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Genetic Modification *see* **Genetics and Genetic Resources**: Genetic Systems of Forest Trees; Molecular Biology of Forest Trees. **Tree Breeding, Principles**: Forest Genetics and Tree Breeding; Current and Future Signposts.

GENETICS AND GENETIC RESOURCES

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Genetic Systems of Forest Trees

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Introduction

The term 'genetic system' was coined in 1932 by C.D. Darlington, one of the renowned pioneers of cytogenetics. His original definition was limited:

> Properties of heredity and variation, methods of reproduction and the control of breeding, we now realize, are in various ways bound up together in each group of organisms. They constitute a genetic system. The genetic systems of different groups of organisms differ widely.

The concept and its definition have later been elaborated as follows. Genetic system refers to any of the species-specific ways of organization and transmission of the genetic material, which determine the balance between coherence and recombination of genes and control the amount and type of gene combinations. Evolution of the genetic systems means the evolution of those mechanisms effecting and affecting genetic variability.

The latter definition contains three crucially significant points:

1. The system is considered species specific.
2. The balance between recombination and maintenance of advantageous gene combinations requires both promoting and restricting mechanisms.
3. Genetic systems are under genetic control and thus subject to evolutionary processes. Species formation is fundamentally based on changes in the genetic system, especially in isolation mechanisms.

A genetic system comprises various components, such as:

- the mode of chromosome organization (genetic information all in one linkage group or distributed to several such groups)

- chromosome cycle (normal meiosis in both sexes)
- recombination index
- mating pattern: outcrossing (allogamy) or self-fertilizing (autogamy), population size, the mode of reproduction (sexual, asexual)
- isolation mechanisms.

Cytological Factors

The genetic information in the nucleus is packed in structures called chromosomes. Each chromosome contains genes in a linear arrangement, with its genes linked together in a consistent sequence, such that the gene programming a given protein (and all its resulting functions) is at a particular position or locus within its chromosome. For higher plants the basic state is diploid, such that there are two homologous versions of each chromosome, one from the mother and another from the father. This comes about from the fusion of haploid gametes, which contain one version of each chromosome from the male and one from the female parent. During meiosis, which is a part of the formation of haploid gametes, maternal and paternal homologs of each chromosome in the parent join together, and these bivalents reassort at random. The higher the chromosome number the larger the number of various combinations of maternal and paternal elements. Furthermore, in a process of duplicating each original chromosome, crossing-over causes exchange of parts of maternal and paternal strains of the chromosome. Towards the end of meiosis the double sets are pulled towards the opposite ends of the mother cell, and finally the single sets draw apart, which leads to a tetrad of four haploid nuclei. Recombination index, a nonlinear function of the chromosome number and the average chiasma frequency, is proportional to the potential number of various recombinant gametes (**Figure 1**). Normal meiosis mixes the maternal and paternal parts of the chromosome set so effectively that the probability of repeating exactly the parental gametes is negligible. Recombination also breaks apart many favorable combinations ('complexes') of genes, but can create some new complexes that are even more favorable in the context of natural selection. Within the overall plant kingdom there are numerous deviations from this classical pattern of meiosis.

Mating Pattern and Gene Flow

The mating pattern, or breeding system, is the second fundamental part of the genetic system. Mating pattern refers to the mode of combining haploid female and male gametes, which leads to the formation of a diploid zygote, embryogeny, and a new individual. The classical function of sexual reproduction is based on cross-fertilization, i.e., the female gamete and male gamete originate from different parents. This process requires cross-pollination, with pollen transported from one individual to the pollen-receptive site of the seed parent. As plants are almost all immobile, an external factor is needed. Wind, insects, birds, and bats are the main pollen vectors, although water rarely and other small mammals occasionally are effective.

