification, in combination with mechanical direct seeding of Scots pine with orchard seed, can achieve desired spacing and different regeneration strategies, at low cost, and on an operational scale. The experiments were performed at four boreal forest sites in northern Sweden with orchard and stand seeds sown with and without microsite preparation (I).
- Quantify early effects on seedling growth, at dense spacing after seeding with a mixture of orchard and stand seed in the boreal forest region of northern Sweden. Effects of mixtures (100, 75, 50, 25 and 0% of orchard seed) at 4-cm target spacing were quantified in one nursery (optimal) and one field (harsh) experiment during a 2-year and 5-year period, respectively. In the field experiment the influence of target spacing at 4-, 8-, and 12-cm target spacing were also studied using 50% mixtures (II).
- Evaluate the effects of seed weight and seed type on early growth and growth allocation in field and in nursery. The study was made with individually weighed orchard and stand seed sown in different mixtures. (III).
- Quantify the effects of seed type on seedling emergence and survival, and early seedling growth at different sites and seeding years. Two experimental series at latitude 61°N and 64°N, respectively, with six orchard seed lots and six stand seed lots of adequate geographical origins in each series were analysed. The effects of latitudinal origin and early growth differences between directly seeded and planted seeds/seedlings of the same seed material were also considered. The experiments were replicated at five sites with up to six seeding years at each site (IV).
- Describe early differences in above soil biomass allocation between two-year-old orchard and stand seedlings in nursery and in field (V).

Results and Discussion

Direct seeding with orchard and stand seeds of Scots pine

Direct seeding with orchard seed compared to high quality stand seed increased seedling emergence 12-41%, in relation to the sown percentage of germinable seeds (**I, III**). With respect to poor quality stand seed, seeding with orchard seed may double or triple seedling emergence (Winsa and Bergsten 1994).

Occasionally, at some sites and during some seeding years, the use of orchard seed compared to stand seed can be low or even negative (**IV**). High predation of the larger seeds and seedlings of orchard seed are a probable reason. Birds may be the most important predator of sown Scots pine seeds (Vaarataja 1950, Heikkilä 1977, Bergsten 1985). Birds rely on vision when foraging (Nystrand and Granström 1997a). The larger orchard seed and seedlings are therefore easier to find and are cost efficient to predate.

The advantage of using orchard seed after scarification seems to be greater on unfavourable than on favourable substrates (Fig. 1). Seedling establishment on undisturbed soil or inverted scalp was increased by more than 100% when orchard seed was used in relation to high quality stand seed (**I**).

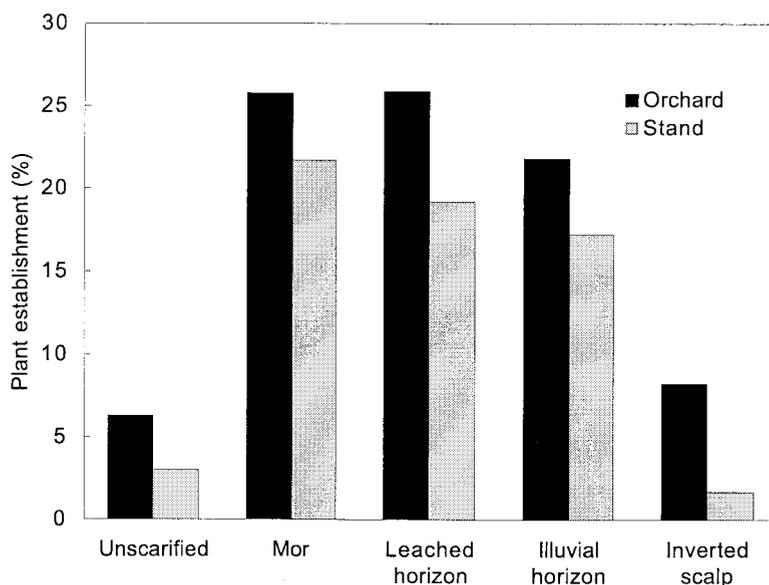


Figure 1. Seedling establishment in relation to sown germinable seeds for mechanically seeded orchard and stand seedlings of *Pinus sylvestris* (L.) in different substrates two years after seeding. Mean value of four sites located between 62°-65° N (**I**).

Correlation between seed quality and seedling establishment seems to be greater in years with good conditions for seedling establishment (IV). In years with poor conditions for seedling establishment, the difference between seed types and seed lots were not significant. Seed predation could be a major cause for poor results, however, poor conditions seem to be the result of complex conditions and differences in sites and years. However, at sites where poor results are caused by frost heaving, the advantage of using orchard seed compared to stand seed is highly significant (I).

Seedlings from directly seeded orchard seed have 13-40% higher height growth than seeds from stand seed after one to five years (Fig. 2; Winsa and Bergsten 1994; I, II, III, IV, V, Wennström In prep.). Plants raised from directly sown orchard seeds were approximately 15% taller than stand seedlings 11 years after seeding (Ackzell and Lindgren 1994). According to results from altogether 15 sites and 51 seeding occasion, the gain from using orchard seed compared to stand seed seems to be highly general (Ackzell and Lindgren 1994, Winsa and Bergsten 1994; I, II, III, IV, V, Wennström In prep.).

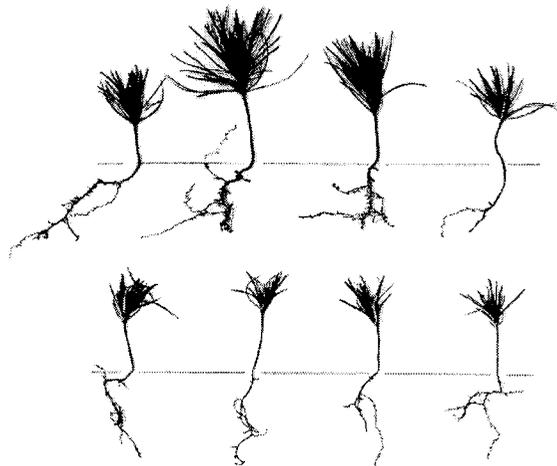


Figure 2. Two-year-old orchard (above) and stand (below) seedlings (*Pinus sylvestris* L.) from an experiment located at 64° N (V).

The gain from using orchard seeds is significantly greater when the regeneration is made with direct seeding than with plants. The gain in height growth was 15% when regenerated with direct seeding and 9% when the regeneration was made with plants five years after seeding and planting using the same seed material for seeding and plants (IV). The results from the planting experiments correspond well to expected genetic gain according to Andersson (1996).

