species such as *E. grandis, E. urophylla, E. nitens*, and *E. globulus*. There are now hundreds of codominant (more informative) microsatellite loci developed for eucalypts that are transferable across species and have allowed alignment of genome maps from different studies and species. High consistency in marker order (synteny) is being revealed, and generic maps are emerging with candidate genes (e.g., for flowering and wood properties) positioned. Considerable progress has been made toward identifying genomic regions and markers associated with variation in quantitative traits (quantitative trait loci, QTL). QTL have been detected for numerous traits of economic significance including growth, propagation and wood properties, and in several cases these have been shown to colocate with candidate genes (e.g., *cinnamoyl* CoA reductase (CCR) gene with pulp yield, cellulose yield, and lignin quality (S/G ratio)). Research is now focusing on identifying genes and alleles responsible for the variation in traits of economic significance, particularly the highly heritable and expensive-to-measure wood property traits, through QTL and association studies. The next decade will see major advances in our understanding of the eucalypt genome and molecular breeding. There are now several privately owned databases containing partial sequences of many of the genes expressed in various tissues (e.g., cambium) of *Eucalyptus*, microchips have recently been produced to study eucalypt gene expression, and there is growing interest in large-scale sequencing of the eucalypt genome.

See also: **Genetics and Genetic Resources**: Genetic Systems of Forest Trees; Propagation Technology for Forest Trees. **Tree Breeding, Practices**: Genetics and Improvement of Wood Properties. **Tree Breeding, Principles**: Breeding Theory and Genetic Testing; Forest Genetics and Tree Breeding; Current and Future Signposts. **Tropical Ecosystems**: Eucalypts.

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Nitrogen-fixing Tree Improvement and Culture

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Introduction

This review focuses on the genetic improvement and culture of important tree species that fix nitrogen. About 700 tree species are known to fix nitrogen, among approximately 3000 suspected to do so. They represent 11 plant families. Most N-fixing trees (NFTs) are multipurpose and tropical in origin. They are often as valuable as fuelwood, green manure, or forage as they are for lumber or craftwood, and they are cultivated in a great diversity of agroforestry

systems. A majority are legumes nodulated by *Rhizobia* or *Bradyrhizobia* bacterial species. However, 10 dicotyledonous families fix nitrogen with the aid of actinomycetes of the genus *Frankia*. Legume trees that fail to fix nitrogen are primarily in the subfamily Caesalpinioideae and include highly selected tropical ornamentals, commonly grown as clones, in genera such as *Bauhinia, Caesalpinia, Cassia, Delonix, Haematoxylon*, and *Parkinsonia*. The great majority of significant NFT species can be thought of as newly domesticated. Only a few NFT genera (e.g., *Acacia, Casuarina, Erythrina, Leucaena, Prosopis*, and *Robinia*) have attracted the investment of provenance collections and strategic plant improvement. The review is in alphabetic order by genus, and within genera by species. An especially useful reference is the book by K.G. MacDicken (see further reading list).

The Genus *Acacia* (Mimosoideae: Leguminosae)

This large genus dominates NFT literature and embraces three great groups of species – about 850 Australian (now assigned by some authors to a genus *Racosperma*), 200 African, and 200 American. Most American species are shrubs and most African species are thorny trees. Diploid species are largely outcrossing, often due to self-sterility, but about one-third of acacias studied are polyploid, and polyploidy in legumes is often associated with self-fertility. Many species of great forestry potential are in early phases of domestication, provenance collection, and evaluation, among them the moist tropical species *A. aulacocarpa, A. cincinnata, A. crassicarpa, A. holosericea, A. leptocarpa*, and *A. polystachya*. Only limited provenance studies or genetic improvement is reported for many important acacias, including the following:

- *A. albida* ($2n = 26$) (= Faidherbia albida): this large, slow-growing tree of dry African tropics is widely distributed for its use as shade and forage on arid lands.
- *A. confusa* ($2n = 26$): 'Formosan koa,' a native of the Philippines and Taiwan, is a small tree grown as fuelwood and as an ornamental and soil-stabilizer, especially on wetter, acid soils. As with many other acacias, some selection has occurred for ornamental use.
- *A. farnesiana* ($2n = 52$): as with other polyploid legume trees, this small, thorny, tropical American tree is widely adapted, self-fertilizing, and often weedy. It has been grown for fuelwood and forage, and provides gum for glue and black dye for ink. It was planted and selected for flowering in France, as the 'cassie' flowers yield a pleasant perfume.
- *A. nilotica* ($2n = 52, 104$): 'Babul' is a thorny Indian and African tree used as firewood, fodder, charcoal, gum, and tannin. A polyploid, it is extremely variable genetically, and several varieties are recognized commercially. These probably include both self-fertile and self-sterile types.
- *A. saligna* ($2n = 26$): this small tree of south-west Australia is highly variable and grows rapidly in a wide range of ecosystems. It provides fodder and fuel and has been planted widely for sand-dune and mine-dump stabilization.
- *A. senegal* ($2n = 26$): this slow-growing, thorny African tree is the source of gum arabic and can be used for fuel, charcoal, and feed. Limited selection has been made to optimize productivity of gum under severe harvest stress conditions.
- *A. tortilis* ($2n = ?$): this thorny, polymorphic African tree (**Figure 1**) provides firewood and fodder in the dry, hot tropics. It tolerates alkaline soils and is often shrubby in growth.

