Impacts of Tree Improvement on Genetic Structure and Diversity of Planted Forests

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After a presentation of basic biodiversity concepts, reviews are made of studies reporting genetic implications of tree improvement activities: seed treatments, seedling production, provenance transfers, plus tree selection, seed production in seed orchards, progeny testing.

Several of the activities may influence the genetic structure and diversity of the planted forests. The general conclusion is, however, that planted forests are at least as genetically diverse as the natural stands that they replaced. The diversity in forest management and use is the best assurance for the future adaptability of the forests.

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1 Introduction

The new forests in the Nordic countries are established by natural regeneration (unmanaged or managed), by sowing or by planting. The majority of seeds for sowing originate from stands, while seeds for planting partly come from seed collections in stands and partly from seed orchards. For Norway spruce, stand seed amounts to the largest proportion of total seed use both in Norway, Sweden and Finland. For the other main conifer species, Scots pine, the larger proportion of seedlings planted in Sweden and Finland originates from seed orchards.

The aim of the artificial regeneration is to replace the harvested stand with a well-stocked stand of high quality. Production of seedlings in nurseries, transfer of species and provenances and seed production in orchards from selected parents are means used to achieve this goal. The growing concern from the society about the forest environment and its conservation has produced critical views on forest management activities in general, and more specificly, of genetic consequences of the tree improvement activities mentioned above. This question is the subject of the present article, which reviews results of studies of the genetic structure and diversity of domesticated tree populations, relevant to Nordic conditions. As many people have only superficial knowledge about the diversity concepts, some definitions are given initially as well as a description of genetic structures and diversity measures used.

2 Basic Concepts

The concept of biodiversity is a widely used term in the present-day discussions of management and conservation of natural resources. A widely accepted definition is that proposed by the U.S: Government's Office of Technology Assessments (U.S. Congress, Office of Technology Assessments 1987, see also Boyle 1992), which stated that:

"Biological diversity refers to the variety and variability among living organisms and the ecological complexes in which they occur. Diversity can be defined as the number of different items and their relative frequency. For biological diversity, these items are organized at many levels, ranging from complex ecosystems to the chemical structures that are the molecular basis of heredity. Thus, the term encompasses different ecosystems, species, genes and their relative abundance".

It is common to consider biological diversity at three different levels: *ecological diversity*, characterizing variation patterns between and within ecosystems; *species diversity*, characterizing the number of species and their distributions; and *genetic diversity*, characterizing the genetic variability between and within poulations of a single species. The present discussion will be limited to the last type of diversity.

The genetic variability of the commercial tree species in the Nordic countries and its organization are influenced by their immigration history, by the processes of mutation, migration and selection and by human activities throughout the centuries. Natural, unmanaged populations still exist. However, none of these can be said to be totally uninfluenced by man. The ability of the natural population to survive and reproduce in a given environment is characterized by its "relative" or "Darwinian fitness", which includes both a fertility and a viability component. In theory, natural selection will maximize total fitness. Management of the forest for human utilization, on the other hand, may have other goals, which may be optimized by a different array of genotypes than those selected by natural selection in the unmanaged stand. This makes it necessary to consider different fitness concepts, such as "domestic" fitness, which may be defined as the ability of a forest stand to survive and produce a specific quality wood product in a managed forest. As multiple use and sustainability are main aims of all forestry practices in the Nordic countries, other fitness concepts may also have to be considered. The important point is that different concepts will apply to different types of forest stands. Geburek and Thurner (1993) fail to take that into account in their rather misleading statement:" ..forest ecosystems will only persist if genetic variation of forest trees is not decreased."

The genetic structure of a population can be described by measures of genetic variation, genotypic associations among gene loci and among traits, the degree of relatedness among individuals and the genetic differentiation of subpopulations (Jain 1975). In addition to the evolutionary processes of mutation, migration and selection mentioned above, the natural mating system and population size will be important determinants of the genetic structure.

Two basically different types of genetic diversity concepts must be considered: *allelic* diversity and *genotypic* diversity (Danell 1992). The first one refers to the number and distribution of allelic variants that exist in the population. It reflects the potential of the population to produce different genotypes and expresses its evolutionary potential. The genotypic diversity characterizes the present population in terms of existing genotypes and their distribution. The one-clone stand has no genotypic diversity. No general statement, based on scientific information, can be given about the relations between the amount of genotypic diversity and the potential performance of the stand under the variable environmental conditions encountered during a rotation.