As shown above, seedlings raised from orchard seed are taller than seedlings raised from stand seed. Seed weight explains approximately 40% of the increased growth, 40% is expected to be the genetic gain and the remainder 20% is due to other factors (III). An increase of the seed weight from 3 to 7 mg increases the

seedling height by 25-66% and the stem volume by 79-182% for directly seeded seedlings from both orchard and stand seed five years after seeding. The influence of seed weight seems to be linear and does not differ between orchard and high quality stand seed, at least in the interval between 3 and 7 mg (III). A reasonable explanation of the unexplained 20% could be a better maturation of orchard seeds. Simak and Gustavsson (1954) found more cotyledons in orchard seed embryos of the same seed weight than in seeds collected from the original plus tree in the stand. More needles mean more photosynthetic surface area. Directly seeded orchard seedlings have twice the needle biomass than stand seedlings after two years (Fig. 3) (V).

Seeding with orchard seeds gives a more even result than seeding with stand seed. The coefficient of variation (standard deviation in relation to the mean value) for plant establishment and height growth is lower for spots sown with orchard seed compared to stand seed (IV).

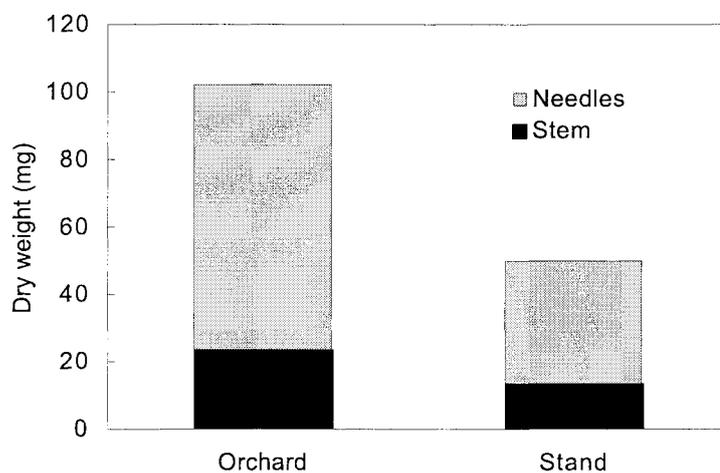


Figure 3. Dry weight biomass of stems and needles of two-year-old orchard and stand seedlings (*Pinus sylvestris* L.) from an experiment located at 64° N (V).

Interactions with environment

Directly sown seeds in undisturbed soil has very low chances to become a mature tree mainly because of high predation (Forsslund 1944, Nystrand and Granström 1997b). Forsslund (1944) found more than 20 forest animals predating seeds of *Pinus sylvestris* and *Picea abies* in undisturbed soil. Scarification increases seedling establishment many times (I). Mainly as a result of decreased predation (Forsslund 1944) and increased water availability during dry periods (Oleskog and Sahlén 2000a, 2000b).

When removing the humus layer the risk of frost heaving increases (Scramm 1958, Bergsten et al. 2001). Frost heaving is a major cause of mortality for post germinated sown seedlings in Sweden (Winsa and Bergsten 1994, Winsa and Bergsten 1995, I). Frost heaving injury is correlated negatively to the mechanical strength of a seedling

(Scramm 1958). Rapid early growth minimise injuries of frost heaving. Orchard seedlings have twice as much stem and needle dry weight biomass than stand seedlings after two years (V). The survival of the faster growing sown orchard seedlings was 8-48% higher than for stand seedlings 2-4 years after seeding (Winsa and Bergsten 1994, I, IV) and the gain in higher survival was largest at sites with high mortality, in these cases caused by frost heaving (Winsa and Bergsten 1994, I).

As result of higher survival of seedlings from orchard seed compared to seedlings from stand seed, seedling establishment, in relation to the sown percentage of germinable seeds, increases slightly (Fig. 4; IV, Wennström in prep.). The increase in seedling emergence from using orchard seed compared to stand seed was 17% the first autumn after seeding, five years after seeding the increase from using orchard seed was 23%.

Drought is another cause for low emergence or early mortality in Scandinavia (Hedemann-Gade 1927, Kinnunen 1982, 1992). Capillarity is high in mineral soils (Grelewicz and Plichta 1983) and mineral soils are a good substrate for germination (Tirén 1934, Kinnunen 1992, Winsa and Bergsten 1995). Seedling emergence and survival can be increased if seeds sown on mineral soil are covered with e.g. anthill material, sawdust or humus (Tirén 1953, Hagner and Lundmark 1982). A thin humus layer left on the mineral soil decreases damage caused by frost heaving (Goulet 1995; Winsa and Bergsten 1995). The capillary action in humus is very low and seeds sown in humus are very sensitive to drought (Winsa 1995, Oleskog et al. 1999). However, the mortality of seed that have emerged in humus is very low. In addition, early height growth of seedlings in humus is approximately 30% higher than for seedlings emerged in mineral soil (Winsa and Bergsten 1995; Wennström In prep.).

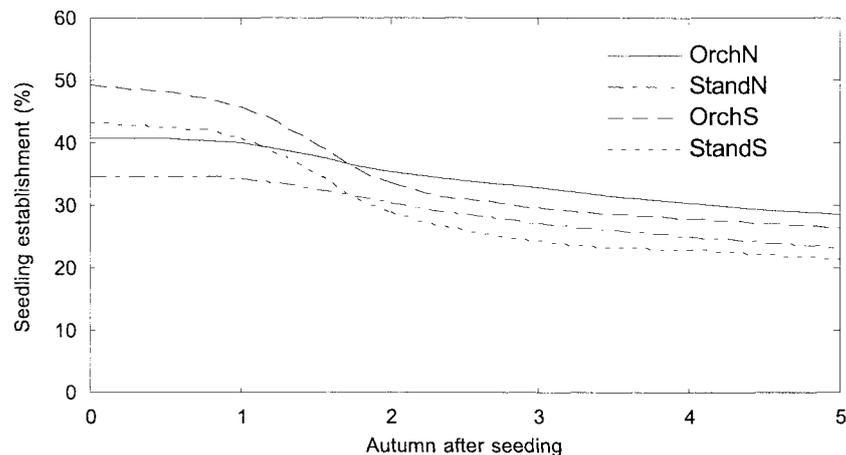


Figure 4. Seedling establishment in relation to sown germinable seeds for orchard and stand seed in northern (Lat. 64°-65° N) and southern (Lat. 61° N) field experiment series zero to five years after seeding (IV, Wennström in prep.). The zero value represents total seedling emergence the first autumn. OrchN and StandN represent direct seeding with orchard and stand seed in northern series, OrchS and StandS represent direct seeding with orchard and stand seed in southern series.