Widely cultivated acacias that have been the subject of provenance and family evaluations and of other genetic improvement include the following species.

Acacia auriculiformis and *A. mangium*

These are related, rapidly growing trees from Australia to New Guinea, whose hybrid is of increasing genetic interest. The former is a smaller, rather crooked tree widely adapted and grown since 1900 throughout the tropics for shade, fuelwood, furniture, and pulpwood. The latter is taller but less forked and has large phyllodes and branches with much fluting; wood is lower in specific gravity. Both are diploids ($2n = 26$) that can be selfed and show low isozymic heterozygosity values, although outcrossing by bees

Figure 1 Naturalized stand of *Acacia tortilis* in Kenya, often coppiced for fuelwood and fodder.

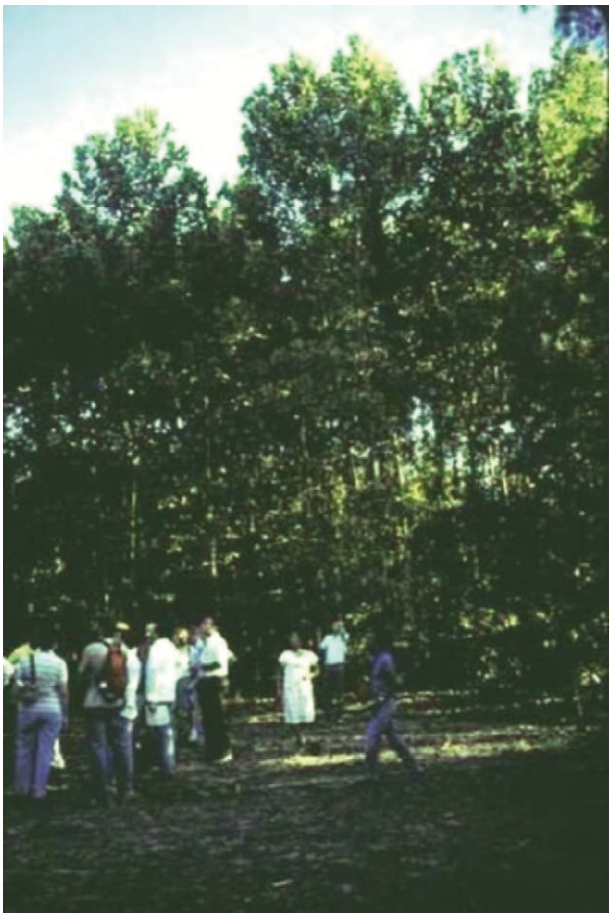

Figure 2 *Acacia mangium* trial in Chumphon, Thailand, age 3 years.

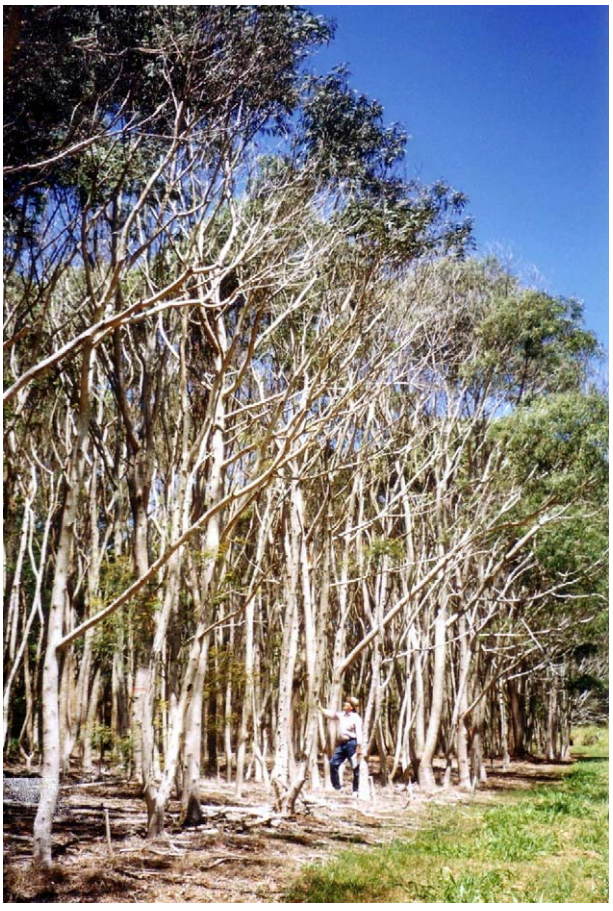

Figure 3 High-value hardwood trials of *Acacia koa* in Hamakua, Hawaii, age 8 years.

occurs (pollen is in polyads). Both can be cloned from cuttings, and both thrive on acidic soils. *A. mangium* (**Figure 2**) was introduced into Malaysia for pulpwood in 1967 (to 25 000 ha) as seeds from a single tree. A broader sample of germplasm was introduced in the 1980s to overcome the loss of form and vigor that occurred due to inbreeding. Extensive provenance collections have been made and evaluated throughout the world for both species. Vigorous hybrids of good form among the two species were then observed and came to dominate scientific interest. As yet the marketing of hybrid seeds or clonal propagules from hybrids is not economic. Provenances from Papua New Guinea have generally dominated yield trials, and growth habit shows startling differences on different sites. Related, interfertile species of interest include *A. aulacocarpa, A. crassicarpa*, and *A. leptocarpa*.

