

## Population, Conservation and Ecological Genetics

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### Introduction

Intraspecific genetic variation is an often overlooked, but none the less essential, biodiversity component of forest ecosystems. Genetic diversity provides the fine-tuning in adjustment to dynamic processes in species and intraspecific competition and determines the pace of adaptation and microevolution on a population level.

Developments in genetic analysis techniques of recent decades yielded an impressive amount of knowledge about reproductive processes in forest tree populations. It turned out that forest trees are unique in their ability to accumulate and maintain exceptionally high levels of genetic variability, compared to other organisms, both plants and animals. Undoubtedly, this strategy must have an evolutionary significance and is related to the long lifespan of trees.

Typically intense gene flow, phenotypic plasticity and other heritable and nonheritable effects contribute to the robustness of tree species, i.e., to their ability to evade genetic degradation and drift even in isolated populations and at low density of occurrence. Nevertheless, genetic analyses also demonstrate effects of human activities on the genetic resources of trees (see Figure 9). Silviculture and various indirect environmental loads have some bearing on the genetic make-up of populations. This fact supports the need to include genetic considerations in both sustained management and conservation strategies of forest ecosystems.

### Significance of Genetic Regulation in Forest Ecosystems

Living systems have a remarkable ability to maintain and restore their uniqueness and identity under both spatially and temporally changing environmental conditions. Ecosystem stability is largely dependent on biodiversity which is detectable at the three main levels of biotic organization: the landscape (associations), species, and genetic levels. Species diversity is generally perceived as biodiversity *per se*. However, it is within-species genetic diversity that safeguards the adaptability and integrity of individual species.

Interbreeding populations are the basic units of adaptation and evolution. An important task of forest genetics is therefore to understand the complexity of genetic regulation and to detect patterns that give it meaning from the gene to the ecosystem level. Within-species genetic patterns determine the rules for use of forest reproduction material and the strategy of conservation of genetic resources.

### Defining and Interpreting Genetic Diversity

Diversity on the genetic level is usually described by the number and frequencies of alleles (different forms of the same gene) per locus in the population or species. Accordingly, two basic components of diversity are the allelic number ( $A$ ) and the proportion of loci that are polymorphic, i.e., with more than one allele. Polymorphism ( $P$ ) is expressed as a percentage of all investigated loci. Expected heterozygosity ( $H_e$ ) is used as the numeric expression of gene diversity within a population or species. Within-species diversity is further characterized by genetic differentiation between populations, i.e., the ratio of variation found among population averages.

**Calculation of gene diversity measures** At a locus, effective number of alleles:  $A_E = 1 / \sum p_i^2$

Expected heterozygosity:  $H_e = 1 - \sum p_i^2$

Genetic differentiation between populations:

$$G_{ST} = 1 - \frac{H_{eP}}{H_{eT}}$$

where  $p_i$  is the frequency of allele  $i$  across loci,  $H_{eP}$  is the average expected heterozygosity within populations; and  $H_{eT}$  is the total expected heterozygosity if all populations are pooled.

Beside gene diversity there are, however, reasons to use a broader definition for genetic diversity. First, the described measures are based on predominantly neutral genetic markers (isozymes, randomly amplified polymorphic DNA (RAPD), restriction fragment length polymorphism (RFLP), microsatellites) which are chosen for being polymorphic. Yet the key importance of diversity is maintaining adaptability and stability, which are expressed in adaptive (nonneutral) quantitative traits in response to the environment. For trees, it is especially true that there is no expression of genotype without environment. Therefore, genetic diversity in the broad sense also includes quantitative genetic variability, i.e., that part of phenotypic variability which can be identified as genetic, based on quantitative genetic analysis.

**Gene diversity characteristics of forest trees** Using genetic marker techniques, the genetic structure of

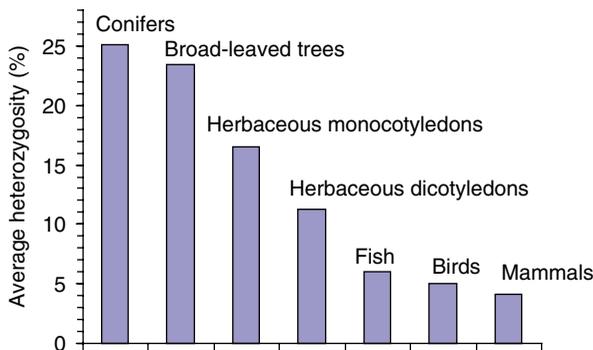
species and populations (gene diversity, level of inbreeding, deviations from Hardy–Weinberg equilibria) can be drawn up and used for comparison. Of great practical importance is the distribution of diversity within and between populations and regions. Compared with other organisms, forest trees generally display high heterozygosity (Figure 1), reflecting relatively high allele numbers.