Within the plant kingdom numerous kinds of deviations from cross-pollination have evolved, from complete self-pollination to partial cross-pollination. Cross-pollination requires large amounts of pollen, especially in wind pollination. Complete self-pollination leads to loss of heterozygosity (diversity between

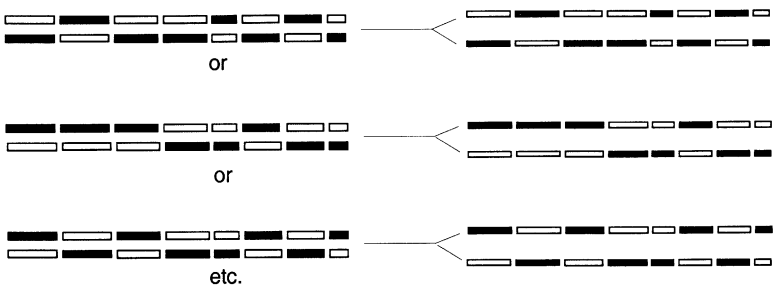


Figure 1 Diagrammatic illustration of chromosomal recombination during meiosis of a species with a diploid chromosome number ($2n$) = 16. The eight chromosome pairs are made up of the maternal part (here white) and the paternal part (here black). During the early part of meiosis the original pairs of chromosomes rejoin and the pairs (bivalents) are assembled to the so-called metaphase plane. The orientation of the maternal and paternal components is random. Consequently, the haploid daughter nuclei (on the right) contain various combinations of maternal and paternal chromosomes. The ideograms show some examples of the orientations. In fact there are 256 different combinations of 8×2 chromosomes. The number of possible combinations (N_R) is a function of the haploid chromosome number (n), $N_R = 2^n$. For instance in case of pines the number of chromosomal recombinants would be 2^{12}, i.e., 4064. Owing to crossing-over, the total number of variations is much higher still. Consequently, the probability of any two of the parental gametes being identical is extremely low in ordinary meiosis.

duplicate copies of the same gene) and recombinants during a few generations, and thus wipes out the original benefit of sexual reproduction. On the other hand, selfing can preserve favorable gene combinations, with minimal allocation of energy to pollen production.

Outcrossing plant species have several mechanisms to enhance cross-pollination. One sure solution is dioecy, i.e., female and male flowers on separate individuals (e.g., *Cedrus* spp., *Populus* spp., *Juniperus* spp.) (**Table 1**). Monoecy means that, while there are separate female and male structures, they both occur in one and the same individual, but it is often combined with features that favor cross-pollination. For instance, female strobili may develop in the upper part of the crown and male strobili in the lower part (e.g., *Abies* spp., *Picea* spp.), reducing chances of self-fertilization. Timing of female and male flowering can be slightly different. When female flowers open prior to pollen shedding in the individual parent, foreign pollen is at an advantage, especially if the space for pollen grains is limited. This phenomenon is called metandry. In monoecious plants sexual asymmetry is common; some individuals carry predominantly female strobili, some others mostly male strobili. Some flowering plants have structural heteromorphism in their hermaphrodite flowers, which results in pollen being deposited on separate parts of the pollinating insects. Cross-pollination requires some external agent to transfer pollen grains of one individual on the receptive organs, ovules, or pistils of another individual of the same species.

Table 1 Occurrence of dioecy and monoecy among 24 genera of conifers. Some genera (e.g., *Cedrus, Juniperus and Podocarpus*) include both monoecious and dioecious species, and exceptional individuals exist in most species.

Genus	*Dioecy*	*Monoecy*
Abies		x
Agathis	x	
Araucaria	x	
Callitris		x
Cedrus	x	x
Cephalotaxus	x	
Chamaecyparis		x
Cupressus		x
Fitzroya	x	
Juniperus	x	x
Larix		x
Libocedrus		x
Metasequoia		x
Picea		x
Pinus		x
Podocarpus	x	x
Pseudolarix		x
Pseudotsuga		x
Sciadopitys		x
Sequoia		x
Taxodium		x
Taxus	x	
Thuja		x
Tsuga		x

Wind pollination is characteristic of gymnosperms, but is also quite common among angiosperms. Wind carries light pollen grains over considerable distances, but successful wind pollination must be based on some key factors: (1) synchronization of flowering time, (2) abundant pollen production and (3) avoidance of harmful effects of pollen from other species. Animal pollination is rather recent in the evolutionary time scale, and it represents a huge diversity of coevolution of generative organs in the plants and the respective animal pollinators. In addition to various kinds of insects, birds and mammals (mainly bats) also transfer pollen while collecting food from flowers. There are many fascinating examples of highly specialized pollination systems. Even though many pollinating insects use pollen for their nutrition because of its high protein content, essentially lower pollen production is sufficient than in wind pollination. On the other hand, the probable distance of pollen transfer is much shorter.