Acacia koa Gray (2*n* = 52)

Koa (**Figure 3**) is a high-value hardwood that is endemic to Hawaii, polyploid, and largely or completely self-sterile. Among 700 accessions evaluated since 1989 in Hawaii, 40 were chosen as parents for seed orchards. Genetic advance through selection was seen in degree of forking, improved bole form, tolerance of koa wilt (*Fusarium oxysporum*), and high wood yield. Seed orchards began bearing in 3–4 years. Genetic advance is sought particularly for tolerance of wilt, a limiting factor in growing koa at lower elevations.

Acacia mearnsii (2*n* = 26)

Australia's black wattle is a temperate tree now found worldwide as a source of tannin (35–40% recovery from bark), fuelwood, charcoal, poles, windbreaks, and other benefits. This self-sterile species is aggressive, however, and can become weedy. Provenance selections in the mid-1900s for high bark tannin contents at the Wattle Research Institute in South Africa (now the Institute for Commercial Forestry) and in Zimbabwe's Rhodesian Wattle Co. led to varieties preferred for production of tannins. Trees were felled after approximately 10 years, selection focusing on rapid growth. Provenance evaluations and plantations for wood also

developed extensively in China. Selected provenances also proved of major value in the reforestation of Korea after the Korean war. With the advent of synthetic tannins and leather substitutes, bark tannin production greatly declined. It is agreed that genetic diversity is great and selection for wood productivity could be profitable, but limited investment is currently made in improvement. Related wattle species of less value for tannins include the green wattle (*A. decurrens*) and silver wattle (*A. dealbata*) that have also been planted widely in the tropics.

Acacia melanoxylon (2*n* = 26)

Australian blackwood is a fine hardwood of the quality of kauri or walnut that occurs over a wide latitudinal range on the east coast of Australia. It is noted for its environmental plasticity and for the importance of locally adapted provenance evaluations. It was introduced widely into East Africa and Sri Lanka in the 1950s.

The Genus *Albizia* (Mimosoideae: Leguminosae)

This is a genus of 150 tropical species of trees, shrubs, and lianas. Many have been domesticated and widely planted but little studied for genetic improvement (e.g., *Albizia chinensis* of the Himalayas, *A. odoratissima* and *A. procera* from South and Southeast Asia). Also important but little bred is *A. lebbek* ($2n = 26$), the 'siris tree,' a widely adapted tree evidently native from Africa to Australia. Limited variation among local and very seedy populations suggests that it is self-pollinated, with abundant dried pods that rattle 'like a woman's tongue.' It is used as an ornamental, for timber and fuelwood, and for fodder. The following species have been the subject of some provenance evaluation, selection and improvement.

Albizia falcataria (2*n* = 26)

Also known as *Paraserianthes falcataria,* albizia (**Figure 4**) is one of the fastest-growing trees of the world. This Southeast Asian tree is planted widely in the tropics as a shade tree and favors moist and acid to neutral soils. Its wood is of low density and of low caloric value, but it is used for pulpwood, boxes, and particle board. Varieties have been selected for use as matchsticks and other products in the Philippines, where plantations are harvested on 10–15-year cycles.

Albizia saman (2*n* = 26) (= *Samanea saman*)

The classic parasol-shaped 'raintree' or 'monkeypod' shares with many legumes a host of Latin and common names. It was distributed worldwide from its Central American center of origin as an ornamental, timber tree, craftwood, and shade tree. It was distributed throughout the tropics from unknown sources and from narrow gene bases, not unlike most tropical trees. Almost no genetic variation occurs, for example, among Hawaii's beautiful, spreading raintrees, that appear to be highly self-pollinated and abundantly seedy in our fuelwood trials. Several accessions of the raintree were included in the gene conservation program of Oxford Forestry Institute.

Figure 4 Naturalized stand of *Albizia falcataria* on acid soils in Hawaii.

