areas in the southern hemisphere where there are massive plantations of *Pinus radiata* and other pine species. Reasons for the widespread use of pines in exotic forestry plantations include their simple design with straight trunks and geometrical branching habitat that makes them ideal for timber production. Moreover, pines grow faster than many other potential species, are easy to manage in plantations, have easily collected seeds, and are ideally suited for planting in marginal forest lands where most plantations are desired. Many pine species – *P. caribaea*, *P. elliottii*, *P. kesiya*, *P. oocarpa*, *P. patula*, *P. radiata* and *P. taeda* – are widely grown in plantations in the tropics and subtropics.

Threats to Pine Species

One-third of all pine species are either threatened in their entirety, or have subspecies or varieties that are threatened. This includes species with naturally restricted ranges and small population sizes as well as others that owe their threatened status to human activities. Even among pine taxa that occupy large ranges, large portions of their genetic diversity have been lost; this may have reduced their ability to respond to changing environmental conditions.

See also: **Biodiversity**: Biodiversity in Forests. **Ecology**: Plant-Animal Interactions in Forest Ecosystems. **Environment**: Environmental Impacts. **Genetics and Genetic Resources**: Population, Conservation and Ecological Genetics. **Hydrology**: Hydrological Cycle. **Landscape and Planning**: Perceptions of Forest Landscapes. **Mensuration**: Tree-Ring Analysis. **Plantation Silviculture**: Forest Plantations. **Temperate and Mediterranean Forests**: Mediterranean Forest Ecosystems; Northern Coniferous Forests; Southern Coniferous Forests; Subalpine and Boreal Forests; Temperate Broadleaved Deciduous Forest. **Tree Breeding, Practices**: *Pinus Radiata* Genetics. **Tree Physiology**: Canopy Processes. **Tropical Ecosystems**: Tropical Pine Ecosystems and Genetic Resources.

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Poplars

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Introduction

The genus *Populus* (family Salicaceae) comprises 29 diverse species found almost exclusively in forests of the northern hemisphere. Considered as a whole, *Populus* covers an impressive ecological amplitude from the tropics to the boreal forests. In China alone, an extraordinary number of species are found in the cold northeast, the arid northwest, and the subtropical Qinghai–Tibetan plateau. No less impressive is the close association between *Populus* forests and the development of humankind that has included their cultivation for shelterbelts, fuel, animal feed and forage, pulp, veneer, lumber, and more lately, engineered wood products. Moreover, this group of trees has lately assumed a vital ecological role in forestalling desertification in Asia and in restoring and maintaining many of the world's degraded rivers and floodplains (**Figure 1**). In the latter regard, conserving the genetic resources embodied in the natural stands of many *Populus* species is critically important. These genetic resources are also an indispensable foundation for many breeding programs that support ongoing *Populus* domestication efforts. As the global forest plantation industry becomes inexorably associated with high-yield plantations of the tropical and subtropical regions, such applied genetics programs will help to sustain *Populus* plantations as the only temperate-zone tree that can be managed for near-comparable yields.

This article is an overview of the genus *Populus* and its members, where they occur, examples of how

Figure 1 *Populus* frequently grows in riparian habitats that are also the base for much of society's agricultural and industrial sectors. The conservation of *Populus* stands in the riparian zone is an integral component of the restoration of such ecologically important habitats.

they have adapted to their environment, the particulars of their genetic recombination systems that allow for future adaptive changes, the needs inherent in their conservation, and the current genetic improvement strategies being used to domesticate *Populus* to meet the demands of a growing world population.

The *Populus* Genus

Populus is mainly found in the northern hemisphere's boreal and temperate forests but is also an inhabitant of the world's tropical and subtropical forests. The genus is divided into six sections. Three sections contain nearly all of the commercial species: section *Populus*, the aspens and white poplars (formerly known as section *Leuce*), section *Aigeiros*, the cottonwoods, and section *Tacamahaca*, the balsam poplars. Section *Populus* is distributed throughout North America, Europe, and Asia. Section *Aigeiros* is best known in North America and Europe, while section *Tacamahaca* has a North American and Asian distribution. Three less economically important sections (*Abaso*, *Leucoides*, and *Turanga*) have less extensive botanical ranges, but include species that greatly extend the class of sites occupied by *Populus* (**Table 1**).

