studies suggest major provenance variations in eco-system adaptability (elevation and cold tolerance).

See also: **Genetics and Genetic Resources**: Cytogenetics of Forest Tree Species; Propagation Technology for Forest Trees. **Tree Breeding, Practices**: Tropical Hardwoods Breeding and Genetic Resources; A Historical Overview of Forest Tree Improvement; Forest Genetics and Tree Breeding; Current and Future Signposts.

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Genetics of Oaks

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Introduction

Oaks (*Quercus* spp.) belong to the most widely distributed genus of forest trees. Besides their economic and ecologic importance, oaks are also considered in many countries as cultural and patrimonial resources. Despite their value, they have received very little and spasmodic attention in genetic research in comparison to other forest trees. They were some of the earliest species that were investigated for inheritance studies in Europe, but were neglected in genetics for almost a century. The first international conference on oak genetics was organized in 1991, whereas international working groups in conifers had been well established for decades. This conference synthesized the state of knowledge in oak genetics. Over the past 10 years, significant contributions have been made in population and evolutionary genetics of oaks. This contribution adds to the 1991 synthesis the genetic knowledge of oaks that has accumulated over the past decade.

Biogeography

The genus *Quercus* is distributed over the northern hemisphere in Asia, North America, Europe, and Africa. There are more American than Eurasian species. The highest oak species diversity exists at 15–30° N, in Central America and Mexico and in Southeast Asia (Yunnan province in China). Species richness decreases northward and southward from both Mexico and southern China. The northern limit of distribution is at 50° N, except for the European *Q. petraea* and *Q. robur*, which extend up to 60° N. The southern limit of the genus is reached in the southern hemisphere in Colombia and Indonesia, where oak species exist at higher altitudes. Oak

species grow from sea level to very high altitudes, up to 4000 m in Yunnan province in China.

Throughout its natural range, the genus has differentiated into numerous species adapted to extremely variable habitats, from swamps to deserts. For example, evergreen species have differentiated under Mediterranean climates as *Q. agrifolia* and *Q. wislizenii* in California, and *Q. coccifera* and *Q. ilex* in southern Europe. Typical examples of extremely wide distribution are *Q. rubra* and *Q. alba* in North America, *Q. acutissima* and *Q. mongolica* in Asia, and *Q. robur* and *Q. petraea* in Europe. In most cases the widely distributed species are those that have received the most intensive genetic studies.

Taxonomy and Phylogeny

Depending on the authors, there are between 300 and 600 reported oak species. Since the beginning of Linnaean taxonomy, classification within the genus *Quercus* has been controversial, and more than 20 classifications have been proposed. Disagreements involve the characters to be used for the classification, the infrageneric subdivisions adopted (subgenera or sections), and species delineation. There is so much variation within some species that several authors have questioned the concept of species, and further complications in taxonomy are due to frequent interspecific hybridization. The most complete classification is that proposed by Camus (1936–1954), which has recently been supported by molecular approaches. Classification criteria are mostly based on foliar and fruit characteristics. In Camus' classification, the genus *Quercus* (*sensu lato*) is subdivided into two subgenera: *Euquercus* (*Q. sensu stricto*) and *Cyclobalanopsis*. About 150 species belong to *Cyclobalanopsis*; these only exist in South Asia, whereas species belonging to *Euquercus* are the more familiar oak species. The subgenus *Euquercus* (now called subg. *Quercus*) has been further subdivided into six different sections by Camus, and into three sections in a more recent review based on phylogenetic inferences of morphological characters. Earlier taxonomists considered *Cyclobalanopsis* and *Quercus* (*sensu stricto*) as two separate genera. Recently taxonomy in the genus *Quercus* has benefited from phylogenetic approaches based on molecular data. Analysis of nuclear and chloroplast DNA sequences showed that the genus was composed of three major clades: *Cyclobalanopis*, *Cerris*, and the remaining three main sections that form one monophyletic group (*Protobalanus*, *Erythrobalanus* (red oaks), and *Lepidobalanus* (white oaks) *sensu* Camus). A major finding of the DNA data in comparison to previous morphological data was the ancient evolutionary separation of *Cerris*.

