

# Evolutionary Forces Influencing Variation among Populations of *Pinus sylvestris*

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The evolutionary forces influencing genetic differentiation among populations are identified. Natural selection, random genetic drift, and mutations promote differentiation while phenotypic plasticity and gene flow delay or prevent differentiation. Evolution is a dynamic force which leads to instability and absence of any perfection in the adaptive process. Natural selection acts mainly on phenotypes and only indirectly on the components of important breeding traits. In the northern part of the distribution of Scots pine there is a large among- and within-population variation in survival. The high among-population variation occurs in spite of an assumed high gene flow. Biomass is a product of many components and it also shows a high population variation. Many markers are neutral and such markers will not reveal adaptive variation.

**Key words** *Pinus sylvestris*, Scots pine, among-population variation, evolutionary forces

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## 1 Introduction

The genetic variation among and within populations is indispensable for efficient tree breeding and gene conservation. These aspects of the genetic structure are in turn dependent on several forces. Understanding of the evolutionary forces is crucial for sensible sampling of populations for gene conservation. The aims of gene conservation are:

- 1) saving alleles with frequencies  $> 0.01$
- 2) capturing existing adaptedness
- 3) creating the best conditions for future evolution.

Understanding among-population variation for different traits is crucial for fulfilment of points 1 and 2 above.

The possibilities for creating desired phenotypes via breeding are best understood after an analysis of the evolutionary forces influencing

different traits. Even trait combinations not existing in the parent population may be created by breeding (cf Ekberg et al. 1994).

The first part of this paper will be devoted to a brief analysis of evolutionary forces influencing the process of differentiation among populations. In the second part observed population differences for some traits are examined in the light of the presentation in the first part of the paper. For the benefit of breeding and gene conservation of *Pinus sylvestris* I hope that this will provide a basis for an examination of the evolution of populational differences in other traits.

## 2 The Process of Population Differentiation

Evolution is frequently looked upon as a two-step process (e.g. Mayr 1988, page 98):

1. Genetic variation is randomly created by new mutations, also accompanied by random recombination
2. Natural selection and/or genetic drift act upon the existing variants

The truth of the first point has been questioned (e.g. Bradshaw 1991).

Natural selection, genetic drift, and mutations tend to increase genetic differentiation among populations, while phenotypic plasticity and gene flow tend to reduce it.

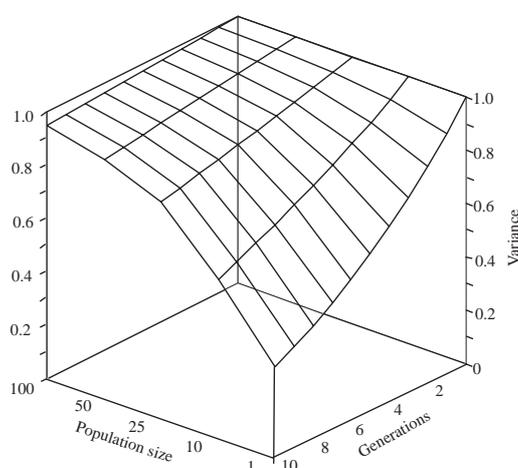
(a) *Natural selection*. The concept of selective environmental neighborhoods (SENs) introduced by Brandon (1990) is useful for an understanding of natural selection and adaptation. A simplified interpretation of SEN is that ranking changes do not take place within its borders. A species growing under several SENs will be exposed to different selective forces of natural selection in the different environments, in this way causing among-population variation. The existence of several SENs within the range of the distribution of a species is a prerequisite for the evolution of among-population variation by natural selection. Some stability over time of SENs is also required. Natural selection is the only force directly connected with adaptation (Brandon 1990). It should be stressed that natural se-

lection mostly operates on the phenotype (cf Mayr 1988). This means that it rarely operates on individual genes. Nor does it usually directly operate on components of a trait.

Since the derivation of the selective effects on genes of varying fitnesses by Haldane (1932), selection in favour of homozygous recessives has been regarded as an extremely slow process owing to the low initial frequency of the recessive gene which in turn means that there are no homozygous recessives to select among. The cases of rapid response to strong toxic agents, e.g. DDT and insects, have been attributed to dominance for tolerance to these substances (Hartle and Clark 1989). Moreover the response to selection was derived for large panmictic populations. However, in many cases in nature the intermating population may be much smaller. For small populations carrying a rare fitness-improving allele the chances of obtaining homozygosity for such an allele increases considerably. In other words in small populations fitness-increasing homozygotes for rare recessive alleles will reach selectable frequencies faster.