Except for dioecious plants, the pollen deposited on the pistils (or ovules of gymnosperms) contains more or less pollen grains of the same individual; in other words, partial self-pollination is common. If the plant's own pollen is accepted, self-fertilization follows. In outcrossing flowering plants (angiosperms) a special self-incompatibility system prevents the germination of own pollen or retards the growth of the pollen tube. This incompatibility mechanism is usually based on one locus, denoted ***s***, with a large number of alleles. If a pollen grain (or even its parent, in some cases) carries the same allele as the pistil, incompatibility prevents fertilization. This kind of system evidently does not exist in conifers, because pollen grains deposit directly on the ovules. After entering the pollen chamber self pollen grains germinate normally and, after the species-specific, shorter or longer rest period, fertilize archegonia as successfully as foreign pollen. During embryogeny, however, most of the selfed embryos abort owing to homozygosity of embryonic lethals. Because there are several archegonia and pollen grains in each ovule, a sound seed may still develop despite the abortion of one or more embryos, if there is at least one outcrossed zygote (or a 'balanced heterozygote' from selfing).

Self-incompatibility and embryonic lethals may be considered a part of the genetic load because they restrict seed production. In combination, however, they maintain high outcrossing rates despite partial

self-pollination. Outcrossing and subsequent heterozygosity must be advantageous in long-lived plants, especially trees, as either self-incompatibility or embryonic lethals in combination with archegonial polyembryony are so predominant. Neither of these systems is absolute; spontaneous selfing does take place, and controlled self-pollination results in some germinable seeds. The inbred seedlings usually display strong inbreeding depression, and most soon die under competition. Self-fertilization can occasionally produce offspring of full vigor, through fortuitous lack of genetic load in parents or fortuitous occurrences of balanced heterozygotes. In this respect the typical genetic system of a gymnosperm is highly flexible in its stochastic (probabilitistic) discrimination against results of self-fertilization rather than self-incompatibility.

Gene flow is a process that affects the rate of recombination and population structure of species. A theoretical, so-called Mendelian population is closed and tends to preserve its genes and its genotype frequencies in a Hardy–Weinberg equilibrium. Exchange of genetic material between populations, however, alters gene frequencies and enhances recombination. As trees are immobile organisms the only option is through reproductive material. The most mobile medium is pollen but many trees have seed that can be transported over considerable distances. Windborne pollen, in particular, may travel hundreds of kilometers without losing viability. On the other hand, pollen must meet receptive female flowers in order to generate a new individual; a pollen grain carries only a haploid genome.

Mode of Reproduction

Simple organisms, such as bacteria, reproduce asexually though cell division. Multiplication of genetically uniform lines is exponential in favorable circumstances. Occasional mutations and recombination events provide adaptability when they are coupled with short generation time and exponential reproductive capacity. Typical sexual reproduction of flowering plants requires considerable allocation of resources to reproductive organs, and the complex array of events is vulnerable. Altogether, sexual reproduction is not optimal in all respects. A large number of plant genera and species have in fact diverged from ordinary sexual reproduction and continue their existence with various forms of reproduction. Cleistogamy, apomictic seed, bulbs, buds, root suckers and other forms of vegetative propagation are common means of reproduction among plants, although in the long term most of these are generally interspersed with at least occasional outcrossing events.

Isolation

Each species is by definition essentially a closed biological unit, within which mating and subsequent sexual reproduction is possible. In the formation of new species the development of isolation mechanisms, following for example disruptive selection, is a crucial step. As long as the new lines that are produced are able to interbreed they are not separate species in the strict sense. Thus, isolation is the factor that is antagonistic to overwhelming recombination and gene flow. The function of isolation is to maintain the species' specific gene complexes and to prevent contamination from other species that will threaten the species' integrity if not its fitness as well. Isolation is predominantly a one-directional phenomenon. The escape of pollen grains from a population of any species does not cause change in the gene pool of the donor population. The participation of the pollen in the paternity of the offspring in the receptor population must be prevented by means of isolation.