When quantifying genetic diversity we have to distinguish between *qualitative* and *quantitative* genetic variation.

A qualitative trait or gene marker indicates the presence or absence of certain genes and ideally allows the assessment of the genotype of the individual (Hattemer 1991). A genetic inventory of a population allows estimates of several types of allelic and genotypic diversity parameters: the average number alleles per locus, the proportion of polymorphic loci and the proportion of heterozygous loci or heterozygote individuals in the population (Hattemer 1991). With forest trees, isozymes is the group of genetic markers most commonly studied. Generally, a low level of associations are found between variation in such markers and traits that are known to have adaptive importance, suggesting that the isozyme polymorphisms have little adaptive significance (Muona 1990). They are therefore often assumed to be selectively neutral and thus representative of the genome, see discussion in Lewontin (1974).

Quantitative traits vary continuously, are strongly influenced by environmental effects and are assumed to be determined by a large number of loci. It is not possible to identify individual genotypes from the phenotypic trait expressions. The phenotypic traits can be characterized by means, variances and covariances in given environments. However, their genetic variation can not be measured directly in any population of trees. Specific family structures are necessary to estimate the genetic parameters from the observed phenotypic variability. Normally, genetic variances, their components and covariances between traits can only be estimated in experimental populations and are defined relative to a specific environment or to a set of environments. Most of the traits characterizing adaptation to environmental conditions, such as time of bud flushing, growth cessation and frost hardiness show quantitative variation, and so do the traits of economic importance selected by the tree breeders.

3 Tree Improvement and Its Genetic Consequences

3.1 Non-Breeding Activities

3.1.1 Seed Treatments

Large differences exist between the seed weights of seed from different mother trees both in seed orchards and in natural stands (e.g. Skrøppa and Tho 1990). Grading or fractioning of seeds from bulked seedlots may therefore have genetic consequences (Lindgren 1982). In one isozyme study in a Scots pine seed orchard, seed grading clearly affected the genetic composition of the seed (Szmidt 1987). Heterozygote excesses were found in embryos from heavy seeds, while homozygote excess was present in embryos from light seeds.

3.1.2 Seedling Production and Planting

In the naturally regenerated forest only a small proportion of the germinating seeds will succeed in producing a member of the production stand. When growing seedlings in a nursery, a large proportion of the germinating seeds will produce seedlings to be planted at a regular spacing in the forest. Muona et al. (1988) studied genetic changes at isozyme loci in the seed and during the first two years in a natural stand of *Pinus sylvestris* and in nursery-grown seedlings originating from the same stand. Although small, less allelic frequency differences were found between the seed and seedlings in the nursery than in the forest stand, indicating that less genetic changes take place in the nursery than in the field. This is most likely due to a faster elimination of inbred individuals in the stand than in the nursery. Evidence of selection in the stand between seeds and the juvenile seedling phase was also shown for the same species by Yazdani et al. (1985) and Muona et al. (1987).

The genetic marker studies indicate that a stronger selection takes place during the establishement in the stand than in the nursery. The consequences for the establishment and subsequent growth of the stand were studied on experimental plots of naturally regenerated, sown and planted *Pinus sylvestris* trees (Ackzell 1993, Ackzell and Lindgren 1994). It was found that the higher selection after sowing than after planting did not have any positive effects at later ages in terms of better survival and/or growth. Planting resulted in the greatest area production after 11 years based on main crop plants. These experiments also clearly demonstrated that the local stand seedlings were not the best in terms of survival and height growth.

Several authors have made comparisons of the genetic diversity (expected heterozygosity) of natural and artificial stands of *Pinus sylvestris* (Szmidt and Muona 1985, Yazdani et al. 1985, Muona et al. 1988, Muona and Harju 1989), see also Savolainen and Yazdani (1991) and Knowles (1985). No consistent differences have been found between the genetic diversity estimates of natural and planted populations from the same origin. Savolainen and Yazdani (1991), however, find this fact not surprising due to the large sizes of the populations studied and the expected neutrality of the markers.

3.1.3 Transfer of Provenances

Transfers of non-indigenous provenances of native species have frequently been made in the Nordic countries, some of which have been successful, others not.