Seedling emergence can be considerably enhanced by making small indentations (so called microsite preparation) in a mineral soil or in a thin humus layer (Fig. 5; Bergman and Bergsten 1984, Bergsten 1988, Van Damme 1992, Winsa and Bergsten 1994, 1995, Winsa 1995, I). The indentations are made with a tool that creates small inverted pyramid-like indentations in the soil. Seedling emergence for seeds, sown in the bottom of the indentations, increases by approximately 50% compared to seeds sown without being placed in indentations (Winsa and Bergsten 1994, 1995, I). The increase in seedling emergence by using microsite preparation is higher in humus rich material than in mineral soil (Winsa and Bergsten 1995, I). The high emergence is due to an increased availability of water (because of increased capillary action and decreased evaporation) and to a reduced predation, because micro erosion from the walls of the indentation covers the seeds. Micro erosion also increases the contact with surrounding soil and thus the surface for water uptake (Oleskog et al. 1999). When using microsite preparation to seed in thin humus, seedling establishment (including early mortality) can be equal or higher than when seeding in mineral soil (Winsa and Bergsten 1995, I, Wennström In prep.). Microsite preparation does not directly influence height growth (I) or survival (Winsa and Bergsten 1994, I). However, microsite preparation allows the seeding to be done in a humus or in a humix (mixture of humus and mineral soil) layer without loss in seedling emergence and this increases survival and growth. The dominant orchard and stand seedling in each seeding spot, when using microsite preparation in thin humus or humix was approximately only 1.5 year behind planted 1-year-old seedlings in height growth when using the same material (Fig. 6; IV). However, more seedling-adjusted scarification, e.g., mounding, would probably have gained height growth of the planted seedlings (Lähde 1978).

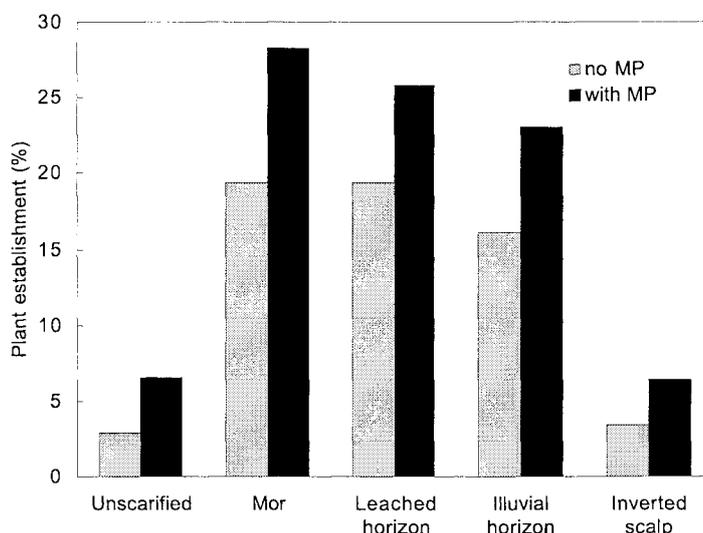


Figure 5. Seedling establishment with and without microsite preparation (MP) in relation to sown germinable seeds for mechanically seeded orchard and stand seedlings of *Pinus sylvestris* (L.) in different substrates two years after seeding. Mean value of the four sites located between 62°-65° N (I).

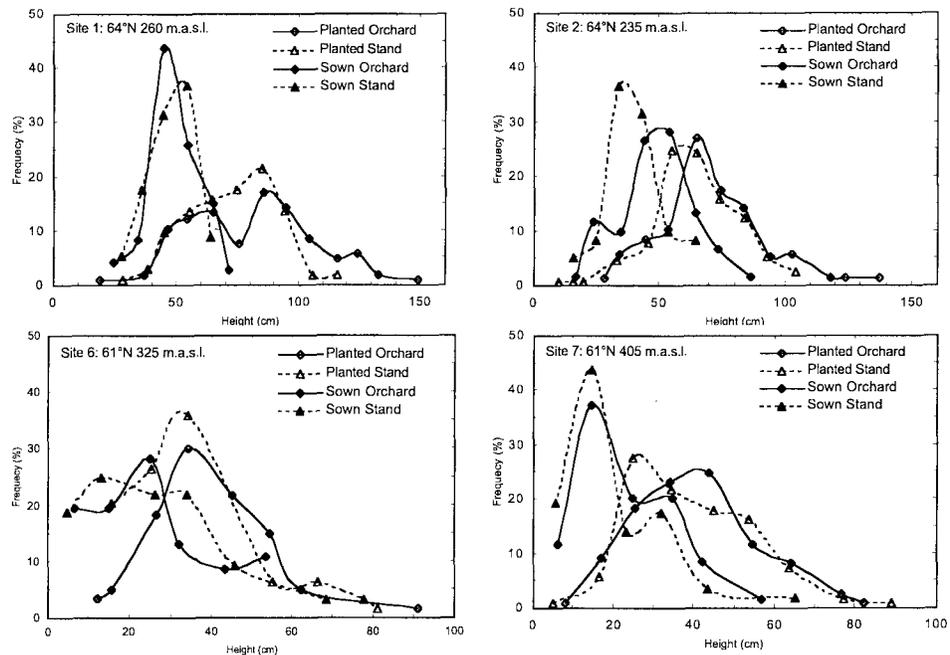


Figure 6. Frequency distribution by seedling height of planted and directly seeded orchard and stand seedlings five years after planting and seeding at four sites (IV).

The increase from using microsite preparation is greater for high quality seed than for low quality seed (Winsa and Bergsten 1994). In Wennström et al. (I), however, there were no differences identified in the effect of microsite preparation between orchard seed and high quality stand seed.