Populus has a pioneering habit, colonizing sites after disturbances; fire and floods are often a prerequisite for good establishment. They are fairly unique among forest trees in their capacity for impressive reproduction by both sexual and asexual means. Very rapid growth rates during the juvenile phase are often exhibited. However, lifespans do not extend much beyond 100 years. In some cases, succession to ensuing seral stages may be postponed by fire or other disturbances; spruce budworm outbreaks in eastern Canada maintain the presence of *P. tremuloides*, preventing its replacement by *Abies* and *Picea*.

Table 1 Sections and species of the genus *Populus* according to Eckenwalder (1996)

Section	*Species*
Abaso	*P. mexicana*
Aigeiros	*P. deltoides*
	P. fremontii
	P. nigra
Leucoides	*P. glauca*
	P. heterophylla
	P. lasiocarpa
Populus	*P. adenopoda*
	P. alba
	P. gamblei
	P. grandidentata
	P. guzmanantlensis
	P. monticola
	P. sieboldii
	P. simaroa
	P. tremula[a]
	P. tremuloides
Tacamahaca	*P. angustifolia*
	P. balsamifera
	P. ciliata
	P. laurifolia
	P. simonii
	P. suaveolens[b]
	P. szechuanica
	P. trichocarpa
	P. yunnanensis
Turanga	*P. euphratica*
	P. ilicifolia
	P. pruinosa

[a] *Populus. tremula* includes *P. davidiana*.
[b] *Populus suaveolens* includes *P. cathayna, P. korena, P. maximowiczii*.
Source: Eckenwalder JE (1996) Systematics and evolution of *Populus*. In: Stettler RF, Bradshaw HD Jr, Heilman PE, and Hinckley TM (eds) *Biology of Populus and its Implications for Management and Conservation*, pp. 7–32. Ottawa, Canada: NRC Research Press.

The species are deciduous in all but a few cases. Their growth habit is indeterminate with the production of neo-formed leaves occurring until growth cessation occurs, triggered in many species by diminishing day length. They are largely shade-intolerant, although there are noticeable differences within the genus ranging from the intolerant (*P. balsamifera, P. trichocarpa*) to the very intolerant (*P. tremuloides, P. deltoides*). The white wood is diffuse–porous with indistinct annual growth rings and comparatively soft and light quality.

The major sections of the genus can also be broadly characterized according to the general class of sites on which they are commonly found. Sections *Aigeiros* and *Tacamahaca* are prominently adapted to lowland riparian zones along major river systems with broad floodplains, but not exclusively; *P. balsamifera* (section *Tacamahaca*) and *P. deltoides* (section *Aigeiros*) have been found respectively, on grasslands and abandoned farm fields and *P. ciliata* (section *Tacamahaca*) is found at higher elevations in the Himalayan foothills. By comparison, the aspens of section *Populus* are more frequently found on drier, less fertile, upland and montane sites; *P. tremuloides* is found at elevations of 3000 m in western North America and *P. tremula* at 3300 m in Mongolia. *Populus euphratica* (section *Turanga*) is typically found in the arid, desertlike environments of Asia, often growing on saline soils, while *P. heterophylla* (section *Leucoides*) is well adapted to prolonged inundation in swamps along the southeastern seaboard of North America.

Botanical ranges in *Populus* typically cover exceedingly wide geographic areas. For example, in section *Populus*, the range of *P. tremuloides* spans approximately 110° of longitude and over 50° of latitude in North America. Even more outstanding is *P. tremula* which grows throughout Europe and Asia, from the Atlantic to the Pacific Oceans, ranging from 70° N latitude in Norway and the tundra in Russia, south to the Mediterranean basin. Similarly, *P. alba* is distributed throughout central and southern Europe and extends southward into Afghanistan, Iran, Iraq, and Syria. In section *Tacamahaca*, *P. balsamifera* has a transcontinental range covering much of Canada, Alaska, and the Great Lakes Region of the United States. *Populus trichocarpa* spans approximately 30° of latitude from southeastern Alaska south to Baja California. The Asian *Tacamahaca* species of widest distribution, *P. suaveolens*, is found from central Asia eastward to the Japanese islands. In section *Aigeiros*, *P. nigra* spans all of Europe, northwestern Africa, western Asia, the Caucasus, and western Siberia. *Populus deltoides* ranges from the Canadian prairie southward to the coast of the Gulf of Mexico and east to the Atlantic seaboard. *Populus euphratica* (section *Turanga*) occurs over an area from North Africa and the Mediterranean through central Asia and northwestern China.