One of the most comprehensive reviews of the occurrence and strength of natural selection is to be found in the book, *Natural selection in the wild*, by Endler (1986). Based on an analysis of hundreds of cases fulfilling certain criteria for being regarded as natural selection (directional, stabilizing as well as disruptive), he concluded that the belief that natural selection is usually weak is not true. Rather natural selection can take any value, weak or strong, and moreover there are many cases in which the selection intensity is as strong as in breeding. Recently Bradshaw (1991) forcefully argued in favour of strong directional natural selection. He listed several cases mostly related to heavy metal tolerance in grass species. In one of the studies he referred to, a build-up of copper tolerance took place in a population within the time frame of no more than four generations.

(b) *Genetic drift*. Random genetic drift will occur in populations with low  $N_e$ s ( $N_e$  = effective population size). Genetic drift causes a loss of additive variance with a rate of  $1/2N_e$  per generation. Its effect on additive variance over ten generations for different population sizes is shown in Fig. 1. From this figure it may be seen that the loss is



**Fig. 1.** The loss of additive genetic variance by random genetic drift over ten generations at population sizes 5–100 individuals.

strongly dependent on population size below a size of 25. Genetic drift will in most cases lead to a reduction in fitness but may in some rare cases also give rise to improved fitness.

(c) *Mutation.* Mutations are assumed to be different in different populations thereby causing differences among the populations. The impact is probably low owing to low mutation rates. Major gene mutation rates are assumed to amount to  $10^{-5}$ – $10^{-6}$ , although higher rates, approximately  $3 \times 10^{-5}$ , have been reported for waxy mutants in pollen grains of maize (Staedler and Sprague 1936, Eriksson 1963). The mutants contributing to additive variance of quantitative traits are of greater interest. They can obviously not be studied individually but estimates from studies in maize, mice, and *Drosophila* suggest rates of  $10^{-2}$ – $10^{-3}$  (Lande and Barrowclough 1987). Unless their mutation rates are much higher than for major genes these figures suggest that genes in a large number of loci are involved in the regulation of the quantitative traits studied. Mutation rates at the genomic level of chlorophyll mutants in *Pinus sylvestris* was estimated by Kärkkäinen et al. (1996) to  $1$ – $3 \times 10^{-2}$  based on original data from Eiche (1955).

(d) *Phenotypic plasticity.* Phenotypic plasticity is defined as the amplitude of the phenotypic expression of a genetic entry studied under two or more environmental conditions. It has to be

emphasized that phenotypic plasticity must be regarded as a genetically regulated trait (for a recent summary see Eriksson 1991). Plants with their indeterminate growth (e.g. Schmid 1992) can show a considerable amount of phenotypic plasticity. However, organs involved in reproduction show much less phenotypic plasticity for obvious reasons. A change of the floral structure of an entomophilous plant species might prevent the pollen vector from visiting the plants. Phenotypic plasticity can be thought of as disguising the genotype and thereby reducing the role of natural selection. When the ratio of the generation time over the selective fluctuations increases, the probability for evolution of phenotypic plasticity increases (Endler and MacLelland 1988). Species which during their lifetime are exposed to selective forces in a multitude of directions must be able to cope with that without a change of the genotype. Therefore it is probable that genotypes with high phenotypic plasticity are favoured under such conditions. For *Pinus sylvestris* this would mean that the probability for development of phenotypic plasticity is high accompanied by a low probability for specific adaptation to environmental fluctuations.

(e) *Gene flow.* Gene flow among populations occupying different SENS reduces previously existing differences and counteracts differentiation. For mobile species gene flow can be accomplished by immigrants. Seeds in seed banks may also be regarded as immigrants from another time with another SEN. For tree species gene flow is a result of pollen and seed dispersal among different SENS.

The mathematics of the process of gene dispersal is fairly complex and different formulae have been derived for different types of population structure; continuous distributions with isolation by distance, island types of structure, stepping stone models (Lande and Barrowclough 1987). In the absence of any other forces, an exchange of one individual between two populations per generation suffices to prevent fixation of different neutral alleles in the same locus in the two populations. In the case of one-dimensional dispersal the figure might be somewhat larger (Lande and Barrowclough 1987, Slatkin 1987). Gene flow among populations must be regarded as an extremely strong force to prevent

population differentiation.