Seeding density

Spot seeding, with high seed densities within spots, has been a commonly used method in Fennoscandia (Kinnunen 1982). High seedling densities have been shown to negatively influence early growth (Varmola et al. 1998, Jansson et al. 1998, I). Other investigations have shown positive influence of seeding density on the tallest seedling in the spot (Tirén 1952, Sirén 1956). However, high seedling densities (because of improved microclimates for seedling emergence) was correlated positively to growth in study II, this was rather an effect of improved microclimate than a stimulation of neighbouring plants. In the same experiment, increased seeding density was correlated negatively to early growth. By increasing the spacing between seeds sown in spots from 4- to 12-cm, height growth was increased by 70% and the stem volume by 530% five years after seeding (Fig. 7; II). The influence of seeding density does not differ between orchard or stand seedlings (II). The increase as the result of increased spacing between seeds can be explained by differences in availability of external resources. Seedlings in 12-cm spacing have 9 times as large area as the seedlings in 4-cm spacing. Water and/or nutrients are thought to be the limiting factor rather than light on boreal clear cuts (Nilsson et al. 1996, Örlander et al. 1996), even in high seeding density spots in early ages (II).

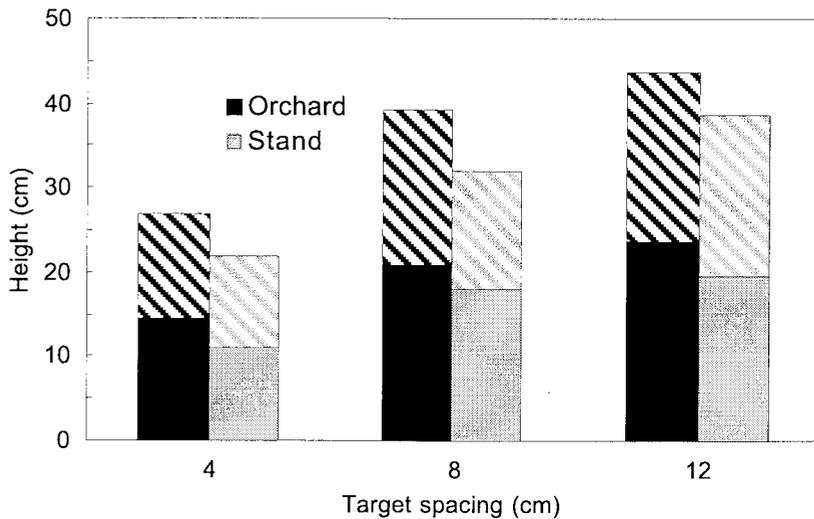


Figure 7. Mean height of the mean (filled) and tallest (striped) orchard and stand seedling (*Pinus sylvestris* L.) in each spot five years after seeding (II).

Mixing orchard and stand seed

Because of the reasons as mentioned above, orchard seeds are preferable for direct seeding. However, the amount of orchard seed is limited (Hannerz et al. 2000) and the costs for orchard seed are high (Hannerz 1995). A compromise would be to mix expensive orchard seed with stand seed. This mix would lower the costs for regeneration and increase the growth potential for the whole rotation period; this may be the most cost efficient way to use orchard seed. It would also distribute the limited amount of genetically improved orchard seed on a larger area. In paper (I) orchard seed was mixed with high quality stand seed. Orchard seedlings were 25% taller than stand seedlings after five years. Although stand seedlings made up less of the seed (25% stand seed and 75% orchard seed) in 4 cm spacing using 64 seeds per spot, the growth of stand seedlings was not negatively influenced after five years. After release thinning, which leaves the tallest seedlings in each spot, sown with equal amounts of stand and orchard seed, 80% of the remaining seedlings after five years were genetically improved orchard seedlings. Future thinnings at higher ages would if desired, probably increase the amount of orchard seedlings. The stand seedlings that become main stems have most probably genetically better growth than the average stand seedlings and the orchard seedlings that are outstripped have genetically lower growth than the average orchard seedling.

Practical implications with examples

Costs for a simulated regeneration, regenerated with plants, mechanised direct seeding, and manual direct seeding using three strategies, are calculated in Table 1. The costs for orchard seed are based on sub-standard seed (OS90%) and high quality orchard seed (OS98%). Sub-standard seed is not always available in northern Sweden. The cost for Or98% is very high partly because of high costs for establishment and nursing seed orchards and partly because nurseries also demand those qualities. OS90% seed is still preferable in relation to high quality stand seed (SS90%). For regenerations in mid Sweden the costs for seed is lower. The possibility of finding OS90% is higher in south and mid Sweden, because of a surplus of orchards (Hannerz et al. 2000). Seed costs and the cost for release thinning greatly influences the costs for direct seeding. Labour cost and labour efficiency greatly influences the costs for planted regenerations. When mechanical direct seeding is compared with manual seeding, seedling emergence greatly influences the cost.

The cost for regeneration was lowest using direct seeding in relation to planting at all strategies (Table 1). The relative cost for regeneration with direct seeding, in relation to planting with strategy 2,000 stems per ha (a typical strategy in Sweden today) was lower for all seed qualities with strategies below 4,000 stems per ha.

Direct seeding, aiming at densities below 2,000 stems per ha is though very risky and it is doubtful that these strategies should be recommended. A failure with such low goal is very costly and will result in severe losses in production.

Due to higher seedling establishment, manual seeding was cheaper than mechanical seeding at all strategies above 1,000 stems per ha. Seed costs influences the total cost at higher degree when mechanised seeding (with low seedling emergence) compared to manual seeding. Seed quality influences the total cost at a higher degree when manual seeding (with high seedling emergence) compared to mechanised seeding.

Although higher seed costs, seeding with OS90% and Mix90/90% was the cheapest alternative at a strategy of 5,000 stems per ha, mainly as a result of the low seed-dosage (<6 seeds/m) that made release thinning not needed. Further development on seeding and harvesting technique might also reduce the need for release-thinning even at higher stem densities. The difference was small between seed lots, OS98% not included, but SS90% was cheaper to use than SS80% at a strategy of 5,000 stems per ha.

Using OS98% for direct seeding when aiming at high densities would lead to high costs in relation to the cost of planting (2,000 stems per ha). High quality orchard seed is though economically interesting when sown in mixture.

Not only the regeneration cost but also future net income should be considered when choosing regeneration strategy. Important factors are wood volume growth

and desired tree and wood properties. These factors are related to the stand density, i.e., yield per ha, and the growth of the individual tree. The use of orchard seed may have impact both on yield and individual tree growth.

The growth potential of the main stems of a seeded mixture of orchard and stand seed can be close to the growth when 100% orchard seeds are sown, since the share of plants originating from orchard seed will increase when the stand is thinned. In the future mature forest, trees from orchard seed will be dominating among the main stems and the stand seedlings that become main stems will be the very best stand seedlings.