Other species have more limited or disjunct ranges. *Populus ilicifolia* (section *Turanga*) is found growing along four rivers in Kenya between 1° N and 3° S latitudes. *Populus heterophylla* (section *Leucoides*) is endemic to the coastal plain of the southeastern USA and then further inland in the Mississippi and Ohio River valleys. Separate populations of the tropical species *P. mexicana* (section *Abaso*) are located along the Pacific and Gulf coasts of Mexico.

Adaptation

The genus *Populus* has successfully adapted to the world's climatic variations. This adaptation may be expressed in a differentiation among populations and its expression is critical to the ecological and evolutionary functioning of individual species and the genus as a whole. One example, adaptive variation in phenology, is of primary importance and is often associated with a population's geographic source. The association is keyed to environmental stimuli, including temperature, photoperiod, and precipitation. In species of the temperate and boreal forests, spring growth takes place only after sufficient winter chilling has occurred which allows a response to warming temperatures, while a reduction in day length towards the end of the growing season cues the process of winter dormancy. Similarly, above-freezing cold temperatures bring about leaf abscission. Populations of *P. balsamifera*, *P. deltoides*, *P. tremuloides*, and *P. trichocarpa* from different latitudes differ in the timing of these spring and autumnal events. Northern populations typically have a lower temperature threshold required for spring growth initiation than their more southerly counterparts. Northern populations also enter the dormant phase under the influence of a longer day length than southern sources of the same species. The synchronization of these growth cycles with the change of seasons has allowed *Populus* species to achieve their characteristically wide geographic distributions.

Other examples of adaptive population variation include:

1. *Populus trichocarpa* from coastal and inland regions of the North American Pacific Northwest are differentiated in their tolerance of winter temperatures. *Populus trichocarpa* populations sampled from contrasting elevations within the same river drainage are differentially adapted to growing season length.
2. *Populus deltoides* from the lower Mississippi River valley has greater chilling requirements for flowering than more northerly populations.
3. *Populus deltoides* populations in southwest North America exhibit differences in drought tolerance that are associated with local precipitation.
4. Differences in crown architecture of Italian *P. alba* populations are correlated with latitude, from which an adaptive strategy for light interception has been inferred.

Adaptations to temperature, photoperiod, light intensity, and precipitation are sufficiently precise that populations of the same species originating from contrasting environments can be differentiated in their response to these environmental cues when tested in a single locale. In nearly all cases, the pattern of adaptive variation in studies sampling populations from latitudinal ranges has been continuous, suggesting the existence of clines. Population differences notwithstanding, genetic systems are such that the larger source of variation in most studies has been found within populations among the individual members; appreciable gene flow between populations partially counters the effects of natural selection. This reservoir of variation allows populations to accommodate yearly variations in climate as well as long-term climatic changes that alter the future adaptive landscape (**Figure 2**).

Next to the importance of climatic adaptations, the resistance to foliar, shoot, and stem diseases also plays a major role in the adaptive strategies of *Populus*. The pathogens of most significant ecological and commercial impact include *Melampsora* leaf rust, *Marssonina* leaf spot, *Venturia* shoot blight, *Septoria* canker, *Hypoxylon* canker, *Dothiciza* canker, and *Xanthomonous* bacterial canker. Pathogenic variation encompasses a range in both virulence and aggressiveness. *Populus* genetic systems have coevolved mechanisms of resistance to both as their pathogens undergo mutation and sexual recombination.

Figure 2 The timing of spring growth initiation in *Populus trichocarpa* is of critical importance to the adaptation of populations to their environment. The adaptive strategy includes differences in the earliness with which individuals of a population initiate growth, perhaps in response to yearly variation in warming spring temperature patterns.

Host–pathogen interactions of *Melampsora* leaf rust have been extensively studied in *Populus*. Resistance involves both major and minor gene systems. Qualitative resistance is expressed in the isolation of the infection by the host's hypersensitive response. If qualitative resistance is lacking and the infection moves throughout the leaf tissue, the rate at which the pathogen spreads and sporulates is controlled by the host's rate-limiting quantitative resistance mechanism. Pathogen interspecific hybridization has been observed and may progress to advanced generations with the formation of hybrid swarms potentially adding a new dimension to the range of variability and virulence; in *Melampsora* leaf rusts, there have been two occurrences of interspecific hybridization.