Also within the plant kingdom, average polymorphism, allelic number, and heterozygosity of trees are conspicuously high, but among-population genetic differentiation is low (Table 1). Weak differentiation in most species with large natural ranges reflects high rates of gene flow in trees. Although the differences in average allele numbers may seem minor, it should be remembered that the potential number of genotypes ( $G$ ) rises sharply with increasing average allele numbers ( $A$ ) and number of loci considered ( $n$ ):

$$G = \left[ \frac{A(A + 1)}{2} \right]^n$$

Counting with just 10 loci, the difference between annual plants and trees of only 0.2 in  $A$  means an increase in potential genotypes from 70 000 to 340 000.

Gene diversity is profoundly influenced by the genetic system (mating pattern, reproductive strat-



**Figure 1** Average heterozygosity (in percent) for some organism groups.

**Table 1** Average genetic diversity within species of different plant life forms

Life form	P	A	$H_e$	$G_{ST}$
Annuals	49.2	2.02	0.15	0.36
Perennials, herbaceous	43.4	1.75	0.12	0.25
Trees	65.0	2.22	0.18	0.08

Genetic diversity is expressed by the measures polymorphism ( $P$ ), average allele number ( $A$ ), expected heterozygosity ( $H_e$ ) and genetic differentiation ( $G_{ST}$ ). For further details, see chapter on defining and interpreting diversity.

egy, genomic organization) of the species and its distribution (e.g., local endemic versus large, continuous). For example, population density of individual species decreases from the boreal zone toward the tropics. With decreasing density, polymorphism and allelic numbers tend to diminish. The effect of evolution, distributional pattern, mating, and reproduction system on species diversity is illustrated by data in Table 2. Failing concrete genetic information, likely genetic characteristics of a species may be inferred from these basic relationships.

### Directed and Random Genetic Changes in Large Populations

Owing to various, partly random genetic effects, such as natural selection (i.e., genetic adaptation), mutation, genetic drift, gene flow, or unequal sexual contribution of individuals, allele frequencies change over time, unlike in idealized populations in Hardy–Weinberg equilibrium. In large populations, gene flow and adaptation are the prime forces influencing genetic diversity and intraspecific variability.

### Hardy–Weinberg Law

In infinite, random-mating populations, allele and genotype frequencies remain constant from generation to generation in absence of selection, migration, drift, and mutation effects. For two alleles of  $p$ ,  $q$  frequency at a locus, the equilibrium ratio of homozygotic ( $p^2$  and  $q^2$ ) and heterozygotic ( $2pq$ ) genotypes will be  $p^2 + 2pq + q^2 = 1$ .

**Table 2** Connection between genetic diversity and distribution, density, and mating type in trees

	P	A	$H_e$	$G_{ST}$
<b>Type of distribution</b>	***	*	***	*
Endemic	42.5	1.82	0.08	0.141
Medium	55.7	1.87	0.17	0.065
Large	67.8	2.11	0.26	0.033
<b>Zonal occurrence (<math>\approx</math> density)</b>	**	**	NS	
Boreal (high)	82.5	2.58	0.21	
Temperate (medium)	63.5	2.27	0.17	
Tropical (very low)	57.9	1.87	0.19	
<b>Mating type, vector</b>	***	**	***	NS
Selfing	11.0	1.15	0.02	—
Allogamous/animal	63.2	2.18	0.21	0.099
Allogamous/wind	69.1	2.31	0.17	0.077

Statistical significance (probabilities of zero difference) of differences within subcolumns indicated as follows: \* 5%, \*\* 1%, \*\*\* 0.1% probability; NS, nonsignificant. For explanation of letters in table heading, see Table 1. Compiled from data of 191 tree species. The calculation is based on the assumption that the population is in Hardy–Weinberg equilibrium.

## Gene Flow

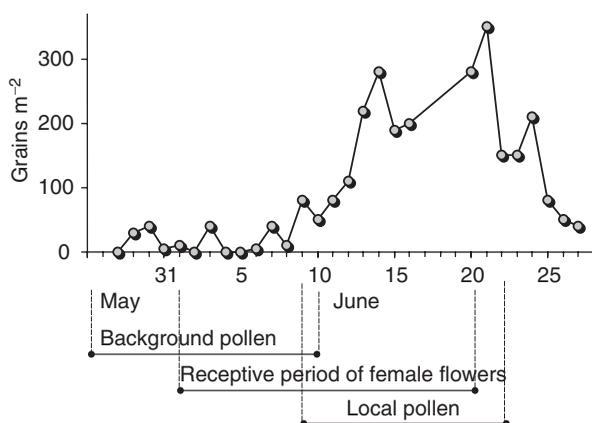
Gene flow describes the spatial movement of genes, typically through seed and pollen dispersal, either within a population or between separated stands. (An alternative term, 'migration,' is reserved here for shifts in time of the geographic range of species or populations.) Wind-pollinated species, producing abundant pollen, such as most temperate forest trees, show major gene flow. In favorable weather, pollen clouds may travel hundreds of kilometers and contribute significantly to local pollination (Figure 2).

Animal-pollinated (mostly tropical) tree species depend on the movement of their pollen vectors. Investigations have shown pollen transport of several kilometers and medium-level gene flow between trees and stands. The very rare apomictic and self-pollinating tree species show the lowest gene exchange rate.

