New Forests **6**: 329—345, 1992.
© 1992 *Kluwer Academic Publishers. Printed in the Netherlands.*

Review paper

Effect of forest management on gene pools

OUTI SAVOLAINEN and KATRI KÄRKKÄINEN
Department of Genetics, University of Oulu, SF-90570 Oulu, Finland

Received 25 October; accepted 13 May 1991

Key words: allozymes, forest management, genetic markers, natural regeneration, seed orchards

Application. Genetic consequences of various modes of forest regeneration are reviewed. Forest regeneration plans should take into consideration both genetic diversity and inbreeding levels. Many forest regeneration practices may influence adaptive quantitative variation in ways that are not reflected by allozyme variation.

Abstract. The influence of current forest management practices on gene pools is discussed. These forest management methods range from natural regeneration to replacing local species with exotics. Genetic changes caused by drift, alterations in the mating system, and directional selection are considered. A baseline is provided by information on genetic variation and demography of natural populations. While biochemical markers are useful for monitoring broad changes in genetic diversity or levels of inbreeding, changes of adaptive characters are likely to go undetected because of the low correlation in level and pattern of variation between biochemical and adaptive characters.

Introduction

Forest management has influenced gene pools of forest trees for long periods. Ancient people of the Middle East used the Cedar of Lebanon (*Cedrus libani* Loud.) for ship building and construction. They cut selectively, picking out the trees with straight trunks. As a result of millennia of dysgenic selection, they left behind only small areas of cedar forests with crooked stems and long branches (Beekeman 1949; Makkonen 1967). In Sweden and Finland, early harvesters of Scots pine (*Pinus sylvestris* L.) cut the tallest trees close to waterways for several centuries. The negative influence of these cutting habits are supposedly still seen along the most heavily used streams in Sweden (Lindquist 1946), but no scientific data are available. In Central Europe, replacing of native species and mixing of seed sources during the centuries has been so extensive that hardly any "natural" forests are left.

At present many tree species are domesticated, and more species are entering tree breeding and forest management programs. We should be well aware of the genetic changes that are caused by forestry practices (e.g., Ledig 1986). Some populations should be left in their natural state for ecosystem conservation and for future plant breeding needs. Tree breeding, considered as part of forest management (see Daniels 1984), by definition influences the genetic composition of populations. Some forest management practices may also result in unintentional changes in gene pools. Are we managing genetic resources better than the ancient Phoenicians did with their cedars? How is modern forestry practice influencing the genetic composition of populations?

The natural state of forest tree populations, their genetic structure and demography, forms a point of reference for managed populations. The natural populations of all forest trees share many important traits. Most trees have high outcrossing rates. Temperate wind-pollinated conifers have average outcrossing rates of 0.9. Some insect pollinated trees have lower outcrossing rates, as for example many eucalypts with an average of 0.7 (see Muona 1989, Table 1 for review).

The outcrossing rates were measured from mature seeds. However, in the adult stage the genotypic proportions in most cases have been found to be in Hardy-Weinberg proportions. Seed production is high, and only a very low proportion of the seed survives to the adult stage. A *Pinus sylvestris* stand may start from a seed cohort of one to two million seeds per hectare, whereas there are less than a thousand adult trees per hectare in a mature stand (Koski and Tallqvist 1978). Some demographic data on *Pinus sylvestris* are given in Table 1. During the early life stages there is heavy mortality. Much of the mortality is random, but intense selection may also take place. For example, most trees display heavy inbreeding depression (see Sedgley and Griffin 1989, p. 208). Inbreds are eliminated in early development, among much random mortality, for example in *Pinus sylvestris* (Yazdani et al. 1985). In this species, as in many others, there is extensive pollen flow (Koski 1970). Due to this pollen migration, and due to segregation, many individual seedlings will not be adapted to the local climate. Part of the selection probably eliminates these individuals. In experimental plantings with seedlings from local seed of *Pinus sylvestris*, Eriksson et al. (1980) observed 20—40% mortality in the first 20 years.

Natural populations may have genetic spatial structure, which would be eliminated by forest regeneration by sowing or planting. However, pollen and seed dispersal are so efficient in most conifers that family structure seems to be weak or nonexistent (e.g., Epperson and Allard 1989). Bird-dispersed pines may occur in clusters of relatives (Furnier et al. 1987), and animal pollinated species may have some family structure (Perry and Knowles 1991). Moran et al. (1989a) suggested that spatial genetic stucturing could explain the higher level of inbreeding in natural stands than in a seed orchard found in *Eucalyptus regnans* Mueller. Microenvironmental selection could also create spatial sturucture, but this is likely reflected in adaptive quantitative characters, usually not in allozymes (e.g., Campbell 1979).

Natural selection in the wild is expected to maximize total fitness, which consists of a viability and a fertility component. Forestry practices shift this goal: instead of maximizing seed yield, the aim is usually to maximize vegetative growth. In trying to achieve the goal, forestry practices interfere with various life stages. Selective cutting, either picking the best trees or leaving the best trees to reproduce, may differ from the effects of natural viability selection. Natural regeneration changes densities and may alter mating systems of reproducing populations. In artificial regeneration, seeds of a different origin may be used. Production of genetically improved material brings about many desired and maybe some other changes in the genetic composition of the new population. Thus forestry influences both the viability and fertility components of selection.