The strategy of disease adaptation in *Populus* is oftentimes tied to environmental conditions that determine selection pressure. *Populus trichocarpa* populations from mesic, low-elevation environments typically exhibit significantly higher overall levels of *Melampsora* resistance, compared with populations native to arid regions that lack rust populations that act as a force of natural selection to heighten host resistance levels. A similar pattern has been observed in *P. deltoides*; populations from the drier portion of the range show lower levels of rust resistance in comparison with populations sampled from more humid, wetter environments.

Recombination System

The *Populus* recombination system is efficient in both the creation of new phenotypes in succeeding generations to allow for adaptation to changing environments, and in preserving the standing adaptability of the parental generation. The recombination system is characterized by mostly dioecious species and is thus outcrossing. Staminate and pistillate flowers are grouped in unisexual inflorescences (hermaphroditism is rare but has been reported in sections *Aigeiros*, *Populus*, and *Tacamahaca*). Sex ratios are balanced in most cases, thereby maximizing the effective population breeding number (sex ratios may shift in favor of females on higher-quality sites). A higher proportion of recombinant progeny is promoted by outcrossing and a large effective breeding number. The following characteristics of *Populus* reproductive biology further promote open recombination (**Figure 3**):

1. Full reproductive maturity is achieved after 10–15 years, ensuring wide participation in the breeding population before individuals are eliminated by stand competition.
2. Periodicity seems to be an unknown in sections *Aigeiros* and *Tacamahaca* with fruiting occurring every year (production of sizable seed crops in section *Populus* occurs on 4- or 5-year intervals).
3. Pollination is anemophilous, achieving wide distribution of male gametes.
4. Each pistillate inflorescence may contain 30–40 flowers, each of which develops into a two- to four-carpelary capsule that can contain upwards of 30 ovules leading to impressive seed production by individual female trees.
5. Seeds are capable of long-distance transport by virtue of their small size and attached cotton fibers that facilitate movement by air and water. Germination is epigenous; stand establishment is prompt and fairly complete when seeds germinate on a moist mineral soil (dormancy is incomplete and stratification is not required).
6. The basic chromosome number of 19 is high in comparison to other dicotyledonous forest trees. Triploids are known in section *Populus* and probably occur in *Tacamahaca* although polyploidy is the exception rather than the rule throughout the genus. The relatively high basic number and the distinctiveness of a diploid chromosome set allows for a higher rate of recombinant gametes during reduction division.
7. The F_2 *P. trichocarpa* × *P. deltoides* generation typically displays large segregation variation for growth and phenology with a relatively high frequency of intermediate types as well as transgressive segregants. This may indicate a loose linkage system that furthers open recombination. Conversely, a physical clustering of genes controlling *Melampsora* leaf rust resistance may lead to an increase in parental phenotypes.

Figure 3 Whilst *Populus* is normally dioecious and outcrossing, departures occur in many species. Shown here is *Populus trichocarpa* cv. PS-53-97 bearing pistillate (center), staminate (upper) and two hermaphroditic inflorescences (left and right) along one long and one short shoot.

Vegetative reproduction is also highly developed in *Populus* which along with stabilizing selection counterbalances the open recombination system of *Populus* preserving the parent generation's refined adaptations. Clonal propagation from roots, stumps, and twigs commonly occurs. Extensive clonal stands of *P. tremuloides* have been established by suckering from root sprouts on upland sites. Similarly, grasslands have been colonized by *P. balsamifera* by suckering from roots of trees growing in surrounding forests. *Populus trichocarpa* reproduces clonally along riparian corridors by a process of cladoptosis. *Populus nigra* establishes along river courses by sprouting from limbs and stems buried in alluvium. Apomixis is also known to occur in the genus, although the frequency of apomictic offspring is probably low and does not significantly restrict the recombination system.

