

# **Seed Orchards – Genetic Considerations on Function, Management and Seed Procurement**

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**Doctoral thesis**  
**Swedish University of Agricultural Sciences**  
**Umeå 2007**

**Acta Universitatis Agriculturae Sueciae**

2007:75

ISSN 1652-6880  
ISBN 978-91-576-7374-9  
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Tryck: Arkitektkopia, Umeå 2007

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## Abstract

Prescher, F. 2007. *Seed orchards – genetic considerations on function, management and seed procurement*. Doctor's dissertation.  
ISSN 1652-6880, ISBN 978-91-576-7374-9

Seed orchards are a cost-efficient way to increase future forest production. This thesis summarizes and discusses the results of eleven studies developing models and evaluating real seed orchard data to improve seed orchard management in *Pinus sylvestris* L. and *Picea abies* (L.) Karst.

When establishing a new seed orchard, not much emphasis should be put on selecting clones with high fertility, since variation in female fertility was found to be rather low and difficult to forecast. For considering active life time of a seed orchard, the possible genetic improvement is an important factor, but there are other factors such as seed production and seed harvest cost that have to be considered as well. The age at which replacement is justified seems to be 30 years for *Pinus sylvestris*, and 40 years for *Picea abies*. The age becomes shorter if forest owners are willing to pay more for genetically better reproductive material.

It is suggested that advanced-generation seed orchards in Sweden should contain 20-25 tested clones, with ramets deployed linearly with respect to breeding value, for an effective number of 15-18 clones. Even considering the complication that outcrossing pollen is more effective than selfing; the linear deployment concept is close to optimal. The linear deployment algorithm was applied to genetic thinning of two orchards, combining desires for high gain and conservation of gene diversity.

The harvesting of cones can often be started as soon as significant amounts of cones develop (typically by age eight in *Pinus sylvestris*), but if contaminating pollen changes the adaptability of the harvested seed, harvest may be postponed until levels of orchard pollen increase or the use of the seeds modified.

Around one quarter of the seed production occurred in the top level of the crown, half in the middle, and one quarter in the bottom. A yield of 9 kg seed per hectare is possible in *Pinus sylvestris* seed orchards. The cone harvest is a dominating cost which has consequences for management, e.g., orchards should be pruned in order to reduce tree height and thus lower harvesting costs.

*Key words:* Seed orchard, fertility variation, clone number, linear deployment, rotation age, orchard management, cone harvest, seed characters

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**This thesis is dedicated to my family, especially  
my late father Max!**

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# Appendix

## Papers I-XI

This thesis is based on the following papers that will be referred to by their respective Roman numerals:

- I.** Prescher, F., Lindgren, D., Almqvist, C., Kroon, J., Lestander, T. & Mullin, T. 2007. Female fertility variation in mature *Pinus sylvestris* clonal seed orchards. Scandinavian Journal of Forest Research 22:00-00 (in press).
- II.** El-Kassaby, Y.A., Prescher, F. & Lindgren, D. 2007. Advanced generation seed orchards as affected by breeding advance, timing of seed crop, and cost components with special reference to Scots pine in Sweden. Scandinavian Journal of Forest Research 22:88-98.
- III.** Moriguchi, Y, Prescher, F. & Lindgren, D. Optimal lifetime for Swedish *Picea abies* seed orchards. (Submitted).
- IV.** Lindgren, D. & Prescher, F. 2005. Optimal clone number for seed orchards with tested clones. *Silvae Genetica* 54(2):80-92.
- V.** Lindgren, D., Tellalov, Y. & Prescher, F. 2007. Seed set for Scots pine grafts are difficult to predict. In Isik, F. (ed) Low input breeding and conservation of forest genetic resources. Proceedings of the IUFRO Division 2 Joint Conference. Antalya, Turkey, 9-13 October 2006. pp 139-141.
- VI.** Kroon, J., Prescher, F., Wennström, U. & Lindgren, D. Cone set over time for different clones in a seed orchard. (Manuscript).
- VII.** Prescher, F., Lindgren, D. & El-Kassaby, Y. 2006. Is linear deployment of clones optimal under different clonal outcrossing contributions in seed orchards? *Tree Genetics and Genomes* 2:25-29.
- VIII.** Prescher, F., Lindgren, D. & Karlsson, B. 2007. Genetic thinning of clonal seed orchards using linear deployment may improve both gain and diversity. *Forest Ecology and Management* (in press).
- IX.** Prescher, F, Lindgren, D., Wennström, U., Almqvist, C., Ruotsalainen, S. & Kroon, J. 2005. Seed production in Scots pine seed orchards. In Fedorkov, A. (ed) Status, monitoring and targets for breeding programs. Proceedings of the meeting of Nordic forest tree breeders and forest geneticists, Syktyvkar. pp. 65-71.
- X.** Bilir, N., Prescher, F., Ayan, S. & Lindgren, D. 2006. Growth characters and number of strobili in clonal seed orchards of *Pinus sylvestris*. *Euphytica* 152:293-301.
- XI.** Bilir, N., Prescher, F., Lindgren, D. & Kroon, J. Variation in seed related characters in clonal seed orchards of *Pinus sylvestris*. (Manuscript).

Publications **I, II, IV, V, VII, VIII, IX** and **X** are reproduced with the kind permission of journal publishers.

## Introduction

Seed orchards are today the link between the breeding population and the production forest of conifers in Sweden, where genetic gain is realized in merchantable wood harvest. A seed orchard is an operation requiring considerable investment; one hectare of *Pinus sylvestris* L. seed orchard in Sweden is estimated to cost about 23 000 € to establish, including the first five years of management (Rosvall et al., 2003). It is important that the orchard functions well, producing as much seed as possible while at the same time efficiently transmitting genetic progress from the breeding population to the forest. A seed orchard that does not produce seed is a failure, not only for the company that owns it, but also for society that loses improved material and the possibility for greater forest production in the future. Furthermore, a non-functioning orchard does not produce income that could fund future seed orchards.

The concept of grafted conifer seed orchards has a long history. The first development in Scandinavia was by Syrach Larsen in Denmark, about 70 years ago (Larsen, 1934; Larsen, 1956). The concept was brought to Sweden by Holger Jensen (Jensen, 1942, 1945) and a large seed orchard program was launched. To make grafts on a large scale was a slow procedure; the selected plus trees in the natural forest were old, producing small numbers of scions that were not very vigorous. It was more feasible, albeit time consuming, to first establish a few grafted plants and then to collect more vigorous scion materials from these. A number of small graft archives and experimental seed orchards were established. The development of orchards in Denmark was hampered by the enemy occupation and the urgency to rebuild after World War II. Sweden on the other hand was less affected and could immediately accelerate its established tree breeding program, stimulated by the large timber demand for rebuilding Europe, where Sweden was the major unharmed supplier. The first full-scale conifer seed orchard in Scandinavia was established 1949 in Drögsnäs at Brunsberg in Värmland (Anonymous, 1962). Many of the guidelines suggested by Larsen (1934) are still used today when establishing new seed orchards in Sweden.

The first round of seed orchards in Sweden was established in the 1950s and 1960s with clones from selected plus-trees. These have produced improved seeds expected to increase volume production by 10% (Rosvall et al. 2002). The most recent reliable Swedish figures suggest that Scots pine plus-tree progenies in northern Sweden produce a stem volume 18.9% greater than unimproved seed at an average age of 27.4 years (Andersson et al., 2007). Jansson (2007) found 12% higher volume growth for Scots pine in southern Sweden at age 26-36. These figures support the final rotation estimate of 10%, if the volume increase is interpreted as a site index increase and growth curves are followed to full rotation age. The second round seed orchards, established during the 1980s and composed of both untested and tested clones, are expected to give genetic gains in the magnitude of 10-25% in height growth (Rosvall et al., 2002). Now, a third round of seed orchards is under establishment with tested clones, and is predicted to produce progenies with about 25% greater production than unimproved seedlots.

Management of a seed orchard involves decisions that have implications for the development of forests long into the future. Today, about 60% of plants delivered from Swedish forest nurseries originate from seed orchards, and this figure is rising. Improving seed orchards is the most cost-efficient way to increase future seed production and sustainable harvests from forest plantations. Seed orchard seeds produce faster and more even germination in the nursery, and more uniform seedling crops (Wennström, pers. comm. 2007). Barnett (1996) ascribes this, not only to the genetic superiority of the clones, but also to the more intensive management of an orchard. Seed orchard seeds are more reliable and predictable than forest stand seeds. Furthermore, selfing is more common in wild stands than in seed orchards (Kjær, 1999), which also affects the uniformity of seedling performance. Factors such as the desire for increased timber production and increasing utilization of biomass for replacement of fossil fuels are reasons for a growing interest in improved seed. Consequently, a programme for establishing new seed orchards called the “third round” (Rosvall & Eriksson, 2002) has been inaugurated in Sweden. At least 360 hectares of new seed orchards for *Pinus sylvestris* and *Picea abies* are planned for establishment during the next decade, some of which have already been planted in recent years.

Clonal forestry is sometimes envisioned as an alternative to seed orchards in Sweden, but currently it is used in a very small scale. Much less than a percent of forest seedlings produced and used are currently cuttings. The use of clones up to year 2000 was reviewed by Sonesson et al (2001), but has declined since that in Sweden. Some trials are currently established with clones produced by SE-technology by some companies, but it will take more than a decade until it is evaluated and production in a commercial scale may be an option (Rosvall, 2007). Clones of *Salix* are used for production of bio energy products, but not on what is regarded as forest land. The total use is in the magnitude of 15000 ha (Gustafsson, Larsson & Nordh, 2006).

The genetic composition of a seedlot is important. Genetic gain, avoidance of inbreeding depression and genetic diversity are essential, and these may be affected, negatively or positively, by factors like self-fertilization, inbreeding, relatedness among parents, pollen contamination, spatial distribution, flowering phenology and synchrony, as well as male and female fertility. To handle calculations, reference is often made to an ideal situation. This however seldom occurs under natural conditions, but is useful as a theoretical reference point or to make calculations about magnitudes manageable, and thus more in accordance with general knowledge and more transparent. The ideal situation entails no pollen contamination, no selfing and otherwise random mating, Hardy-Weinberg equilibrium, no linkage disequilibrium, no inbred or related clones, and equal gamete contributions from all clones to the seed crop.