Conclusions

Orchard seed can be used advantageously for direct seeding. In general, sown orchard seed had higher seedling emergence (12-41%), survival (8-48%) and growth rates (13-40%) than stand seed. The disadvantages of using orchard compared to stand seed for direct seeding are potentially higher predation on orchard seed and seedlings and a higher cost per seed as a result of a limited amount of available orchard seeds. Using orchard seed for direct seeding decreases the variation between years and sites. However, at year with very poor seedling emergence the difference between seed lots of any type is small.

Microsite preparation allows seeding with low seed dosage in thin humus or humix with high survival and growth. The gain of using microsite preparation could thus be higher for orchard than for high quality stand seed if the seed cost should be considered.

After consideration of seedling emergence, survival, and growth seed dosage can probably be further reduced when orchard seed is used. Seedling establishment is more evenly distributed, plant establishment is greater where scarification fails, and seedlings are more even in height when orchard seeds are used in relation to stand seed. This gives us more candidates for main stems when orchard seeds are used in relation to stand seed.

Besides the “seed effect” of using orchard seed, using high quality seed with low seed dosage will reduce competition between seedlings and thus increase growth and reduce the costs for release thinning.

The high cost of orchard seed makes a mixture of orchard and stand seed as a suitable alternative in several regeneration strategies. The higher growth of orchard seedlings does not negatively influence early growth of stand seedlings when sown in mixture. Stand seeds can be used to increase stand density and thus reduce the cost of seeds, as insurance if seedling establishment is low, and to increase the total wood production and timber quality. The genetically improved orchard plants will be dominant after future thinnings.

Strategy	Method	Scarification ^{a)}	Seed cost ^{b)}	Used seed ^{c)}			Planting ^{d)}	Release thinning ^{e)}	Restocking ^{f)}	Sum of costs	Rel. cost ^{g)}	
				g/ha	No./ha	No./m						
1 000	Planting	Manual	1 000	0	6	1 039	0.3	3023	0	283	4 305	66
- "	DS SS80%	Mechanised	1 300	298	83	18 402	4.1	0	0	706	2 304	35
- "	DS SS90%	- "	1 300	308	70	15 540	3.5	0	0	706	2 314	35
- "	DS OS90%	- "	1 300	382	72	12 012	2.7	0	0	706	2 388	37
- "	DS OS98%	- "	1 300	1 019	66	11 031	2.5	0	0	706	3 026	46
- "	DS SS80%	Manual	1 600	119	33	7 364	1.6	0	0	706	2 425	37
- "	DS SS90%	- "	1 600	123	28	6 216	1.4	0	0	706	2 429	37
- "	DS OS90%	- "	1 600	153	29	4 805	1.1	0	0	706	2 459	38
- "	DS OS98%	- "	1 600	408	26	4 413	1.0	0	0	706	2 714	42
- "	DS Mix90/90%	- "	1 600	130	28	5 791	1.3	0	0	706	2 437	37
- "	DS Mix90/98%	- "	1 600	199	28	5 665	1.3	0	0	706	2 506	38
2 000	Planting	- "	1 000	0	17	2 770	0.6	5 537	0	0	6 537	100
- "	DS SS80%	Mechanised	1 300	596	166	36 805	8.2	0	538	706	3 141	48
- "	DS SS90%	- "	1 300	615	140	31 080	6.9	0	300	706	2 922	45
- "	DS OS90%	- "	1 300	763	144	24 024	5.3	0	0	706	2 769	42
- "	DS OS98%	- "	1 300	2 039	132	22 063	4.9	0	0	706	4 045	62
- "	DS SS80%	Manual	1 600	238	66	14 722	3.3	0	0	706	2 545	39
- "	DS SS90%	- "	1 600	246	56	12 432	2.8	0	0	706	2 552	39
- "	DS OS90%	- "	1 600	305	58	9 610	2.1	0	0	706	2 611	40
- "	DS OS98%	- "	1 600	815	53	8 825	2.0	0	0	706	3 122	48
- "	DS Mix90/90%	- "	1 600	261	56	11 582	2.6	0	0	706	2 567	39
- "	DS Mix90/98%	- "	1 600	399	55	11 330	2.5	0	0	706	2 705	41
5 000	Planting	- "	1 000	0	42	6 925	1.4	14 519	0	0	13 519	207
- "	DS SS80%	Mechanised	1 300	1 491	414	92 012	20	0	1 274	283	4 347	66
- "	DS SS90%	- "	1 300	1 538	350	77 699	17	0	1 166	283	4 287	66
- "	DS OS90%	- "	1 300	1 908	360	60 060	13	0	987	283	4 478	68
- "	DS OS98%	- "	1 300	5 365	348	58 060	13	0	962	283	7 909	121
- "	DS SS80%	Manual	1 600	596	166	36 805	8.2	0	538	283	3 017	46
- "	DS SS90%	- "	1 600	615	140	31 080	6.9	0	300	283	2 798	43
- "	DS OS90%	- "	1 600	763	144	24 024	5.3	0	0	283	2 646	40
- "	DS OS98%	- "	1 600	2 039	132	22 063	4.9	0	0	283	3 921	60
- "	DS Mix90/90%	- "	1 600	652	141	28 954	6.4	0	168	283	2 703	41
- "	DS Mix90/98%	- "	1 600	996	138	28 324	6.3	0	120	283	2 999	46

Table 1. Cost for regeneration with 1000, 2000, and 5000 seedlings year 4 when regenerated with planted seedlings, mechanised direct seeding (DS) and manual DS at 64°30' N, 250 m.a.s.l. (in SEK). DS was performed using four seed lots: Low quality stand seed with 80% germination capacity (SS80%), high quality stand seed with 90% germination capacity (SS90%), sub-standard orchard seed with 90% germination capacity (OS90%), and high quality orchard seed with 98% germination capacity (OS98%). Two mixtures are also included, SS90% mixed with OS90% and SS90% mixed with OS98%, aiming at 25% orchard seedlings after 4 years. DS costs have been calculated using 10% and 25% seedling emergence after seeding with SS90% with mechanical and manual seeding, respectively. Costs and data for seeds, seedlings, seedling emergence, etc. are based on actual costs and practical experiences (Bäckström pers. com., Wilhelmsson pers.com., Hannerz 1995, I, IV, Wennström in prep.).