The evolutionary and practical significance of gene flow is high. Its function is to counter genetic drift (random fluctuations in allele frequencies) within the range, to disperse fitness-improving mutant alleles, to maintain high levels of genetic variation and adaptability, and to avert inbreeding in fragmented populations. Gene flow has therefore a decisive role in shaping within-species genetic variation patterns (Table 2), and consequently influences appropriate strategies for forest reproductive material use and conservation.

## Natural Selection, Adaptation

The prerequisite of the selective force described by Darwin and Wallace is easily visible in forests, namely conspicuous differences between individual



**Figure 2** Density (grains m<sup>-2</sup>) of pollen in a Scots pine seed orchard. Fifty percent of the female strobili was receptive before the appearance of local pollen. Reproduced with permission from Lindgren D, Paule L, Xihuan S, *et al.* (1995) Can viable pollen carry Scots pine genes over long distances? *Grana* 34: 64–69.

trees in competitive and reproductive ability, the two key components of fitness. Natural selection acts through higher mortality and fewer offspring of less-fit individuals. Consequently, the gene pool of the next generation will be selected for greater fitness.

The shift in genetic variability tends to change the population profiles and over several generations may lead to evolution. Darwinian natural selection is an important, although not exclusive, driving force of evolution, as random effects play an important role too.

**Genetic adaptation and fitness** While natural selection explains the 'statistical' aspect of selection, adaptation describes the sum of biological processes that safeguard the survival of the population under constantly changing conditions. Some of these mechanisms are nonheritable.

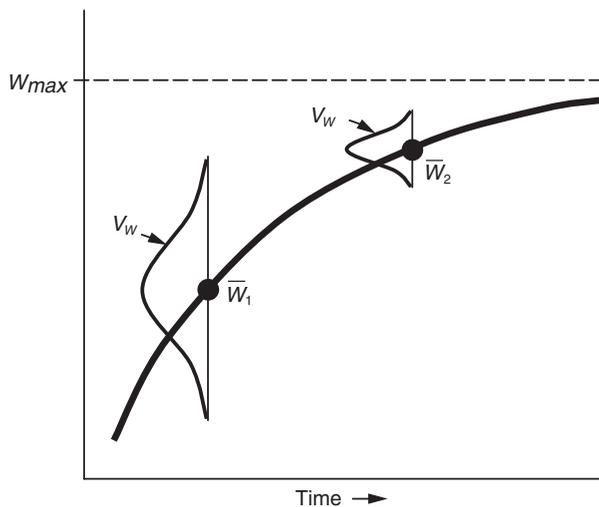
Genetic adaptation operates on populations through fitness selection. Fitness encapsulates the differential effect of many traits expressed during the life cycle. The selective value of individual traits depends on the actual environment, which can change constantly. In environments influenced by humans, e.g., in managed forests or plantations, fitness will be modified (cultivation- or domestic fitness).

Fisher's fundamental theorem of natural selection postulates that the increase of average fitness ( $\Delta\bar{W}$ ) is a function of the average relative fitness of the parent population ( $\bar{W}$ ) and the within-population additive genetic variance ( $V_W$ ):

$$\Delta\bar{W} \approx \frac{V_W}{\bar{W}}$$

i.e., progress of natural selection depends on adaptedness ( $\bar{W}$ ), and adaptability of a population depends on the available genetic variance – if genetic variability is depleted, adjustment to a changed environment becomes difficult or impossible (Figure 3).

The consequences of reduced genetic diversity on adaptability on species level can be illustrated by the examples of two contrasting boreal pine species, jack pine (*Pinus banksiana*) and red pine (*P. resinosa*), which have similar life histories and ecological niches in boreal forests of eastern North America. While the former displays very broad genetic variability, the latter seems practically devoid of diversity. Regarding distributions, red pine has only restricted, fragmented occurrences and is becoming rare in certain areas, while jack pine is the dominant species in many forest associations. The difference in distribution pattern may be attributable to the loss of diversity in red pine, probably through 'genetic bottlenecks' of glacial periods.



**Figure 3** Improvement of the fitness average of populations over time in a theoretical niche. The progress of population 1 is slower toward the fitness maximum ( $W_{max}$ ), because its genetic variability is smaller, and its average fitness is closer to the maximum. Population 2 has a larger genetic load ( $L$ ), but also the selection pressure is stronger. In practice, the progress is not very effective owing to environmental fluctuation and heterogeneity, resulting in ever-changing fitness optima. The precondition for the improvement of fitness is sufficient genetic variability!