Genomics

Although a few cases of naturally occurring triploids have been mentioned in the literature, oaks are diploid species, bearing $2n = 24$ chromosomes. Extra chromosomes ($2n = 24 + 1$, 2, or 3) have been reported as consequences of irregular segregation in mitoses. The diploid DNA content per cell is remarkably homogeneous across species and botanical sections, as reported values only vary between 1.88 and 2.00 pg ($= 10^{-12}$ g per cell). The DNA content of two widely separated sections was 1.88 pg for *Lepidobalanus* (*Q. petraea* and *Q. robur*) and 1.91 pg for section *Cerris* (*Q. cerris* and *Q. suber*), and these species are representative of the most widely separated sections (*Lepidobalanus* and *Cerris*). The genome of oak species contains 40% guanine + cytosine (G + C) base composition, which is similar to most higher plants. Genetic mapping in *Q. robur* resulted in 12 linkage groups and a total map length ranging between 1200 and 1800 cM. The map length of the different linkage groups in *Q. robur* varies between 10 and 200 cM. Eighteen percent of the genetic markers used in the mapping study deviated from Mendelian segregation as a result of a high genetic load in the species. The physical characteristics of the oak genome (number of chromosomes, physical and genetic size, genetic map length) are similar to tomato (*Lycopersicon*)! The oak genome is six times larger in physical size and three times larger in genetic size than *Arabidopsis*, the prime model species in plant genomics.

Genomic research has further addressed the molecular differentiation among species and gene discovery. Phylogenetically closely related oak species exhibit limited molecular variation among species, as a result of their interfertility. In the case of *Q. robur* and *Q. petraea*, the interspecific differentiation, regardless of the molecular markers used, is only slightly larger than the intraspecific variation. Hence genomic regions responsible for species variation are extremely rare. As a result of the similarity between genomes, molecular markers as microsatellites could easily be transferred across species and botanical sections.

Evolutionary Biology

Origin and Diversification

Fossil remains of oaks are common and have been discovered on the three continents. Earliest remains found in China, Europe, and North America come from the Eocene. The almost simultaneous appearance of the genus on the three continents has raised the question of its geographic origin and radiation.

Two scenarios were proposed to reconstruct the history of the species. In the first, the genus appeared in Southeast Asia, deriving from a sister genus *Trigonobalanus* during the Palaeocene, and migrated in two directions: to Europe and America via the North Atlantic land bridge before the Eocene, and via the Bering strait after the Miocene. In the second scenario, the genus *Quercus* derived from the widely distributed boreal–tropical deciduous forest that occupied the northern hemisphere at the beginning of the Tertiary. The genus further differentiated as the continents separated further. As a result, oak species arose 'simultaneously' on the different continents and differentiated from the ancestral group composing the boreal–tropical forest. Between the Oligocene and Miocene, oaks diversified extremely rapidly as a response to important climatic changes. Most fossil remains of that period are similar to extant samples. Hence it is believed that most of the extant species already existed at the mid-Miocene.

Postglacial Migration

During the Quaternary, oaks underwent important migrations in response to climatic changes. There were about 17 Milankovitch climate oscillations (alternation of glacial and interglacial periods) when oak species, like other plants, were subjected to successive contractions and expansions of their distributions. A glacial period lasted 50–100 thousand years, whereas interglacial periods were much shorter and lasted 10–20 thousand years. Climatic oscillations were strong selective forces, favoring species that were vagile enough to track their moving habitats. They were most likely responsible for the selection of a reduced number of species that occupy today large continental distributions (*Q. robur* in Europe, *Q. alba* in America, or *Q. acutissima* in Asia). These movements have profoundly influenced the genetic diversity of the species, but in rather different ways between North America and Europe. A large survey conducted recently in Europe comparing the remaining historical footprints (pollen deposits) with genetic fingerprints (chloroplast DNA (cpDNA) polymorphisms) demonstrated how the extant distribution of genetic diversity was shaped by the dynamics of postglacial colonization. At the end of the last glaciations, European oaks were restricted to three major refugia (southern Iberian peninsula, central Italy, and southern Balkan peninsula). As glacial periods lasted up to 100 000 years, species were most likely genetically differentiated among these refugial zones, as shown by the completely different haplotype lineages (=cpDNA variant) occupying these regions. In less than 7000 years (from 13 000 to 6000 years ago), oaks recolonized the majority of their modern ranges. On average, the migration was extremely rapid (300–500 m year^{-1}). Rare long-distance dispersal events contributed significantly to the rapid spread of the species. These dynamics had various consequences for the diversity of the species. Despite the strong founder effects that accompanied the recolonization, oaks were able to maintain high levels of genetic diversity. Although the highest neutral diversity is restricted to the southern areas of Europe, the level of diversity is still important in the central part of Europe, where the different migration fronts originating from the refugial zones merged. However, today's distribution of adaptive diversity is not correlated with neutral diversity; there is no footprint left by the maternal origin on the variation of adaptive traits. Genetic variation for adaptive traits resulted from more recent local selection pressures. Interspecific hybridization was a key migration mechanism as it facilitated the introgression of late-successional species (*Q. petraea*) into the pioneer species (*Q. robur*). The systematic sharing of the same cpDNA haplotype by different white oak species occupying the same stands indicates that hybridization was extremely important during recolonization. Postglacial colonization dynamics in North America were quite different from Europe. Species were not restricted to genetically separated refugial zones. Furthermore, oak stands persisted as low-density populations close to the Laurentide ice sheet. Hence postglacial recolonization was more diffuse than in Europe.