Introgression and the Recombination System

Introgression can alter the genetic composition of populations of the participating parental species. Although phenological barriers to the cross-pollination of distinct *Populus* species appear to be insubstantial in most instances, the reproduction of interspecific crosses usually functions at a lower level than their intraspecific counterparts owing to problems with either prezygotic (pollen–stigma interactions) or postzygotic (embryo abortion, low seed germination, seedling mortality) effects. Nevertheless, interspecific hybridization is known to occur in the wild between members of the same section. *Populus* × *canescens*, the hybrid offspring of *P. alba* and *P. tremula*, is widely distributed throughout Europe. *Populus grandidentata* hybridizes with *P. tremuloides* (*P.* × *smithii*) in the upper Midwest of North America. Furthermore, intersectional hybridization between *Aigeiros* and *Tacamahaca* has been observed; in California and Nevada, hybridization between *P. fremontii* and *P. trichocarpa* (*P.* × *parryi*) occurs, whilst *P. deltoides* reproduces with *P. trichocarpa* (*P.* × *generosa*) at the western limit of its range in Washington and Idaho where the two species come into contact. Hybrids of *P. deltoides* and *P. balsamifera* (*P.* × *jackii*) are found in Ontario and Alberta.

A quite large hybrid swarm involving *P. trichocarpa, P. balsamifera, P. angustifolia*, and *P. deltoides* is being studied along several rivers in southern Alberta.

Although interspecific hybrids have largely formed the foundation of commercial *Populus* plantations with vigorous growth rates and substantial disease and insect resistances, they are often less disease-resistant, less tolerant of herbaceous competition, and more palatable as herbivore browse when grown in the wild without benefit of cultivation, a phenomenon known as hybrid breakdown. But despite their reduced fitness, barriers to continuous backcrossing and introgression are not absolute. Persistent hybrid swarms are a force that opens the recombination system of the participating species, especially at the fringes of their ranges, where the pressure to adapt may be greatest. Natural hybrid zones are also of ecological significance to the degree that they foster an extensive diversity of associated plant and animal species.

Conservation

Sections *Aigeiros* and *Tacamahaca* are commonly found occupying floodplain and riparian habitats, at times growing in large contiguous, pure stands. The construction of dams, revetments, levees, and channelization projects along many of the world's rivers has reduced the frequency with which their banks are scoured and gravel bars created, both of which are essential to the establishment of a next generation of *Populus* stands. Construction of levees along the Mississippi River has eliminated much of the natural cycle of flooding and meandrous flow and, consequently, a noticeable decline in the regeneration of *P. deltoides*. The same can be said of many river systems in Europe and Asia.

The conservation of the genetic resource contained in riparian *Populus* species include *ex situ* preservation of wild *Populus* collections in cultivated arboretums. Some arboretums may incorporate a multiple population breeding system to direct and enhance within-species genetic variation. The European Forest Genetic Resources (EUFORGEN) Program to conserve *P. nigra* is perhaps the most advanced *ex situ* effort today with a collection of nearly 2800 clones from 19 countries. Similarly, an *ex situ* collection of *P. trichocarpa* from 100 stands has been assembled in the Pacific Northwest of the USA by GreenWood Resources in response to the loss of riparian forests along the Columbia and Willamette Rivers and their tributaries. Alternatively, *in situ* conservation efforts secure native *Populus* populations in large nature reserves and, in some cases, may include efforts to restore degraded habitats. A major *in situ* effort has been initiated in China's Xinjiang Autonomous Region with the establishment of the Tarim River nature reserve; a critical component is the conservation of *P. euphratica* riparian forests that have shrunk in area by nearly two-thirds.

Other conservation examples include a long-standing effort to preserve *P. nigra* in the Netherlands where it has been replaced *Populus* hybrid plantations. Similarly, the conservation of Italian *P. alba* populations has been proposed in view of the loss of native germplasm in the wake of expanding agriculture. Finally, the Indian government with support from the International Poplar Commission and the United Nations Development Program has surveyed *P. ciliata* populations in the Himalayan foothills as the first step in implementation of its conservation.

Relatively recent changes in air quality are now known to have impacted *Populus* genetic resources. A well-documented example is *P. tremuloides* in North America; populations sampled from regions with a history of chronic exposure to polluted air show significantly higher tolerances to ozone, as natural selection has eliminated sensitive individual phenotypes. The long-term effect of this narrowing of the *P. tremuloides* genetic resource is not known but no less an important concern. Natural selection and loss of diversity is likely to be occurring in polluted areas of Europe and Asia. Conservation efforts here are worthwhile to the extent that populations undergoing selection may also be losing potentially valuable alleles.