The location of a seed orchard has been widely discussed. In early years, this discussion focused on where highest seed yields could be obtained; later, attention shifted to the genetic consequences of locating a seed orchard outside its target utilization area. The production of seed is limited by harsh climatic conditions at



high altitudes and latitudes, and a southward transfer of seed orchards has been advocated by numerous authors (Wright, Lemmien & Bright, 1966; Sarvas, 1970; Molotkov, Patlaj & Davidova, 1982). Mátyás (1991) summarized the expected advantages as:

- accelerated initial development and increased cone production; and
- phenological isolation from local populations as temperature sum requirements for flowering of different sources are dissimilar.

It has been shown, since the onset of flowering varies among clones (Jonsson, Ekberg & Eriksson, 1976), that contaminating pollen from surrounding stands can decrease the hardiness of offspring and change the seed crop's degree of adaptation (Pulkkinen, Haapanen & Mikola, 1995; Nikkanen, 2002). Furthermore, as pollen contamination can vary over time, both in quantity and quality, contamination from a source with different adaptation reduces the predictability of orchard seed performance. Owens et al. (2001) pointed out a number of negative effects of a southern location, such as environmental preconditioning and genetic aftereffects. These have been demonstrated to occur in *Pinus sylvestris* (Andersson, 1994), *Picea abies* (Skrøppa & Johnsen, 1994; Johnsen et al., 1995, 1996), *Picea glauca* (Stoehr et al., 1998) and *Larix laricina* (Greenwood & Hutchinson, 1996).

A rather high level of pollen contamination is something forestry and seed orchard managers have to tolerate for *Pinus sylvestris* and *Picea abies* in Sweden. It reduces the genetic gain, but provides some assurance that the orchard seeds originate from a large number of parents, representing many gene variants. Several studies have been conducted to estimate levels of contamination in *Pinus sylvestris* seed orchards, with reports between 2 and 74% (Müller-Starck, 1982; Nagasaka & Szmids, 1985; El-Kassaby Rudin & Yazdani, 1989; Harju, 1995; Wang et al. 1991; Pakkanen & Pulkkinen, 1991; Yazdani & Lindgren, 1991; Paule & Gömöry, 1992; Harju & Nikkanen, 1996). For *Picea abies*, levels between 43 and 71% have been reported (Paule, Lindgren & Yazdani, 1993; Pakkanen, Nikkanen & Pulkkinen, 2000). Nikkanen (2002) showed that pollen contamination can be reduced if a *Picea abies* orchard is exposed to more sunlight. Kang (2001) concluded that pollen contamination often exceeds 30-40%, even in mature conifer seed orchards. The latest estimate for Swedish conditions is 30-50%, sometimes even extending to 70% (Almqvist, 2007). Also foreign investigations using modern molecular markers point on high number rates of contamination, compatible with the Swedish estimates (e.g. Moriguchi, 2005). Contamination levels in the order of 50% decrease the genetic gain of seed orchard crop by about 25%. Throughout this thesis, a value for pollen contamination of 50% is used as a standard assumption when relevant.

Early contamination estimates are predominantly based on isozymes, which give some room for different interpretations and require rather large "corrections" for non-detected contaminants. It is now possible to make more accurate and precise estimates with molecular tools, and perhaps the estimates will be somewhat modified downwards.

The most natural way to decrease pollen contamination is to locate a seed orchard rather far away from other stands of the same species. This is not so easy, as windborne pollen can travel as far as 2 000 km (Koski, 1987). In Sweden, where seed orchards are normally pruned, it is thought that by not pruning to reduce the height of two or more border rows around the orchard, a “protective curtain” can be created. The border rows can also act as pollen producers, even if their seeds are not normally harvested due to higher collection costs. It has been shown by Yazdani & Lindgren (1991) and Nikkanen (2002) that pollen contamination is reduced on the lea-side as well as in the centre part of the orchard compared to the edge, indicating that these border rows are beneficial. Thus, the larger the seed orchard is, the less impact contamination has on the seed crop. As an alternative, the border can be planted with a non-orchard species, which may help to filter out some of the alien pollen (Mátyás, 1991).

The negative effects of pollen contamination can be reduced or eliminated by adding pollen, and this can also manipulate the balance of parental contributions. So-called “supplemental mass pollination” (SMP) has been widely described in the literature (e.g., Franklin, 1971; Eriksson, 1996), but has not been applied to a great extent, due to limited success and high cost. Controlled mass pollination (CMP) is more expensive than SMP, since the female strobili must be isolated and pollinated artificially, but this provides seeds with much-improved genetic quality (Bridgwater et al., 1998). CMP is today used in some south-eastern US *Pinus taeda* seed orchards as a standard procedure for more than 3 per cent of the plant production (McKeand et al., 2007). In New Zealand *Pinus radiata* seed orchards are established as controlled pollination orchards today; the produced seed is then usually amplified by vegetative propagation (Sweet, 1995). One further step is to asexually propagate elite genotypes by somatic embryogenesis (SE). A thorough review of this technique and its application to practical forestry is given by Nehra et al. (2005). In Europe, however, seed orchards are often only seen as the main source of forest tree germplasm, providing stable and sufficient seed production at a reasonable cost (Giertych, 1987). The rotation times of forests in Europe are longer and the willingness to pay for the additional gain much less than, say, the south-eastern US. It is thus likely that SMP, CMP, and SE will not have an impact on practical conifer seed orchard management in Sweden, at least not in the foreseeable future.

Clone-wise harvest and planting of only the best, open-pollinated (OP) families can dramatically increase productivity of forest plantations. Today, 59% of *Pinus taeda* and 43% of *Pinus elliottii* are deployed to plantations as half-sib families in the south-eastern US (McKeand et al., 2007). However, this is only possible if there is a surplus of seed, which today is not the case in Sweden.

Seed orchards have become the main suppliers of seed, not only for nursery production, but if there is a surplus of seed, also for direct seeding in the boreal forest. In this case, it is not only the genetic superiority of orchard seeds that matters, but perhaps even more important is their physiological advantage (Wennström, 2001). The current trend is to replace natural regeneration of Scots pine with seeding of genetically improved seed (Ahtikoski & Pulkkinen, 2003).

This has encouraged selective harvest from seed orchards to produce a genetically best fraction for use in nurseries, and a second fraction for direct seeding.

## **Objectives**

This thesis deals with factors influencing the seed crop from clonal seed orchards of *Pinus sylvestris* and *Picea abies*, with the overall goal of improving their efficiency. The specific objective is to give the seed orchard manager tools to assist in management decisions based on both developed models and real seed orchard data. The following questions are discussed:

- 1) How great is the variation in female fertility in a mature seed orchard, and what impact does this have on the composition of the seedlot? **(I)**
- 2) When should a seed orchard be replaced by a new one and what factors - including genetic progress in long-term breeding - are most important for this decision? **(II, III)**
- 3) What is the appropriate number of tested parental genotypes in a seed orchard, and what are the relevant factors to be considered in its determination? **(IV)**
- 4) Is it possible to predict the seed production ability of clones and to use this information when establishing a seed orchard? **(V, VI)**
- 5) How can genetic gain and gene diversity be combined in an efficient way through the establishment of clones in a seed orchard or during genetic thinning? **(VII, VIII)**
- 6) What potential seed production can be expected and how variable is it? **(IX, X)**
- 7) What variation in seed-related characters can be expected and what impact has this on seed procurement? **(XI)**

## Materials and methods

The material used in the thesis is of two types: a) seed orchard data, collected by the authors (**I, V, VI, IX, X, XI**) and/or extracted and analysed from the published work of others (**I**); and, b) models developed using real data or data estimated from best knowledge (**II, III, IV, VII, VIII**). This section gives a brief summary of the materials and methods used in the different papers; for detailed information, please refer to the respective paper.

### Seed orchard data

In paper **I**, data on cones and seeds per ramet from six Swedish, two Finnish, one American and one Polish mature *Pinus sylvestris* seed orchard were used to describe clonal variation in female fertility. From five of the orchards, records for two or more consecutive years were available. Variance components were estimated by ANOVA or restricted maximum likelihood using ASReml (Gilmour et al., 2002) for among-clone variation, among-ramet-within-clone variation, and clone-by-year interactions. The variance components were used to calculate the sibling coefficient,  $\Psi$  (Kang, 2001). The variance components were standardized to a ramet mean of 100, which can be seen as a percent average scale, to facilitate comparisons among the datasets.

The cone set in a clonal archive was compared to that for the same clones in four *Pinus sylvestris* seed orchards (Skaholma, Robertsfors, Klocke and Sävar) and some clone trials in paper **V**. Correlations between observations in the clonal archive and the seed orchards, and gain possible by selecting the top-ranking cone producers in the archive, were calculated to estimate how efficient it is to consider estimates of clone fertility as criteria for seed-orchard inclusion.

Paper **VI** studied the relationships among cone set for different clones at different times. Records of cone set for years 11 to 30 in an experimental Scots pine seed orchard at Sävar (latitude 64° N) were used.

In study **IX**, data from five Scots pine seed orchards in central and northern Sweden were used, as well as those from the experimental seed orchard (paper **VI**). The age of the orchards was between 20 and 41 years at time of assessment. Per-unit-area seed production was calculated for these orchards. The following characters describing female fertility were assessed at two seed orchards (Långtora and Skaholma): number of filled seeds; weight of filled seeds; volume of cones; number of cones; and seed weight. Furthermore, numbers of cones were counted from the ground to estimate the accuracy of such visual assessments. The variation (CV) among grafts was calculated for the aforementioned characters.