The intensity of forest management varies from natural regeneration to intensive industrial forestry. Forestry can cause many kinds of genetic changes. We shall consider whether forestry practices cause directional changes, whether drift due to small population sizes is important in causing decreases in diversity, and whether management practices cause alterations in the mating system that in turn influence the level of inbreeding. Forest management could also break microgeographic patterns of variation, where they exist. The aim is to evaluate critically what changes genetic markers, allozymes or restriction fragment length polymorphisms, will be able to detect, and where other kinds of methods must be employed. We start with the most natural forestry practices and then consider modern intensive industrial forestry.

Natural regeneration

Selective cutting

The ancient way to regenerate forest was to harvest the best trees and leave the rest to reproduce. The effects of this kind of management depend on the intensity of selection on parental trees (Zobel and Talbert 1984). Even if heritabilities for height growth are fairly low in the natural populations, long lasting intensive phenotypic selection may bring about genetic change, as in *Cedrus libani*.

In shelterwood and seed tree regeneration, a relatively few large trees are left to reproduce. Will this kind of stands maintain sufficient genetic variability, or does selection of big trees result in directional change in genetic composition? Table 2 shows that the level of genetic variability is little altered in shelterwood and seed tree stands (Neale 1985; Yazdani et al. 1985; Cheliak et al. 1988). Nor was evidence of directional changes in frequencies of genetic markers found. Thus, selection for size has not influenced allozyme frequencies systematically, and population sizes are not small enough for drift to have a measureable influence in one generation. From allozyme evidence, shelterwoods or seed tree stands seem to be a very natural way to regenerate forests. Forest fires have similar effects: after fires the biggest trees are most likely to remain alive and contribute progeny to the next generation (Wyant et al. 1986).

Effects of the density of reproducing trees

In seed tree and shelterwood stands the density is lower than in forests normally. If only a few trees are reproducing, the probability of inbreeding increases. The level of inbreeding can rise because of higher levels of selfing or matings between relatives.

Farris and Mitton (1984) found some evidence of higher levels of selfing in low density stands of *Pinus ponderosa* Laws. On the other hand, Neale (1985), Neale and Adams (1985a), and Yazdani et al. (1985) did not find any additional selfing in low density stands of *Pseudotsuga menziesii* (Mirb.) Franco or *Pinus sylvestris*. In *Pseudotsuga menziesii* (Neale and Adams 1985a), the differences between densities were large, but no sign of increased selfing was found (see Table 3). In animal pollinated plants, the density of populations could be more important, as Ellstrand et al. (1978) found in *Helianthus annuus*.

The level of inbreeding is also affected by the size of the trees. Both very small conifer trees (Neale and Adams 1985b) and very big ones (Shea 1987) can have a higher level of selfing than average size trees. In small trees this may be due to weak separation of male and female strobili (Neale and Adams 1985b), and in big trees due to their high production of pollen (Shea 1987). However, increased selfing is not a problem in natural stands because of the early selection against inbreds. Loehle and Namkoong (1987) have pointed out that selection of the biggest trees could also mean that seed yields are lowered, if there is a negative correlation between seed production and growth, as was found by Schmidtling

(1981). However, as long as a sufficient number of trees are left, such selection would be advantageous for future timber production.

Role of natural regeneration

Natural regeneration allows only minor improvement because of low heritabilities. However, this kind of regeneration will probably be used in many areas for a long time to come. In some areas artificial regeneration is too expensive, in others natural regeneration is the method that works best. Environmental considerations may also lead to this kind of regeneration (Mahlein and Hemstrom 1988). Of the total area of *Pinus sylvestris* regenerated in Finland, almost half is natural (Yearbook of Forest Statistics 1987).

Artificial regeneration: bulk seed

Origin of the seed source

In large clearcuts, where no shelterwood is left, regeneration must be artificial. Since seed orchards of many species are young, and their seed production insufficient, bulk seed lots from natural forests are commonly used (Zobel and Talbert 1984). Foresters have often used seed lots from outside the local area in order to improve yields, e.g., in northern Finland when regenerating *Pinus sylvestris*. When the biology of the species is not known sufficiently well, such transfers have resulted in failure of regeneration due to heavy mortality. Many wind pollinated conifers have large continuous populations, but they are highly differentiated in many characters. For example, *Pinus sylvestris* has steep clinal variation in growth characteristics. In common garden experiments with Finnish material (lat. 60—70 °N), Mikola (1982) found a two month range in bud-setting in the autumn. The correlation of median budset date with latitude of origin was −0.968. Similar latitudinal and altitudinal differentiation has been found in *Pseudotsuga menziesii* (Rehfeldt 1989) and *Pinus contorta* Loud. (Rehfeldt 1988). In transfer experiments such latitudinal and altitudinal differentiation is observed clearly. Even short range transfers of seedlings either to the north or to higher altitudes result in increased mortality in *Pinus sylvestris* (Eriksson et al. 1980). Provenance differentiation may also exist for other characters, e.g., disease resistance in *Pseudotsuga menziesii* (McDermott and Robinson 1989). Much of the quantitative variation is presumably adaptive in present environments, however, geographic variation may also be generated by historical patterns of migration (Lagercrantz and Ryman 1990).