The Conservation Role of Commercial *Populus* Plantations

Production plantations established with highly selected interspecific hybrid varieties and intensive agronomic-style tending practices, are among the highest-yielding crop trees in the temperate zone. For example, growth rates of 21–33 $m^3\,ha^{-1}$ have been achieved at age 7 in *P.* × *generosa* plantations in the Pacific Northwest. High-yield plantations allow for the preservation of natural forested lands while meeting the fiber and fuel needs of a growing world population.

Beyond North American *P.* × *generosa* plantations, other worldwide plantations programs include cultivation of *P.* × *canadensis* (*P. deltoides* × *P. nigra)* in France's Loire River Valley and the Po Valley of Italy, *P. simonii* × *P. nigra* in northeastern China, *P.* × *tomentosa* (*P. alba* × *P. adenopoda*) in the northern plains of China, and *P. tremuloides* × *P. tremula* in western boreal Canada. Plantations of *P. deltoides* have been established in the southeastern USA, southern Brazil, Argentina, northern India, and southern China. These plantations are managed for a range of products including fuelwood, chips for paper, and logs for veneer and sawnwood products. Intercropping with soya, ryegrass, and corn during the first several years of a *Populus* rotation is practiced in agroforestry programs in China, India, and elsewhere where labor costs are low and arable land is scarce.

A reduction in soil erosion and an increase in water quality are often claimed as environmental benefits of *Populus* cultivation. *Populus* plantations have also been used extensively in various afforestation projects in India and China to address wood shortages while also slowing desertification. Over 1 million ha of *Populus* plantings were established during the 1970s as part of China's 'Green Great Wall' project to slow the spread of the northern deserts (**Figure 4**).

Their environmental benefit notwithstanding, the degree of gene flow between plantations of exotic species or interspecific hybrids and neighboring wild *Populus* populations is an important question in the context of native species conservation. Low levels of gene flow between *P.* × *generosa* plantations and native *P. trichocarpa* stands in the Pacific Northwest have been observed. The level of gene flow between *P.* × *canadensis* plantations and *P. nigra* stands in France may be higher, however.

Domestication

As high-yield plantations become ever more important in meeting the world demand for wood and fiber, novel genetic improvement strategies become an integral component of intensive plantation management practices. A unique combination of classical plant breeding methods and contemporary molecular approaches is used in *Populus*.

Figure 4 *Populus simonii* × *P. nigra* hybrid plantation Shanxi Province, China along the Inner Mongolian frontier. *Populus* stands are being used to reduce the severity of sandstorms and to contain the spread of China's northern deserts. Courtesy of Dave Austin.

Classical *Populus* breeding strategies

Breeding and selection of *Populus* has a lengthy and distinguished history among trees, beginning with a large-scale commercial improvement program conducted in North America in the late 1920s. Successful breeding programs have since been initiated in Europe, Asia, and North America in many cases relying upon nonrecurrent, first-generation (F_1) interspecific hybridization. Hybridization brings the variation encompassed by separate species into a single generation that often exhibits heterosis for yield. Although controlled reproduction may be difficult when some species are hybridized, the ease with which superior individual selections can be vegetatively propagated promotes F_1 hybridization as a popular breeding method (**Table 2**). Advanced generation breeding into the second generation (F_2) is sometimes accompanied by diminished vigor most likely due to the disruption of coadapted linkage groups that occurs during F_1 gametogenesis or to a reduction in overdominant gene action, although transgressive segregants are occasionally found. Backcross breeding is used to introduce a single, highly heritable trait from a donor species to improve an otherwise suitable recurrent parent. For example, in the North Central region of the USA, *P. deltoides* × *P. suaveolens* F_1 hybrids are crossed (back) to unrelated *P. deltoides* selections in an attempt to introduce the strong adventitious rooting ability of *P. suaveolens* into the recurrent *P. deltoides* parent that shows superior resistance to *Septoria* canker (F_1 *P. deltoides* × *P. suaveolens* hybrids are themselves highly canker susceptible).