The Genus *Alnus* (Betulaceae)

This amazingly widespread genus of alders is largely temperate. It includes 35 species, all NFT through association with *Frankia* actinomycetes. They grow rapidly and aggressively (to 30 m in 10 years), and are often considered weeds, although they provide significant soil improvement for forests. Most are $2n = 28$ and outcrossing. Like many NFTs, the alders are widely planted, fully domesticated, poorly

represented by forest genetic resources, and managed with little view to genetic improvement. Among these are:

- *A. acuminata*: a Central and South American species planted extensively throughout Latin America for timber and fuelwood.
- *A. glutinosa*: black alder, a widely distributed European species that provided wood for early violins and that is grown as a fuelwood and craftwood and as a stabilizing tree along rivers and roadsides.
- *A. nepalensis*: the Nepal alder of Himalayan origin, planted extensively worldwide for timber, forage, and firewood.
- *A. rubra*: the red alder of northwest North America, a tree up to 40 m tall that is used for construction and furniture, as fuel and in pulpwood mixtures. It can become annoyingly weedy in young stands of pines. As with other alders, the red alder varies greatly in ecosystem adaptability (latitudinal, elevational).

The Genus *Calliandra* (Mimosoideae: Leguminosae)

Most of the 132 species of this predominantly American genus are shrubby, and few enter commerce, but the genus is noted for growth on acid tropical soils. Several are common as ornamental shrubs or trees selected for red, pink, or white flowers, including *C. inaequilatera* and *C. haematoma*.

Calliandra calothyrsus (2*n* = 22)

Calliandra is a small, clonable, rapidly growing tree used less in its native America than in countries like Indonesia, where it serves as fuelwood, green manure, and fodder. It is sparsely seedy due to its nocturnal flowering habit and cross-pollination largely by bats and moths. The US National Academy of Science supported an early publication on calliandra, and Oxford Forestry Institute provided seed collections for >120 international trials of different seedlots and species. Wide variations were recorded in wood yield, branching, and growth habits. Selection in Australia and Costa Rica has focused on variations in fodder utility and digestibility, which are very low in fresh foliage due to high condensed tannin contents.

The Genus *Casuarina* (Casuarinaceae)

This Australian genus is now recognized to include 17 tree species, with about 70 related polymorphic species assigned to the genera *Allocasuarina, Ceuthostoma,* and *Gymnostoma*. The true casuarinas are noted for hardwood, fuelwood, and shade on tropical beaches and waterways. Major shelterbelts occur along coastlines in China and in Pacific islands. N fixation is by *Frankia,* pollination is by wind, and some species are dioecious. The species below have been hybridized and evaluated widely in China.

Casuarina cunninghamiana and the related (and cross-fertile) *C. glauca* (2*n* = 18)

These are of less significance as plantation species than *C. equisetifolia*, but their genetic variation is much better studied. *C. glauca* can be weedy due to root-sprouting. These species have a broad ecological range as riverine species of eastern Australia, and extensive provenance collections have been made and studied, e.g., in California, China, and Egypt. Genetic diversity was similar to that of other tropical wood species (0.2–0.3, probabilities that any two alleles are different) with unusually large between-provenance variations. Significant variations are reported in traits like freezing survival, tree height, and diameter. Clinal variations by latitude were very significant. Selected families and species hybrids dominate modern plantings.

Casuarina equisetifolia (2*n* = 18)

The 'ironwood' is the most extensively planted casuarina, noted for fuelwood, pulp, and timber, and as a shade tree. Provenance collections are somewhat limited and significant variations occur among them. Clones based on its stately hybrid with *C. junghuniana* (= *C. montana*) are prominent in Thailand and India (**Figure 5**).

The Genus *Dalbergia* (Papilionoideae: Leguminosae)

The 'rosewoods' of fame occur among the 100 species of this tropical papilionoid genus of trees, shrubs, and lianas. Many species are known for their high-value hardwood and widely planted, but have been the subject of no major genetic improvement. These include *D. decipularis* (Brazilian tulipwood), *D. latifolia* (Indian rosewood, blackwood), *D. melanoxylon* (African blackwood), and *D. nigra* (Brazilian rosewood). The rosewoods are often endangered by deforestation and major genetic erosion.

Dalbergia sissoo Roxb. (2*n* = 20)

'Sissoo, shisham' is a widely planted high-value hardwood endemic to the Himalayas (**Figure 6**). It is also recognized for shade, soil enrichment,

Figure 5 Three years' growth of hybrid *Casuarina equisetifolia* × *C. junghuniana* in Chumphon, Thailand.

Figure 6 Logs of *Dalbergia sissoo* with Director C. Sheikh of Pakistan Forest Institute.

fuelwood and charcoal, honey, and traditional medicines. While it thrives on gravelly outcroppings in the terai at the foot of the Himalayas, it also grows under a wide range of stressing environmental factors, including aridity, mild frost, and very high

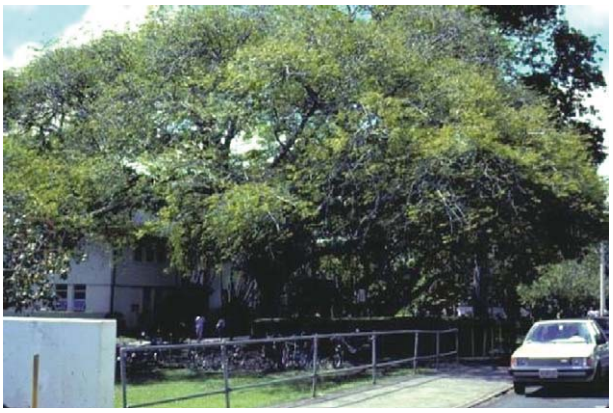

Figure 7 Hawaii's largest tree is the Costa Rican earpod, *Enterolobium cyclocarpum*.