Several types of isolation exist. Geographic isolation, i.e., isolation by distance, is a special case. It has come as a result of ancient external forces, such as tectonic processes or climate changes, that separated parts of the original range by even thousands of kilometers. The evolutionary processes caused divergence in morphological and ecological characteristics of those sister species or allopatric species, but there was no pressure to develop cross-incompatibility barriers. Consequently, sister species from Europe and North America often hybridize if artificially grown next to each other. Species hybrids of larch (*Larix*), fir (*Abies*), and poplar (*Populus*) are well known examples in many arboreta. The lack of isolation causes trouble in certain instances of gene conservation, when autochthonous populations are subject to pollution from stands of introduced species. The problem may be even more serious in case of *ex situ* conservation of species, especially rare (e.g., *Abies*) species with extremely small, endangered natural stands. When species share a common territory, in other words they are sympatric, they must have effective mechanisms to preclude interspecific hybridization.

Spatial Isolation

Spatial isolation at least reduces interspecific pollination in animal-pollinated species, especially when they grow on ecologically different habitats. On the other hand, bats and solitary bees can travel significant distances while visiting different trees of a species. Windborne pollen of forest trees can travel over 10 km, and spatial isolation is rather ineffective.

Temporal Isolation

Temporal isolation is caused by nonoverlapping flowering times. Typically wind pollination occurs during a short seasonal period, being heavily dependent on close synchrony among individuals in their flowering times. This kind of behavior, in addition to being needed for effective pollination, facilitates the avoidance of interspecific pollination.

Incompatibility

Incompatibility, i.e., a biochemical mechanism that prevents the normal functioning of pollen grains of foreign species, is the most effective barrier against interspecific hybridization. This barrier may sometimes partly fail such that hybrids appear at low frequency. Sometimes the hybrids may lack fitness in the wild, but sometimes they may even show hybrid vigor.

Hybrid Sterility

Hybrid sterility is the final alternative of culling species hybrids. Sterility is thought to be mostly caused by meiotic disturbances, when the homology of chromosomes is imperfect, or when the chromosome numbers do not match. There are still other isolation mechanisms even though the hybrid may be fertile. They may for example have poor field survival, or segregation may cause unbalanced phenotypes in the second generation. On the other hand, rare coincidences of successful hybrids and 'failure' of isolation, often coupled with polyploidy, have resulted in new species.

Forest Trees

Forest trees are large, long-lived organisms, which have immense ecological and economic value. The sustainability of forest ecosystems and the maintenance of genetic diversity may be threatened by exploitation and changes in land use. As the genetic system and its components determine the capability of a population to adapt and to undergo evolutionary changes, the components promoting genetic variability and regeneration are considered to be of utmost importance. From the biological point of view, however, isolation mechanisms must not be neglected. Introduced tree species may hybridize with autochthonous ones, which is usually undesirable (e.g., in black poplar, *Populus nigra*).

Forest trees comprise a huge number of species, which in terms of plant systematics do not form any uniform group. Even though conifers represent only a small fraction of the total, the components of their genetic systems have been investigated much more comprehensively than those of angiosperms. This is mainly due to the great economic value and ecological significance of many conifers. Also, their chromosomes are much easier to study, and their reproductive organs, pollen grains and ovules are large enough to study with small magnification.

Conifers

The number of remaining genera of conifers is around 50 and the number of species close to 600. The numbers of genera and species vary among textbooks and catalogs, depending on each author's taxonomic views. The crucial fact is that the extant species are only a small fraction of the ancient diversity.