#### Variation in Reproductive Fitness: Unequal Sexual Contribution of Individuals

Differences between genotypes in flowering and seeding vary over 10-fold, even among dominant trees in a forest stand. Owing to unbalanced flowering and seeding, neither natural regeneration nor the seed crop collected in a stand or in a seed orchard is genetically identical to the gene pool of the parents. Many genotypes contribute insignificantly to the next generation. The top quartile of genotypes may be represented in over two-thirds, and the bottom quartile in less than 3% of the progeny. Therefore the effective population size ( $N_e$ ) is usually far smaller (by roughly an order of magnitude) than the total number of individuals, and can be calculated for a monoecious species from the reproductive contribution of each individual ( $W_i$ ):

$$N_e = \frac{1}{\sum (W_i^2)}$$

#### Effectiveness of Fitness Selection in Natural Populations

The effect of fitness selection on individual traits depends strongly on both the (adaptive) importance of the trait for total fitness (e.g., budbreak timing versus leaf morphology) and on the simplicity of the traits' inheritance. Rapid adaptation could be de-

monstrated, e.g., in 'industrial melanism' in various insect species, or in heavy-metal tolerance in grasses growing on mine spoils. In trees, diversity patterns of adaptive traits indicate more gradual adaptive shifts.

#### Constraints on 'Perfect' Adaptation

The idea of perfectly adapted natural populations is a widespread misconception. There are several genetic reasons why 'perfect' adaptation is impossible, such as:

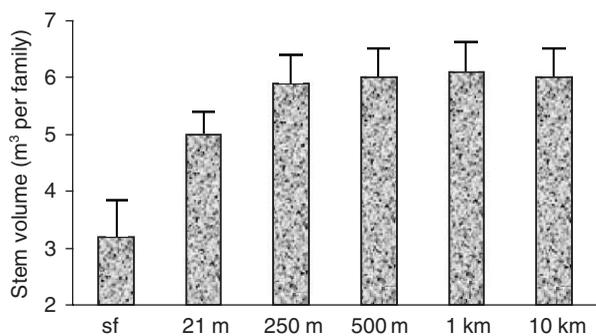
- genetic interdependence of traits, making simultaneous adaptive shifts relatively slow
- polygenic inheritance of quantitative traits, preventing ready fixation (attaining 100% frequency) of favorable alleles
- trade-offs between reproductive and vegetative traits in contributions to fitness, which maintain a conspicuous variation of reproductive ability within populations
- environmental heterogeneity and fluctuations (on the life-cycle scale of trees, the changes are two orders of magnitude faster than for annual plants)
- gene flow: the more continuous the distribution, the stronger the effects to limit differentiation between populations
- biotic complexity: e.g., long-term competition, and spasmodic epidemics of pests and diseases, which point toward evolutionary complexity rather than toward precise adjustment to local conditions.

Adaptation lag can be demonstrated in comparative experiments, where populations of local origin often show less adaptedness than introduced ones.

#### Local Patterns Arising from the Balance of Gene Flow and Adaptation

Genetic neighborhoods are intermating groups of related individuals within larger populations. The size and even the existence of such neighborhoods depend on the sexual system and dispersal pattern of the species. In outcrossing, wind-pollinated species, occurring at high density, neighborhoods cannot readily develop. In some species with more restrictive sexual systems (e.g., mixed-mating eucalypts) neighborhoods are much more extensive than usually suspected (Figure 4).

The balance of gene flow and adaptation forms adaptively homogenous areas (AHAs) within the species, which should serve as a basis for seed and conservation zones. Within the AHAs populations vary little in adaptive features. Owing to gene flow, AHAs are much larger than selective environments with roughly uniform ecological conditions.



**Figure 4** Average stem volume of 4-year-old progenies of a selected tree of *Eucalyptus globulus* from controlled crossings (*sf.*, selfed). The crossing partners were chosen at various distances (horizontal axis) from the subject tree. The poorer performance from pollination by closer neighbors is probably caused by inbreeding depression, which indicates the existence of genetic neighborhoods in this species. Reproduced from Hardner CG, Potts BM, and Gore PI (1998) The relationship between cross success and spatial proximity of *Eucalyptus globulus* parents. *Evolution* 52: 2, 614–618.

## Nonheritable Ways of Adaptation

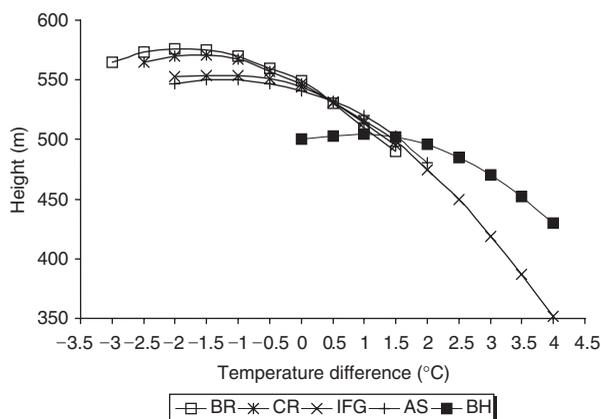
### Phenotypic Adjustment

A genotype may grow and develop in different ways, in interaction with the environment, resulting in the actual phenotype. The change of the phenotype of a population or an individual genotype may be plotted along site factor gradients. Genotypes clearly vary in their phenotypic responses to environment, and this is termed genotype  $\times$  environment interaction. (Naturally, the ability itself is genetically determined.) Populations or genotypes maintaining their relative performance (relative to a standard genotype or experimental average) across sites are considered phenotypically stable and, if inherently productive, are highly desirable.