Data from three Turkish *Pinus sylvestris* seed orchards between 12 and 21 years of age were used in papers **X** and **XI**. In **X**, the characters studied were: number of male and female strobili; length of the trunk below and above the longest branch; total height; diameter at base and breast height; crown diameter; and number of

branches. Variation, broad-sense heritability ( $H^2$ ) and correlations between characters were estimated. In paper **XI**, cones were counted and collected on three grafts, chosen at random from 14 to 25 clones in each orchard, and from three heights above the ground. The cones were assessed for: number; diameter; length; form; fresh weight; dry weight; percentage of moisture; number of filled seeds per cone and per graft; number of total seed per cone and graft; and percentage of filled seed per cone and graft. Variance components were calculated for the characters using ANOVA and  $H^2$  was estimated. Genetic and phenotypic correlations were estimated using ASReml (Gilmour et al., 2002).

## Developed models

A model was developed in paper **II** to study and evaluate various biological, genetic, economic and management factors associated with advanced-generation seed orchard establishment using parameter estimates for *Pinus sylvestris* in Sweden. The factors considered were: planting density; rate of genetic advance in the breeding population; timing of first seed collection; seed value; seed production cost; orchard rotation age; and pollen contamination level. The model was formulated as a Microsoft Excel spreadsheet, where different inputs were tested to optimize rotation age and age of first cone harvest. The model was also applied in a simplified form to *Picea abies* in paper **III**, with some factors regarded as unimportant for spruce. The programme and model itself is applicable to a wide range of species, seed orchards and situations, but the specific inputs and applications must refer to actual data or case-specific estimates. The worksheets are currently available on the website managed by Dag Lindgren: <http://www-genfys.slu.se/staff/dagl/index.htm>.

A model is constructed in paper **IV** to maximize a goodness criterion or “benefit” for seed orchards. This can be seen as an effort to express “value for forestry” in a single quantity and to optimize the number of clones to be included in seed orchards. The benefit is a function of:

- number of tested genotypes available for selection;
- number of top-ranking clones planted in seed orchard;
- contribution to pollination from:
  - o the ramet itself;
  - o the closest neighbours;
  - o the rest of the orchard; and
  - o sources outside the orchard (contamination);
- variation among genotypes for fertility;
- variation among genotypes in “value for forestry”
- efficiency of self pollination;
- production of selfed genotypes (reduction in “value for forestry”);
- gene diversity (expressed as Status Number);
- the “value for forestry” of gene diversity;
- genetic variation among the candidates;
- correlation between selection criterion (e.g., height in progeny test) and “value for forestry” (e.g., production in forests from the orchard); and
- the number of top-ranking ones clones harvested.

Appropriate values for these factors were established for two scenarios (one for *Pinus sylvestris* in Sweden and a second for *Pinus taeda* in the south-eastern USA) and the number of clones for a seed orchard was optimized.

Paper **VII** presents a theoretical framework considering the influence of outcrossing pollen frequency on differences in reproductive success of clones and how this should influence the deployment of clones. Formulae for effective clone numbers are presented based on the number of gametes produced by the clones as well as the number of successful gametes (“outcrossing effective number”). The Excel tool ‘Solver’ was used to search for optimal clonal contributions. This tool was applied to different effective clone numbers, with the algorithm searching to maximize genetic gains. The model was also applied to a real case to optimize the establishment of a clonal *Picea abies* seed orchard, where the breeding values of 161 candidate clones were known, and the model results compared to linear deployment.

In paper **VIII**, two Swedish *Picea abies* seed orchards were genetically thinned using linear deployment. The linear deployment algorithm was first presented by Lindgren and Matheson (1986), and later developed for application to genetic thinning by Bondesson and Lindgren (1993). One operation was a seed orchard in Lagan (latitude 57°N), which was established with cuttings (a selection of clones referred to in paper **VII**) at a dense spacing. Since the establishment of this orchard was with left-over cuttings from a clonal forestry programme, there are huge differences in number of ramets from each clone. The seed orchard was thinned in 2006, using breeding values (Boije, 2001) as inputs in the algorithm. Another thinning operation was applied to an old grafted seed orchard at Maglehem (latitude 56°N), originally composed of 36 clones. Breeding values were obtained from measurements in four progeny trials, using the BLUP technique. The orchard was genetically thinned 1994 with the linear deployment algorithm.

## Mathematical framework

Some of the formulae presented in the original papers, and which are essential for the transparency of this thesis, are presented below.

The sibling coefficient,  $\psi$ , expresses the probability that successful gametes (“sibs”) will originate from the same parent compared to the case with no differences in parental fertility. The concept was introduced in Kang and Lindgren (1999):

$$\psi = N \sum_{i=1}^N p_i^2$$

where  $N$  is the census number of the parents; and  $p_i$  is the probability that a gene in the offspring originates from parent  $i$ . The sibling coefficient is a probabilistic interpretation, where the corresponding variance interpretation is expressed by the

coefficient of variation ( $CV$ ) for fertility. The relationship between them can be formulated

$$\psi = \frac{CV^2(N-1)}{N} + 1$$

The sibling coefficient cannot be less than 1. If  $\psi = 1$ , all individuals have the same fertility; if  $\psi = 2$ , it means that the probability that two randomly drawn successful gametes share the same parent is twice that where fertilities are equal across the population. A sibling coefficient  $\psi=2$  also means that variable fertility among clones can be compensated for by choosing twice as many as the desired number of clones with equal fertility.

Sibling coefficient can be seen as a part of a larger theory including the concepts of status number and effective number of clones and effective number of seed crops. These concepts and theories and the relation between status number and the “classical effective numbers” as well as to gene diversity are described and discussed in more detail e.g. by Lindgren & Kang (1997), Lindgren & Mullin (1998) and Kang (2001).

Part of the theory of the relation between female and male fertility relating to their correlation is dealt with by Kang & El-Kassaby (2002). Often the variance in total fertility is lower than either female or male taken separately.

Broad-sense heritabilities for female fertility were calculated as:

$$H^2 = \frac{VC_C}{VC_C + VC_R}$$

where  $VC_C$  is the variance component among clones in an individual year; and  $VC_R$  is the variance component among ramets within clone and year.

Broad-sense heritability is somewhat doubtful as concept. There are many reasons clones may behave differently in a seed orchard, and all of them are not genetic. Seed orchards are usually not regarded as randomized experiments, thus less effort has been done to manage ramets from different clones equally, than in an experiment. Scions of different clones may be harvested at different times and on different objects. The physiological state of the mother tree may be reflected in its grafts; grafting is typically done clone-wise; the root-stocks may be different for different clones; clones may be grown together in the nursery; different clones may be planted at different years. All these differences may have effects which appear as clonal differences, and are interpreted as genetic differences when broad-sense heritability is estimated. It is thus likely that the actual broad-sense heritability is somewhat lower than expressed here. It might have been better to talk about clonal repeatability instead to consider this difficulty. Even the genetic variation among clones is likely to be exaggerated of this reason; it does not matter so much as long as it is just a question about the actual fertility differences within a seed orchard, but may be more disturbing in other connections.

## Results and Discussion

### Variation in fertility

Fertility variation is an important factor in evolution, and thus deserves much attention from a basic scientific point of view.

Some of the data here may be relevant for that, but the emphasis in this thesis has been from a seed manager's point of view. For an orchard manager, there are several reasons to consider fertility of female parents before that of male parents: 1) seeds are the source of income from a seed orchard; 2) cones and seeds are used to audit the operation; 3) about two-thirds of the tree improvement effect comes from the seed parents as half of the pollen parents are outside the seed orchard; and 4) seeds from a known tree can be harvested and counted, which can be considered as the exact number of successful female gametes of that parent, while male gamete contributions are more tricky to estimate. About half of the male gametes do not origin from the seed orchard at all. Even if molecular techniques are available today to determine the pollen parent (Buiteveld et al., 2001; Moriguchi et al., 2004; Hansen & Kjær, 2006), they are laborious and costly, require much competence, are somewhat inaccurate, and can be done only for a limited amount of material by an organisation with good resources.

Variation in genetic contributions to seed crops depends of course also on male fertility. Paper **X** gives some estimates about the variation in male strobili. The variation among clones for male strobili was low and similar variable as the female. The numbers of male and female strobili were positively correlated. Furthermore, both the numbers of male and female strobili increased with the stem diameter of the ramet. Thus it seems reasonable that male and female fertility are correlated in rather young seed orchards, as both depend on the size of the graft. Savolainen et al. (1993) investigated mature seed orchards (study **I** uses some of these data) and reported negative genetic correlations ( $r_g = -0.135$  to  $-0.593$ ) between male and female fertility. Negative correlation between male and female tends to make reproduction more equal among genotypes and reduce the total fertility variation (Kang & El-Kassaby, 2002). Considering the large uncertainties in estimates of male fertility variation regarding statistical error and methodology, it seems likely that much of negative correlations found are non-significant noise or caused by special circumstances with limited general significance. Kang et al. (2003) found that variations in fertility are similar for both genders but it seems to be somewhat smaller for male than for female fertility. Kang & El-Kassaby (2002) reported a weak positive correlation between male and female fertility. These observations support that the fertility variation among trees and clones can be somewhat, but not much, smaller if both female and male fertility variations are considered compared with only female. If 50% of the pollen is contamination, the fertility variation on the male side of seed orchard clones is much reduced in the seed crop compared to among the clones. Thus it seems likely that fertility variations in seed orchard crops usually are smaller if both genders are considered than what this thesis focus on - female fertility variations.



An extensive review of fertility variation in forest trees was done by Kang et al. (2003), including conifer clonal seed orchards. As a rule of thumb, it was suggested that the variation among clones typically corresponds to a coefficient of variation  $CV=1$  and sibling coefficient  $\Psi=2$ . The variation in fertility seemed to be higher in young seed orchards and in years when seed production is low. These suggested values, or calculations based on them, probably overestimate the relevant variability in seed productivity per ramet among clones. Variation among ramets within clones combined with small ramet samples, interaction between years and clones, scale effects, differences among clones in the relationship between observed female strobili and final yield of good seeds, probably all contribute to overestimates of clone variability. Additionally, the ambition to express a rule of thumb with a numerically simple but somewhat upward truncated value and a smaller variation in seed production in mature seed orchards and in good seed years than reported in the experiments reviewed, also contributes to this overestimate.