The chromosome numbers of conifers are extremely uniform when compared to those of angiosperms. With very few exceptions, the somatic chromosome number ($2n$) is 22, 24 or 26. Thus, almost the entire group is diploid. There are differences in the chromosome morphology, e.g., in the length of the arms among species, so that the karyotypes are variable. Normal meiosis, including crossing-over, takes place in both female and male gametes. The chiasma frequency is above 2; in other words there are, on average, at least two crossing-over events in each bivalent. These figures indicate that the potential for recombination is high, owing to recombination of maternal and paternal chromosomes and is further increased by numerous chiasmata. The huge amount of gametes, especially pollen grains, makes possible the manifestation of immense numbers of potential recombinants.

Conifers are wind-pollinated plants. Most species are monoecious, but there are dioecious species (e.g., *Cedrus* spp., *Juniperus* spp., Podocarpaceae) too. As the transport of pollen grains from male catkins to the female inflorescence is largely a random process, the effective pollination of ovules requires abundant and simultaneous pollen shedding. One big tree produces several hundreds of grams of pollen at one time, even though the individual pollen grains of conifers are very light. One tree releases some 10^{10} pollen grains, and on a per-hectare basis the order of magnitude is 10^{12}. Air currents carry pollen grains far from a source and only a very small fraction happens to hit the female strobili of the neighborhood. Conifer pollen is quite resistant to desiccation and ultraviolet radiation. So the pollen cloud immigrating from another stand of the same species can cause effective gene flow. This kind of gene flow has been detected as pollen contamination in many seed orchards (**Figure 2a**).

Partial self-pollination is common in monoecious species despite the temporal and spatial differences