Reproduction and Mating System

Reproduction in oaks can be either vegetative or sexual. Coppicing has been a widely used vegetative system to regenerate oak stands. Stump sprouting is also a natural way of propagation for oaks after forest fires and, when repeated over generations, creates clonal structures in natural stands. The production of root suckers is a less frequent natural means of propagation, but has been reported in *Q. pyrenaica* and *Q. ilex*. Oaks are predominantly monoecious species with distinct male and female flowers, although cases of floral hermaphroditism have been reported. *Quercus* is anemophilous (wind-pollinated) whereas other genera of Fagaceae (except *Fagus* and *Nothofagus*) are entomophilous. There are important differences among species groups in the lag between pollination and fertilization. In the *Lepidobalanus* section (white oaks), acorns mature at the end of the growing season in which the pistillate flower is pollinated. In contrast, in the

Erythrobalanus and *Cerris* sections, fertilization occurs more than 12 months after pollination.

Oaks are also predominantly outcrossing species. All reported values of effective outcrossing rates using the mixed-mating model exceed 0.90. Hence it has often been suggested that a self-incompatibility mechanism existed in oaks, although no experimental data have yet been published on the subject. Mating studies have also indicated that crosses among related trees are rare.

Hybridization

There is much literature on oak hybridization. Hybridization was first investigated by using morphological traits as diagnostic markers, but this has raised controversy as the range of within-species variation of morphological features remains largely unknown. During the past 10 years, gene markers have been applied to study introgression that provided new interpretations on the ecological and evolutionary role of hybridization in sympatric oak species. In two examples, one in European oaks (*Q. petraea* and *Q. robur*) and one in North American oaks (*Q. grisea* and *Q. gambellii*), hybridization was shown to be asymmetric. In the European example, *Q. petraea* preferentially pollinated *Q. robur*, whereas in the other example *Q. grisea* was the predominant male parent. As indicated earlier, asymmetric hybridization can reinforce the succession of species replacing the pioneer species (*Q. robur*) by a late successional species (*Q. petraea*) and is thought to have facilitated the dispersal of species during the postglacial recolonization. The use of molecular markers also permitted estimation of the level of introgression and revisiting of former interpretations of the geographic distribution of hybrids. Occurrence of hybrids has been reported more frequently at the margins of the natural distributions of sympatric species where typical parental habitats are less frequent. The hypothesis of higher fitness of hybrids under nonparental habitats has recently been challenged by an alternative interpretation. In the *Q. grisea*/*Q. gambellii* example, it was suggested that the mate-recognition systems can be impaired under stress conditions prevailing at the margin of a species' range. It was found in this example that the formation of a hybrid zone resulted from the diminishing male function due to environmental stress.

Hybridization in natural stands was further confirmed by artificial crossings. Extensive controlled crossing was done within and between species belonging to the three sections *Lepidobalanus*, *Erythrobalanus*, and *Cerris*. Among the 75 intersectional crosses, only three resulted in viable seedlings (*Q. turbinella* (section *lepidobabanus*) × *Q. cerris* (section *cerris*), *Q. turbinella* (section *lepidobabanus*) × *Q. suber* (section *cerris*), and *Q. turbinella* (section *lepidobabanus*) × *Q. marilandica* (section *erythrobabalnus*)), and were confirmed by segregation analysis of the progeny. Hence hybridization is mostly intrasectional, as has been extensively reported in the *Lepidobalanus* section. Artificial controlled crosses also confirmed the preferential asymmetric crosses between *Q. petraea* and *Q. robur*, and challenged the use of morphological features for hybrid identification. Hybrids resulting from controlled crosses between *Q. petraea* and *Q. robur* exhibited foliar characteristics that were not intermediate between the parental forms, as they resemble more the female parent.