In contrast to studies of adaptive traits, studies of biochemical markers have shown a near lack of differentiation between populations, with very low G_{ST} values, usually less than 10 % (Hamrick 1983; Muona 1989). A cline of acid phosphatase allozymes in *Picea abies* (L.) Karst is one of the rare exceptions (Bergmann 1978), but Tigerstedt (1973) found no differences between a northern and a southern population in the same species at the same locus. Some indication of edaphic differentiation was given by data of Mitton et al. (1989) in *Picea engelmannii* (Parry) Engelm. and Millar (1989) in *Pinus muricata* D. Don.

Common garden experiments show strong differentiation with respect to latitude or of origin in timing of growth or survival in *Pinus sylvestris* and several other species. Allozyme variability shows very low levels of differentiation. This poses a limit on the usefulness of allozymes in controlling seed origin.

Direct seeding

Regeneration by sowing is used for *Pinus sylvestris* in Finland on about 10% of the yearly regeneration (Yearbook of Forest Statistics 1987). The seed used for this purpose is normally bulk seed, from any natural stands or sometimes from selected seed collection stands. The number of seeds per hectare will be initially quite high, e.g., 50 000 (Table 1). This is, however, far lower than would obtain in a natural population, but does allow for heavy mortality in the early life stages. If the seed source was initially chosen correctly, the genotypic composition of the adult stand may resemble that of local stands. As more genetically improved seed becomes available, the use of sowing will probably decline.

Seedlings from bulk seed

We will here discuss general questions dealing with regenerating with seedlings, specifics of seed orchard seed will be dealt with later. Seedlings are produced in nurseries, under close to optimal conditions. These are then planted at a low density in regeneration areas (Table 1). Selection intensities in nurseries may be low, or the selection may differ from that in natural stands (see Kitzmiller 1990). The mortality in natural populations brings about genetic changes, e.g., elimination of inbreds. Some mortality is probably also due to lack of climatic adaptation in the seedlings (due to segregation and pollen migration). If such selection does not operate in nurseries, the result may be poor growth or heavy mortality in the field.

Table 1. Demography of natural and artificial regeneration of *Pinus sylvestris* in Finland

Life stage	Natural stands	Sowing	Planting
Seeds	2000000	50000	
Seedlings (3 yr.)	50000		2500
Adult trees	<1000	<1000	<1000

(*n* of individuals/hectare).

This may result in stands that are too scarce. Such growing conditions will lead to decreased quality of the timber (see e.g., Barbour and Kellogg 1990).

A possible way to study selection in nurseries using allozymes is to monitor the elimination of inbreds, or to follow allelic frequency changes. We compared genetic changes that took place in a natural stand of *Pinus sylvestris* during the first years to those in a nursery (Muona et al. 1988), but found only small differences at marker loci. It would be important to monitor the fate of inbreds in nurseries in species where the level of selfing is considerable and inbreds in natural stands are eliminated in the early years, as e.g., *Eucalyptus regnans* (Moran et al. 1989a).

Regeneration with seed orchard seed

Seedlings from seed orchard seeds are the most extensively used genetically improved material for regeneration of coniferous forests. Wheeler (1992, this issue, pp. 311—328) has reviewed the use of allozymes in monitoring seed orchard function. Our perspective will deal with those genetic changes that are really a byproduct of the intended genetic improvement.

Genetic variability and inbreeding

Seed orchards should provide genetically variable seeds. Most of the effort in measuring genetic variability in any organism has centered on expected heterozygosity. Measured in this way, drift depletes genetic variability very slowly, at the rate of $1/2N_e$ per generation (where N_e is the effective population size). It is evident that seed orchards with even moderate numbers of clones or genotypes will lose very little of the expected heterozygosity in one generation. The regenerated forests are not going to continue with this small population size. Instead, they will be regenerated with seed from orchards again. Additive genetic variability behaves as expected heterozygosity, and is likely to be retained to a high degree. However, some of the important genetic variability may be in the form of rare alleles, e.g., disease resistance. Seed orchards typically contain such low numbers of clones that even fairly common alleles are lost (see Hattemer et al. 1982). Empirical results on variability in natural stands and seed orchards crops confirm that expected heterozygosities are similar in natural and managed populations (Table 2).

Table 2. Expected heterozygosities (H_e) at isozyme loci in natural and managed forests

Species	Natural	Managed	Stage	Reference
Pinus sylvestris	0.28	0.27 (SO)	seeds	Muona and Harju 1989
Pinus sylvestris		0.35 (SW)	seeds	Yazdani et al. 1985
Pseudotsuga	0.21	0.23 (SO)	seeds	Shaw and Allard 1982
menziesii	0.22	0.23 (SW)	adults	Neale 1985

SO — seed orchard, SW — shelterwood or seed tree stand.