In Sweden, southward transfers of Scots pine provenances led to an increase in survival, higher yield and better stem quality compared to the local provenance being used (e. g. Persson 1994). Similarly, transfers of late flushing Norway spruce provenances from White Russia and the Baltic countries to latefrost exposed sites in southern Sweden have reduced frost damage and improved growth (Werner et al. 1991).

Norway spruce provenances from Austria and southern Germany were extensively planted in southeastern Norway during a 20-year period starting in the 1950s. A survey of 79 planted stands of Central European origin and 21 of local orgin, all at the age of 27 years, was recently made in Østfold County, Norway (Skrøppa et al. 1993). In the stands of local origin 30 % of the trees were classified as having saw timber qualities, whilst only 7 % of the trees in the Central European stands obtained the same quality classification. These results show that this provenance transfer generally had a negative effect on timber quality and a small positive effect on volume production, even if a few of the planted stands with southern provenances had both high volume production and good stem quality.

Provenance transfers have been sucessful in several cases when specific adaptive properties have been sought. In other cases, maladaptation has occurred. The transfer of provenances, in particular from a mild to a severe climate, requires a specific knowledge of the climatic conditions at the planting site which should match with the inherent growth rhythm of the provenance. In areas with large topographic variation such transfers are in particular risky and have given variable results.

The many successful provenance transfers will produce healthy and productive forest stands and may also give rise to well adapted new generations on the same site if natural regeneration will be considered advantageous. However, the pollen cloud from stands of transferred provenances may give rise to provenance hybrid progenies which may be less adapted to climatically more severe localities. This has consequences both for natural regeneration and for seed collection. Model calculations made by Dietrichson (1991) showed that under certain conditions 5–10 % of the seed in the local stands may be from provenance hybrid pollinations in areas where 10–20 % of the flowering stands are of introduced provenances. This fact should be considered when cones are collected in areas where in particular north-transferred provenances have been extensively planted.

3.2 Breeding Activities

The early seed orchards were established with grafts of selected plus trees without progeny testing. The far largest amounts of seed orchard seed used are from these seed orchards. However, progeny test information has in some cases been used for clonewise collection of cones, to thin orchards and to establish new orchards based on a selected sub-set of the original parents. Below, reviews will be given of known genetic implications of the different activities, first in the untested seed orchard programs and finally of effects of progeny testing. Vegetatively reproduced materials (i.e. clones) will not be considered as they have been used to a small extent with conifers in the Nordic countries.

3.2.1 Phenotypic Selection of Plus Trees

The so-called plus trees were originally selected in stands, based on volume growth and stem and branch quality traits. If the selection were effective, then the seed orchard population of plus trees should be genetically different from the original populations in these traits and less variable. However, they may also be different in their genetic structure and in their genetic diversity in general.

Comparisons of the isozyme variation between groups of phenotypically selected trees and random stand trees of the North-American conifers white spruce and black spruce showed no substantial genetic heterogeneity between the groups (Knowles 1985, Cheliak et al. 1988). In terms of alleles represented, the selected trees had a reduction of 25 % compared to the alleles in the non-selected group, none of which belonged to the set of common widespread alleles. This could be interpreted as a sampling effect due to a smaller number of selected trees.

Bergmann and Ruetz (1991) compared the isozyme variability of 45 phenotypically selected Norway spruce trees and a set of randomly selected trees. They found no differences between the groups in gene frequency distributions and gene diversity measures. However, they found a higher degree of average heterozygosity in the selected clone group. A similar increase in heterozygosity was found in phenotypically selected seed orchard populations of Sitka spruce (El-Kassaby 1992). Neither for this species nor for western red cedar did the selection cause any reduction in variability compared to the natural populations.

These studies indicated that the selected clones in a seed orchard reflect the population from which they were sampled at the level of overall genetic structure and in terms of isozyme variability.

Progeny tests with families from plus trees demonstrate a large variation between families for most quantitative traits, including the traits selected for by the plus tree selection. A large genetic variance is therefore present in the populations of plus trees. Johnsen and Østreng (1994) compared frost hardiness of offspring of selected plus trees with the offspring of random trees from the same five natural stands of Norway spruce in northern Norway. They found large variation in frost damage after artificial freezing tests within each stand, but no differences between the selected plus tree progenies and the random stand tree progenies. This experiment shows that the phenotypic selection of plus trees had no correlated effects on the two traits characterizing the growth cessation and frost hardiness development.