### Genetic Imprinting

Genetic regulational changes triggered by environmental signals that lead to persistent phenotypic change are termed genetic imprinting or epigenetic effects. Indications that epigenetic effects may contribute across generations to the phenological and growth differentiation of populations in different environments were recently traced in certain boreal conifer species. The extent and inheritance of this effect in trees are still unexplored.

The importance of nonheritable adaptation is that it allows adjustment to the environment by reducing the role of natural selection; this offers a saving of resources and of response time. Nonheritable adaptation 'masks' the true genotype and contributes therefore to the maintenance of a broader adaptability.



**Figure 5** Response regressions calculated for 12-year height of *Pinus ponderosa* progenies in five Californian tests (different plotting symbols). The horizontal axis shows differences in average temperature between the original and the test site (0 means local). Almost without exception, populations transferred from warmer environments performed better.

## Intraspecific Genetic Variation Patterns

### Large-Scale Adaptive Geographic Variation

Provenance research, which has a tradition of more than a hundred years of study in forestry, has revealed a clear geographic differentiation between populations for adaptive traits in widely distributed species. Provenance is a population originating from a defined geographic location or area.

**Clinal variation** Genetic variation showing gradual trends linked to ecological gradients is termed clinal. In continuously distributed, wind-pollinated species clinal variation is caused by gradually changing selection effects despite gene flow, leading to gradual allele frequency changes; however, a gradual allele frequency trend itself may also reflect gene flow effects. In temperate species, variations in daylength and temperature cause latitudinal clines in stem form, phenology, and growth potential. In temperate pines, for example, southern origins exhibit faster growth, extended vegetation period, longer needles, but poorer stem form than northern ones. Particularly steep clinal variation may occur on mountain slopes. Significant differences appear over altitudinal differences of only 200–300 m (at high elevations, even less). Such differentiation tends to be weaker in broad-leaved than in coniferous species (Figure 5).

**Ecotypic variation** An ecotype is a population adapted to local site (usually edaphic) conditions that occur in patches rather than in gradients. Traditionally, within-species genetic variation is considered by most silviculturists as ecotypic. However, site differences seldom exert enough selection

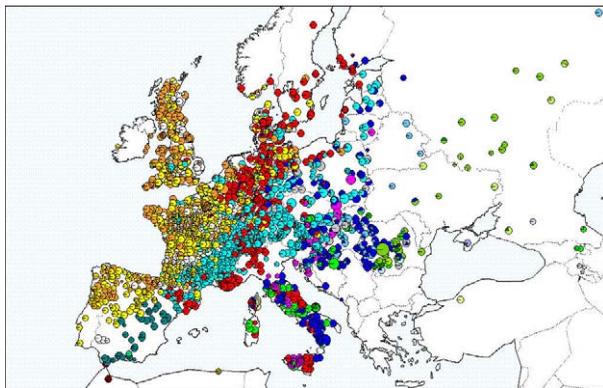
pressure to override gene flow. Accordingly, there are very few proven cases of ecotypes in forest trees. Their existence may be restricted to species with minimal gene flow between populations (Table 2). European ash (*Fraxinus excelsior*), for example, occupies conspicuously different habitats. Still, even thorough field tests could not reveal any clear genetic differentiation between populations of ‘water ash’ of the floodplains and ‘lime ash’ of dry, calcareous mountain ridges.

### Nonadaptive Geographic Variation

**Racial differentiation** Historical fragmentation of species ranges during Ice Ages (and associated migration) affected the genetic diversity of species, causing genetic bottlenecks, as mentioned for *Pinus resinosa*. For many others (e.g., beech or firs) the loss of alleles along the migrational route could be demonstrated. In many cases migration and isolation have led to fragmentation and strong within-species differentiation and even speciation. The effect of the migrational past persists especially on neutral loci (Figure 6). These patterns reflect combinations of adaptive and random effects and therefore have limited or no ecological significance. This variation is therefore not ecotypic and should be better termed racial.

### Polymorphism

**Phenotypic (quantitative) polymorphism** A well-known feature of many forest trees is the broad variation of traits and the parallel presence of alternative phenotypes (morphs) in the population. Some of these have clear ecological-adaptational significance (early- or late-flushing, branching types),