The effective population size is usually much lower than the true number of clones because of variation in progeny number. In the orchards studied by Muona and Harju (1989), the effective sizes were about half the number of clones. Even so, little variability is lost in one generation. Even if variability was lost, it would be partly compensated for by background pollination, which is extensive and difficult to avoid in the Finnish orchards studied. The number of alleles in the seed crop was clearly higher than in the orchard parental clones, due to background pollination (Harju and Muona 1989). These studies suggest that hardly any changes of variability occur in seed orchards at allozyme loci, though other genetic changes may occur (see below).

Table 3 shows that in general seed orchards have no more inbreeding than natural stands. In *Eucalyptus regnans* less inbreeding was found in an orchard (Moran et al. 1989a).

Directional genetic changes due to fertility selection?

In the ideal seed orchard no fertility selection occurs. However, clones do not contribute equally to the offspring generation. There is extensive variation in female flowering and cone crops between the clones of e.g., *Pinus sylvestris* (e.g., Jonsson et al. 1976; Muona and Harju 1989), *Picea abies* (Eriksson et al. 1973), *Pseudotsuga menziesii* (El-Kassaby et al.

Table 3. Multilocus estimates of outcrossing (t_m) in natural and managed forests

Species	Natural	Managed	Reference
Pinus sylvestris	0.94	0.98 (SO)	Muona and Harju 1989
Picea mariana	0.70	0.84 (SO)	Barrett et al. 1987
Pseudotsuga menziesii	0.98	0.95 (SW)	Neale and Adams 1985
Eucalyptus regnans	0.74	0.91 (SO)	Moran et al. 1989a

SO — seed orchard, SW — shelterwood or seed tree stand.

1989) and *Pinus kesiya* Royle ex Gordon (Sirikul and Luukkanen 1987) (see Muona 1989 for further references). The coefficients of variation of cone production ranged from 0.5 to 1 in *Pinus sylvestris*. Likewise, male fertility varies between clones in *Pinus sylvestris* and in other species (Muona and Harju 1989). The variation in male strobilus production is also reflected in the actual participation in fertilizations of the different clones, as shown by paternity analysis for *Picea glauca* (Moench) Voss by Schoen and Stewart (1986) and *Pinus sylvestris* by Muona and Kärkkäinen (1989). However, phenological effects may also be very important in determining mating success (Erickson and Adams 1989). In addition, male fertilities may vary after pollination (Schoen and Cheliak 1987). Total fertility variation thus is an important selective factor. This will probably not influence the frequencies of biochemical markers, which are likely to vary independently of the flowering variables. However, flowering variation may be negatively correlated with growth (e.g., Loehle and Namkoong 1987). Surprisingly, few data are available on such correlations (Sedgley and Griffin 1989). Skroppa and Tutturen (1985) found no correlation between flowering and growth in young *Picea abies*, but Schmidtling (1981) demonstrated a negative correlation in *Pinus taeda* L. Nikkanen and Velling (1987) found a negative correlation between vegetative growth and flowering in clones of *Pinus sylvestris*. Loehle and Namkoong (1987) also suggested that variation in sexual reproduction may be negatively correlated with resources allocated to defenses against pathogens.

Even if there are some potential problems with seed orchards, genetic gains are achieved even in first generation orchards. Matheson et al. (1986) showed that in *Pinus radiata* Don trees from first generation seed orchards had considerably better volume growth (15—30%) than control seed lots, due to genetic improvement.

Correlations between levels of variability

The use of biochemical markers in monitoring variability within populations is based on the idea that they reflect the genome in general. How true is this assumption? There are examples of widespread species that have extensive allozyme and morphological and physiological variability, as for example *Pinus sylvestris* (Mikola 1982; Szmidt and Muona 1985; Muona and Harju 1989). *Picea omorika* (Pančić) Purkyne is a species with low morphological variability (Langner 1959), but it has been shown to have extensive genetic variability at marker loci (Kuittinen et al. 1991). One of the important trees in the reforestation of tropical areas is *Acacia mangium* Willd. This species is known to have hardly any allozyme variability, with expected heterozygosity 0.02 (Moran et al. 1989b). However, the populations contain much genetic variability for growth and physiological characters (Atipanumpai 1989). Finally, *Pinus torreyana* Parry ex Carr. has little variability in both kinds of traits (Ledig and Conkle 1983). Despite these examples of lack of concordance between levels of variability, allozymes are obviously useful when variability is monitored over time in a population or species, even if bottlenecks may have somewhat differing influences on variation at single loci and in quantitative characters (Lande 1980).

Clonal forestry

Clonal forestry is currently used for many broad-leaved species, e.g., eucalypts and poplars. Among conifers, *Cryptomeria japonica* (L. F.) D. Don, *Pinus radiata* and *Picea abies* are species where the technology is available (Zobel and Talbert 1984). As techniques are developed, the share of clonal forestry will increase. Modern biotechnology can be most rapidly integrated into tree breeding with the aid of vegetative propagation (Cheliak and Rogers 1990). In theory clonal forestry allows complete control over the genotypic composition of the plantation. The risks associated with a genetically uniform plantation with a low number of clones have been discussed intensively for years (see e.g., Benzer et al. 1988 for references). Many technical problems, for example with respect to genetic variation between genotypes in the ease of cloning, remain to be solved. As discussed above in connection with flowering variation, genetic correlations could lead to concomitant selection on other traits. The clones to be used in plantations are thoroughly tested for their production and adaptive characters. Marker genes have a minor role in monitoring genetic changes due to these practices. In species where regeneration takes place by seeds, the markers allow observation of the genetic effects of the reproductive cycle. Since this cycle is missing in clonal propagation, the genetic composition of the population can be monitored directly. Marker genes are used as technical aids, for example in identifying clones.