3.2.2 Loss of Genetic Variability Due to Sampling Effects

A seed orchard contains only a finite number of clones, which is considerably smaller than the number of parents in the natural stand. This may lead to a reduced genetic variability due to sampling effects on allelic frequencies. As shown by Hattemer et al. (1982) this may in particular lead to the loss of rare alleles. However, as pointed out by Danell (1992), there are small chances that rare alleles can be of large importance, either it be in the evolution of natural populations or in breeding. The expected loss of heterozygotes among the seed orchard offspring due to the reduced population size should be very small with the number of clones used in the seed orchards (equals 1/2N, N=effective population size).

3.2.3 Mating Pattern in Seed Orchards

Ignoring the gene flow by pollen coming from outside the seed orchard, it is clear that the effective number of parents of the seed orchard pooled seed lot is lower than the census number of clones in the orchard which again is lower than the effective number of parents in a forest stand. This is due to the very unequal clonal contribution both to female and male flowering (e.g. Eriksson et al. 1973, Skrøppa and Tutturen 1985) which reduces the effective number of parents and may influence both selfing rates and loss of genetic variability due to genetic drift. However, even if the effective number of parents in the seed orchard may be as low as half the census number of clones, it still seems in most cases to be high enough to avoid depletion of genetic variability due to genetic drift (Savolainen and Kärkkäinen 1992).

Results from isozyme studies show that selfings rates may be lower in *Pinus sylvestris* seed orchards than in natural stands (Rudin et al. 1985, Muona and Harju 1989).

The seed orchard clones are generally sampled from many stands in a large geographic area. This has at least two consequences for the genetic structure of the offspring population: a possible level of spatial family relationships in a natural stand is broken, thus inbreeding is reduced. There is also the possibility of obtaining a wider sample of genetic variability as many populations are sampled. This may have a negative effect on the adaptive properties of the orchard offspring if adaptation has resulted in co-adaptation of different gene loci. However, as several studies show that the genetic variation in most traits is largely additive, such effects are unlikely to be of importance.

3.2.4 Pollen Contamination in Seed Orchards

A major problem with seed production in orchards is the gene flow into the orchard by pollen from the outside (Savolainen 1991). The relative amount of background pollination will vary between orchards and also between years in the same orchard. An immediate consequence is an increase of the genetic diversity of the orchard offspring compared to pollination with orchard pollen alone. This will reduce the gain obtained by selection of the parents. A more severe effect arises if the orchard is located in a warmer climate outside the climatic region of the orchard clones. The background pollen will in that case originate from parents adapted to a warmer climate, and the adaptational properties of the orchard offspring may be changed. Such effects have been observed on Scots pine families of northern origin produced in seed orchards in southern Finland (Aho and Pulkkinen 1991). In such cases, the intended region for the orchard seed should be redefined or the orchard must be abandoned.

3.2.5 Overall Genetic Composition of Seed Orchard Seed

Isozyme studies have been made on seed orchard seeds from six seed orchards of Scots pine in Sweden (Szmidt and Muona 1985) and two orchards in Finland (Muona and Harju 1989). These studies showed no visible reduction of the genetic diversity in the seed orchard seed compared to seed from natural stands. Some differences in genetic diversity were found between orchards, but these differences could not be related to the number of clones in the orchard and variation in the origin of the clones. This shows that the genetic structure of seed orchard seed, measured on assumingly neutral traits, is not very different from that of stand seed, taking all influencing factors into account.

3.2.6 Correlations between Flowering Characteristics and Quantitative Traits

Fertility selection will always occur in the seed orchard and traits that have positve genetic correlations with preferred types during reproduction will increase. The few results on this do not give any conclusive answers of the effects. One may ask whether such effects in the seed orchard are different from similar selections that occur in the natural stand.