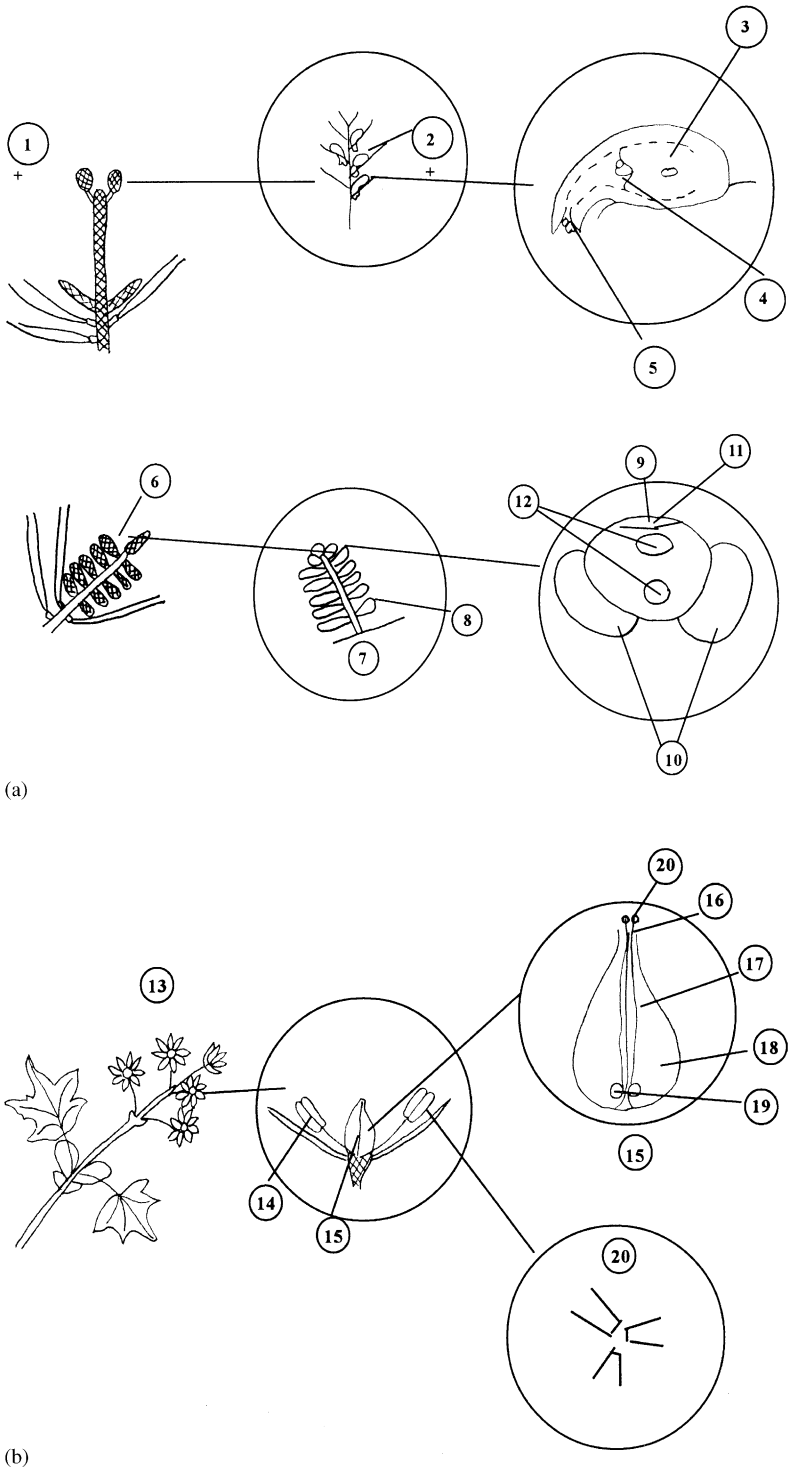


Figure 2 Schematic illustration of the differences in the floral organs of (a) conifer (pine) and (b) angiosperm (maple). (a) A female strobilus (1) of pine consists of an axis, supporting scale and ovuliferous scales. There are two ovules (2) at the base of each fertile scale. An ovule consists of nucellus (3), pollen chamber (4), and micropyle (5). Pollen grains attach on the micropylar filaments and they are transported into the pollen chamber by a pollination drop. Male strobili (6) of pine are on the basal part of the new shoot, mainly in the lower part of the crown. A male (7) strobilus (catkin) has nothing but an axis and scales (microsporophylls) (8) with saclike microsporangia that are filled with pollen. Pollen grains (9) are rather big and they have two air sacs (10). The body of the pollen grain contains a few haploid cells (11) and two haploid sperm nuclei (12). (b) In angiosperms the basic type of flower has both female and male parts. Often numerous flowers make up an inflorescence (13). A single flower of maple has four sepals, four petals, eight anthers (14), and a pistil (15). The pistil consists of stigma (16), style (17), and ovary (18). The ovules (19) are inside the ovary, and the pollen grains (20) are deposited on the stigma (by insects). Pollen tubes have to grow through the style until they reach the egg cells within the ovary. Immense variability of structure of the reproductive organs exists especially among angiosperms.

of female and male flowering. Inbreeding is, however, significantly restricted by embryonic lethals, which cause abortion of selfed embryos. The embryonic lethals are recessive genes which make their homozygotes nonviable. They are a part of the genetic load. Conifer species with large distributions and a continuous population structure usually carry numerous such embryonic lethals. Some species with a small distribution area have been purged and they may be relatively self-fertile. Altogether, most conifers studied so far display high rates of outcrossing and large genetic diversity among individuals in populations. Conifers have never been found to have self-incompatibility mechanisms as such to prevent self-fertilization, but incompatibility does exist to some extent between even closely related species.

Angiosperms

Broadleaved trees are representatives of flowering plants, which are younger than conifers from the evolutionary point of view. Diversity is characteristic of broadleaved trees when compared to conifers. An estimate of species is 25 000, all belonging to the group dicotyledons. The number of genera is in the thousands, and numerous families include trees. Often there are both herbaceous and woody plants in the same genus. In fact there are probably still numerous broadleaved tree species undiscovered, especially in tropical forests. On the other hand, the components of the genetic system have been investigated only in relatively few species. The commercially important species of the temperate and boreal zones are fairly well known, but many basic features of flowering biology and cytology of most species are unknown.

The chromosomes of broadleaved trees are very small, which does not mean that they contain less genetic information than the large chromosomes of conifers. The minute size causes problems in cytological studies. Even the counting of the exact number is tedious, and a detailed survey of meiosis is most difficult.

The chromosome numbers vary widely. This is not surprising because the group consists of various taxonomic categories. Polyploidy has played an important role in species formation, and different levels of ploidy are found even within one genus (e.g., *Betula*). Sometimes the geographical races of one species can have different levels of ploidy. In any case, the chromosome numbers are large enough to produce a large number of chromosome recombinations in meiosis (**Figure 2b**).