Given that the entire range of genetic variation can be exploited by clonal selection, a very significant advantage compared to other species that rely upon seedling-based family selection programs, *Populus* programs have frequently focused solely on the selection of superior individuals as opposed to efforts to improve the average performance of whole populations. A complete strategy incorporates recurrent breeding of parental populations so as to improve their hybridizing quality thereby more fully guaranteeing future genetic gains. The ideal is a reciprocal recurrent breeding program. But this has often proved too expensive to implement. Moreover, a lack of full reproductive compatibility between species can greatly complicate the estimation of parental hybrid breeding values required by a reciprocal recurrent

Table 2 Examples of applied *Populus* genetic improvement programs

Pedigree	*Breeding centers*
Populus alba × *P. adenopoda*	China[b]
Populus alba × *P. alba*	Italy[u]
Populus alba × *P. deltoides*	Spain[j]
Populus alba × *P. grandidentata*	Canada,[d] Serbia[f]
Populus alba × *P. tremula*	China,[c] Italy,[u] Korea[o]
Populus alba × *P. euphratica*	Iran[t]
Populus ciliata × *P. deltoides*	India[e]
Populus ciliata × *P. suaveolens*	India[e]
Populus ciliata × *P. yunnanensis*	India[e]
Populus deltoides × *P. deltoides*	Argentina,[k] Beligum,[m] Canada,[d] USA,[h,n,p,q] France[i]
Populus deltoides × *P. balsamifera*	Canada[d,r]
Populus deltoides × *P. nigra*	Belgium,[m] Canada,[d] France,[i] Italy,[l] Serbia,[f] USA[q]
Populus deltoides × *P. suaveolens*	Canada,[d,r] China,[c] USA[h,q]
Populus deltoides × *P. trichocarpa*	Belgium,[m] France,[i] USA[h,q]
Populus nigra × *P. nigra*	Belgium,[m] Italy[l,u]
Populus nigra × *P. suaveolens*	Canada,[d,r] China,[c] Korea[o]
Populus simonii × *P. nigra*	China[c,s]
Populus tremula × *P. tremuloides*	Canada,[a,d] Finland,[g] Serbia[f]
Populus tremuloides × *P. tremuloides*	Canada[d]

[a] Alberta-Pacific Forest Industries, Inc., Boyle, Alberta, Canada.
[b] Beijing Forestry University, Beijing, People's Republic of China.
[c] Datong Poplar Bureau, Jinshatan, People's Republic of China.
[d] Direction de la Recherche Forestière, Sainte-Foy, Québec.
[e] Dr. Y. S. Parmar University of Horticulture and Forestry, Solan, India.
[f] Faculty of Agriculture, Poplar Research Institute, Novi Sad, Serbia.
[g] Finnish Forest Research Institute, Vantaa, Finland.
[h] GreenWood Resources, Portland, OR, USA.
[i] Institut National de la Recherche Agronomique, Ardon, France.
[j] Instituto Nacional de Investigación y Tecnologia Agraria y Alimentaria, Madrid, Spain.
[k] Instituto Nacional de Tecnologia Agropecuaria, Buenos Aires, Argentina.
[l] Istituto di Sperimentazione per la Pioppicoltura, Casala Monferrato, Italy.
[m] Instituut voor Bosbouw en Wildbeheer, Geraardsbergen, Belgium.
[n] Iowa State University, Department of Forestry, Ames, IA, USA.
[o] Korea Forest Research Institute, Kyunggi-do, Korea.
[p] MeadWestvaco, Corporation, Wickliffe, KY, USA.
[q] Natural Resources Research Institute, University of Minnesota, Duluth, MN, USA.
[r] Prairie Farm Rehabilitation Administration, Indian Head, Saskatchewan, Canada.
[s] Poplar Research Institute of Liaoning Province, Gai, People's Republic of China.
[t] Research Institute of Forests and Rangelands, Tehran, Iran.
[u] Università della Tuscia, Viterbo, Italy.

breeding. Consequently, many *Populus* programs substitute intraspecific breeding values as a guide for the manner in which parental populations are refined for interspecific hybridization.

The traits targeted for *Populus* improvement are usually the agronomic ones of yield, stem form, pest resistance, tolerance of cold and drought, wind firmness, and adventitious rooting. All have exhibited pronounced rates of genetic variation and have responded well to clonal selection programs. Field evaluations typically involve a multistage process to sequentially refine large populations until a group of elite selections has been identified. Other selection criteria may include wood and fiber properties for the veneer and sawnwood industries and the calorific quality of biomass for the heat- and power-conversion industries.