Notes:

- a) Costs for microsite preparation and seeding are also included when direct seeding. Manual seeding, capacity of work: 2.5 ha/day
- b) The cost is calculated with: Seed: SS80% 3,800 SEK/kg, SS90% 4,400 SEK/kg, OS90% 5,500 SEK/kg, OS98% 16,000 SEK/kg; 1000-sw: SS80% and SS90%: 4.50 g, OS90% and OS98%: 6.00 g; Seedling emergence: SS90%=0.10 (mechanised) and SS90%=0.25% (manual), SS80%=0.95xSS90%, OS90% and OS98%=1.20xSS90%; Survival from year 1 to 4: SS80% and SS90%=72%, OS90% and OS98%=80%
- c) Used seed for planted seedlings is calculated as follows: 1000-sw: 6.00; Germination capacity: 95%, Plant establishment in nursery: 95%; direct seeding see 'b'
- d) The cost is calculated as follows: Labour: 1,500 SEK/day; Capacity for work: 1.200 seedlings/day; Seedlings: 0.95 SEK/seedling; Seedling survival: 80%; Transformation: $1/(\text{SQRT}(\log(\text{number of seedlings}))-0.85)$
- e) The cost is calculated as follows: Labour: 1,500 SEK/day; Capacity for work: 1.4 ha/day; Transformation: $\log(\text{sown seeds/m} - 5)$. No release thinning needed for planted seedlings or when less than 6 seeds/m are sown.
- f) The cost is calculated as follows: Labour: 1,500 SEK/day; Capacity for work: 800 seedlings/day; Need: 100 seedlings/ha for direct seeding with strategy 5,000 and planting with strategy 1,000; 250 seedlings/ha for direct seeding with strategy 1,000 and 2,000; Seedlings: 0.95 SEK/seedling; No restocking needed for planted seedlings with strategy 2,000 and 5,000.

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Crouch down elks, the thesis is finished...

References

- Ackzell, L., and Lindgren, D. 1994. Some genetic aspects of human interventions in forest regenerations: Considerations based on examples from an experiment in northern Sweden. *Forestry* 67(2): 133-148.
- Almqvist, C., Bergsten, U., Bondesson, L., and Eriksson, U. 1998. Predicting germination capacity of *Pinus sylvestris* and *Picea abies* seeds using temperature data from weather stations. *Can. J. For. Res.* 28(10): 1530-1535.
- Andersson, B. 1996. The risks and benefits of using different Scots pine stock in northern Sweden. The Forestry Research Institute of Sweden. Redogörelse 1: 101-107. (In Swedish with English summary).
- Anon 1979. Skogsvårdslag (SFS 1979:429). (In Swedish).
- Anon 1990. Skogen, Sveriges national atlas. 144 pp. ISBN 91-87760-05-3. (In Swedish).
- Anon 1993. Skogsstyrelsens föreskrifter och allmänna råd till skogsvårdslagen (SKSFS 1993:2), 26 pp. (In Swedish).
- Anon 2001. Statistical yearbook of forestry 2001. Official statistics of Sweden, National board of forestry, Jönköping 2001. 337 pp. (In Swedish with English table-text).
- Bergman, F., and Bergsten, U. 1984. Improvement of germination by direct seeding through mechanical soil preparation. P. 291-307. In: K. Perttu (Ed), Ecology and management of forest production systems. Swedish University of Agricultural Sciences, Dep. of Ecology and Environmental Research, Uppsala. Rapport 15.
- Bergsten, U. 1985. A study on the influence of seed predators at direct seeding of *Pinus sylvestris* L. Swedish University of Agricultural Sciences, Dep. of Silviculture, Rapport 13. 16 pp.
- Bergsten, U. 1988. Pyramidal indentations as a micro site preparation for direct seeding of *Pinus sylvestris* L. *Scan. J. For. Res.* 3: 493-503.
- Bergsten, U. 2000. Ny markbehandling för skogsförnyelse från frö till planta. In: Forskningsprogram för den boreala skogens nyttjande. Resultat från perioden 1997-2000. Swed. Univ. Agri. Sciences, Vindelns försöksparker. p. 27-33. (In Swedish).
- Bergsten, U., Goulet, F., Lundmark, T., and Ottosson Löfvenius, M. 2001. Frost heaving in a boreal silt soil in relation to soil scarification and snow cover. *Can. J. For. Res.* 31(6): 1084-1092.
- Castro, J. 1999. Seed mass versus seedling performance in Scots pine: a maternally dependent trait. *New Phytol.* 144: 153-161.
- Danell, Ö. 1993. Förädlingsvinster och diversitet (in Swedish with English summary). In: Produktion av förädlad frö (ed. Wilhelmsson, L., Eriksson, U. and Danell, Ö.) The Forestry Research Institute of Sweden, Redogörelse 3, 11-16.
- Eiche, V. 1966. Cold damage and plant mortality in experimental plantations with Scots pine in northern Sweden. *Stud. For. Suec.* 36: 1-218.
- Eriksson, G., Andersson, S., Eiche, V., Ifver, J., and Persson, A. 1980. Severity index and transfer effects on survival and volume production of *Pinus sylvestris* in northern Sweden. *Studia forestalia Suecica*, no. 156. 32 pp.
- Forsslund, K.H. 1944. Något om djurlivets inverkan på barrskogens naturliga förnyring. *Svenska Skogsvårdsföreningens Tidskrift* 42: 366-376. (In Swedish).
- Grelewicz, A., and Plichta, W. 1983. Water absorption of xeromor forest floor samples. *For. Ecol. Manage.*, 6: 1-12.
- Goulet, F. 1995. Frost heaving of forest tree seedlings: a review. *New Forest* 9:67-94.
- Hadders, G. 1963. Some causes of variation in the initial development of Scots pine (*Pinus sylvestris* L.). In *Proceeding of the World Consultation on Forest Genetics and Tree Improvement*. Vol. 1 FAO/FORGEN 63-2a/8. Food and Agriculture Organization of the United Nations, Rome, Italy. 10 pp.