Ellstrand and Elam (1993) reported on estimates of the number of migrants among populations in several plant species including Eucalypts. They varied between 0 and 15 per generation and they found no relationship with the pollination pattern of the species. In contrast, Govindaraju (1988) summarized published data on gene flow in 115 plant species. Generally the gene flow was highest in anemophilous plants and lowest in selfing species. Entomophilous plants took an intermediary position.

These five forces hardly ever operate in isolation, rather one or more of them operate simultaneously. Theoretical derivations of formulæ for the effects of these factors are available and some basic information will be given.

Loss of variance due to genetic drift can be compensated for by variance contribution by new mutants. If the figure for the pooled mutation frequency in genes regulating a quantitative trait amounts to  $10^{-3}$  as mentioned above, the  $N_e$  must be 500 ( $1/2N_e = 10^{-3}$ ) to compensate for the loss of additive variance caused by drift.

As a rule of thumb it is usually stated that genetic drift will reduce the additive variance of a population when the mutation rate is much less than  $1/4N_e$ . The same is true for the coefficient of selection ( $S$ ), defined as  $S = (100-w)/100$ , in which  $w$  is the fitness as a percentage of the fitness of the genotype with highest fitness. The formula indicates that extremely high mutation rates or selective forces are needed to overcome the effect of drift when  $N_e$  is low.

A decrease in the size of the recipient population increases the fraction of immigrants which implies that immigration to small populations should be more effective in levelling population differences. However with decreasing size of the population the effect of genetic drift increases. Therefore, there seems to be a balance between these two forces such that there is no population size dependence for the impact of gene flow (Slatkin 1987).

The speed of evolution is also influenced by all five forces discussed above. Contrary to the popular belief, the speed can be faster in small populations than in large populations (cf Endler and MacLelland 1988). One reason is that recessive or additive genes contributing to fitness can

appear faster in homozygous conditions in small populations than in large populations. In a population with  $N_e = 25$  there is no gene frequency lower than 0.02. Genetic drift may contribute considerably to evolution in such small populations. The role of genetic drift as an evolutionary agent is often overlooked. One reason for this may be that drift itself does not contribute to improve fitness directly, but via a faster creation of new genotypes natural selection can operate more rapidly.

With all the complexity caused by counteracting forces it is easy to understand that perfection in the process of adaptation cannot be expected (cf Mayr 1988). Perfection would require

- total independence of traits
- no environmental variation
- no intermating among members from different selective environmental neighborhoods
- no genetic drift
- that two different genotypes never create the same phenotype.

For an elaboration of these requirements the reader is referred to Eriksson et al. (1993). In conclusion the genotype favoured in natural selection must be regarded as a compromise resulting from simultaneous selection for a whole array of traits.

For breeding it is also important to distinguish between *domestic fitness* and Darwinian fitness. The former is the ability of a genetic entry to meet human demands whereas Darwinian fitness is the ability to transfer genes to the next generation. These two types of fitness may be the same but are more likely to differ considerably. One example may suffice to exemplify this statement. A pine tree may produce one million seeds during its lifetime. To keep the population size it is required that one seed gives rise to a new tree for the next generation. Contrary to this a forester wants to have 100 % survival in his plantation.

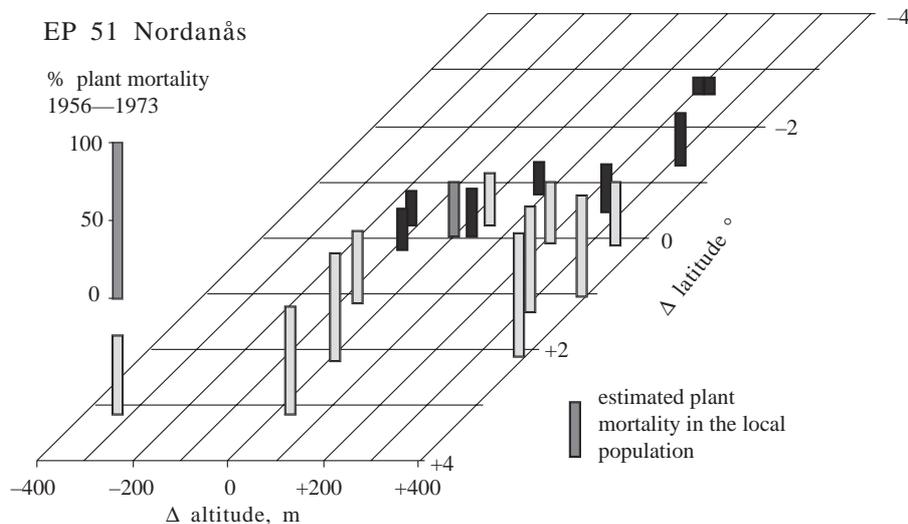
In summary genetic differentiation among populations will be perpetuated concomitant with an improvement of the fitness as long as there are several SENs and natural selection outweighs the impact of other evolutionary forces. Natural selection is the only evolutionary force that directly enhances fitness.