Exotic species

Exotic tree species have been used extensively for centuries to increase yields (Zobel et al. 1987). In Europe, conifer forests have to a large degree replaced native deciduous forests. The species that are used as exotics are often ecologically and genetically well known, as *Pinus contorta*, *Pinus radiata*, many eucalypts or acacias (see e.g., Turnbull 1987). One of the reasons for growing exotics rather than local species is that their biology and silvicultural requirements are well known (Evans 1987; Booth et al. 1988). Similar genetic considerations apply to these species as have been discussed above. Genetic markers are helpful in assessing how much of the variation in native populations has been included with the introductions. For older introductions, the initial sources may be unknown. Moran and Bell (1987) were able to infer the main sources of Australian *Pinus radiata* by comparing the original and introduced populations.

When exotics are planted, native forests are being replaced. In Europe this occurred so long ago that it is hardly remembered. At present, the disappearance of tropical rain forests is a major concern. Currently, every minute, 20 ha of forest are being converted or destroyed, and less than one hectare for every 10 hectares is reforested (Burley 1988). Much of the disappearance of forests is not due to "forest management," but to diverse social and economic pressures (FAO 1985). Plantation forestry may sometimes reduce pressure on natural tropical forests, because the yields can be four to ten times higher than in natural forests (FAO 1985; Gladstone and Ledig 1990). The protection of genetic diversity in tropical forests should be of interest to foresters. The genetic resources of tropical species are needed for future breeding, and for ecosystem stability (Ledig 1986).

Conclusions

Foresters interfere massively with many aspects of the trees' life cycle in tree breeding and silviculture. Forestry practices range from selective cutting and leaving of seed trees to replacing local species with exotics. It is important to be aware of the kinds of genetic changes that are to be expected along with these practices. There are both short term and long term considerations. In the short term, forestry practices should result in productive stands that are able to tolerate the environmental variation for the duration of the rotation. Natural regeneration and regeneration with bulk or orchard seed should mostly satisfy the requirements for genetically variable non-inbred seed. Foresters are also concerned with the quality of the wood produced (e.g., Barbour and Kellogg 1990). If plantations start with a low density, and heavy mortality occurs, the resulting stand will be quite sparse. Even with good genetic material, the result may be of poorer quality wood due to excessive branching. In using clonal forestry, the level of genetic variability may decrease considerably from that of natural populations. However, in this case foresters opt to take a calculated risk. The desired level of diversity will depend on the species, environment, and rotation age.

The longer term concern is the maintenance of reservoirs of genetic variability. This is needed for current breeding programs, and more importantly, for future needs. Important changes in the environmental conditions occur with climates being changed by the greenhouse effect and environmental pollution. Also, the requirements set by industry for wood production may change. As more and more forest land comes under intensive management practices, do any forests remain in a completely natural condition? Even if populations are maintained in a natural condition, isolation is not possible, and pollen from commercial stands will form part of the next generation's gene pool. Forest geneticists are exploring the need for differently managed populations for breeding and conservation (e.g., Namkoong 1989).

Current public debate on forestry practices deals mainly with two topics. In temperate areas, the debate revolves around choices between intensive industrial forestry and a more "natural" kind of management, often called New Forestry (Hasenkamp 1978; Mahlein and Hemstrom 1988; Franklin 1988). Genetics does not enter into the discussion often, except at the level of maintaining species diversity (e.g., Mahlein and Hemstrom 1988). When diversity within tree species is considered, most alternative modes of regeneration will likely maintain sufficient diversity.

The other intensely discussed topic is tropical forestry. Genetic resources are frequently mentioned as a reason for conserving native rainforests (e.g., Burley 1988). Again, the genetic issues primarily concern species-level diversity. The extinctions of species due to modification of environment are taking place so rapidly that the question of loss of genetic variability within species is moot: all individuals may have disappeared before drift has a chance to operate. The many ecological causes of extinction often operate before lack of genetic variation becomes an issue (Lande 1988).

What role do genetic markers have in following these changes? So far, the research has mainly used allozymes, but in the near future more numerous DNA markers will become available (Neale 1992, this issue, pp. 391—407). Allozymes have proved useful in measuring mating systems and inbreeding levels. So far, there have been few reports of a useful correlation between levels and patterns of variability of allozymes and adaptive morphological and physiological characters. This limits the usefulness of allozyme markers in monitoring the important genetic changes. Random DNA-level markers are not likely to fare much better. However, by saturating chromosomes, eventually we should be able to use DNA-markers to identify important quantitative trait loci (QTLs). If sufficiently tight associations between markers and QTLs are found, then maybe DNA markers can provide a short cut to monitoring to what happens with adaptive characters, at least in specific families or populations. Strauss and Tsai (1988) demonstrated that there is some clinal variation in the number of rDNA repeat units in *Pseudotsuga menziesii.* Methods are being improved for detecting variation at single copy regions (Neale 1992, this issue, pp. 391—407). The main use of this variation will certainly be to aid directly in tree breeding, but when such variation is detected, it can also be used for monitoring genetic changes in cultivated and conservation populations.