- Hagner, M., and Lundmark, A. 1982. Täckning med humus vid radsådd. Umeå Universitet, Institutionen för Skoglig Produktionslära, Reprot 129: 1-47. (In Swedish).
- Hagner, S. 1958. On the production of cones and seed in Swedish coniferous forest (in Swedish with English summary). Meddelande från Statens Skogsforskningsinstitut. 47(8): 120 pp.
- Hanerz, M. 1995. Skogssådd – Fröförsörjning och ekonomi. The Forestry Research Institute of Sweden. Arbetsrapporter, nr: 308: 1-16. (In Swedish).
- Hanerz, M., Eriksson, U., Wennström, U., and Wilhelmsson, L. 2000. Scots pine and Norway spruce seed orchards in Sweden – a description with an analysis of future seed supply. The Forestry Research Institute of Sweden. Redogörelse 1, 40 pp. (In Swedish with English summary).
- Hedemann-Gade, E. 1927. Undersökningar angående lämpligaste tiden för sådd av barrträdsfrö. Svenska Skogsvårdsföreningens Tidskrift., 25: 5-50. (In Swedish).
- Heikkilä, R. 1977. Destruction caused by animals to sown pine and spruce seed in northern Finland. Commun. Inst. For. Fenn. 89(5). 35 pp. (In Finnish with English summary).
- Houllier, F., Leban, J.M., and Colin, F. 1995. Linking growth modelling to timber quality assessment for Norway spruce. Forest Ecology and Management. 74(1-3): 91-102.
- Hultén, H. 1982. In: H. Hultén (Ed), Root deformation of forest seedlings - Proceedings of a Nordic Symposium. Department of Forest Yield Research, Swedish University of Agricultural Sciences, Umeå. Rep. 11.
- Hynynen, J. 1993. Self-thinning models for even-aged stands of *Pinus sylvestris*, *Picea abies* and *Betula pendula*. Scand. J. For. Res. 8(3): 326-336.
- Jansson, G., Jonsson, A. and Eriksson, G. 1998. Efficiency of early testing in *Pinus sylvestris* L. growth under two different spacings in growth chamber. *Silva Genetica* 47(5-6): 298-306.
- Johnsson, H., Kiellander, C.L., and Stefansson, E. 1953. Kottutveckling och fröbeskaffenhet hos ympträd av tall. Svenska Skogsvårdsföreningens Tidskrift. 51: 358-389. (In Swedish.)
- Kinnunen, K. 1982. Scots pine sowing on barren mineral soils in western Finland. *Folia For.* 531:1-24. (In Finnish with English summary).
- Kinnunen, K. 1992. Effect of substratum, date and method on the post-sowing survival of Scots pine. *Folia For.* 785:1-45. (In Finnish with English summary).
- Kohh, E. 1968. Sommarvärme och tallfröets mognad i Norrland. Sveriges Skogsvårdsförbunds Tidskrift. 1968(5): 381-526. (In Swedish).
- Lähde, E. 1978. Effect of soil treatment on physical properties and on development of Scots pine and Norway spruce seedlings *Comm. Inst. For. Fenn.* 94.5, 59 pp.
- Long, J.N. 1978. Root system form and its relationship to growth in young planted conifers. P. 222-234. In E. van Erden and J.M. Kinghorn (Eds), Proceedings of the Root Form of Planted Trees Symposium, Victoria, British Columbia, 1978. British Columbia Ministry of Forests and Canadian Forestry Service. Joint Rep., 8.
- Maltoni, A., and Tani, A. 1997. Influence of seed weight on the growth of *Pinus nigra* seedlings. *Italia Forestale e Montana.* 52(4): 261-273.
- Marshall, D.L. 1986. Effect of seed size on seedling success in three species of *Sesbania (Fabaceae)*. *Am. J. Bot.* 73: 457-464.
- Mikola, J. 1985. Relationships between height growth differences of Scots pine full-sib families and variation in seed size, annual growth rhythm, and some foliage characteristics. In Tigerstedt, P. M. A., Puttonen, P. and Koski, V. (eds.). Proceeding of an International Conference on Managing Forest Tree as Plants, Crop Physiology of Forest Trees: 23-28 July 1984, Helsinki, Finland. pp 233-243. ISBN 951-45-3705-X.
- Morén, A-S., and Perttu, K.L. 1994. Regional temperature and radiation indices and their adjustment to horizontal and inclined forest land. *Stud. For. Suec.* 194: 1-19.

- Nilsson, U., Gemmel, P., and Hällgren, J-E. 1996. Competing vegetation effects on initial growth of planted *Picea abies*. *New Zealand J. For. Sci.* 26(1-2): 84-98
- Nystrand, O., and Granström, A. 1997a. Post-dispersal predation on *Pinus sylvestris* (L.) *Oecologia* 110: 353-359.
- Nystrand, O., and Granström, A. 1997b. Forest floor moisture controls predator activity on juvenile seedlings of *Pinus sylvestris* (L.). *Can. J. For. Res.* 27: 1746-1752.
- Oker-Blom, P., Kellomäki, S., Valtonen, E., and Väsinen, H. 1988. Structural development of *Pinus sylvestris* stands with varying initial density: a simulation model. *Scand. J. For. Res.* 3:185-200.
- Oleskog, G., Grip, H., Bergsten, U., and Sahlén, K. 2000. Seedling emergence of Scots pine (*Pinus sylvestris* L.) in characterised seedbed substrates under different moisture conditions. *Can. J. For. Res.* 30: 1766-1777.
- Oleskog, G., and Sahlén, K. 2000a. Effects of seedbed substrate on moisture conditions and germination of *Pinus sylvestris* (L.) seeds in a clear-cut. *Scand. J. For. Res.* 15: 225-235.
- Oleskog, G., and Sahlén, K. 2000b. Effects of seedbed substrate on moisture conditions and germination of Scots pine (*Pinus sylvestris* L.) seeds in a mixed conifer stand. *New Forests* 20: 119-123.
- Örlander, G., Nilsson, U. and Hällgren, J-E. 1996. Competition of water and nutrients between ground vegetation and planted *Picea abies*. *New Zealand J. For. Sci.* 26(1-2): 99-117.
- Persson, A. 1976. The influence of spacing on the quality of saw timber from Scots pine. Swedish University of Agricultural Sciences, Dep. of Forest Yield Research. Research notes 42:1-122. (In Swedish with English summary).
- Persson, B., and Ståhl, E.G. 1993. Effects of provenance transfer and spacing in an experimental series of Scots pine (*Pinus sylvestris* L.) in northern Sweden, Department of Forest Yield Research, The Swedish University of Agricultural Sciences, Garpenberg. Report 35: 1-92. (In Swedish with English summary).
- Persson, B. 1994. Effects of provenance transfer on survival in nine experimental series with *Pinus sylvestris* (L.) in northern Sweden. *Scand. J. For. Res.* 9: 275-287.
- Persson, B., Persson, A., Ståhl, E.G., and Karlsmats, U. 1995. Wood quality of *Pinus sylvestris* progenies at various spacings. *Forest Ecol. and Manage.* 76: 127-138.
- Reich P.B., Oleksyn, J., and Tjoelker, M.G. 1994. Seed mass effects on germination and growth of diverse European Scots pine populations. *Can. J. For. Res.* 24: 306-320.
- Remröd, J. 1976. Choosing Scots pine (*Pinus sylvestris* L.) provenances in northern Sweden – analysis of survival, growth and quality in provenance experiments planted 1951. Department of Forest Genetics, Royal College of Forestry. Research notes, 19: 1-132. (In Swedish with English summary).
- Rosvall, O. 1994. Stability in Lodgepole pine and resistance to wind and snow loads. The Forestry Research Institute of Sweden. Redogörelse 2, 47 pp. (In Swedish with English summary).
- Schramm, J.R. 1958. The mechanism of frost heaving of tree seedlings. *Proceedings of the American Philosophical Society.* 102:333-350.
- Simak, M., and Gustafsson, Å. 1954. Seed properties in mother trees and grafts of Scots pine. *Meddelanden från Statens Skogsforskningsinstitut* 44(2), 73 pp. (In Swedish with English summary).
- Sirén, G. 1956. Thinning of pine stands (In Finnish with English summary). *Metsätaloudellinen aikakauslehti* 2-3: 40-49.
- Stanton, M.L. 1984. Seed size variation in wild radish: effect of seed size on components of seedling and adult fitness. *Ecology* 65: 1105-1112.
- St. Clair, J.B., and Adams, W.T. 1991. Effect of seed weight and rate of emergence on early growth of open-pollinated Douglas-fir families. *For. Sci.* 37: 987-997.