3.2.7 Translocation of Seed Orchards and After-Effects

A different aspect of the location of seed orchards are effects on the progenies due to the climatic conditions during the generative reproductive process. The seedlings produced in Norway spruce

seed orchards in Norway where the parental clones are transferred to seed orchard sites 6–8 degrees of latitude southwards or to 500–600 m lower in altitude, do not retain the annual growth rhythm of their parents, see Johnsen (1989b), and Skrøppa and Johnsen (1994) for reviews. Progenies after controlled crosses in such orchards, as well as the open-pollinated pooled orchard offspring, have in particular a later growth start in the spring, a delayed growth cessation and a later development of autumn frost hardiness than their sibs after pollination, fertilization and seed maturation in their native environment. The effects have been shown in freezing tests on one or two year old seedlings, but are verified by growth rhythm studies in experiments with ten-year-old trees (Skrøppa 1994) and after a clonal propagation (Johnsen 1989a). The population mean of seed orchard offspring is changed, but the genetic variation between different families for the traits seems to be maintained.

Results from field trials and in practical plantings indicate that the observed after-effects may have practical consequences under extreme climatic situations in the field (Skrøppa, unpublished). The effects may either be positive or negative for the survival and quality of the plantation, depending on how the climatic extremes are related to the annual growth rhythm of the material. The situation seems to be similar to that of a provenance transfer. It will be adavantageous under certain environmental conditions, but the opposite under other conditions.

3.2.8 Effects of Progeny Testing

The plus tre selection did not provide a sufficient gain in the traits under improvement. Progeny testing has been found neccessary. Seed production based on a set of selected parents may clearly have genetic implications quite different from those of the untested seed orchard. However, rather little information is available on the genetic structure of seed from orchards of strongly selected parents, and a part of the reasoning must be based on theoretical considerations and from experimental populations.

In theory, the genetic diversity of seed orchard offspring produced by parents selected after an efficient progeny test will be influenced in three ways: the population mean for the trait(s) selected for will be changed, the genetic variation for the quantitative trait will be reduced, and the genetic variance of correlated traits will be influenced.

Both the allelic and genotypic diversity of the offspring from the selected set of parents will depend to a large extent on the number of selected parents, as will the population mean and a possible reduction of the genetic variance. On theoretical grounds, and has been shown by isozyme studies, a set of parents of 20–30 individuals, all producing pollen and cones, will guarantee a sufficently high effective population size. This number will also provide a large genotypic diversity in the plantation.

It has been argued that the selection for increased growth rate will decrease the general hardiness of the offspring population, due to a negative correlation between growth rate and hardiness. A negative relationship between hardiness and growth rate at the provenance level under northern condition may be the reason for this kind of speculation. However, a similar negative correlation may not occur at the individual level, and it may be possible to select for both traits simultaneously or at least keep the hardiness at a constant level. Two examples will show this.

After shoot elongation measurements in a provenance trial it was found that the provenance variation in the length of the shoot elongation period accounted for 80 % of the variation in shoot length (Skrøppa and Magnussen 1993). However, in full-sib family tests consisting of families from three natural populations and tested at the same site and in the same year as the provenance trial, it was found that the duration of the growth period accounted for less than 50 % of the variation in annual shoot growth (Skrøppa, unpublished). Some families seemed to achieve superior growth in a short growth period, and had a fast development of autumn frost hardiness.

Among the 73 clones from Svenneby Norway spruce seed orchard tested at two sites, 8 of the top parents and 8 of the lower ranked parents for height growth at age 10 years were remated in a factorial scheme. One-year-old seedlings were tested in articificial freezing test with assessments of height and bud-set. The two sets of families after crosses among the superior and among the lower ranked families parents had a similar timing of bud-set and the same level of frost damage in freezing tests (Johnsen and Skrøppa, unpublished).

The conclusion is that with a large set of parents included in the test and testing for several traits simultaneously, it is possible to select a sufficent number of parents for a seed orchard so that the planted offspring population will both have a large genotypic diversity and no negative correlation between growth rate and hardiness. However, under extreme climatic conditions care must be taken, and selection for climatic adaptation alone may be the proper action.

4 Conclusions

The presented results show that some tree improvement activities clearly influence the genetic structure and diversity of the planted forest. These influences may in some cases reduce the adaptability of the planted stand and its value for human use. The best example is the cases of non-successful provenance transfers. The majority of experimental results, however, show that planted forests are as least as genetically diverse as the natural stands that they replaced. When considering the overall genetic diversity of the tree species it must also be remembered that a large proportion of the forests is naturally regenerated. The future forests will consist of mosaics of naturally regenerated stands and planted stands, the last ones originating partly from stand seed and partly from seed orchard seed. In addition we have areas set aside for nature protection and conservation and specific gene conservation activities. The diversity in manangement and forest use will, as stated by McNeely (1994), be the best assurance for the future adaptability of our forests.