### 3 Evolution of Different Traits in Scots Pine

At the cellular level there are a huge number of metabolic processes. Thus Endler and MacLeland (1988) reported that an ordinary cell has 500 metabolic reactions and some 10 000 proteins. Whether this is true for *Pinus sylvestris* has to be proven but it suggests that complex interactions occur at various levels of organization, gene, cell, tissue, and whole individual, as well as with the environment. As a consequence of this, natural selection and other evolutionary forces will act differently on different traits. Most traits must be regarded as composite, possibly with a separate set of genes regulating each component, which complicates the understanding of the evolutionary forces acting on such a trait. The possibility of different SENs for a given trait should be considered before any hypothesis about genetic variation of that trait is put forward.

#### 3.1 Survival and Phenology

Owing to the large climatic variation in the area of distribution of *Pinus sylvestris*, among-population variation in survival is expected to be large. For harsh environmental conditions it has repeatedly been shown that there is great variation among populations with respect to survival (Eiche 1966, Eriksson et al. 1976, Remröd 1976, Eriksson et al. 1980). The severity index coined by Eriksson et al. (1980) is an estimate of the survival 20 years after plantation. This index clearly indicates that there is limited survival of the local population at high latitudes and altitudes. All data from northern Sweden indicate a strong clinal variation (Remröd 1976, Eriksson et al. 1980 and Fig. 2). In his classical study of dry matter content in different populations Langlet (1936) was the first to show clinal variation, which is so apparent for *Pinus sylvestris* in Scandinavia. Moreover, the cause of poor survival can probably be attributed to late inwintering of the plants. Giertych (1991) recently reviewed the variation in phenology of *Pinus sylvestris*. The pattern was



**Fig. 2.** The tree mortality of populations at the test site at latitude 64.32° and 400 meters above sea level. The locations of the columns in the grid indicates the latitudinal and altitudinal transfers. Columns below the horizontal 0-line indicate populations which are moved in a northward direction. Columns to the right of the diagonal 0-axis show populations which are moved to a higher altitude. The estimated mortality of the local population is given. The different types of screen show whether a population has a higher or lower mortality than the value estimated for the local population.

the usual one with early onset of growth in high altitude and latitude populations. These populations also had the earliest growth cessation. In the parts of the distribution area in which frost is a selective agent we expect a population differentiation in growth rhythm such that in each SEN the highest fitness is to be found in genotypes where inwintering is completed before low and harmful temperatures appear.

The data presented by Eriksson et al. (1976) indicate that there is a large within-population variation in survival in northern Scandinavia (Fig. 3).

How can this high among- and within-population variation be evolutionarily explained? What we know about survival is based on common garden experiments. Thus it would be possible to regard this as solely a domestic fitness. However, the selection in the wild is certainly not less than in common garden experiments. The among-population variation is present in spite of the levelling out of population differences by large long-distance transfers of pollen among populations. The among-population variation must be attributed to a strong selection for adaptation to macroclimatic conditions.

The high within-population variation can either be explained by:

- 1) Selection for adaptation to microclimatic conditions. – Selection to microclimatic conditions may occur. However, the pollen exchange within a population would probably lead to a selective advantage of genotypes with high fitness over the whole zone of intermating of such a population.
- 2) The evolutionary advantage of broad genetic variation in a long-lived tree species growing under varying weather and climatic conditions. – A simplified phrasing would be to say that a high within-population variation prepares the population, such that there are always genotypes available which are well adapted to the conditions at the time of regeneration (cf Levins 1963).

A broad genetic within-population variation may increase the adaptability of a population. The large variation observed, though, probably exceeds what might be an evolutionary advantage.