Variation in female fertility, assessed by the number of cones per ramet or seeds per ramet, in mature Scots pine seed orchards was found to be less than expected when the study was initiated (**I**). The variation among clones is of the same magnitude as variation among ramets within clones. The average sibling coefficient,  $\Psi$ , was 1.35 among clones in single years, and 1.26 among clones over years, which is much lower than the rule of thumb suggested by Kang et al. (2003). Table 1, based on a similar table in paper **I**, includes additional data that became available from the two mature seed orchards reported in paper **XI**. When the variance components from these Turkish seed orchards are included, the sibling coefficient decreases even more among clones in single years,  $\Psi=1.24$ . The rather low among-clone variation is somewhat surprising; it does not seem to be in accordance with casual observations, common opinions or earlier studies (e.g., O'Reilly, Parker & Barker, 1982; Schmidting, 1983; Matziris, 1993). In this case, the seed orchards are mature, i.e., they have reached an age when there is abundant flowering on most of the orchard trees (c.f. **VI**). This decrease in variation as a seed orchard ages is also supported by the studies of Byram, Lowe & McGriff (1986). The trees have also generally been pruned, so they are similar in size. The rather low variation suggests that seed production in a seed orchard is not expected to increase to a large extent if clones that seem to be characterized by low cone production are avoided during orchard establishment.

Clone-by-year interactions between adjacent years were found to be significant, but were slightly lower (about 80%) than the among-clone variation (**I**). In paper **VI**, the results indicated that the interactions in cone set between adjacent years were even lower, and decreased as the orchard trees aged.

The effective number of clones in a seed orchard can be expressed as the census number divided by the sibling coefficient,  $\Psi$ . In a seed orchard with 40 equally deployed clones (same number of ramets) and  $\Psi=1.24$ , the effective number of clones will be  $40/1.24 \approx 32$ . The typical variation in fertility among clones results

in the effective number of clones being 20% lower than the census number, in a seed orchard where clones are equally represented.

In a seed orchard there are at least two factors which increase the sibling coefficient (and thus decrease the effective number and gene diversity) than given in Table 1. The first factor is that there are a limited number of ramets of each clone and a variation among these ramets. Thus, there will be a variation among different samples of ramets. As most seeds in a seed orchard crop come from clones with many ramets (the magnitude 50) in Swedish conifer seed orchards this effect can usually be assumed to be small. It will be smaller in future seed orchards which will have more ramets of fewer clones (c.f. study **IV**). Another, quantitative more important, factor is that ramet number varies among clones (Kang et al., 2001), and thus have impact on the fertility variation among clones in a seed orchard.

This implies that the seed crop will seldom be dominated by progenies from a few clones, especially not over the harvest of several years, and that fertility variation among clones seems to reduce “gene diversity” of seed orchard crops less than was earlier suggested (Matziris, 1993; El-Kassaby, 1995). These results agree with those reported for *Picea glauca* (Moench) Voss and *P. engelmanni* Parry ex Englem. by Stoehr et al. (2005). The variance component among clones in single years describes how much gene diversity a customer receives when using a commercial seed crop, whereas the average clonal variation in seed production over several years is more relevant to the gene diversity over the whole forest area regenerated with seed from an orchard.

Table 1. Variance components and percentages of total variance for cones/ramet, seeds/ramet and female strobili/ramet (values standardized to ramet mean = 100), broad-sense heritability, and sibling coefficient,  $\Psi$ .

Seed orchard	Trait	Between clones a individual year			Between clones over years			Clone by year interaction		Between ramets within clone and year		$H^2$ (individual year)
		Variance component	Percent of total variance	$\psi$	Variance component	Percent of total variance	$\psi$	Variance component (years)	Percent of total variance	Variance component	Percent of total variance	
Askerud, SE	Seeds/ramet	3813 <sup>b</sup>	68% <sup>c</sup>	1.38	2318	41%	1.23	1495 (3)	27%	1856	32%	0.67
Lustnåset, SE	Seeds/ramet	5830 <sup>b</sup>	64% <sup>c</sup>	1.58	4751	52%	1.48	1079 (2)	12%	3302	36%	0.64
Långtora, SE	Seeds/ramet	0 <sup>a</sup>	0%	1.00	*			*		4775	100%	0.00
Robertsfors, SE	Cones/ramet	2455	55%	1.25	*			*		2029	45%	0.55
Skaholma, SE	Seeds/ramet	5466	74%	1.55	*			*		1946	26%	0.74
Sävar, SE	Cones/ramet	1258	38%	1.13	*			*		2039	62%	0.38
Gnievkovo, PL	Cones/ramet	313 <sup>b</sup>	25% <sup>c</sup>	1.03	149	12%	1.01	164 (2)	13%	976	75%	0.24
Nebraska, US	Cones/ramet	10271 <sup>b</sup>	79% <sup>c</sup>	2.03	3242	25%	1.32	7029 (2)	54%	2896	21%	0.78
Viitaselki, FI	Cones/ramet	*			2824	75%	1.28	*		940	25%	
Vilhelminmäki, FI	Female strobili/ramet	2541 <sup>b</sup>	31% <sup>c</sup>	1.25	1970	24%	1.20	571 (2)	7%	5607	69%	0.31
Vilhelminmäki, FI	Cones/ramet	*			2722	34%	1.27	*		5281	66%	
Sogutlu, TR	Cones/ramet	115	20%	1.01	*			*		458	80%	0.20
Mengen, TR	Cones/ramet	104	17%	1.01	*			*		505	83%	0.17
Average all SOs		2380	53%	1.24						2114	47%	0.42
Average for SO with clone-by-year interaction					2568	34%	1.25	2068	28%	2893	38%	0.52

\*) no observation; **a)** non significant negative variance component set to 0; **b)** the value is given when there are observations for several years and is the sum of the variance component between clones over years and the variance component for interaction; **c)** is the sum of the percentage of variance component between clones over years and the percentage of the variance component for interaction

## Seed orchard turnover

Long-term breeding successively increases genetic gain in the breeding population, such that seed orchards become genetically outdated (Nanson, 1986; Williams & Askew, 1993; El-Kassaby, 2003), as the gain from a new seed orchard will be considerably greater. The manager must decide when to establish a new seed orchard, and the critical factor may be additional genetic gain, rather than biological or management problems with existing orchards. There are several biological, genetic, economic and management factors to be considered to optimize seed orchard turnover. A model was developed to evaluate the benefit of various options to enhance and give support for such decisions. The options and variables included in the model are:

- seed orchard area (size);
- planting density of the orchard;
- type of orchard material (grafts, cuttings (**III**));
- establishment and management costs;
- cone harvest (and its dependence of tree height) and seed processing costs;
- development over time of the seed orchard crop;
- rate of genetic progress in long-term breeding;
- genetic penalty, representing the gain differential between the seed orchard and a hypothetical new orchard incorporating the latest genetic progress in the breeding population;
- impact of pollen contamination;
- how the genetic quality influences the value of the seeds; and
- the orchards productive lifespan (from establishment to the last year of operation).

The model appear to deal with an individual seed orchard, but actually it deals with a permanent seed supply programme which is planned to last forever, and is a part of such a programme. It could be seen as new small seed orchards started every year covering an equal share of the seed need, thus the manager works at no specific age of seed orchard. But it makes it easier to develop the model by regarding it as a single seed orchard. The application of the model in **II** and **III** meets an annual seed need from forestry. There are annual income and expenses, and the aim is to maximize the profit, i.e. the difference between income and expenses. The model does not calculate the monetary value of improved seed, it just evaluates the consequences for seed orchard establishment. The monetary value of improved seeds as a function of their genetic value have been analysed in other independent calculations (e.g. Ahtikoski & Pulkkinen, 2003) and are not a part of this model. The model does not include interest and should thus not be seen as an investment calculus. It aims at developing tools for those responsible for seed orchards, to act in the best way. Income or expenses can be seen as occurring at the same time as all phases and ages are considered. Thus it may not be motivated to correct for that they occur at different times. Gain is less worth in monetary units if it occurs later, as the value of genetically updated seeds is the same over time and does not increase. Thus seed of a certain genetic quality loose

their value the later they occur. The market will demand successively higher genetic quality over time, but will pay the same price. Like computers, the price will not increase over time even if the quality of the product continuously increases. The monetary value of seeds, which are the best the breeding population have to offer, is constant, although the genetic value of the breeding population improves.

Genetic thinning or selective harvest has not been included in the model. Future seed orchards (from what is called “1.5-generation” and forwards) will mainly be established with tested clones with known breeding values, and additional precision in breeding values, when time comes for thinning, will be marginal, thus genetic thinning is unlikely. Even if new breeding values for phenotypic selections become available, the gain by thinning and selective harvest would be small compared to the gain when establishing a new seed orchard, using the same data as the selection intensity will be much higher for a new seed orchard. The model may be less applicable without modification for situations where strong genetic thinning is foreseen as an important tool. The model is, as said before, not an investment model; more factors must be considered in a less generalised way for detailed analyses when the establishment of a new seed orchard in a specific case is justified.

The model is applicable to a wide range of species, seed orchards and situations; however, the specific inputs and applications used here refer to typical Swedish grafted clonal *Pinus sylvestris* (II) and *Picea abies* (III) seed orchards, currently in use. Annual variation is experienced in factors such as flowering among clones, flowering among ramets within clones, pollen contamination, costs, etc. These variations change with age (I, Byram, Lowe & McGriff, 1986) and tree species. *Picea abies*, for example, has a large annual variation in cone production (Nikkanen & Ruotsalainen, 2000; Eriksson, Ekberg & Clapham, 2006). The model uses fixed or gradual changes over time, and deals with expectations, predictions and averages over time, so that the annual variations are levelled out and therefore of minor interest.

For *Pinus sylvestris* (II), the cone harvest is a major component of the total cost; in the base scenario for the model it accounts for 77% of the seed cost. Establishment (10%) and/or management (13%) costs should therefore not be limiting when planning a new orchard. In *Picea abies* (III), harvest costs are lower, since the cones are mainly harvested from the ground after topping the orchard trees. Here the number of seeds produced at a given planting density is more important for the benefit of the seed orchard. Differences in planting density within the studied range seem not to be so important in either *Pinus sylvestris* or *Picea abies*. The current practice is around 400 per hectare for Scots pine and Norway spruce in northern Sweden, and 200 for Norway spruce in southern Sweden where the trees are not so slender (Sylvén, 1909, 1916); this seems in agreement with the model scenarios.