Flowering biology and pollination mechanisms are extremely diverse. The wind-pollinated species of the temperate and boreal zones have rather similar pollination to that of conifers. Where the pollen vectors are animals, the pattern is highly variable. Most of these tree species grow in mixed forests and do not occur in stands or even groves but as scattered individuals. In general, animals do not carry pollen over such long distances as wind does. Thus gene flow through pollen migration tends to be lower than in wind-pollinated species. On the other hand, fruit and seed may be dispersed by animals or float on water over considerable distances.

The structure of the gynoecium of angiosperms facilitates the functioning of incompatibility mechanisms. Outcrossing tree species have self-incompatibility, and interspecific incompatibility very often prevents the germination of foreign pollen grains.

Conclusion

The life-form and strategy of forest trees is typically coupled with high degrees of heterozygosity and potential to produce broad genetic variation in the offspring. The genetic system of successful species must have met this requirement. These features of the genetic system appear to have been crucial to the long-term success of forest tree species. The profuse production of pollen and seed becomes understandable against this background.

A sound knowledge of the structure and functioning of the genetic system of trees not only helps to understand trees' life but it is also essential when planning the management of genetic resources. This applies especially to all efforts to conserve genetic resources and to maintain genetic diversity of forest trees. Even though many species are capable of vegetative regeneration, e.g., coppicing or root suckers, sexual reproduction is essential and outcrossing seems to be the predominant mating pattern. Therefore, in addition to a sufficient number of trees to sample an adequate proportion of the gene pool, the requirements of the functioning of the genetic system deserve attention. As regards wind-pollinated species the stands should be fairly large and separated from undesirable pollen sources. In any case of animal pollination the pollen vector should be known, too, and its environment be maintained.

See also: **Ecology**: Reproductive Ecology of Forest Trees. **Genetics and Genetic Resources**: Cytogenetics of Forest Tree Species. **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement; Breeding Theory and Genetic Testing; Forest Genetics and Tree Breeding; Current and Future Signposts.

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Quantitative Genetic Principles

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Introduction

Response to selection is the basic prerequisite for successful genetic improvement. Within a species, the entities that are selected can be populations (or provenances) or individuals that can be used as seed parents or as clones for mass propagation. Where selection of individuals is involved the genetic improvement amounts to breeding, in which cumulative genetic gain is sought over successive generations. Efficient breeding is dependent on an understanding of the factors governing response to selection, in both the short term and the long term. Prediction of response can indicate what genetic gain is achievable and, when applied to alternative selection scenarios, it can be used to indicate how best to achieve the gain.

The classical tool for predicting response to selection, and optimizing various selection procedures, is quantitative genetics. This is based upon a model of individual gene action. It embodies the neo-Darwinian synthesis, which reconciles the usual pattern of continuous variation with Mendel's discovery that units of heredity represent discrete factors. Practical implementation is usually based on assuming that each trait is controlled by large numbers of genes ('polygenes'), each of very small effect, at widely dispersed sites or loci in the genome. This treatment will often be a major oversimplification of reality. Nevertheless, it is typically a powerful and remarkably robust framework for predicting response to selection and illustrating various guiding principles.

After a basic exposition of the genetic model, important topics are:

- how response to selection is governed by the different parameters, which need to be known at least reasonably well
- how the same principles can be extended to responses to progeny testing
- the factors governing the efficiency of various forms of indirect selection for breeding goals
- how the principles can be applied to multitrait selection
- how genotype × environment interaction can affect response to selection, appropriate structuring of a breeding program, and appropriate deployment of genetic material
- factors governing longer-term response to selection, as opposed to short-term, which need to be considered in structuring populations.

Complementary information needed by the breeder (but often very imperfectly known) includes the cost structures for the various breeding operations, and the economic worth functions for metric values of various traits. Such information allows efficient allocation of effort, and enables the breeder to decide on the appropriate emphasis to place on different traits.

The principles are far from specific to forest tree breeding, but certain features of forest tree breeding,