- 3) High gene flow from other populations, mainly via the long-distance transfer of pollen. – Long-distance pollen dispersal evidently occurs (Koski

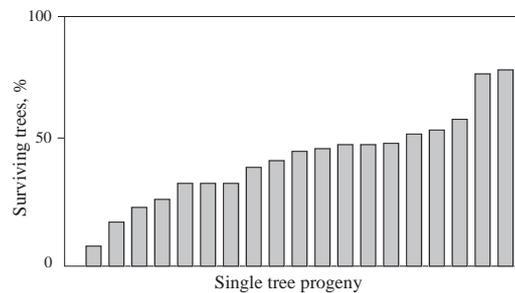


Fig. 3. The percentage of surviving trees of individual open pollinated families from population Korpi-lombolo, latitude 66.83°, altitude 180 meters, at a test site at latitude 66.27° and 440 meters above sea level.

1970, Lindgren et al. 1991, Savolainen 1991) although its participation in fertilization is unsettled so far. Since pollen dispersal is believed to be most important from mild to harsh climates (Savolainen 1991), it may be responsible for part of the within-population variation on the low-hardiness side of the distribution.

Based on the discussion above it may be concluded that natural selection for survival is probably very strong and at the population level it outweighs the high gene flow via pollen (cf Savolainen 1996).

### 3.2 Growth

By analogy with what was stated about survival, growth is expected to show a high among-population variation owing to the wide range of the species. As with survival there are large variations in biomass per tree and per area unit (Remröd 1976, Eriksson et al. 1987, Giertych 1991, Persson 1994). The conspicuous differences in growth following transfer must be attributed to differences in growth rhythm among populations.

Several attempts have been made to analyze growth in other species (eg. Kremer and Larson 1983). One is illustrated in Fig. 4, in which I have split growth into two major components, growth rate and growth period duration. Growth rate in turn may be split into different major physiological processes. Kramer (1986) in his

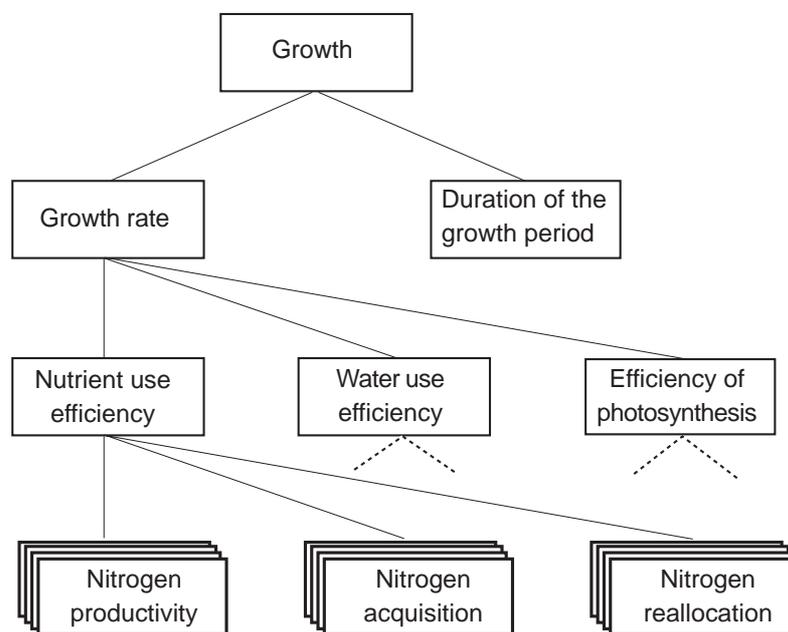


Fig. 4. One possible analysis of growth into growth components.

review of the potentials for improvement of growth via different processes was fairly sceptical about the possibilities of improvement via some of the basic processes such as photosynthesis and utilization of nutrients. One reason for this is that these processes are so fundamental or fine-tuned that all mutants will have a lower fitness. One example from our laboratory will be used to exemplify the complexity.