Acknowledgments

We thank V. Koski, J. Lumme, T. G. Harmsen, T. Prout and P. M. A. Tigerstedt for discussions, encouragement, and comments on the manuscript. Our research has been financially supported by the National Research Council for Agriculture and Forestry and the Foundation for Natural Resources in Finland.

References

Atipanumpai, L. 1989. *Acacia mangium*: Studies on the genetic variation in ecological and physiological characteristics of a fast growing plantation tree species. Acta Forestalia Fennica 206: 1—92.

Barbour, R. J. and Kellogg, R. M. 1990. Forest management and end-product quality: a Canadian perspective. Can. J. For. Res. 20: 405—415.

Barrett, J. W., Knowles, P. and Cheliak, W. M. 1987. The mating system in a black spruce clonal seed orchard. Can. J. For. Res. 17: 379—382.

Beekeman, W. B. 1949. Hout in alle tijden. I. Prae-historie en Historie tot en met de Iraniers. Kluwer, Deventer/Batavia/ Bandoeng/Semarang/Soerabaia, 714 pp.

Benzer, B. G., Foster, G. S., Hellberg, A. R. and Podzorski, A. C. 1988. Genotype x environment interaction in Norway spruce involving three levels of genetic control: seed source, clone mixture and clone. Can. J. For. Res. 18: 1172—1181.

Bergmann, F. 1978. The allelic distribution at an acid phosphatase locus in Norway spruce (*Picea abies*) along similar climatic gradients. Theor. Appl. Genet. 52: 57—64.

Booth, T. H., Nix, H. A., Hutchinson, M. F. and Jovanovic, T. 1988. Niche analysis and tree species introduction. For. Ecol. Manage. 23: 47—59.

Burley, F. W. 1988. The tropical forestry action plan: recent progress and new initiatives. pp. 403—408. In: Wilson, E. O. (Ed) Biodiversity. National Academy Press, Washington, DC, 521 pp.

Campbell, R. K. 1979. Genecology of Douglas-fir in a watershed in the Oregon Cascades. Ecology 60: 1036—1050.

Cheliak, W. M., Murray, G. and Pitel, J. A. 1988. Genetic effects of phenotypic selection in white spruce. For. Ecol. Manage. 24: 139—149.

Cheliak, W. M. and Rogers, D. L. 1990. Integrating biotechnology into tree improvement programs. Can. J. For. Res. 20: 452—463.

Daniels, J. D. 1984. Role of tree improvement in intensive forest management. For. Ecol. Manage. 8: 161—195.

El-Kassaby, Y. A., Fashler, A. M. K. and Crown, M. 1989. Variation in fruitfulness in a Douglas-fir seed orchard and its effect on crop-management decisions. Silvae Genet. 38: 113—121.

Ellstrand, N. C., Torres, A. M. and Levin, D. A. 1978. Density and the rate of apparent outcrossing in *Helianthus annuus* (Asteraceae). Syst. Bot. 3: 403—407.

Epperson, B. K. and Allard, R. W. 1989. Spatial autocorrelation analysis of the distribution of genotypes within populations of lodgepole pine. Genetics 121: 369—377.

Erickson, V. J. and Adams, W. T. 1989. Mating success in a coastal Douglas-fir seed orchard as affected by distance and floral phenology. Can. J. For. Res. 19: 1248—1255.

Eriksson, G., Andersson, S., Eiche, V., Ifver, J. and Persson, A. 1980. Severity index and transfer effects on survival and volume production of *Pinus sylvestris* in northern Sweden. Studia Forestalia Suecica 156: 1—32.

Eriksson, G., Jonsson, A. and Lindgren, D. 1973. Flowering in a clone trial of *Picea abies*. Studia Forestalia Suecica 110: 1—44.

Evans, J. 1987. Site and species selection — changing perspectives. For. Ecol. Manage. 21: 299—310.

FAO (Food and Agriculture Organization) 1985. Tropical Forestry Action Plan. Food and Agriculture Organization of the United Nations, Committee on Forest Development in the Tropics, Rome, 159 pp.

Farris, M. A. and Mitton, J. B. 1984. Population density, outcrossing rate, and heterozygote superiority in ponderosa pine. Evolution 38: 1151—1154.

Franklin, J. F. 1988. Structural and functional diversity in temperate forests. pp. 166—175. In: Wilson, E. O. (Ed) Biodiversity 5. National Academy Press, Washington, DC.

Furnier, G. R., Knowles, P., Clyde, M. A. and Dancik, B. P. 1987. Effects of avian seed dispersal on the genetic structure of whitebark pine populations. Evolution 41: 607—612.