References

Ackzell, L. 1993. A comparison of planting, sowing and natural regeneration for Pinus sylvestris (L.) in boreal Sweden. Forest Ecology and Management 61: 229–245.

— & Lindgren, D. 1994. Some genetic aspects of human intervention in forest regeneration: considerations based on examples from an experiment in northern Sweden. Forestry 67: 133–148.

Aho, M.-L. & Pulkkinen, P. 1991. Effect on pollen origin on frost hardening of one-year-old northern Scots pine seed orchard seedlings. Swedish University of Agricultural Sciences. Department of Forest Genetics and Plant Physiology. Report 10: 6–13.

Bergmann, F. & Ruetz, W. 1991. Isozyme genetic variation and heterozygosity in random tree samples and selected orchard clones from the same Norway spruce populations. Forest Ecology and Management 46: 39–47.

Boyle, T. J. B. 1992. Biodiversity of Canadian forests: Current status and future challenges. The Forestry Chronicle 68: 444–453.

Cheliak, W. M., Murray, G. & Pitel, J. 1988. Genetic effects of phenotypic selection in white spruce. Forest Ecology and Management 24: 139–149.

Danell, Ö. 1992. Genetisk variation på olikt sett. Skog & Forskning (1): 28–44.

Dietrichson J. 1991. Genspredning fra plantet mellomeuropeisk gran (Picea abies (L.) Karst.) på Sør-Østlandet. Summary: Gene flow from planted continental Norway spruce (Picea abies (L.) Karst.) in southeastern Norway. Research paper of SKOGFORSK 11/91. 11 p.

El-Kassaby, Y. A. 1992. Domestication and genetic diversity – should we be concerned? The Forestry Chronicle 68: 687–700.

Eriksson, G., Jonsson, A., & Lindgren, D. 1973. Flowering in a clone trial of Picea abies. Studia Forestalia Suecia 110: 1–44.

Geburek, T. & Thurner, G. 1993. Verändert sich der Genpool von Waldbeständen durch forstwirtschaftliche Massnamen? Centralblatt für das gesamte Forstwesen. 110: 49–62.

Jain, S. 1975. Population structure and effects of breeding system. In: Frankel O. H. & Hawkes, J. G. (eds.). Crop genetic resources for today and tomorrow. Cambridge University Press, Cambridge, p. 15–36.

Hattemer, H. H. 1991. Measuring genetic variation. In: Müller- Starck, G. & Ziehe, M. (eds). Genetic variation in European populations of forest trees. Sauerländers Verlag, Frankfurt am Main. p. 2–19.

— ,Gregorius, H.-R., Ziehe, M. & Müller-Starck, G. 1982. Klonzahl forstlicher Samenplantagen und genetische Vielfalt. Allgemeine Forst- und Jagd-Zeitung 153: 183–190.

Johnsen, Ø. 1989a. Phenotypic changes in progenies of northern clones of Picea abies (L.) Karst. grown in a southern seed orchard. I. Frost hardiness in a phytotron experiment. Scandinavian Journal of Forest Research 4: 317–330.

— 1989b. Phenotypic changes in progenies of northern clones of Picea abies (L.) Karst. grown in a southern seed orchard. II. Seasonal growth rhythm and height in field trials. Scandinavian Journal of Forest Research 4: 331–341.

— & Østreng, G. 1994. Effects of plus tree selection and seed orchard environment on progenies of Picea abies. Canadian Journal of Forest Research 24: 32–38.

Knowles, P. 1985. Comparison of isozyme variation among natural stands and plantation: jack pine and black spruce. Canadian Journal of Forest Research 15: 902–908.

Lewontin, R. C. 1974. The genetic basis of evolutionary change. Columbia University Press, New York. 346 p.

Lindgren, D. 1982. Fractionation of seed orchard seed by weight does have genetic implications. Silva Fennica 16(2): 156–160.