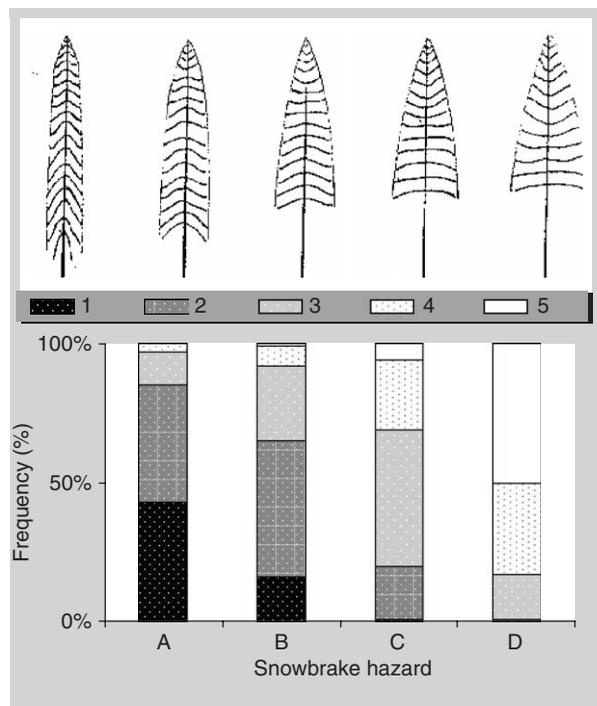


**Figure 6** Beside the nuclei, chloroplasts also contain genetic material which is inherited maternally in broad-leaved species. A Europe-wide analysis of chloroplast haplotypes of white oaks revealed the prolonged effects of postglacial migration from South European refugia. Reproduced with permission from Kremer A *et al.* (2002) Chloroplast DNA variation in European white oaks. *Forest Ecology and Management* 156: 5–26.

while others obviously not (cone scale form, male flower color in conifers). Ecologically relevant differences between populations can be expected only for traits of adaptive value (Figure 7).

**Polymorphism at genetic marker level** In contrast to quantitative traits, most of the marker-allele polymorphism of forest trees exists within populations. In widespread species, differentiation between populations ( $G_{ST}$ ) seldom exceeds 4–5%. Exceptions are species with fragmented or dispersed distribution (e.g., *Pinus radiata* isozymes: 16%), and some tropical forest trees of low density (<1 flowering tree ha<sup>-1</sup>; e.g., *Cavanillesia platanifolia*: 26%). Obviously, an adaptive geographic variation pattern, as is observable with quantitative traits, is seldom evident in genetic markers. This phenomenon raises the question of interpreting results of genetic marker analysis. From the neutralist viewpoint, gen(etic) diversity at the marker level is held in equilibrium by mutation and genetic drift. The selectionist interpretation maintains that frequency differences have selective value; even neutral alleles may mark adaptive effects if genetically linked to loci of adaptive significance.

In fact, for a few isozyme systems the selective value of alleles could be proven. For example, the  $B_1$  allele of the enzyme gene *IDH-B* (isocitrate



**Figure 7** Frequency of spruce crown types in the Slovenian Alps. The diagrams represent different categories of snow-break hazard: (A) extreme cold, hazardous sites, (B) exposed sites on a plateau, (C) transitory sites, and (D) low hazard sites.

dehydrogenase-B) has a lower temperature sensitivity than allele  $B_2$ . In silver fir (*Abies alba*) populations, the higher frequency of  $B_1$  in Mediterranean populations as compared to temperate-montane populations was confirmed.

### Gene Pool Changes in Small Populations

Small, isolated populations are often considered as resulting from human activity, but many species have naturally restricted, or scattered distributions. Reduced population size becomes problematic if random genetic forces prevail over selection and adaptation.

#### Genetic Drift

Differential pollen and seed production means a 'random genetic sampling' of the parent population. The smaller the sample, the more the offspring depart from the Hardy–Weinberg allelic ratios. If the population size remains low, drift recurs every generation. Drift effects may persist long after the population regains its size, if the original allelic richness is not replenished through gene flow, e.g., after a demographic bottleneck (through a catastrophic fall in numbers), or if very few individuals colonize a new habitat (founder effect). For example, the loss of alleles during postglacial recolonization is still evident in many temperate species, despite gene flow over many generations.

Figure 8 shows that diversity loss in small populations depends on the effective number of population members. Through random fluctuations, alleles might be lost or fixed even if their initial frequencies were high or low respectively.

As a result, small populations typically show an excess of homozygotes due to a higher number of fixed (monomorphic) loci. Random fixation of some deleterious alleles (harmful mutants) is also probable

if the effective number is small or if selection pressure ( $s$ ) is mild. At the species level, drift in single fragmented populations does not necessarily lead to loss of diversity and may even increase among-population additive variance. For example, in island populations of sugar maple (*Acer saccharum*), fragmented by agricultural fields, polymorphism was found to be higher than in closed, large stands.

Genetic drift may be compensated by gene flow. Model calculations show that relatively low migration rates suffice to offset drift effects. The maintenance of gene flow between scattered stands is therefore important for avoiding divergence of species fragments.

#### Inbreeding

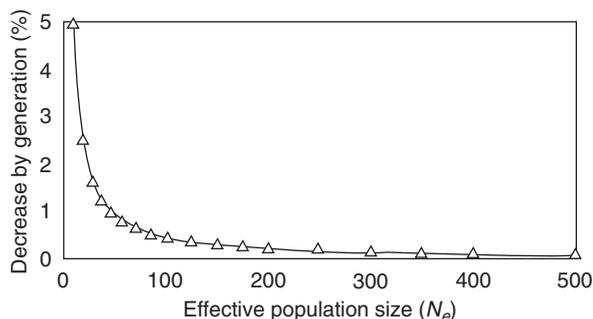
Inbreeding happens if individuals of common ancestry mate. Selfing is an extreme form of inbreeding, which can only happen in monoecious species. The inbreeding coefficient ( $F$ ) depends, like genetic drift, on the size of the effective population ( $N_e$ ):  $F = 1/2N_e$ .