Gladstone, W. T. and Ledig, F. T. 1990. Reducing pressure on natural forests through high yield forestry. For. Ecol. Manage. 35: 69—78.

Hamrick, J. L. 1983. The distribution of genetic variation within and among natural populations. pp. 335—348. In: Scoenewald-Cox, C. M., Chambers, S. M., MacBryde, B. and Thomas, W. L. (Eds) Genetics and conservation. Benjamin Cummings, Menlo Park.

Harju, A. and Muona, O. 1989. Background pollination in *Pinus sylvestris* seed orchards. Scand. J. For. Res. 4: 513—520.

Hasenkamp, J. G. 1978. Betriebswirtschaftliche Auswirkungen der naturgemässen Waldwirtschaft. Der Forst- und Holzwirt 33: 278—280.

Hattemer, H., Gregorius, H.-R., Ziehe, N. and Müller-Starck, G. 1982. Klonenanzahl forstlichen Samenplantagen und Genetische Vielfalt. Allg. Forst U. J. Ztg 153: 183—191.

Jonsson, A., Ekberg, I. and Eriksson, G. 1976. Flowering in a seed orchard of *Pinus sylvestris* L. Studia Forestalia Suecica 135: 1—38.

Kitzmiller, J. H. 1990. Managing genetic diversity in a tree improvement program. For. Ecol. Manage. 35: 131—149.

Koski, V. 1970. A study of pollen dispersal as a mechanism of gene flow. Communicationes Instituti Forestalis Fenniae 75(3): 1—30.

Koski, V. and Tallqvist, R. 1978. Tuloksia monivuotisista kukinnan ja siemensadon määrän mittauksista metsäpuilla. Folia Forestalia 364: 1—60.

Kuittinen, H., Muona, O., Kärkkäinen, K. and Borzan, Z. 1991. Serbian spruce, a narrow endemic, contains much genetic variation. Can. J. For. Res. 21: 363—367.

Lagercrantz, U. and Ryman, N. 1990. Genetic structure of Norway spruce (*Picea abies*): concordance of morphological and allozymic variation. Evolution 44: 38—53.

Lande, R. 1980. Genetic variation and phenotypic evolution during allopatric speciation. Am. Nat. 116: 463—479.

——. 1988. Genetics and demography in biological conservation. Science 241: 1455—1460.

Langner, W. 1959. Selbstfertilität und Inzucht bei *Picea omorica* (Pancic) Purkyne. Silvae Genet. 8: 84—93.

Ledig, F. T. 1986. Conservation strategies for forest gene resources. For. Ecol. Manage. 14: 77—90.

Ledig, F. T. and Conkle, M. T. 1983. Gene diversity and genetic stucture in a narrow endemic, torrey pine (*Pinus torreyana* Parry ex Carr.). Evolution 37: 70—85.

Lindquist, B. 1946. Den skogliga rasforskningen och praktiken. Svenska Skogsvårdsföreningens förlag. Stockholm, 176 pp.

Loehle, C. and Namkoong, G. 1987. Constraints on tree breeding: growth tradeoffs, growth strategies, and defense investments. Forest Sci. 33: 1089—1097.

Mahlein, D. and Hemstrom, M. 1988. Ecosystem management, a new forestry. Forest Watch 8(8): 8—10.

Makkonen, O. 1967. Ancient forestry. An historical study. Part I. Facts and information on trees. Acta Forestalia Fennica 82.3: 1—84.

Matheson, A. C., Eldridge, K. G., Brown, A. G. and Spencer, D. J. 1986. Wood volume gains from first-generation radiata pine seed orchards. CSIRO Div. For. Res. User Ser no. 4, 13 pp.

McDermott, J. M. and Robinson, R. A. 1989. Provenance variation for disease resistance in *Pseudotsuga menziesii* to the Swiss needle-cast pathogen, *Phaeocrytopus gaeumannii*. Can. J. For. Res. 19: 244—246.

Mikola, J. 1982. Bud-set phenology as an indicator of climatic adaptation of Scots pine in Finland. Silva Fennica 16: 178—184.

Millar, C. 1989. Allozyme variation of bishop pine associated with pygmy-forest soils in northern California. Can. J. For. Res. 19: 870—879.

Mitton, J. B., Stutz, H. P., Schuster, W. S. and Shea, K. L. 1989. Genotypic differentiation at PGM in Engelmann spruce from wet and dry sites. Silvae Genet. 38: 217—221.

Moran, G. F. and Bell, J. C. 1987. The origin and genetic diversity of *Pinus radiata* in Australia. Theor. Appl. Genet. 73: 616—622.

Moran, G. F., Bell, J. C. and Griffin, A. R. 1989a. Reduction in levels of inbreeding in a seed orchard of *Eucalyptus regnans* F. Muell. compared with natural populations. Silvae Genet. 38: 32—36.

Moran, G. F., Muona, O. and Bell, J. C. 1989b. *Acacia mangium*: a tropical forest tree of the coastal lowlands with low genetic diversity. Evolution 43: 231—235.