The waiting period before beginning seed harvests is critical, both for the economic return and the genetic superiority of seeds from the orchard. When

harvests begin early, pollen contamination affects the seed orchard crop more and decreases the genetic quality compared with a later onset of harvest. In young orchards, where pollen production has not started, contamination level is 100%. If the seed orchard is located outside the target planting zone of the selected clones, pollen contamination will also affect the seed crop's adaptation to environmental and climatic factors (Pulkkinen, Haapanen & Mikola, 1995). This suggests that, where early harvests are planned, seed orchards should preferably be situated near the utilization area so that the contaminating pollen has hardness similar to that of the orchard's own pollen. There can also be positive effects of pollen contamination; it reduces inbreeding (selfing and mating among relatives) and increases gene diversity. Were it not for pollen contamination, early seed crops would not occur. The estimated impact of pollen contamination is shown in Table 2 (from paper II).

Table 2. Assessment of the amount of gain/loss caused by contamination and selfing, and the corresponding reduction in genetic diversity in tested clonal *Pinus sylvestris* seed orchards (adopted from IV and Nilsson & Lindgren (2005)).

Source of gain/loss	Orchard	
	Young	Mature
<b><u>Losses due to contamination:</u></b>		
Number of clones	20	20
Average BV <sup>1</sup> (%)	20	20
Contamination level (%)	100	50
Seed crop BV (%)	10.0%	15.0%
<b><u>Losses due to Selfing:</u></b>		
Within ramet Selfing	0	-1.6%
Among ramet Selfing	0	-0.7%
<b><u>Diversity loss:</u></b>		
	-0.5%	-1.1%
<b><u>Adaptation uncertainty:</u></b>		
	-2.0%	-1.0%
<b>Total:</b>	<b>7.5%</b>	<b>10.6%</b>

<sup>1</sup> Breeding value.

Pollen contamination is not the only problem arising with early cone harvests. As described above (I), the variation in female fertility is greater in young orchards than in mature ones. This means that the composition of the seed crop also differs on the maternal side compared to a more mature crop where the genetic base is broader. Years with poor flowering give a similar result (Schmidting, 1983; Matziris, 1993). Such early or poor crops should be used carefully (Gömöry, Bruchanik & Longauer, 2003), or collection avoided entirely due to high harvest costs and a low seed yield.

The main reason to begin harvesting early is to capture the higher genetic gain from clones in a newly established seed orchard. With the above-stated advantages and drawbacks (IV), it seems justified to start seed collection as quickly as

economically feasible, and this usually means a starting age of 8 years for *Pinus sylvestris* and 15 years for *Picea abies*. The later age for spruce is due to differing biology, as it normally starts flowering later than pine.

Another part of the puzzle is the annual genetic progress in the breeding population. In study **III**, it was shown that faster progress shortens the optimal productive life of a seed orchard. In other words, the genetic penalty imposed by producing seeds from older selections increases, and the benefit (value of seeds minus production costs) decreases over the life of the orchard. An annual rate of genetic progress of 0.35% was used in the base scenario for both *Pinus sylvestris* and *Picea abies* (**II**, **III**, Rosvall et al., 2002).

Under many scenarios, including the most reasonable, the point when a seed orchard is genetically outdated occurs before production is limited for biological or management reasons (**II**, **III**). Therefore, the optimal rotation age for *Pinus sylvestris* is suggested to be around 30 years (**II**). This is lower than the typical 40-year productive life of today's orchards; the Långtora and Skaholma orchards studied in papers **I** and **V** were even older. The differential between the breeding and production population will hence be smaller, and the value to the forest owner, who has access to more-improved material, will increase. In practice, this conclusion is, of course, dependent on the actual breeding population, where gain typically progresses in jumps, rather than the steady progress assumed in the models. As a rule of thumb, it seems that the seed orchard manager should begin planning for a new seed orchard 15 years after the establishment of the earlier one, even if the old seed orchard is expected to retain good seed production to age 45. In practice, the old seed orchard constitutes a backup if the new one does not produce up to expectations or if seed demand increases. Selective harvest of clones with high breeding values in the old seed orchard can be considered, so that even when the seed demand can be largely met by the new seed orchard, the best parents in the old orchard can continue to contribute. If seed demand for direct sowing grows, which seems to be the case for the moment, the old seed orchard can help supply that need.

It is suggested in paper **III** that the corresponding rotation age for *Picea abies* should be 40 years. The turnover of orchards is much dependent on the market value for improved material. If forestry is willing to pay more for a unit of genetic gain, the optimal rotation age decreases; however, the establishment of a new seed orchard also depends on the genetic gain currently available from the breeding population. Annual progress is an estimated average over time, while the actual gain possible increases stepwise depending on periodic activities such as measurements in progeny tests and calculation of breeding values. This is important for individual establishment decisions.

### **Optimal number of clones**

Not much has been presented in the literature concerning the optimal number of clones that should be deployed in a seed orchard (**IV**; Lindgren, 1974). The focus

of other authors has been to establish minimum standards regarding selfing and the loss of biodiversity, rather than to balance advantages and disadvantages. The topic is important, especially as it applies to advanced-generation seed orchards. The number of clones is one of the first choices to be made when considering a new seed orchard, and it is a critical decision point in the establishment. The number of clones is one of the most commonly reported statistics for seed orchards, and is easily understood. Selection intensity, and thus the genetic gain, will be higher if fewer tested clones are used; there can be considerable cost in lost gain, if many unnecessary clones are used. Environmental and legal requirements also tend to favour large numbers of clone, because it is regarded as safer, even in the absence of a quantitative measure of what this safety is worth or how it relates to the number of clones. Several factors are related to the context of clone numbers, and will be discussed below.

One must first decide which criteria to use in order to suggest a suitable number of clones for an orchard. In paper **IV**, this criterion is expressed as benefit for forestry. The value for forestry is mainly predicted forest production, but possible risks for lost production are considered as well, and expressed as a negative effect on benefit. When a formula for benefit has been developed, it was maximized (**IV**).

There are factors associated with the number of clones in a seed orchard and, if these factors and their dependence on clone number are quantified, it becomes possible to find an optimum. The most problematic in this context is to quantify the value of gene diversity, i.e., the positive value of having many clones in a seed orchard, and to quantify the relationship between that value and number of clones. The subject that often is mentioned in conjunction with diversity is susceptibility or resistance to pests and diseases. It is widely accepted that greater gene diversity decreases this risk. Furthermore, if a disaster occurs, the ecological niche that is released would be faster exploited by other genetic materials if gene diversity within stand is high. The loss of gene diversity is expressed as the difference to the gene diversity in the population the initial plus trees was selected from. The loss of gene diversity accompanying a low number of clones can logically be quantified as the inverse of clone number (**IV**), however, a quantification of what gene diversity is worth must also be considered. A factor is needed which sets the loss of gene diversity proportional to the inverse of the number of clones on the same scale as the genetic gain. This factor is called *DivCoeff* in paper **IV**.

To make *DivCoeff* more understandable, numeric examples are given. If *DivCoeff* has the value one, and the seed crop is a homozygous line, then the seed crop has no value. If *DivCoeff* is zero, it means that the benefit of a seed orchard crop is independent of its gene diversity, thus the amount of gene diversity does not matter and need not be adjusted for. In the calculations of optimum clone number for Scots pine, a value of *DivCoeff* = 0.4 (or rather -0.4 as lack of gene diversity has a negative impact on benefit) has been used, based on considerations of upper bounds compatible with no observed negative effects in materials with low gene diversity. That means that the quantitative value of the lack of diversity, which is



withdrawn from the gain to get the benefit, is 40 % of the loss of gene diversity in the seed orchard crop.

In a seed orchard, there may be different sources of pollen involved in fertilizing female strobili:

- selfing pollen from the orchard tree itself;
- selfing pollen from other ramets of the same clone in the orchard;
- outcrossing pollen from other clones in the orchard; and
- contaminating pollen from outside the orchard.

The different pollination patterns tested in the model, however, did not have a major influence on the optimal number of clones in the seed orchard.

A high number of candidate clones favours marginally a high number of selected clones. This is as the selection intensity, and thus the gain becomes more sensitive to the selected number if there are fewer candidates, and it thus becomes more favourable to use few clones in the seed orchard the fewer alternatives there are.

Self-pollination is another factor that influences the optimum number of clones. If selfing does not result in seeds or reduced seed production, or if seeds from selfing do not result in inbreeding depression, there is little need to avoid selfing by using a high numbers of clones.

High genetic gain and strong correlations between estimated and true breeding values favour a low optimal number of clones.

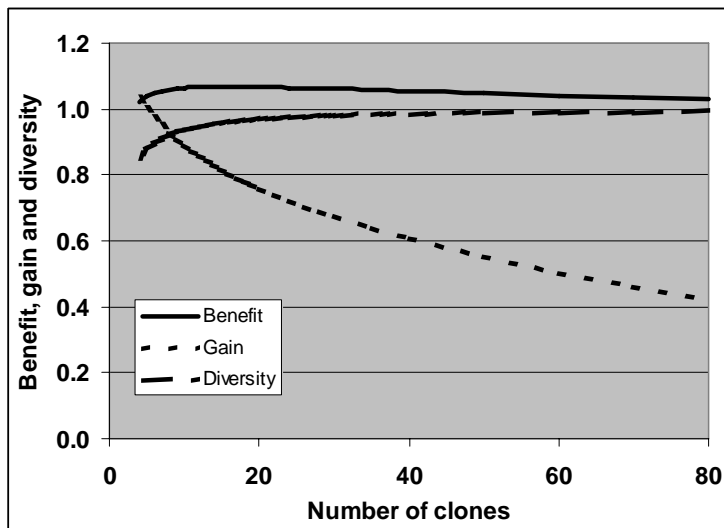


Figure 1. Example of how benefit, gene diversity and genetic gain depend on number of clones. The gain and benefit are in compatible units, but the value for gene diversity loss has to be multiplied with the factor *DivCoeff* to make the unit compatible with the two others.