Gene Flow in Natural Populations and Neighborhood Size

Oaks have small pollen grains that can be physically transported over long distances. Physical models of oak pollen dispersal pointed to maximum theoretical distances of several hundreds of kilometers. Investigations on oak pollen production and dispersal in California indicated that pollen grains can be transported at least 16 km. In Finland, at the northern margin of *Q. robur*, pollen grain capture on traps along a gradient was recorded at 7 km from the source stand. However, pollen may lose viability quite rapidly. Effective pollen dispersal has recently been measured using parentage analysis with microsatellite fingerprinting obtained in *Q. macrocarpa* and in *Q. petraea* with *Q. robur*. In both examples, it was shown that more than half of the male parents contributing to pollination of female parents on a 5-ha study stand were actually located outside the stand, and that the mean distance of pollen dispersal exceeded several hundred meters. Although nearest neighbors contributed preferentially to pollination in these two examples, pollen dispersion curves are clearly composed of both a short- and a long-distance contribution, most likely related to different wind-transport mechanisms. These data were obtained in rather dense stands (10–100 trees ha^{-1}), and contrasted sharply with those obtained in a savanna landscape where oak trees are more sparsely distributed. In a pollen-dispersal study of the Californian *Q. lobata* (1–2 trees ha^{-1}), effective pollen flow was much more limited (mean dispersal distance = 65 m) as a result of the low density of trees. There is an important asymmetry between pollen and seed dispersal: the ratio of the number of gene migrants by pollen and seed between

populations amounts to several hundreds, even though parentage analysis has indicated that long-distance seed dispersal can also occur. Based on dispersal curves from gene-flow data, attempts were made to estimate neighborhood sizes. In dense stands (100–200 trees ha^{-1}), as with Q. petraea and Q. robur, the neighborhood size was estimated at 12–20 ha, representing 1200–4000 trees. However, these numbers are lower for more sparsely distributed species, as for Q. lobata where a male neighborhood size of 3 ha was inferred.

Genetic Diversity

Genetic variation for morphological and adaptive traits has been investigated in oaks for more than a century. Provenance tests were established in Europe at the end of the nineteenth century, and progeny tests in the 1950s. Similar efforts were made in North America in the second part of the twentieth century. During the past 15 years, genetic surveys have been conducted in many oak species to monitor the level and the distribution of genetic diversity with various molecular tools in response to conservation issues. While investigations of phenotypic traits were mostly concentrated on economic important species for which provenance tests were established, molecular diversity was assessed for a greater range of species.

Diversity of Phenotypic and Adaptive Traits

Levels of diversity Phenotypic and adaptive traits exhibit extremely high levels of diversity, even for fitness-related traits. Heritability values (h^2) were estimated by many authors in progeny and clonal tests for the commercially important species (Q. petraea, Q. robur, Q. rubra, and Q. acutissima). The highest estimated heritabilities were for phenological characters like bud burst (0.35–0.80) and leaf retention (0.35–0.65), and for wood quality (0.15–0.87). Genetic variability for height growth is extremely variable among species and case studies (in Q. petraea estimated h^2 ranges from 0.15 to 0.78, in Q. acutissima from 0.43 to 0.44, and in Q. rubra from 0.15 to 0.25). Most of the crown-architecture characters of oaks have given low estimates of heritability (<0.05) except for the presence of epicormic shoots (0.38). These heritability values are statistical estimates and their range of variation does not correspond to confidence intervals but rather variation between estimates made among different experiments.

Geographic distribution of diversity Phenotypic traits exhibit important population differentiation but not as much as for the chloroplast genome.