An imperative for production programs that incorporate clonal stands is a diverse pool of operational selections to help minimize the risk of plantation failures due to unforeseen climatic and biotic events. Most plantation programs are therefore allied with an ongoing hybridization program that continuously feeds new selections into production use. Continuous turnover of the commercial pool of clones is a safeguard against catastrophic failures due to coevolution of associated pests.

Application of Molecular Tools to Tree Improvement

Populus, by virtue of its relatively small genome, ease of cloning, and use of interspecific hybridization, has emerged as the model species for the application of molecular tools (genomic mapping and genetic engineering) to more traditional tree improvement approaches. Genomic markers associated with quantitative trait loci could lead to new approaches to the evaluation of full-sib seedling populations for superior selections that normally would not be revealed until conventional field tests are conducted for a half rotation or longer. Genomics could eventually lead to map-based cloning of important genes that are then used in transformation projects. The Joint Poplar Genome project is scheduled to complete sequencing of the *Populus* genome by the end of 2003.

Genetic transformation methodologies are well developed in *Populus*. Transformation can improve existing varieties for desired traits that otherwise are unavailable to conventional hybridization programs using recombinant DNA. *Populus* varieties have been modified for herbicide resistance, altered lignin content, and leaf beetle resistance. Currently field trials of genetically modified varieties have been conducted in North America with *P. deltoides* and *P. trichocarpa* × *P. deltoides* hybrids. In Europe, more than 20 field trials have been established using genetically modified *P. tremula*, *P. tremuloides, P. deltoides*, and *P. alba* × *P. tremula* selected varieties. The use of genetically modified plants has raised concerns over the risk posed to the fitness or future adaptability of wild relatives with whom transgenic plantations might reproduce. Consequently, a major ongoing effort has been sterility transformation that would prevent completely the sexual reproduction of transgenic plantations.

See also: **Genetics and Genetic Resources**: Propagation Technology for Forest Trees. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance; Genetics and Improvement of Wood Properties. **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement; Breeding Theory and Genetic Testing; Conifer Breeding Principles and Processes; Economic Returns from Tree Breeding; Forest Genetics and Tree Breeding; Current and Future Signposts.

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Spruces, Firs and Larches

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Introduction

Together with the genera *Pinus* (subfamily Pinoideae), *Cathaya*, *Pseudotsuga* (subfamily Laricoideae), and *Cedrus, Keteleeria, Nothotsuga, Pseudolarix, Tsuga* (subfamily Abietoideae), the genera *Picea* (subfamily Piceoideae), *Abies* (subfamily Abietoideae), and *Larix* (subfamily Laricoideae) belong to the family Pinaceae. The subfamilies are distinguished by cone and seed characters like the existence of an umbo or the existence of resin vesicles on the seed.

Species of the genera *Picea* (spruce), *Abies* (fir), and *Larix* (larch) are exclusively distributed in the northern hemisphere from 22° N in the south to 73° N forming the polar borderline of trees. Several species of these genera cover wide areas in boreal Eurasia and North America. They contribute to a major extent to the northern coniferous forests which stretch from coast to coast across these latitudes and form the greatest expanses of continuous forests. Many species of these genera are also found in mountainous regions of the more temperate zones often forming the alpine tree border line.

Picea, Abies, and *Larix* species occur in a wide range of habitats with very different soil and climate conditions. They are associated with various tree species depending on certain site conditions but they can also be found in pure stands under extreme site conditions. Mainly reproducing sexually by wind pollination, vegetative reproduction is the dominant mode of propagation if sexual reproduction is limited due to climatic limitations.

The lifetime of *Picea, Abies*, and *Larix* species ranges variously from 150 to 900 years. Under favorable conditions they grow to tall trees often forming dense forests with considerable growing stocks. Among populations of most species genetic differences can be observed in various traits. Due to their wood characteristics, the timber of spruces, firs, and larches can be used for a wide variety of purposes and is therefore of high economical importance.

Spruces

The genus *Picea* (subfamily Piceoideae) is related most closely to the genus *Pinus* (subfamily Pinoideae), but differs significantly by, e.g., cone and