temperatures. Sissoo is self-fertile but appears to be partially outcrossed in nature and provenance variations are large. Like most legume trees, sissoo is light-seeking and invariably crooked, and genetic variability is high for stem form and growth habit. Estimates of heritability for stem form are high (40–50%) but these assume complete outcrossing. They have led to optimistic projections for expanded use of genetically improved sissoo throughout the tropics, despite its relatively slow growth and lack of institutional investment.

The Genus *Elaeagnus* (Elaeagnaceae)

This European genus includes 40 species of shrubs and trees that fix nitrogen through association with the actinomycete *Frankia*. Similar American NFTs occur in the genera *Shepherdia* and *Hippophae*, often noted as fodder trees but 'armed' with spines for protection. *Elaeagnus angustifolia*, the Russian olive, is commonly cultivated as an ornamental and has been planted widely as a shelterbelt companion of trees that do not fix nitrogen. Selected cultivars and clones are reportedly of better form and appearance.

The Genus *Enterolobium* (Mimosoideae: Leguminosae)

A small genus of five tropical American species, this is related to the genus *Albizia*. A widely cultivated rapidly growing ornamental (**Figure 7**) is the giant, spreading *Enterolobium cyclocarpum*, known as 'guanacaste' or 'elephant's ear.' Like *Albizia saman*, its roots are often superficial and it is undesirable as a street tree. The wood ranges widely in density and quality, and the wood dust causes allergies. Foresters favor trees with dark walnut-like wood, but there is no evidence that these selections are prominent in

plantations. Fuelwood plantings in Hawaii (1×1 m spacing) yielded well but showed great intraprovenance variations.

The Genus *Erythrina* (Papilionoideae: Leguminosae)

The 112 species of 'coral trees' are tropical and worldwide in origin, with *E. fusca* native to three continents, its seeds surviving in sea water. Most are small thorny trees with soft wood and high alkaloid contents in leaves. Truly multipurpose but low in value, their uses range from fodder, food, and medicinal to fencepost, shade tree, green manure, and ornamental. Interspecific hybrids were evaluated widely and proved highly interfertile. All appear to be $2n = 42$ and outcrossed by hummingbirds. Many are American in origin, with one endemic to Hawaii, *E. sandwicensis*. *E. abyssinica* and *E. cristagalli* are grown as ornamentals worldwide. Erythrinas are easily cloned from stakes or cuttings. Centro Agronomico Tropical de Investigacion y Enseñanza (CATIE) in Costa Rica maintains a clonal and provenance collection, and the following species are largely grown as locally adapted clones selected for specific use.

- *E. berteroana*: a coral tree that is highly tolerant of aluminous clays, and is often cloned to serve as fence posts in its native tropical America.
- *E. fusca*: the most international species, a classic multipurpose tree. It often serves as shade and green manure for coffee and cocoa and as fenceposts.
- *E. poeppigiana*: a tall South American tree that serves widely as a shade or nurse tree for coffee and as fodder (despite high alkaloid contents).
- *E. variegata* ($= E. indica$): used as a thorny living fence, ornamental, shade for coffee, and support for viny crops. A fastigial, erect cultivar is widely cultivated throughout the Pacific as hedgerows.

The Genus *Gliricidia* (Papilionoideae: Leguminosae)

This small meso-American genus (four species) is known primarily for the species *G. sepium*.

Gliricidia sepium ($2n = 20$)

Gliricidia (**Figure 8**) is a small, rapidly growing, and thornless tree with bright pink flowers in the spring that appear to be entirely outcrossing. It has been spread internationally as an ornamental, green manure, fodder, and firewood tree. The trees clone easily from stem cuttings but develop better roots from seedlings. Planting of gliricidia clones as living fences, as support trees for peppers and yams, and as shade for cacao and coffee, often involves 'seat of the pants' selection of erect, less-forked types. A joint series of provenance collections was made in the 1980s, with inputs from International Livestock Center of Africa, University of Hawaii, Nitrogen Fixing Tree Association, Oxford Forestry Institute, Food and Agriculture Organization of the UN and other organizations. Genetic variations were great both between and within provenances. An outstanding provenance, Tequisate, from Guatemala, was observed in trials from Hawaii and the Philippines to Nigeria. Its superior growth was evident in both fodder and total biomass. Extensive studies were conducted in Nigeria of gliricidia in alley farming systems with crops like maize, and as a leguminous fodder supplement in animal diets. The fresh fodder was not palatable to animals, but palatability increased upon drying, and digestibility of the pure legume was relatively low (55%) but increased when in grass mixtures. Improvement in forage quality with selection was predicted among gliricidia provenances and clones.