McNeely, J. A. 1994. Lessons from the past: forests and biodiversity. Biodiversity and Conservation 3: 3–20.

Muona [Savolainen], O. 1989. Population genetics in forest tree improvement. In: Brown, A.H.D., Clegg, M.T., Kahler, A.L. & Weir, B.S. (eds.). Plant population genetics, breeding and genetic resources. Sinauer, Sunderland, Mass., p. 282–298.

— & Harju, A. 1989. Effective population sizes, genetic variability, and mating system in natural stands and seed orchards of Pinus sylvestris. Silvae Genetica 38: 221–228.

— , Yazdana, R. & Rudin, D. 1987. Genetic change between life stages in Pinus sylvestris: allozyme variation in seeds and planted seedlings. Silvae Genetica 36: 39–41.

— , Harju, A. & Kärkkäinen, K. 1988. Genetic comparison of natural and nursery grown seedlings of Pinus sylvestris using allozymes. Scandinavian Journal of Forest Research 3: 37–46.

Persson, B. 1994. Effects of climate and provenance transfer on survival, production and stem quality of Scots pine (Pinus sylvestris L.) in northern Sweden. Swedish University of Agricultural Sciences, Department of Forest Yield Reserach. Report 37. 42 p. + appendices.

Rudin, D., Muona, O. & Yazdani, R. 1986. Comparison of the mating system of Pinus sylvestris in natural stands and seed orchards. Heriditas 104: 15–19.

Savolainen , O. 1991. Background pollinatiom in seed orchards. Swedish University of Agricultural Sciences. Department of Forest Genetics and Plant Physiology. Report 10: 6–13.

— & Kärkkainen, K. 1992. Effect of forest management on gene pools. New Forest 6: 329–345.

— & Yazdani, R. 1991. Genetic comparisons of natural and artificial populations of Pinus sylvestris. In: Müller-Starck, G. & Ziehe, M. (eds). Genetic variation in European populations of forest trees. Sauerländers Verlag, Frankfurt am Main. p. 228–234.

Skrøppa. T. 1994. Growth rhythm and hardiness of Picea abies progenies of high altitude parents from seed produced at low elevations. Silvae Genetica 43: 95–100.

— & Tutturen, R. 1985. Flowering in Norway spruce seed orchards. Silvae Genetica 34: 90–95.

— & Tho, T. 1990. Diallel crosses in Picea abies. Variation in seed yield and seed weight. Scandinavian Journal of Forest Research 5: 355–367.

— & Magnussen, S. 1993. Provenance variation in shoot growth components in Norway spruce. Silvae Genetica 42: 111–120.

— ,Martinsen, D. R. & Følstad, A. 1993. Vekst og kvalitet av mellomeuropeiske og norske granprovenienser plantet i Østfold. Summary: Growth and quality of Central European and native Norway spruce provenances planted in Østfold. Research Paper of SKOGFORSK 7/93. 20 p.

— & Johnsen, Ø. 1994. The genetic response of plant populations to a changing environment. In: Boyle, T.J.B. & Boyle, C.E.B. (eds.). NATO ANSI Series, Vol I20. Biodiversity, Temperate Ecosystems, and Global Change. Springer Verlag, Berlin Heidelberg. p. 183–199.

Szmidt, A. 1987. Genetic composition of seed orchard crops. Forest Ecology and Management 19: 227–232.

— & Muona, O. 1985. Genetic effects of Scots pine (Pinus sylvestris L.) domestication. In: Gregorius, H.-R. (ed.). Population genetics in forestry. Lecture Notes in Biomathematics 60. Springer Verlag, Berlin, Heidelberg. p. 241–252.

U.S. Congress, Office of Technology Assessments. 1987. Technologies to maintain biological diversity. OTA-F-330, US Government Printing Office, Washington DC.

Werner, M., Karlsson, B. & Palmér, C.H. 1991. Ortens gran – et osäkert alternativ i Götaland. Summary: Domestic provenances of Norway spruce – a risky alternative for Southern Sweden. Institutet för skogsförbättring, Information Skogsträdsförädling Nr 4 1990/1991. 4 p.

Yazdani, R., Muona, O., Rudin, D. & Szmidt, A.E. 1985. Genetic structure of a Pinus sylvestris L. seed tree stand and a naturally regenerated understory. Forest Science 31: 430–436.

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