The mating probability of identical alleles matters if the allele adversely affects fitness, causing inbreeding depression. Forest trees are typically outbreeders and carry relatively high genetic loads (deleterious alleles) to avoid inbreeding. Experiments with conifers show that growth depression of selfed plants typically reaches 20–25%. The practical importance of selfing is generally low, owing to mechanisms that effectively limit fertilization with self-pollen (in angiosperms, self-incompatibility alleles; in conifers, embryonic lethals). Viable offspring from selfing and matings between close relatives are therefore uncommon, and few survive competition.

### Human Effects on Forest Gene Resources

Selective cutting has been practiced over millennia in most of the accessible forest complexes in inhabited areas. Negative effects of associated dysgenic selection ('high-grading') on both gene diversity and quantitative traits have been proven. Consequences may be especially serious if the species occur at low density, such as in tropical forests. For instance, as a result of overexploitation, Cuban mahogany (*Swietenia mahagoni*) presently reaches only shrub size in the Caribbean.

Various other silvicultural practices may cause dysgenic effects, such as the unconsidered introduction of certain exotics (causing introgression between related, otherwise separated species), but especially the uncontrolled collection and commerce of reproductive material blurred the pattern of natural genetic variation in managed forests (Figure 9).



**Figure 8** Decrease of gene diversity (heterozygosity) by generation (as a percentage) in function of effective population size. Adapted from Wright JW (1976) *Introduction to Forest Genetics*. New York: Academic Press.



**Figure 9** Scots pine provenances in a comparative test in the Ukraine. Compared to the autochthonous population (right), the German population (Darmstadt, left) shows the effect of severe dysgenic selection.

Proper forest management, however, may also have positive effects. In some cases genetic improvement of growth and resistance traits has been found to follow proper silviculture, certainly for introduced species.

Contrary to many beliefs, well-managed artificial stands display gene diversity characteristics comparable or even superior to natural forests. **Table 3** illustrates that statistics of controlled artificial regeneration and of first-generation seed orchards are not inferior to those of natural populations.

### Conservation and Management of Genetic Resources

Genetic resources are elements of genetic variability that are (or might be) used to meet human needs and objectives. In forestry, the term covers naturally occurring populations and individuals, plantations, and collections, which carry currently or potentially valuable genetic information, and their protection is considered necessary from standpoints of economics, ecology, or conservation.

A basic concept for conservation is minimum viable population (MVP) size – the number of

**Table 3** Comparison of gene diversity statistics of natural and artificial populations of Douglas fir in British Columbia. A negative effect on genetic diversity can be traced after intense genetic selection only

Population type	P (%)	A	H <sub>e</sub>
Natural stand	53	2,14	0,171
Artificial regeneration	65	2,65	0,167
First-generation seed orchard	63	2,28	0,172
Second-generation seed orchard	56	2,25	0,163

For explanation of letters in table headings see **Table 1**. Reproduced with permission from Mátyás C (ed.) (1999) *Forest Genetics and Sustainability*. Forestry Sciences vol. 63. Dordrecht, The Netherlands: Kluwer.

individuals that is necessary for the long-term survival of a population. It has to be large enough to conserve genetic diversity and to safeguard evolutionary ability. One approach to estimate MVP size is to calculate the probability of loss of low-frequency alleles. **Table 4** shows that MVP should include several hundred individuals. The numbers refer to effective population sizes; so gene reserves may need to be at least an order of magnitude larger. MVP size may largely vary according to species, depending on diversity conditions, mating patterns, dispersion, and density.

**Table 4** Estimation of minimum viable population size (MVP) based on probabilities of allele loss ( $P$ )

P	q	Population size			
		M = 1	M = 10	M = 100	M = 1000
0.01	0.05	45	67	90	113
	0.01	230	343	458	573
	0.005	460	689	919	1148
0.005	0.05	52	75	97	119
	0.01	264	379	493	622
	0.005	529	758	988	1217

The table gives estimates for three allele frequencies ( $q$ ) and different number of rare alleles at unlinked loci ( $M$ ). The calculation is based on the assumption that the population is in Hardy-Weinberg equilibrium. Reproduced with permission from Mátyás C (ed.) (1999) *Forest Genetics and Sustainability*. Forestry Sciences vol. 63. Dordrecht, The Netherlands: Kluwer.

### Why Specific Forest Gene Conservation Strategy is Needed

Although nature conservation areas protect valuable genetic resources, they are not sufficient because:

- the areas do not necessarily represent ecological conditions typical and important for silviculture
- there may be legal obstacles to management interventions in protected areas (regeneration/or seed collection).

A strategy of forest gene conservation should be based on some knowledge of past and present human influence, the diversity conditions and genetic system of the species, the probable size of MVP, and of adaptively homogenous areas.