Figure 8 *Gliricidia sepium* managed for alley farming trials at Ibadan, Nigeria.

The Genus *Inga* (Papilionoideae: Leguminosae)

Over 200 species of tropical American origin are in this genus of woody shrubs and trees, studied taxonomically by the Oxford Forest Institute. The species *Inga laurina* ('icecream bean') is used as a food and shade tree in Latin America, *I. vera*, *I. edulis*, and others serve variously as shade, fuelwood, and food (sweet pulp), notably on acid soils in humid tropics. Seeds are recalcitrant, restricting the cultivation and improvement of these species.

The Genus *Intsia* (Caesalpinioideae: Leguminosae)

This tropical Asian genus of three species includes *Intsia bijuga* ($2n = 24$), a handsome timber tree called 'ipil' in the Philippines. The hard, rot-resistant timber of this and *I. palembanica* (Borneo teak) are noted for use in decking and truck bodies. Ipil is believed to be highly variable genetically in the Philippines but there is little evidence of selection and breeding. Debate also exists about its ability to fix nitrogen.

The Genus *Leucaena* (Mimosoideae: Leguminosae)

No NFT genus has been selected or bred more extensively than this American genus of 22 species ranging from Peru to Texas, from sea level to 3000 m. Among the fastest-growing trees, all are woody and most will flower the first year. All are polyploids, ranging from $2n = 52$ to $2n = 112$. The predominant diploid species ($2n = 52$, 56) are self-sterile, while three of the four polyploids ($2n = 104$, 112) are self-fertilized. A single self-pollinated variety of the $2n = 104$ species, *Leucaena leucocephala*, circumnavigated the world four centuries ago, accounting for early interest in this model multipurpose tree for agroforestry systems. Cultivation and management systems differ greatly for leucaenas; some are maintained as shrubs for fodder, some as trees for a wide variety of uses. All species have been included in >2500 seed collections made by University of Hawaii, Oxford Forestry Institute and Commonwealth Scientific and Industrial Organization (CSIRO) of Australia, with evaluations in Hawaii, Queensland, and Nicaragua. In Hawaii, 232 interspecific hybrids were made among 16 species, resulting in 77% interfertility. Many of the 73 hybrids grown were heterotic for growth rate and involved attractive combinations of parental traits. Many species are widespread, at least partially domesticated and of use as fodder or fuelwood, e.g., *L. collinsii, L. lanceolata, L. macrophylla, L. shannonii*, and *L. trichandra*. Much current breeding is based on populations from interspecific hybrids, involving taxa such as *L. pallida* ($2n = 104$), *L. diversifolia* ($2n = 104$), and *L. pulverulenta* ($2n = 56$). Species fully domesticated and of breeding interest include the following:

- *L. diversifolia* ($2n = 104$): self-fertile tree of highland Mexico, now widespread, used as coffee shade, fuelwood, and green manure. Fertile hybrids with *L. leucocephala* are being evaluated for timber and fuelwood.
- *L. esculenta* ($2n = 52$): widely grown outcrossing food tree (edible pods) of highland Mexico, also used as shade. Seedless hybrids with *L. leucocephala* are attractive as high-value hardwood, widely adapted in elevation and resistant to psyllid insects.

Leucaena leucocephala ($2n = 104$)

Leucaena leucocephala is the familiar leucaena throughout the lowland tropics on less acid soils, known by a hundred vernacular names. Among 700 international collections of this self-fertile species grown in Hawaii, most were identical seedy shrubs, the 'common type' widely used for fodder and fuelwood in warm tropics. In contrast, seed collections in its native Mexico and Central America range widely in ideotype, including arboreal types from which 'giant' cultivars have been bred and are now international in use. These are distributed largely as pure lines, e.g., K8, Cunningham, K636, and Tarramba, for fodder and wood uses, and are not inclined to be weedy. Hybrids among pure lines show some heterosis, and one F_2 population (K636 × K584) is marketed. However, interspecific hybrids with highland species are of great commercial interest. KX2 derives from the fifth cycle of recurrent selection following the crossing of *L. leucocephala* with a small Mexican tree, *L. pallida*, a self-sterile polyploid that confers resistance to psyllids and to cold weather. Another, KX3 (**Figure 9**), is from hybrids with *L. diversifolia*, described above. An attractive, clonable, seedless triploid hybrid is K1000 (**Figure 10**) showing impressive hardwood quality and growth rate derived from the cross with *L. esculenta*.

Figure 9 High-value hardwood from 12-year old hybrid, *Leucaena leucocephala* × *L. diversifolia*, in Waimanalo, Hawaii.

Figure 10 Seedless triploid clone K1000, *Leucaena esculenta* × *L. leucocephala*, age 7 years, Waimanalo, Hawaii.

The Genus *Millettia* (Papilionoideae: Leguminosae)

This genus of 90 African and East Asian species now embraces the genera *Pongamia* and *Derris,* and includes a number of lesser-known fuelwood and timber trees. The pongam or Indian beech is *Millettia* spp., formerly known as *Pongamia pinnata* and as *Derris indica*. It is a native of East Asia that is now widespread and used in many ways, providing a seed oil as fuel and medicinal, fuelwood, postwood, shade, and ornamental. Profuse root suckers and weediness limit its use.