An example of the relationship between clone number and benefit (goodness of a seed orchard), gene diversity and gain is shown in Figure 1 (from paper **IV**). As clone number increases, gene diversity also increases, slowly approaching unity; the genetic gain drops and the benefit reaches a maximum. The maximum is broad; minor deviations in clone number from the optimum are not critical. Little benefit will be lost when the number of clones is somewhat larger than the optimum, but even one percent has an immense economic value in forestry.

The optimum number of clones calculated in paper **IV** is 16 for Swedish *Pinus sylvestris* seed orchards. In this scenario, sibling coefficient  $\Psi=2$  was used. According to paper **I** and the extended Table 1 in this thesis, the average sibling coefficient  $\Psi=1.24$  for mature *Pinus sylvestris* orchards, which when inserted into the model reduces the optimum number to 11 clones. As explained earlier, the model assumption  $\Psi=2$  recommended by Kang et al. (2003), is actually somewhat high and can be said to discount for some unintentional inequality in ramet number. Factors like mortality causes such inequalities, and thus “the effective clone number” based on the number of ramets may turn out some years after establishment to be slightly higher than originally planned by tools like linear deployment.

The calculations assume that the clones are deployed to the orchard with equal numbers of ramets, which is seldom the case in a real orchard due to technical problems during establishment. Since equal deployment is not optimal (**VII**; Lindgren & Matheson, 1986), and that unequal deployment will be more favourable when breeding values are better estimated, a larger number of clones are recommended. In a seed orchard with a similar effective number of clones, the census number of clones can be 25 or 50% higher when deployed unequally, which results in an orchard that is somewhat more optimal than if the clones were deployed equally. On the other hand, the advantage of a few clones is mainly the greater genetic gain, a benefit that becomes more pronounced that in advanced-generation orchards established with clones having known breeding values.

The use of genetic thinning and selective harvest could justify an increase in the number of clones. Advanced-generation seed orchards will be established with tested clones and the additional gain in reducing the number of remaining or harvested clones will thus be less than in a seed orchard established with untested material.

Self pollination has a lower efficiency in fertilizing the ovule than outcrossing (**VII**; Koski, 1973; Woods & Heaman, 1989; Williams & Savolainen, 1996; Nikkanen, Pakkanen & Heinonen, 2002) and this increases the share of zygotes with fathers outside the orchard. Therefore, as the fraction of contaminating pollen increases with decreasing number of clones, this will reduce the value of the seed crop. This is an argument for a larger number of clones.

A larger number of clones give freedom of action later on in the seed orchard's life, to make adjustments for new techniques, etc. Future options can be based on information that was not available when the seed orchard was established.

Furthermore, consideration should be given to seed production and pollen production potential, in addition to the breeding values of selected clones. Some clones may fail after establishment, due to incompatibility, a technical malfunction in the system, or other such losses. This could lead to a lower number of clones, compared to what was originally planned. To be prepared for such events, a larger number of clones than appears theoretically optimal may be justified, and the penalty for using a larger number seems low (Figure 1).

The abovementioned factors combine to influence the number of clones that should be selected. For Swedish conifer seed orchards, 20 clones seem to be appropriate in a standard situation, where unrelated, tested clones are deployed in reasonably equal proportions, although this number is somewhat reconsidered later in this thesis. Paper **IV** also includes a scenario for *Pinus taeda*, and here about 10 clones are recommended under the same circumstances as above, because specific circumstances in the two scenarios suggest different model parameters.

### **Prediction of fertility prior to orchard establishment**

Normally, breeding values are given more emphasis during selection of clones to a seed orchard than is their capacity to produce seed (Sorensen & Webber, 1997). For the economy of the seed orchard, it could be more important to select clones able to produce seeds. When practical decisions are made about what clones to place in a seed orchard, the cone-set ability of candidate clones is often reviewed, and seemingly poor cone producers are not selected. Knowing both breeding values and fertility of candidate clones, these characters may be balanced to establish seed orchards in an optimal way considering both factors (Lindgren et al., 2004). To consider fertility, however, requires knowledge about how well it can be predicted. Papers **V** and **VI** discuss the prediction of female fertility prior to orchard establishment.

Seed production in *Pinus sylvestris* starts at about age 8 (**IV**) and becomes more abundant from age 15 (**VI**; Matyas & Rauter, 1987). After age 15, annual fluctuations are more important than the continuous increase in cone production over time; single-year observations do not give a reliable estimate of future rank for cone set in the orchard. Broad-sense heritability was low for cone set at young ages (0.1-0.3), indicating that the onset of cone set is strongly environmental. The heritability rises as the orchard matures, with values reported in the range of 0.5-0.6 (**I**; **VI**; Byram, Lowe & McGriff, 1986). It can be discussed if conclusions are correct when studying an experimental seed orchard with different treatments in plots as in paper **VI**. The model however “corrects” for plot effects, and age of the graft, thus much of the reasons for environmental variation in a common seed orchard has been removed. The model considers just the within plot variation (thus variation over 50\*50 m) while a typical seed orchard spans over 10 hectares. As it is not a common seed orchard but considered as an experiment located on the site of a major experimental research station, the management can be assumed to be better and more uniform than in a common seed orchard. Thus the heritability obtained can be expected to be higher than in an ordinary seed orchard.

The observed female fertility for clones can have other causes than genetic; clones may be different because of how they are produced. These differences are not likely to repeat if a new seed orchard is established. The broad-sense heritability may be overestimated and not be a good guidance for how well clonal characteristics are repeated if the vegetative multiplication is repeated under other circumstances.

The correlation between cone set for a clone in a particular year and the observation at age 30 becomes stronger over time. The genetic correlation is more than twice as high ( $r_g \approx 0.5$ ) for cone set at mature age (>20 years) compared to that at a more juvenile age (<13 years). As cone production is accumulated, stronger genetic and phenotypic correlations are found with the end of the observation period (age 30).

Collection of cumulative cone-yield data would provide greater reliability when ranking candidate clones for seed production. This has not been done in practical operations in Sweden and probably seldom elsewhere, except for the experimental seed orchard studied in **VI**. Neither is it seems worthwhile to do in the future, since the information on accumulative cone production over a decade of mature production in a seed orchard would come too late to be useful. Genetically better genotypes would be preferred when reliable cone-set data of old material become available. Furthermore, it would mean a considerable long-term-investment for an uncertain output to collect and register individual clone seed set for a large number of years.

In paper **V**, correlations are calculated between female fertility in clone archives or grafted plus-trees and performance of these same clones in seed orchards. The 18 comparisons showed correlations close to zero, and in none was there a significant relationship between cone-set observations in the archive or plus-trees and female fertility in seed orchards, for the same trial. The two lowest correlations were found in the experimental seed orchard, described in paper **VI**, where the orchard and the archive actually grow only a few hundred meters from each other.

Zobel & Talbert (1984) suggested that seed characters could be used as criteria during selection of parental trees to a seed orchard, thus enhancing seed production. Lindgren et al. (2004) suggested that breeding value and predicted seed yield could be balanced when determining the number of ramets for different clones. Our results, however, indicate that there are logistic and practical difficulties in predicting the fertility of a clone prior to orchard establishment, and that little or no effort seems justified to collect and consider such data as a selection criterion when designing new seed orchards.

### **Deployment of clones to a seed orchard**

Equal deployment of tested clones to a seed orchard is not optimal from a genetic standpoint (c.f. **IV**, **VII**, **VIII**). Lindgren & Matheson (1986) introduced an algorithm for “linear deployment”, to deploy clones proportional to their breeding

values, in order to optimize genetic gain at a given gene diversity. Clones are assumed to contribute to the offspring as a linear function of the number of ramets deployed.

In a seed orchard, ramets of different clones do not contribute equally to the seed crop. There are variations in seed set, pollen production, phenology etc. However, as studied in this thesis, it is difficult, uncertain and does not seem practically feasible to predict how ramets from different clones will differ in fertility, and the actual differences may be smaller than earlier visualised (**I**). Linear deployment need not be applied for predicted contribution of clones based on ramets used, but other fertility predictions can be used, and the ramet number adapted to make the contributions linear depending on these values. But it seems hard to predict fertility in an efficient way. It has not been studied how well the linear deployment algorithm functions for stochastic variations, but it seems likely that the average quantitative superiority to truncation selection, which is subject to the same stochastic variation, should remain. That the contribution of a clone is direct proportional to its number of ramets seem a safe consideration. However, it is probably not exactly so.

If fertility of clones to be deployed were known, the linear deployment could be modified to consider fertility. However, other studies (mainly **V** and **VI**) in this thesis seem to indicate that it is not practically possible to make accurate predictions of fertility.

A higher proportion of pollen from a clone also constitutes a higher probability of self-fertilization, and selfing in conifers seldom leads to fertile seed (**VII**, Koski, 1973; Woods & Heaman, 1989; Williams & Savolainen, 1996; Nikkanen, Pakkanen & Heinonen, 2002), such that the clone's contribution to the seed crop can be different than would be expected from the number of ramets. This is a mechanism that could reduce the efficiency of the linear deployment algorithm, an effect which is quantified in paper **IV**.

The share of outcrossing pollen from a clone will decrease as its representation in an orchard increases. Outcrossing pollen is more efficient than pollen that is delivered to ramets of the same clone. The term “outcrossing effective number” is therefore coined to describe the balance between the number of ramets and the effective number of the realised seed crop. The optimal deployment of clones, i.e., considering outcrossing effective number as well as the average breeding value for successful outcrossing gametes, was compared to linear deployment of clones, where effective number and gain are based on the number of ramets. The comparison between the optimal and linear deployments, under the same outcrossing effective number, generally produced similar results for breeding value by outcrossing contributions, effective clone number, average breeding value of ramets, and number of selected clones (Figure 2). At low effective numbers, the impact of selfing will be greater than in seed orchards with larger number of clones, due to the significant contribution of self-pollen to the pollen cloud. The outcrossing effective number will, however, be somewhat different than the effective number of clones based on contributions proportional to the

number of ramets. So, even if linear deployment is near-optimal if only outcrossing is considered, the actual effective number, genetic gain and gene diversity characterizing a seed orchard will be slightly different.