However, differentiation values (Q_{st}) reach 0.06–0.6 for height and phenological traits in Q. petraea. Geographic trends of variation exist for phenological growth, and form traits. Geographic gradients are, however, most evident in phenological traits (dates of bud break and growth cessation). In the European species, Q. petraea, there is a clinal trend of variation with latitude and altitude, with southern origins flushing earlier than northern origins; these trends are consistent across the different, widely scattered provenance tests that were established. In the widely distributed American species, Q. rubra, there are contrasting patterns depending on the site where the provenance test was established. Longitudinal clines were observed in tests planted in Nebraska whereas an altitudinal cline was found in tests established in Tennessee. These trends are different from those observed in widely distributed north temperate conifers, suggesting that not only climatic factors may impose selection pressures, but most likely also biotic factors, such as defoliating insects. For other traits such as growth and form, no consistent geographic gradient of variation was observed in either American or European species.

DNA and Protein Diversity

Levels of diversity There is now evidence that, in respect of their DNA features, oaks are among the most diverse species of forest trees. This is particularly so for species with large continental distributions, such as Q. robur and Q. petraea in Europe, Q. macrocarpa in North America, or Q. acutissima in Asia. These can exhibit high levels of heterozygosity both within a population and throughout their ranges. For microsatellites, the number of identifiable alleles present at a locus within a population can frequently exceed 20. There is also evidence that levels of diversity differ between the two major botanical sections: white oaks (section Lepidobalanus) are more variable than red oaks (section Erythrobalanus), as shown by a comparative allozyme analysis between these two sections. High levels of diversity are most likely due to the maintenance of large population sizes, the ability for long-distance gene flow, and prevalent interspecific hybridization. Long generation intervals may be advocated for managing oak populations, to minimize the allele losses associated with genetic drift.

Geographic distribution of diversity Most nuclear genetic diversity resides within populations, as is usual for wind-pollinated species. With a few exceptions, genetic differentiation among populations (F_{st} or G_{st}, which are analogs of Q_{st}) is less

than 10%. Earlier results obtained with allozymes were confirmed by other molecular markers, random amplified polymorphic DNA (RAPD), amplified fragment length polymorphisms (AFLPs), or microsatellites (simple sequence repeats). As for the level of diversity, substantial pollen flow, large populations, and long generation intervals may account for these results. The geographic distribution of genetic diversity of chloroplast genomes is strikingly different from those of nuclear markers. Oak stands tend to be completely fixed within populations for the chloroplast genome but fully differentiated among stands. Hence differentiation values (F_{st} or G_{st}) in most cases exceed 0.80. The discrepancy between nuclear and chloroplast genome differentiation is due to their different inheritance. As chloroplast genomes are maternally inherited, and as seed exhibits restricted dispersal, diversity within a stand rapidly becomes eroded as a result of stochastic effects. These trends are facilitated during the initial establishment of the stand, which is often associated with low population sizes due to founder effects. Fixation of chloroplast genomes is enhanced by the limited number of founder individuals and the restricted dispersal of seed. When these mechanisms are extended to larger geographic scales, they lead to strong geographic patterns of cpDNA diversity that reflect the colonization dynamics of the species, resulting in strong phylogeographic structures. In conjunction with historical records gathered from fossil pollen, phylogeography of cpDNA permitted reconstruction of postglacial colonization pathways of oaks throughout Europe.

Genetic Improvement

Oaks have several features that limit operational breeding. Besides the biological constraints of longevity, such as delays in the onset of flowering, and the impossibility of seed storage, the uncertainty of long-term breeding objectives makes the implementation of improvement programs economically questionable. Hence research in breeding and improvement has been much less intensive than in shorter-rotation species, even for highly valuable tree species. The general understanding is that tree improvement would be a rather risky initiative for such long-lived species and that research in genetics should be oriented towards a sustainable management of oak stands rather than to the improvement of the existing resources by breeding and selection methods. Hence objectives of tree improvement initiatives were limited to the selection of seed stands, or the installation of first-generation seed orchards.

Europe

There is a long tradition of oak improvement in Europe, although it has not taken the typical form of a modern tree-breeding program. In the Netherlands, it was traditional to raise *Q. robur* for several years in the nursery and to select for stem form. These procedures resulted in the selection of various cultivars that were used in horticulture. Classical tree breeding started in the early 1950s in Germany, and even earlier in Eastern European countries when the earliest plus-tree selection was done and clonal seed orchards were established. Ongoing activities in tree improvement are being conducted on three species: *Q. petraea*, *Q. robur*, and *Q. suber*. For these species, European countries have selected seed stands which are clustered in provenance regions following European Community regulations on reproductive material. For *Q. petraea* and *Q. robur*, progeny tests associated with seed orchards were installed in Belgium, Croatia, Denmark, Hungary, Germany, Ireland, Lithuania, Netherlands, Slovakia, Ukraine, and the UK. Objectives of improvement are wood quality (including the quality of cork for *Q. suber*), stem form, and adaptation to the site. Research to solve the problems posed by the poor storage ability of seed was also pursued. Besides improvement of seed-storage protocols, techniques were developed for vegetative reproduction either by traditional cutting propagation or by using *in vitro* techniques and somatic embryogenesis.