The Genus *Mimosa* (Mimosoideae: Leguminosae)

Few arboreal species occur in this large genus of 400 species, and these are often thorny and shrubby. *Mimosa scabrella* ($2n = ??$), bracatinga, is an exception. It is a fast-growing Brazilian legume of good form with diverse use as fuelwood, lumber, charcoal, ornamental, pulpwood, and shade for coffee. It is believed to be outcrossing and one study showed wide provenance variations.

Figure 11 Variegated-leaf clone of *Pithecellobium dulce* as ornamental, Honolulu, Hawaii.

The Genus *Parkia* (Mimosoideae: Leguminosae)

Forty species of this genus range from Africa to Southeast Asia, and a few are now worldwide. They are bat-pollinated and probably self-sterile, and have recalcitrant seeds. They are observed to vary genetically, but with no evidence for breeding and selection. Two species are outstanding:

- *P. javanica* (= *P. roxburghii*): an imposing tree to 40 m with umbrella crown, used as ornamental or timber tree, with seeds used medicinally.
- *P. speciosa*: a source of food in Southeast Asia (seeds, from the large pods), known to produce hybrids with *P. javanica*.

The Genus *Pithecellobium* (Mimosoideae: Leguminosae)

The 20 tropical American trees of this genus are largely thorny and best known as sources of sweet fruit. It was earlier treated by early botanists as a much broader taxon, including genera like *Albizia*.

Pithecellobium dulce ($2n = 26$)

Manila tamarind is a thorny American tree up to 15 m tall that can be found throughout the drier tropics (**Figure 11**). Its multiple roles include food use of the pods and seeds, honey, postwood, fuelwood, shade, and ornamental. It is alternately planted and cursed, as its thorns and weediness (seeds are spread by birds) reduce its utility and attractiveness. Variegated mutants are selected as ornamental trees, and thornless mutants (as in *Prosopis*) are known to occur.

The Genus *Prosopis* (Mimosoideae: Leguminosae)

The 44 species of this genus are American in origin, and most are drought- and salt-tolerant, thorny,

$2n = 28$ and self-sterile. They include the mesquites of fuelwood and charcoal fame (*Prosopis glandulosa* in North America) that add flavors to many a grill. They are also known as honey and fodder trees and occasionally provide high-value hardwood. Among species that are fully domesticated and widely planted but little studied genetically are *P. cineraria* (= *P. spicigera*), a widespread Indian tree of the hot tropics used as firewood, fodder, green manure, and charcoal. It segregates for thorns, and thorny trees are favored for goat-proof fences. Also of fame is *P. tamarugo*, a slow-growing Chilean species widely planted locally for its saline tolerance under annual rainfall <100 mm. It has not been adapted effectively outside of Chile. The following two species complexes have been more widely evaluated as provenances or localized selections. However, as with most NFTs, expert panels routinely recommend the increased availability of genetically improved materials, if research money could accompany the recommendations.

Prosopis alba (2n = 28) and *P. chilensis*

These are algaroba trees from a related complex largely found in highland subtropics that also includes *P. flexuosa* and *P. nigra*. All serve as sources of honey, firewood, and charcoal, and the sweet succulent pods are used for food and cattle fodder. Seedlot variations are reported for growth rate, limbiness, stem form, and thorniness. Phenotypic selection in natural stands was declared ineffective, due to environmental plasticity, a phenomenon with which all NFT breeders are familiar.

Prosopis pallida (2n = 28) and *P. juliflora*

These ($2n = 28$, 56) are two closely related mesquites from Peru north into Central America that are now abundant worldwide; their awkwardly forking trees often dominate arid landscapes and seascapes (**Figure 12**). Known best for their excellent charcoal and dense fuelwood, they were also planted internationally as animal fodder (pods). The wood has very high calorific value (4200–4800 kcal kg^{-1}), and the relatively slow-growing trees offer a durable postwood and an excellent source of honey. *Prosopis pallida* in Hawaii segregates about 1/8 thornless, suggesting single-gene control based on the presumed two-tree origin (introduced from Paris Botanical Garden in 1828). Such a narrow gene base is undoubtedly common in many countries. Trees are coppiceable and cuttings and grafts take fairly well, permitting some use of clones. Thornless trees are universally favored for tropical beaches but do not breed true due to self-sterility. Some selection has also occurred for pod yields, tree form, and growth, but serious genetic improvement awaits financial support.

Figure 12 The Peruvian *Prosopis pallida* dominates Pacific beaches, such as this in Molokai, Hawaii.