At outcrossing effective numbers of the magnitude planned for use in Swedish seed orchards (paper IV) the differences are exceedingly small between optimal selection considering self-pollination and linear deployment. In study VII, equality between male and female outputs was assumed; in a real situation, they may not be so. This may slightly enhance the effect of outcrossing deficiency for clones with greater representation; thus, linear deployment will be a better approximation.

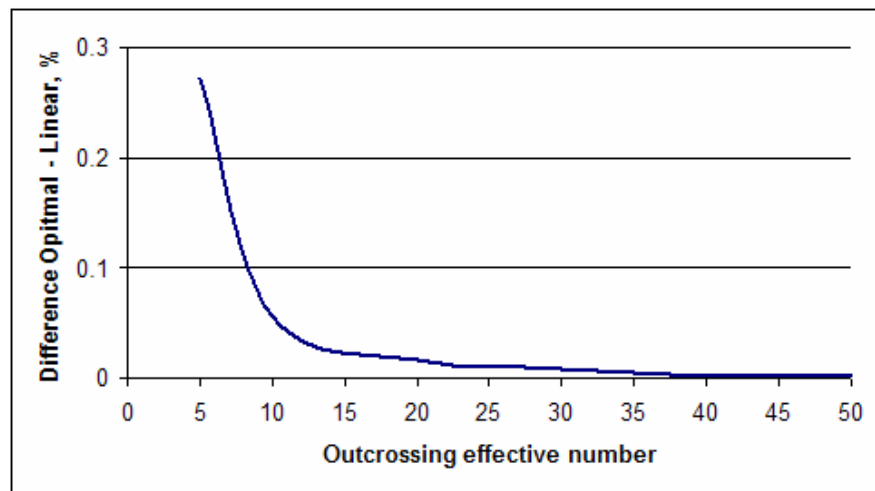


Figure 2. The difference in gain (percent of total gain obtained) between “optimal selection” considering the reduction in fertility by self-pollination and linear deployment. Generally, the differences are negligible and become smaller as the effective number increases.

Compilation of the results from IV and VII suggest that *Pinus sylvestris* seed orchards should be established with between 20 and 25 tested clones, linearly deployed according to their breeding values, with an effective number of 15-18 clones based on number of ramets planted.

### **Thinning of seed orchards using the linear deployment algorithm**

The linear deployment algorithm can also be applied to thinning operations in seed orchards (VIII; Bondesson & Lindgren, 1993). In one case of operational thinning, it was actually possible to increase both gain and effective number at the same time (VIII); it seems almost like magic that these seemingly conflicting goals can both be achieved by the same action. The orchard where this occurred had a highly variable number of ramets per clone and linear deployment made these numbers more equal.

The major factors for the genetic quality of seed orchard crops are gain and diversity (Stoehr, Webber & Woods, 2004). Thinning by linear deployment has the feature that it is optimal in the sense that no other thinning regime can result in greater genetic gain, higher effective clone number, and lower thinning intensity, simultaneously, without sacrificing any of these characteristics. A slightly higher genetic gain can be obtained by conventional truncation thinning at the same selection intensity, but this is accompanied by a considerable loss in effective clone number and number of remaining clones. Silvicultural considerations, such as spacing considerations or mortality of ramets, may reduce the theoretical optimality of linear deployment thinning. How large this reduction is, depends on the original deployment of clones at establishment, but it generally seems negligible. Silvicultural irregularities can cause larger problems with truncation selection. With linear deployment thinning, it is possible in some degree to consider the health of individual ramets and avoidance of unproductive gaps in the seed orchard, while still respecting the algorithm, while there is no such flexibility in truncation selection. However, in practice truncation selection thinning is normally modified. The worst clones are removed, and silvicultural thinning of the remainder is guided by a ranked list of breeding values. Thus this is closer to optimal than rigid truncation selection; obtaining some, but not all the, benefits of linear deployment.

Thinning by linear deployment preserves more of the variance and a higher number of clones than truncation selection, which gives the seed orchard manager more flexibility in the future for additional thinning, mass production of controlled crosses, selective harvest for specific goals, etc. (VIII, Varghese, Lindgren & Ravi, 2006; Kang et al., 2001). A high effective number of clones are accompanied by higher gene diversity, which can be seen as politically correct by regulating authorities who approve seed orchard's certification for trade. Authorities usually only use census numbers, not effective numbers, and thus it may be easier to get political acceptance with linear deployment, as it implies more clones at the same effective number.

### **Biological seed production**

There is a need for prognoses of seed set for projection of future seed production and for operational decisions on orchard size, spacing, etc. (IX). Historic records help, but considerable differences exist among definitions of "seed production", which adds complication. Reports on seed orchard harvests are often available, but these do not always reflect the actual seed production, as the total biological seed production potential is seldom utilized for operational harvests. The amount of cones and seeds harvested usually drops when the orchard ages, due in part to higher cost and difficulty harvesting from larger trees, while at the same time better alternatives to obtain seeds may have become available.

Biological seed production is often expressed per unit area, eg., seeds/m<sup>2</sup>. Compared to a natural stand, seed production in an orchard is characterized by larger cone volume as well as cone size, while the number of seeds per cone is

about the same. The fact that seed orchards are often located on abandoned farm land, with favourable climate and soil conditions, increases the production potential, and high seed production is normally a goal of both location and management. Under these conditions, at least 120-150 seeds/m<sup>2</sup> or 10 kg/hectare would be possible (IX). Seed orchards are generally young compared to seed stands, which may be a reason why the production potential of seed orchards is commonly underestimated. Usually, seed orchards have more cones per unit area than natural stands, although the cone production and seed set of natural stands may be considerably increased, at least temporarily, by intensive thinning. Studies of seed trees released for natural regeneration have shown a biological seed production of >200 seeds/m<sup>2</sup> (Karlsson, 2000), which suggests that seed production obtained in natural stands is also attainable in seed orchards if properly managed.

Data from six different *Pinus sylvestris* seed orchards (IX; Eriksson, Jansson & Almqvist, 1998; Almqvist et al. 1996), some with replications in different years, had an average biological seed production (filled seeds) of 165 seeds/m<sup>2</sup> (70-349 seeds/m<sup>2</sup>). The orchards were between 20 and 41 years old at time of assessment. The two oldest seed orchards, Långtora and Skaholma (41 and 40 years, respectively) produced 349 and 153 seeds/m<sup>2</sup>, or 19 and 8.5 kg/hectare, respectively. These figures indicate that there is no biological drop in seed production of seed orchards when they become old. The average biological seed production from the orchards studied indicates a production of 9 kg/hectare.

Results from the experimental seed orchard in Sävar (IX) showed that, at different initial spacing (269 and 525 grafts/hectare), similar numbers of seeds/m<sup>2</sup> were obtained at age 29 (191 and 192, respectively). This indicates that initial spacing has little influence on per unit area seed production beyond 30 years of orchard age. When a tree acquires more space, the crown develops to a larger size, with more potential shoot tips where strobili can form. Positive correlations were found between number of male and female strobili and size of the ramet expressed as crown diameter or breast-height diameter (X), strengthening the observation that trees respond to wider spacing by developing crowns with more cones. Diameter at breast height was suggested as a possible predictor for number of strobili per tree (X) as both height and crown diameter can be affected by pruning.

Clonal variation in various female fertility traits was studied at Långtora and Skaholma (IX), which are among the oldest active seed orchards in Sweden. The traits studied included filled seeds, weight of filled seeds, volume of cones, number of cones, and number of cones observed from ground. All showed similar coefficients of variation, CV  $\approx$  0.7. Probably all measures give usable estimates of female fertility variation and the most cumbersome methods need not be used. A quick way to estimate the female fertility is to visually count cones from the ground, even if only about 10% of the cones are visible from the ground by a stationary observer (Figures 1 and 2 in IX).



## Impact of growth and seed related characters on seed procurement

Traits such as growth, morphology, and number of strobili seem to have limited genetic variation in seed orchards and low  $H^2$  (Table 2 in **X**), so that consideration of these traits is not warranted when selecting clones for orchards. Since the environmental within-clone variation is large, there ought to be potential to manipulate environment through cultural management. Such treatments may have more potential to increase production of seeds than pollen, as the environmental variation observed was larger for female than for male strobili (**X**). Since the cost for harvesting cones in Scots pine is highly dependent on the height of cones above the ground (**II**, Lindgren et al., 2005), pruning is recommended. Pruning results in more potential shoot tips (Ho & Schooley, 1995; Kim et al., 2007) and encourages formation of strobili at a lower height, thus lowering harvest costs. Almqvist (2004) showed that cone and seed production in *Pinus sylvestris* are possible at low orchard-tree heights.

Seed-related characters such as number of cones per ramet, cone diameter, length, form, weight and moisture content, number of filled seeds, and total number of seeds per cone and ramet, and percentage of filled seeds per cone and ramet, all have an impact on seed procurement. Knowledge about these characters can be as important for efficient seed orchard management as the breeding value and fertility relations of the orchard clones, as they more directly affect seed production and procurement. Paper **XI** presents results on seed-related characters from three Turkish *Pinus sylvestris* seed orchards. Assessments were made at three levels in the crown, the bottom, middle and top thirds.

Clonal variation is considerable for cone dry weight and number of filled seeds per cone. Broad-sense heritabilities were about 0.4 for the traits studied. Cones in the top of the crown were larger and heavier than those in the bottom. The percentage of filled seeds varied among the seed orchards, indicating that environment and graft age are important factors for this trait, but variation within the crown was negligible. These figures are in agreement with previous studies (Koski, 1971; Yazdani et al., 1995). Seed weight was slightly heavier in the middle part of the crown. Differences in cone production among clones did not seem to be large; on average, 36% of the cones were produced by the 25% highest-producing clones (cf. **I**).