North America

At the first international conference on oak genetics held in 1991, 27 ongoing oak improvement programs were reported on a total of nine species (*Q. alba*, *Q. falcata*, *Q. macrocarpa*, *Q. nigra*, *Q. phellos*, *Q. prinus*, *Q. robur*, *Q. rubra*, and *Q. velutina*). These programs were mainly conducted by public agencies and institutions in the eastern USA, whereas two projects in Canada were mentioned. In this period, some of the oldest provenance and progeny tests were established for *Q. rubra*. Objectives of breeding programs were timber and veneer for *Q. rubra* but more generally, juvenile growth and plantation success. Other objectives were also pulp production or use as shelterbelts (for *Q. macrocarpa* in the Great Plains). Breeding efforts varied from only plus-tree selection (in about half of the programs) to also producing seedlings or clonal seed orchards. However, owing to the decline of oak plantations and to reduced public budgets (national or state agencies), these projects have all been reduced in the past 10 years. Recent initiatives have, however, revitalized tree improvement activities in

northern red oak, such as the creation of the Hardwood Tree Improvement and Regeneration Center (HTIRC) in Purdue (Indiana). HTIRC aims to improve the genetic quality and regeneration of *Q. rubra* through application of classical breeding, genomics, and advanced propagation technology.

Exotics

Oaks have been transferred to various regions in the world. Red oaks from the eastern USA have been introduced in Europe, and *Q. rubra* is currently used throughout western Europe, not only as an ornamental tree but also as a plantation species for veneer or timber production. Hence tree improvement activities in *Q. rubra* were implemented in France, Germany, and the UK, starting with the installation of combined provenance and progeny tests. As the introduction in Europe began at the end of the eighteenth century, there have been only a few generations since the species was introduced in Europe but landraces (a landrace is a population that became adapted in a new environment to which it was transferred) have already been genetically differentiated in Europe. Similarly, *Q. robur* was introduced in many countries throughout the world, but no genetic improvement program has been reported outside its natural range and Europe.

See also: **Genetics and Genetic Resources**: Cytogenetics of Forest Tree Species; Genecology and Adaptation of Forest Trees; Genetic Systems of Forest Trees. **Genetics and Genetic Resources**: Molecular Biology of Forest Trees; Population, Conservation and Ecological Genetics. **Temperate Ecosystems**: Fagaceae. **Tree Breeding, Principles**: Breeding Theory and Genetic Testing; Conifer Breeding Principles and Processes.

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Pinus radiata Genetics

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Introduction

Pinus radiata is arguably the most domesticated of all forest trees. It is grown in exotic plantations occupying over 4 million ha, an area roughly 500 times its natural extent. Overall these plantations are highly productive, and many are intensively managed. Associated with the intensive management, several large-scale, intensive genetic improvement programs have developed, which have prompted a large volume of genetic research on the species. Indeed, this genetic research, and commercially motivated research on most other aspects of the species' biology, have led to the species assuming the role of a model species for research into forest trees. The genetics of the species are of twofold interest. On the one hand, the story typifies that of many conifers, and pines in particular, in respect of karyotype, genomic characteristics, and genetic system in general. On the other hand, there are a number of features that are highly distinctive of the species. Notable among these are the biogeography, with five discrete natural populations that are differentiated by a combination of adaptive features and apparent founder effects, and the conspicuously high level of functional genetic variation from tree to tree. Intensive genetic improvement began from around 1950, and is now being pursued at varying levels of sophistication in at least five countries. It has delivered major genetic gains, in growth rate, tree form, and disease resistance. Improvement work is shifting in emphasis towards improving wood properties, while differentiated breeds are being developed. Challenges remain in the management of gene resources.

The Genetic System

Breeding System

Like almost all pines (*Pinus* spp.), *P. radiata* is an outbreeder. Effective self-fertility, reflected in filled