### Methods of Gene-Resource Management

1. Dynamic, *in situ* (on site) conservation of natural or naturalized populations is the ideal. Although natural forest dynamics should usually be preferred, human intervention to regulate succession or density, and even to regenerate artificially (with authentic material), is acceptable. The species-oriented protection of evolutionary potential is best served by a network of gene reserves.
2. *Ex situ* conservation: reproductive material is brought to units outside the natural habitat. Gene banks include seed-, pollen-, and tissue-culture banks, as well as field collections (clonal archives, stool beds, etc.). *Ex situ* conservation stands (progeny stands) may be established with evacuated populations where the original site is threatened, or with plantations of valuable selected populations or exotic species.

**Gene conservation and sustainability** Gene conservation forms part of the conservation of biodiversity

and, more generally, of nature conservation. The general aim of conserving genetic resources of forest trees, i.e., to safeguard adaptability and long-term evolutionary potential, has high priority given the current pace of environmental changes in relation to trees' generation intervals.

The emerging concept of ecosystem management includes the sustained management of genetic resources. Genetic sustainability depends on the maintenance of processes determining genetic diversity, such as population size, conditions of gene flow, mating, and reproduction. In a world dominated by humans, genetic sustainability cannot rely on nature conservation and gene reserves alone. Genetic principles must form part of national forest policy, especially with regard to the management of close to natural forests.

**International scope of gene conservation** As the distributions of some key forest trees straddle many countries, reasonable conservation of genetic resources requires international collaboration. At present no binding international agreement exists for forest genetic resources. However various international initiatives (notably the Convention on Biodiversity) and institutions (such as the Food and Agricultural Organization of the UN, International Plant Genetic Resources Institute, Rome) promote internationally coordinated conservation efforts. Perhaps the most advanced is the European initiative (EUFORGEN), with nearly 30 actively participating countries.

*See also: Genetics and Genetic Resources: Genecology and Adaptation of Forest Trees; Genetic Systems of Forest Trees; Molecular Biology of Forest Trees. Tree Breeding, Practices: Genetics of Oaks. Tree Breeding, Principles: A Historical Overview of Forest Tree Improvement; Conifer Breeding Principles and Processes; Forest Genetics and Tree Breeding; Current and Future Signposts.*

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## Genecology and Adaptation of Forest Trees

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### Introduction

Genecology is the study of intraspecific genetic variation in relation to environmental conditions. It reveals patterns of adaptation of populations to their environments that result from differences in natural selection among locations. Genecological studies are conducted for the practical purposes of: (1) determining how far seed can be moved from the collection site to a reforestation site without risking maladaptation of the trees to the planting site; (2) delineating geographic breeding zones for which a single breeding program would suffice; (3) selecting optimal provenances within the native range for nonnative (introduced) species; and, more recently, (4) predicting the ability of populations of forest trees to adapt to rapidly changing climates.

To meet these objectives, seed is collected from different provenances (geographic origins) throughout all or a portion of a species range and planted in one or more field or nursery common-garden experiments. The survival and growth of trees of different provenances are observed under the same set of environmental conditions, allowing for the separation of genetic and environmental effects. Genetic variation in resistance to biotic (e.g., insects and diseases) or abiotic (e.g., cold and drought) stresses can also be observed in different environments or tested artificially. Variation among provenances is quantified and related to patterns of geographic variation in climate

or other environmental factors. Species that show a high degree of genetic differentiation among provenances require the management of genetic resources on a more local scale than those that show relatively little genetic variation. If seed for reforestation is moved too far from the environments to which it is well adapted then losses in growth, health, and survival may result. The ability of populations to adapt to climate change will depend on current geographic patterns of genetic differentiation as well as the amount of genetic variation for adaptive traits that exists within populations.

### Background

The recognition of genetic variation among populations of trees occupying different environments is not new. A full century before both Darwin's theory of evolution was published in *On the Origin of Species*, and Johann Gregor Mendel determined the mechanics of heredity, Carl von Linné (also known as Carolus Linnaeus, the father of modern taxonomy), reported in 1759 that yew trees (*Taxus baccata*) from France were less cold-hardy than those from Sweden. Around the same time, Henri Louis Duhamel du Monceau, Inspector-General of the French navy and noted botanist, established the first forest genetic trials on record. He collected seed from Scots pine (*Pinus sylvestris*) from various locations across Europe and established plantations in France in which to compare the performance of different provenances (seed origins). Later in the eighteenth century, the importance of provenance was recognized by guidelines of the Swedish Admiralty for selection of seed sources of pine and oak, and in Germany for the use of tree species introduced from North America. Similarly, the importance of using local, well-adapted provenances was recognized in Japan centuries ago.

While early botanists and foresters lacked an understanding of evolution and genetics, they recognized that the survival, health, and growth of planted individuals of a tree species depended jointly on the location where seed was collected and the environment in which the resulting seedlings were planted. Maladaptation can result in slow growth, and injury or mortality due to biotic (e.g., insects, diseases, or competition) or abiotic (e.g., cold or drought) agents. When seed was planted in an environment very different or very far from the one in which it was collected, the likelihood of maladaptation was clearly high; however, nonlocal provenances sometimes outperformed local material.

Investigations of provenance variation continued through the nineteenth century, most notably for