Around one quarter of the seed production occurred in the top level of the crown, half in the middle, and one quarter in the bottom. As the cost of seed production is dominated by the cone harvest cost, and as this cost is highly dependent on where in the crown seeds are produced, this is economically significant information for seed orchard management.

The fresh weight of cones has an impact on seed procurement, especially when harvest starts early, since the fresh weight is related to ripening (Hartmann et al., 1997). The variation in ripening among clones of *Pinus taeda* can be up to one

month, so it is now common practice to harvest the cones clone wise according to the degree of cone ripening (D. Gerwig, pers. comm., 2006). In Swedish *Pinus sylvestris*, clone-wise harvest has not been motivated by differences in ripening, but rather as selective harvest of a fraction of clones with the highest breeding values.

The genetic variation among clones for numbers of female strobili and conelets was much less than for cones and seeds. On average, broad-sense heritabilities were below 0.5 for all characters studied, which was slightly lower than reported in paper I. Differences in gamete contributions clones could be genetic (Eriksson, Jonsson & Lindgren, 1973), but the environment seems more important for the performance of grafts (cf. Hedegart, 1976) than their genetic constitution, indicating the importance of management to achieve a high seed production. One example of this is given by Varghese et al. (2006), who found significant differences in fertility among grafts due to position in the orchard and effects of openings due to thinning of adjacent trees. Clonal variation in seed and cone production capacity also has an impact on the balance between maximizing genetic gain and maintaining seed production capacity when thinning a seed orchard (Ying & Illingworth, 1985).

Genetic and phenotypic correlations differed between characters and orchards (XI). Cone number and cone dry weight showed significant correlations with the studied seed characters. The results agree with previous studies in *Pinus sylvestris* or other tree species (Shen & Lindgren, 1981; Ying, Murphy & Andersen, 1985; Reynolds & El-Kassaby, 1990; El-Kassaby & Cook, 1994; Matziris, 1998).

The variances and correlations reported in paper XI are likely also applicable to Scandinavian *Pinus sylvestris*, even if absolute seed weights or numbers of cones per graft are not directly comparable. The cones are more numerous and seeds heavier in Turkish seed orchards, but there are fewer seeds per cone. In Swedish seed orchards the frequency of empty seeds is considerably higher in the bottom portion of the crown, while this difference is negligible in Turkish orchards. The reason for this difference is not well understood, but it suggests that selfing is either less frequent or the inbreeding depression following selfing is less severe in Turkey than in Sweden.

## Suggestions for future seed orchard management

The following suggestions for future seed orchard management of *Pinus sylvestris* and *Picea abies* are based on the studies in this thesis.

- When establishing a new seed orchard, little emphasis should be put on selecting clones with high fertility, since the variation in female fertility is rather low and methods of forecasting fertility are often unreliable, particularly at younger ages.
- A seed orchard with tested clones should contain 20-25 clones, with ramet numbers linearly deployed with respect to breeding value, resulting in an effective number of 15-18 clones.
- While harvesting of cones can often be started as soon as the first cones are available (age 8 in *Pinus sylvestris* ), contaminating pollen may change the adaptability of the seed, suggesting that the harvest be postponed until levels of orchard pollen increase or the use of the seeds modified.
- For *Pinus sylvestris*, the optimal active life time of seed orchards seems to be 30 years, and for *Picea abies* 40 years. It gets shorter if forest managers are willing to pay more for genetically better reproductive material.
- For seed orchards of *Pinus sylvestris*, the high cost of cone harvest suggests that trees should be pruned to reduce height and thus cost of collection.
- Clonal seed orchards, similar to those used for the last half century, will probably remain the most realistic way to genetically improve forest production in coming decades.

## Suggestions for further research on seed orchards

More effective seed orchards are the most realistic way to improve the production forests of Sweden and increase the potential harvest (cf. Rosvall, 2007), as well as an important mean to counter global warming. During the work with this thesis, I have detected several topics referring to seed orchards that are not fully explained or covered. Some of those I have tried to list below:

- Variation in fertility has been studied for Scots pine in this thesis. The other important tree species in Sweden is Norway spruce, and for this species the knowledge of fertility variation is much more limited. New Norway spruce seed orchards are established now, which will have a big impact on future forest production in Sweden, and thus this knowledge is important.
- Pollen contamination is a big thief of genetic gain, and the quantitative importance of contamination will increase as more advanced genetic material will be used. We still do not fully understand why it is so, neither how important different countermeasures are. It seems important that research in this field is intensified. Molecular tools will probably make the studies more accurate.
- Forward selection will probably be more important for the establishment of future seed orchards, but then the technique to make many copies of a perhaps four meter high superior genotype in a field trial, in a short time, must be improved, especially for Scots pine.
- Coordination of activities in the breeding stock and establishment of seed orchards must be improved. The logistics would probably benefit from defining some research projects in this area.
- Selective harvest in seed orchards is nowadays becoming more accepted in Sweden. The knowledge of the clone's breeding values gives us reasons to study the potential of using different fractions of the seed orchard crop on different planting sites. Especially to use the best fractions on the best sites to utilize them so that a gain percentage gives more gain in national wood production. Furthermore, the impact of forest management with respect to e.g. gene diversity on such plantations should be studied further.
- The production of seed in a seed orchard must be maximized to make the investment as profitable as possible. The research on techniques for increasing seed production and for protection of the crop from pests and insects must be intensified.
- An improvement of the theory of handling advanced generation material is needed. E.g. in the future, inbred and related clones will probably occur in seed orchards. Today's knowledge is limited to low generation numbers, which can result in an inefficient management of the breeding populations.

- Knowledge and experience relevant for seed orchard clone number accumulates and in a decade or two it is motivated to reconsider the clone number recommendations given here. Probably it could be revised somewhat downward, but it is felt that such decisions should not be made fast.
- In order to optimize seed use and seed orchard size it is important to estimate the drawbacks of using the same improved material over a wide range of environments as well as the consequences of the uncertainty about future environments.
- It seems now so likely that a global warming during the coming century will occur and thus it is motivated to let this knowledge affect the establishment of new seed orchards. Advice for seed orchard managers considering the increased temperature climate needs to be made more specific than currently. When material for a new seed orchard is chosen, it may have been tested and bred for other conditions than the seed orchard crop will be used under. It is important to study which impact this global warming has on the long-term breeding and how to cope with it.

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## Acknowledgements

I am very happy to have had Dag as my supervisor, guiding me through these last years of my PhD-studies. Dag, you have been incredible in the way you have encouraged me, supported me, mail-bombed me and helped me in all various ways with never-ending eagerness and joy. I thank you especially for being patient during times when my ordinary work as seed manager took more time from me than the work with scientific papers and this thesis. I know this must have been very frustrating to you, and I recognised that you sometimes had doubts about if I really would carry this thesis to a finish. But now we together reached the goal and I am very grateful to you for this.

Thank you, Ola, for acting as my co-supervisor. Your great wisdom and support has been very valuable, and has given the thesis a more practical approach.

I am furthermore greatly indebted to my prior supervisor, late Professor Anders, who encouraged me to start the PhD-studies during my years at SLU in Garpenberg. When I left Garpenberg, I had to take a time-out in my studies due to a heavy work load, and I'm sorry that you couldn't experience the result of what you once started.

Thank you, all co-authors in the papers on which this thesis is based on! Without your tremendous work with discussing, writing, commenting and revising the papers, the thesis would have been much thinner. Yousry, I remember the nice days we had together in Umeå in the summer 2005 writing on a paper and fighting with mosquitoes in the seed orchard. Your enormous knowledge of forest genetics and its practical implementation has inspired me and your always generous way of sharing this knowledge has learned me a lot. Nebi, it was a pleasure to work together with you and your data on the Turkish seed orchards. You have always been helpful and your unselfish way of helping me is gratefully acknowledged. Yoshinari, I really appreciated to get acquainted with you. Your great knowledge about molecular genetics has given me another dimension in my thoughts. Tim, thank you for taking your valuable time and contribute to our common paper. Thank you also for your extensive editing and commenting on my thesis. Your long experience in the seed orchard business and practical tree breeding, have been a great asset for me. Curt, Torbjörn, Ulfstand, Bo, Seppo, Johan, Sezgin and Yordan, thank you for sharing your knowledge, collected data and writing skills with me, and Jon for helping in collecting data in Skaholma. Your support has made it possible to make new calculations enhancing a development in seed orchard management. Finally, Dag, you have participated in all of the eleven papers included in this thesis and put great effort in teaching me how a scientific paper should be written. Thank you for all your help!

During my studies I have had a lot of discussions about forest genetics and seed orchards in several different ways. I really enjoyed our discussions and learnt a lot from you, Bengt, my friend and colleague since more than 30 years. I also acknowledge all participants in seminars and conferences who asked questions



and discussed the topics I presented, and through which I could improve the writing of the papers. Thank you all, no one mentioned and no one forgot colleagues in Sweden and abroad for fruitful discussions.

I am indebted to the staff at UPSC and Skogforsk for all help I have got. Especially I would like to mention Katarina and Stefan. Katarina helped me in the beginning with all practical and administrative matters concerning my studies and arranged with housing during one summer period, big thanks! Stefan, your technical assistance and computer arrangements very much enhanced my studies. I also want to thank all fellows in the Research School for Forest Genetics and Tree Breeding, which actually was one reason and inspiration for me to take up my PhD studies again.

I also want to thank all unknown referees who have struggled with bad language and unclear statements in my papers and made comments so that they could be improved and readable. I'm gratefully indebted to the evaluation committee for suggestions that improved the thesis further.

My employer, Svenska Skogsplantor AB, has supported me to a great extent with time for studying during these last three years. Thank you, CEO Lena, for not pushing me too hard with excel ordinary duties during this period. I am furthermore gratefully indebted to our president Urban, who persuaded me to break the time-out and encouraged me to finish my studies.

I gratefully acknowledge The Foundation for Forest Tree Breeding who financially supported me.

Last but not least I would like to thank my wife Elisabeth and my sons Michael, Daniel and Thomas who had patience with me during these last three years of paper writing and travelling.