- Ståhl, E.G., Persson, B., and Prescher, F. 1990. Effect of provenance and spacing on stem straightness and number of stems with spike knots in *Pinus sylvestris* L. - northern Sweden and countrywide models. *Stud. For. Suec.* 184. 14 pp.
- Surles, S.E., White, T.L., Hodge, G.R. and Dureya, M.L. 1993. Relationship among seed weight components, seedling growth traits, and predicted field breeding values in slash pine. *Can. J. For. Res.* 23: 1550-1556.
- Tirén L. 1934. Några iakttagelser över den naturliga förnyringens uppkomst på Kulbäckslidens försökspark. *Svenska Skogsvårdsföreningens Tidskrift.*, 32: 251-274 (In Swedish with German summary).
- Tirén L. 1952. On experiments in sowing pine and spruce seed in northern Sweden . *Meddelanden från Statens Skogsforskningsinstitut*, 41(7): 5-110. (In Swedish with English summary).
- Tirén L. 1953. Comparison between different sowing methods. *Meddelanden från Statens Skogsforskningsinstitut*, 43(9): 83 pp. (In Swedish with English summary).
- Uusvaara, O. 1989. Effect of spacing and site quality on branchiness and wood quality in Scots pine plantations. P. 243-253. *In*: R.N. James and G.L. Tralton (Eds), *New approaches to Spacing and Thinning in Plantation Forestry, Proceedings of an IUFRO Symposium 10-14 Apr. 1989, Rotorua, New Zealand.* Forest Research Institute, New Zealand. FRI Bull. 151.
- Vaartaja, O. 1950. On factors affecting the initial development of pine. *Oikos* 2:1 89-108.
- Väisänen, H., Kellomäki, S., Oker-Blom, P., and Valtonen, E. 1989. Structural development of *Pinus sylvestris* stands with varying initial density: a preliminary model for quality of saw timber as affected by silvicultural measures. *Scand. J. For. Res.* 4: 223-238.
- Valtunen, J. and Engberg, M. 1987. The result from Kainuu and Pohjanmaa of the ploughed-area reforestation experiment begun during 1970-1972. *Folia For.* 686:5-42. (In Finnish with English summary).
- Van Damme, L. 1992. Microsite soil compaction enhances establishment of direct-seeded Jack pine in Northwestern Ontario. *North. J. Appl. For.* 9(3):107-112.
- Varmola, M., Kolström, T. and Mehtälö, E. 1998. The effect of release cutting on the growth and external quality of the dominant trees in a *Pinus sylvestris* stand established by spot sowing. *Scand. J. For. Res.* 13: 151-159.
- Wennström, U., Bergsten, U., and Nilsson, J-E. 1999. Mechanised microsite preparation and direct seeding of *Pinus sylvestris* in boreal forests - a way to create desired spacing at low cost. *New Forests* 18(2): 179-198.
- Wennström, U., Bergsten, U., and Nilsson, J-E. 2001. Early seedling growth of *Pinus sylvestris* (L.) after sowing with a mixture of stand and orchard seed in dense spacing. *Can. J. For. Res.* 31(7): 1184-1194.
- Wennström, U., Bergsten, U., and Nilsson, J-E. (In review). Effects of seed weight and seed type on early seedling growth of *Pinus sylvestris* (L.) under harsh and optimal conditions.
- Wennström, U., Bergsten, U., and Nilsson, J-E. (Manuscript). Effects of seed type, seed origin and seeding year on plant establishment and seedling growth after direct seeding with *Pinus sylvestris* (L.).
- Wennström, U. (Manuscript). Early differences in biomass allocation for directly seeded *Pinus sylvestris* (L.) orchard and stand seedlings.
- Wennström, U. (In prep.). Correlation between laboratory seed analysis data and seedling emergence, survival and early growth of directly seeded *Pinus sylvestris* (L.) seeds.
- Wibäck, E. 1910. Om sambandet mellan fröets beskaffenhet samt återväxtens mängd och fördelning vid grupsådd. *Skogsvårdsföreningens tidskrift*, 7-8: 243-269.

- Winsa, H. 1995. Influence of rain shelter and site preparation on seedling emergence of *Pinus sylvestris* L. after direct seeding. *Scand. J. For. Res.* 10(2): 167-175.
- Winsa, H., and Bergsten, U. 1994. Direct seeding of *Pinus sylvestris* using microsite preparation and invigorated seed lots of different quality: 2-year results. *Can. J. For. Res.* 24:77-86.
- Winsa, H., and Bergsten, U. 1995. Seedling emergence, survival and early growth after direct seeding of *Pinus sylvestris* L. using different combinations of site and microsite preparation. Appendix 5, 19 pp. In Winsa, H. Effects of seed properties and environment on seedling emergence and early establishment of *Pinus sylvestris* L. after direct seeding. Ph.D. dissertation. Swedish University of Agricultural Sciences, Dep. of Silviculture.
- von Hofsten, H. and Weslien, J. 2001. Föryngring av brända hyggen I Norrland med hänsyn till snytbagge –slutresultat. SkogForsk, Arbetsrapport nr 483, 22 pp. (In Swedish).

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