The Genus *Pterocarpus* (Mimosoideae: Leguminosae)

Many fine timbers (bloodwood, narra, padouk, Philippine mahogany, vermilion wood) derive from the 20 species of this tropical Indian and African genus of tall leguminous trees. Narra is probably the best known and most widely cultivated. Timber, dye, and shade use are also made of many other taxa, notably *Pterocarpus erinaceus* (kino, Burmese rosewood), also referred to as *P. angolensis* and *P. echinatus*. Other important species include *P. dalbergioides* (Andaman padauk), *P. macrocarpus* (Burma padauk), *P. marsupium* (malabar kino, source of astringent resin), *P. santalinus* (red sandalwood), and *P. soyauxii* (West African padauk). All are characterized by winged pods, presumed outcrossing, clonability, and extensive natural variability.

Pterocarpus indicus (2n = 22)

This majestic spreading tree (up to 40 m tall) is known as narra, Burmese rosewood, and Andaman redwood, and is native over a wide ecological range from Myanmar to Borneo and the Philippines. It is cultivated as an ornamental and street tree and is harvested as a choice timber for furniture and flooring. Flowering occurs in short intervals and pod set appears to be due to self-pollination. Much variation is seen in tree form, fluting, forking, and growth rates of narra. Cuttings root easily from trees of all ages and clones have been selected for adaptability to location, ecology, and use. It responds well to deep, high-quality soils of reduced acidity.

The Genus *Robinia* (Papilionoideae: Leguminosae)

Four interfertile species make up this North American temperate genus, a relict of tropical origin related to gliricidia and sesbania that becomes deciduous only upon frost. Like sesbania, it has a unique N-fixing spectrum of rhizobia. The shrubby species *Robinia hispida*, rose acacia, is planted as an ornamental but has little selection history. In contrast, the black locust is among the most intensively studied and bred NFTs.

Robinia pseudoacacia ($2n = 20$)

The black locust (or false acacia) is widely naturalized throughout North America, where the borer *Megacyllene robiniae* has restricted commercial plantings to erosion control, land stabilization, and as postwood. It is nodulated by both *Rhizobium* and *Bradyrhizobium* bacteria and can become weedy. Away from the borer, black locusts have been planted worldwide and cultivated intensively in Eastern Europe as a pulpwood, postwood, and fuelwood tree. Its outcrossed papilionoid flowers also serve as a bee pasture for honey and cultivars have been selected for use as an ornamental. It was introduced to Europe in the 1700s, where 'shipmast locust' arboreal types were selected and grown intensively (250 000 ha in Hungary) as a timber tree on a 30-year harvest cycle. Great genetic variability (average heterozygosity 0.30) and breeding progress were recorded for height, yield, spinelessness, and coppiceability. In contrast, much less variation was observed in specific gravity (average 0.62 at age 20 years). Intensive studies have been made to accelerate planting of uniform clones from vegetative and root cuttings, tissue cultures, and from grafts.

The Genus *Sesbania* (Papilionoideae: Leguminosae)

This genus includes 50 species of shrubs and small trees in the section Robinieae, now scattered worldwide. Most species are annuals, of which many are important as fodder (**Figure 13**) and ornamental. All nodulate aggressively, some having nodules on the stems. A very fast-growing fodder and multipurpose species is *Sesbania sesban* ($= S.\ aegyptica$; $2n = 12$) a short-lived shrub or tree now planted worldwide, and a similar shrub called 'ohai' is native to Hawaii, *S. tomentosa*.

Sesbania grandiflora ($2n = 24$)

S. grandiflora, called 'agati,' is a small polyploid tree from Southeast Asia or Indonesia with showy flowers

Figure 13 Forage trials in Maseno, Kenya, of several arboreal and shrubby species of the genus *Sesbania*.

that are self-fertile but largely outcrossed. It is planted internationally as a multipurpose tree for fodder, fuelwood, ornamental use and often for food (flowers, young pods, and leaves). It is recognized by farmers as a source of fixed nitrogen and green manure. It coppices vigorously for use as fodder or fuel (fast-burning), and selections have been made for ornamental or food use, e.g., with larger flowers or with red (versus white) flowers.

The Genus *Sophora* (Papilionoideae: Leguminosae)

This genus includes 52 species of temperate and tropical origin, several noted as ornamentals or as source of hardwood and of toxic or medicinal chemicals. *Sophora japonica* ($2n = 28$; Japanese pagoda tree) is a large deciduous tree native to China and Korea that has been cultivated for more than 30 centuries in China as an ornamental, dye, and medicinal plant. Flowering begins only on very old trees and the outcrossed flowers cause stains to form where they fall. Genetic variations exploited by horticulturists include weeping, fastigiate, and variegated-leaf trees, and cloning or grafting is common.

The Genus *Tipuana* (Papilionoideae: Leguminosae)

This is a monotypic South American genus with *Tipuana tipu* ($2n = 20$) as the sole species. The 'pride of Bolivia' is a fine timber (rosewood) and ornamental, and is widely planted for fodder, windbreak, and as a street tree to 20 m height in Argentina and Bolivia (to 3000 m elevation). The outcrossed large yellow flowers produce winged one-seeded pods, and it can be weedy. It has an irregular bole similar to most legume trees and it is coppiceable and clonable. Limited

studies suggest major provenance variations in ecosystem 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