In our efforts to understand nutrient use efficiency we have carried out experiments according to the steady-state philosophy introduced by Ingestad (1979), in which the production of assimilates per nitrogen content in the tissue were estimated. Pots with seedlings were given nitrogen treatments according to a prescribed scheme adapted to a certain growth rate. Steady-state cultivations are generally restricted to part of the first growth period, whereas we ran the experiment for two full growth periods. In our estimations of the nitrogen productivity we have considered the duration of the growth period. In Fig. 5 the total biomass is plotted against the nitrogen productivity and duration of the growth period, respectively. There is a positive relationship between the family mean values for the two sets of

traits which is expected to occur between a component and the composite trait. However, the precision is fairly low, nitrogen productivity alone explaining 33 per cent and the duration of the growth period explaining 23 per cent of the variation. This example is given to illustrate that it is hardly probable that natural selection would individually influence the components of a composite trait unless the component is the only important contributor to the composite trait or is strongly correlated with the end product. Components of composite traits can play different roles in different populations as described for *Picea abies* populations by Skrøppa and Magnussen (1993) who studied the role of growth rhythm on growth. Similarly the components can have different roles at the population and within-population levels as described by Skrøppa (1982) for the impact of growth rate and duration of the growth period on total height in *Picea abies*. The discussion above does not mean that I advocate against studies of components, rather that the outcome of natural selection as stated in the introduction constitutes a compromise. There are reasons to believe that components of a trait are regulated by a lower number of genes than com-

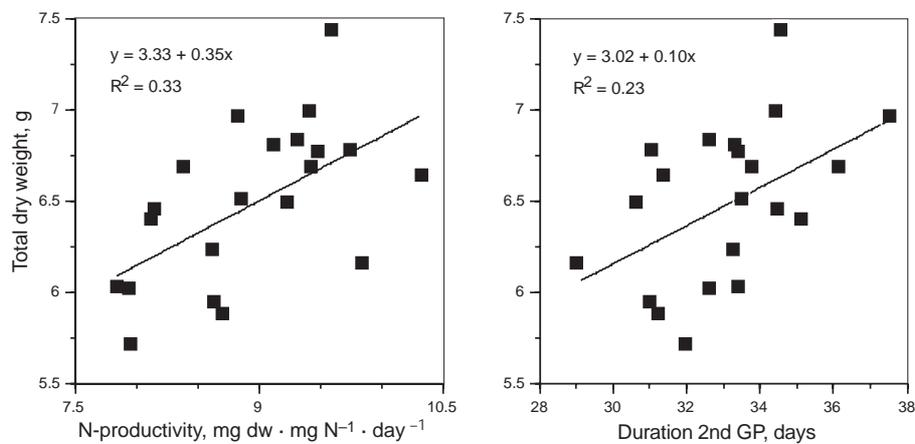


Fig. 5. The plotting of total family mean biomass against nitrogen productivity and duration of the growth period in an experiment with steady state cultivation of *Pinus sylvestris* seedlings under controlled conditions.

posite traits (cf Eriksson 1991). Therefore, the better we understand the genetic regulation of components the closer to the full understanding of a composite trait.

### 3.3 Markers

Mainly three categories of markers have come into use in forest genetics. They are isozymes, secondary metabolites such as terpenes and phenols, and DNA fragments. Isozymes and terpenes have been used in forest tree genetics research for a few decades. Different DNA techniques have been incorporated into forest tree genetics during the last decade. Before some observations on among-population differentiation in *Pinus sylvestris* are presented for various types of markers, their usefulness for this kind of study will briefly be summarised. Kremer (1995) discussed the merits of molecular markers as means to identify different populations. For neutral markers like isozymes and DNA segments the among-population differentiation is expected to be low with the possible exception of species with a scattered distribution. This has been confirmed for isozymes (summarised by Kremer 1995) as well as for ribosomal DNA, RFLPs, RAPDs and microsatellites in a study of *Pinus sylvestris* populations (Karhu et al. 1996). Generally the more loci

that are combined to estimate the among-population differentiation the better the chance to reveal differentiation (Kremer 1995, Kremer et al. 1997). For that reason the relatively low number of loci identified for isozymes and terpenes is a constraint on their utility in studies of population differentiation (Kremer 1995). The among-population differentiation is usually much lower for isozymes than metric traits such as phenology and growth (Karhu et al. 1996, Kremer et al. 1997). Chloroplast DNA has extensively been used in studies of migratory pattern after the last glaciation in European oak species (eg. Petit et al. 1993). A particular feature of conifers is the paternal inheritance of chloroplast DNA (Neale and Sederoff 1988). The use of chloroplast DNA haplotypes makes discrimination between female and male migrants easy. In species with a scattered distribution among-population variation may be revealed, as was the case for *Ulmus laevis* Finnish populations (Mattila and Vakkari 1997). However, this kind of among-population differentiation is probably not adaptive, rather it may be attributed to genetic drift in small marginal populations. A comprehensive summary of the use of markers in forest tree improvement was recently written by Forrest (1994). Therefore, only a few examples will be used to illustrate some characteristics of the markers.