Muona, O. 1989. Population genetics in forest tree improvement. pp. 282—298. In: Brown, A. H. D., Clegg, M. T., Kahler, A. L. and Weir, B. S. (Eds) Plant population genetics, breeding and genetic resources. Sinauer, Sunderland, Mass.

Muona, O. and Harju, A. 1989. Effective population sizes, genetic variability, and mating system in natural stands and seed orchards of *Pinus sylvestris*. Silvae Genet. 38: 221—228.

Muona, O., Harju, A. and Kärkkäinen, K. 1988. Genetic comparison of natural and nursery grown seedlings of *Pinus sylvestris* using allozymes. Scand. J. For. Res. 3: 37—46.

Muona, O. and Kärkkäinen, K. 1989. Reproductive effort and reproductive success in *Pinus sylvestris*. Abstracts of 2nd European Conference on Evolutionary Biology, Rome, Italy, 1989.

Namkoong, G. 1989. Population genetics and the dynamics of conservation. pp. 161—181. In: Knutson, L. and Stoner A. K. (Eds) Biotic diversity and germplasm preservation, global imperatives. Kluwer Academic Publishers, Dordrecht.

Neale, D. B. 1985. Genetic implications of shelterwood regeneration of Douglas-fir in Southwest Oregon. Forest Science 31: 995—1005.

——. 1992. Use of DNA markers in forest tree improvement research. This issue (pp. 391—407).

Neale, D. B. and Adams, W. T. 1985a. The mating system in natural and shelterwood stands of Douglas-fir. Theor. Appl. Genet. 71: 201—207.

——. 1985b. Allozyme and mating-system variation in balsam fir (*Abies balsamea*) across a continuous elevational transect. Can. J. Bot. 2448—2453.

Nikkanen, T. and Velling, P. 1987. Correlations between flowering and some characteristics of grafts of *Pinus sylvestris*. For. Ecol. Manage. 19: 35—40.

Perry, D. J. and Knowles, P. 1991. Spatial genetic structure within three sugar maple (*Acer saccharum* Marsh.) stands. Heredity 66: 137—142.

Rehfeldt, G. E. 1988. Ecological genetics of *Pinus contorta* from the Rocky Mountains (USA): a synthesis. Silvae Genet. 37: 131—135.

——. 1989. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. glauca): a synthesis. For. Ecol. Manage. 28: 203—215.

Schmidtling, R. C. 1981. The inheritance of precocity and its relationship with growth in loblolly pines. Silvae Genet. 30: 188—192.

Schoen, D. J. and Cheliak, W. M. 1987. Genetics of the polycross. 2. Male fertility variation in Norway spruce, *Picea abies* (L.) Karst. Theor. Appl. Genet. 74: 554—559.

Schoen, D. J. and Stewart, S. C. 1986. Variation in male reproductive investment and male reproductive success in white spruce. Evolution 40: 1109—1120.

Sedgley, M. and Griffin, A. R. 1989. Sexual reproduction of tree crops. Academic Press, London, 378 pp.

Shaw, D. V. and Allard, R. W. 1982. Isozyme heterozygosity in adult and open-pollinated embryo samples of Douglas-fir. Silva Fennica 16: 115—121.

Shea, K. 1987. Effects of population structure and cone production on outcrossing rates in Engelmann spruce and subalpine fir. Evolution 41: 124—136.

Sirikul, W. and Luukkanen, O. 1987. Promotion of flowering using exogenous plant hormones in tropical pines. For. Ecol. Manage. 19: 155—161.

Skroppa T. and Tutturen, R. 1985. Flowering in Norway spruce seed orchards. Silvae Genet. 34: 90—95.

Strauss, S. H. and Tsai, C.-H. 1988. Ribosomal gene number variability in Douglas-fir. J. Heredity 79: 453—458.

Szmidt, A. E. and Muona, O. 1985. Genetic effects of Scots pine (*Pinus sylvestris* L.) domestication. pp. 241—252. In: Gregorius H.-R. (Ed) Population genetics in Forestry. Lecture notes in biomathematics 60. Springer Verlag, Berlin.

Tigerstedt, P. M. A. 1973. Studies on isozyme variation in marginal and central populations of *Picea abies*. Hereditas 75: 47—60.

Turnbull, J. W. 1987. (Ed) Australian Acacias in developing Countries. ACIAR Proceeding no. 16. 196 pp.

Wheeler, N. 1992. The use of electrophoretic markers in seed orchard research. This issue (pp. 311—328).

Wyant, F. G., Omi, P. N. and Laven, R. D. 1986. Fire induced mortality in Colorado ponderosa pine/Douglas-fir stand. Forest Sci. 32: 49—60.

Yazdani, R., Muona, O., Rudin, D. and Szmidt, A. E. 1985. Genetic structure of a *Pinus sylvestris* seed-tree stand and naturally regenerated understory. Forest Sci. 31: 430—436.

Yearbook of forest statistics 1987. Folia Forestalia 715: 1—245.

Zobel, B. J. and Talbert, J. T. 1984. Applied forest tree improvement. John Wiley and Sons. New York. 505 pp.

Zobel, B. J., van Wyk, G. and Stahl, P. 1987. Growing exotic forests. John Wiley, New York. 508 pp.