### 3.3.1 Terpenes

Secondary substances such as terpenes are believed to be involved in the protection of conifers by retarding the digestion of needles by herbivores (Rhoades 1985). They are believed to be unspecific with respect to defence against herbivores (cf Futuyma 1983). It is conceivable that Scots pine with its long generation time cannot build up specific defence systems to compete with the short generation turn-over of pathogens and pests, which would easily be overcome by the pathogens and pests. Forrest in his review (1994) states that the existing genetic variation in terpenes might lead to adaptive evolution but few cases have been reported.

Since the first report on genetic variation in terpenes in *Pinus sylvestris* (Tobolski and Hanover 1971) several reports on population differentiation have been published. The genetic distance estimates though are low (eg. Kinnloch et al. 1986,  $G_{ST} = 0.02$ ). The mode of inheritance of terpenes is claimed to be either monohybrid or dihybrid. However, Birks and Kanowski (1988) conclude that alternative interpretations may be equally valid. One problem is that there is sometimes no sharp boundary between the low- and high-content classes of an individual terpene. One interpretation of the inheritance may be that there are some genes with a large effect on the content of a particular terpene concomitant with many modifying genes, thus blurring the pattern of inheritance. With such an interpretation the observed clinal variation might be attributed to the presence of quantitatively acting genes which may be pleiotropic and also influence traits exposed to natural selection.

### 3.3.2 Isozymes

Today most forest geneticists seem to agree that isozymes are neutral markers in the sense that they cannot be utilized to detect adaptive variation (eg. Gregorius and Bergmann 1995, Kremer 1995, Karhu et al. 1996, Savolainen 1996). Therefore, with respect to the SEN concept, only one SEN would exist. Contrary to this (Bush and Smouse 1991) claimed that isozymes might be used to reveal adaptive variation in other pine

species.

The study of Gullberg et al. (1985) will be used to exemplify the differences in among-population variation when estimated by isozymes and as survival. In that isozyme study the genetic distances between populations, estimated in the traditional way, were low. One of the Stockholm area populations was found to be more closely related to a northern population, more than four degrees further north, than to a neighbouring population. Few if any trees from the Stockholm populations would survive at the site of origin of the northern population. All isozyme studies in *Pinus sylvestris* that I am aware of have low  $G_{ST}$  values rarely larger than 0.05, the highest, 0.09, being reported by Mejnartowicz (1979).

In the absence of other forces, one exchange of migrants per generation is enough to prevent fixation of neutral alleles at a locus. Therefore, it is logical to conclude that the isozyme alleles studied must be regarded as neutral. The small among-population differences observed can be interpreted as due to too small samples for detection of a total homogeneity. Alternatively some alleles have not had time to spread to all populations owing to the long distances. Even for wind-pollinated species there must be an isolation by geographic distance.

If my interpretation that isozymes are neutral markers, or very nearly so is correct, they have no use in the identification of existing adaptiveness for breeding or gene conservation purposes. This is in agreement with the statement by Gregorius and Bergmann (1995) in their review article that isozymes are of restricted use for detection of adaptive differentiation (cf Savolainen and Kärkkäinen 1992). They may on the other hand be useful tools for studies of mating patterns thanks to their neutrality.

### 3.3.3 DNA Markers

Karhu et al. (1996) reported low among-population variation for RFLP, RAPD ( $G_{ST} = 0.02$ ), and microsatellites ( $G_{ST} = 0.014$ ) in Finnish *Pinus sylvestris* populations originating from the latitude range 60–69°. This means that there is almost no difference between northern marginal populations and the central populations and that the marginal

ones are not less variable than central populations. Noteworthy is that RFLP and microsatellite within-population variation was higher than for isozymes of the same populations. Ribosomal DNA differentiation was several times higher but still lower than among-population differentiation in bud-set of the same populations. No geographic trends could be revealed for the ribosomal DNA variation (Karvonen and Savolainen 1993). Szmidt et al. (1996) reported no RAPD variation between two Swedish *Pinus sylvestris* populations from latitudes 64° and 67°, respectively. Owing to the high variability in some of the DNA markers as well as their presumed neutrality they are excellent tools for studies on gene flow.

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