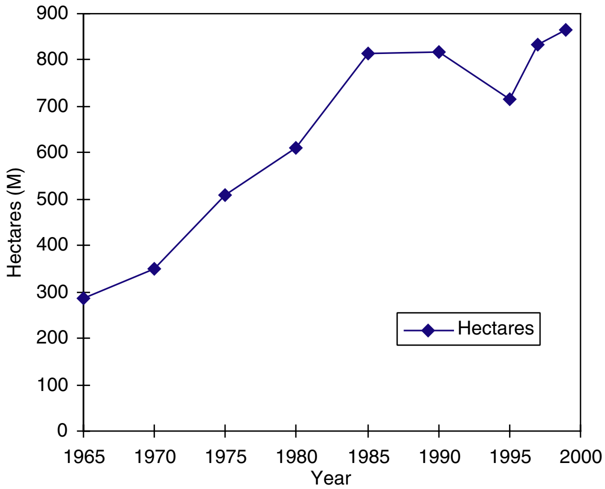

Figure 7 Area planted annually in the southern USA from 1965 through 2000. Based on data in Southern Forest Resources Assessment Draft Report. Data from USDA Forest Service, Southern Research Station.

effect of genetic improvement and more intensive management has far exceeded expectations, to the point that the timber shortages predicted less than a decade ago are not materializing.

The cooperatives are making a concerted effort to preserve all the genotypes included in the breeding population forming a genetic base far greater than the trees included in the production orchards. These so-called scion banks combined with the genetic tests form an invaluable genetic resource in addition to the extensive natural stands.

See also: **Genetics and Genetic Resources**: Molecular Biology of Forest Trees. **Tree Breeding, Practices**: 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. **Tropical Ecosystems**: Tropical Pine Ecosystems and Genetic Resources.

Further Reading

Byram TD, Lowe WJ, and Gooding GD (2000) Western Gulf Forest Tree Improvement Program gene conservation plan for loblolly pine. *Forest Genetic Resources* 27: 55–59.

Dorman KW (1976) *The Genetics and Breeding of Southern Pines*, Agriculture Handbook no. 471. Washington, DC: US Department of Agriculture.

Dvorak WS, Jordan AP, Hodge GR, Romero JL, and Woodbridge WC (2000) The evolutionary history of the Mesoamerican Oocarpae. In: *Conservation and Testing of Tropical and Subtropical Forest Tree Species by the CAMCORE Cooperative*. Raleigh, NC: North Carolina State University.

Lowe WJ, McKinley CR, and Toliver JR (eds) (1986) *Advanced Generation Breeding of Forest Trees*, Southern Cooperative Series Bulletin no. 309. Baton Rouge, FL: Louisiana Agricultural Experiment Station.

Schmidtling RC (2001) *Southern Pine Seed Sources*, General Technical Report no. SRS-44. Asheville, NC: US Department of Agriculture, Forest Service, Southern Research Station.

Schulz RP (1997) *Loblolly pine*, Agriculture Handbook no. 713. Washington, DC: US Department of Agriculture.

van Buijtenen JP(ed.) (1983) Progeny Testing of Forest Trees, Proceedings of workshop on progeny testing, 15–16 June 1982, Auburn, AL. College Station, TX: Department of Agricultural Communications, Texas A&M University.

van Buijtenen JP (1984) Genetic improvement of forest trees through selection and breeding. In: Wenger KF (ed.) *Forestry Handbook*, pp. 457–488. New York: John Wiley.

Wells OO (1983) Southwide pine seed source study: loblolly pine at 25 years. *Southern Journal of Applied Forestry* 7(2): 63–71.

Wells OO and Wakeley PC (1966) *Geographic variation in survival, growth, and fusiform infection of planted loblolly pine*, Forest Science Monograph no. 11. Bethesda, MD: Society of American Foresters.

Williams CG and Byram TD (2001) Forestry's third revolution: integrating biotechnology into *Pinus taeda* L. breeding programs. *Southern Journal of Applied Forestry* 25(3): 116–121.

Zobel BJ and Sprague JR (1993) *A Forestry Revolution: The History of Tree Improvement in the Southern United States*. Durham, NC: Carolina Academic Press.

Zobel BJ and Talbert J (1984) *Applied Forest Tree Improvement*. New York: John Wiley.

Tropical Hardwoods Breeding and Genetic Resources

E D Kjaer, The Royal Agriculture and Veterinary University, Hoersholm, Denmark

© 2004, Elsevier Ltd. All Rights Reserved.

Introduction

The tropical flora includes thousands of tree species that have proven to be of high value to humans. Products from trees include an almost endless number of goods: timber, fuelwood, edible fruits, medicinal compounds, fibers for clothing, latex, and oils. The genetic diversity of these species represents an enormous biological resource in terms of options for human utilization. Research into the application and conservation of this genetic resource has provided important guidelines on its sustainable genetic management. Tree breeding has focused on relatively few hardwood species considered to have high potential in industrial plantations. However, more recently a broader scope has been applied, and the research and development have focused on a substantially larger number of species including domestication of trees planted by farmers.

Genetic Resources

The term 'genetic resources' refers to genetic variation in trees of potential or present benefit to humans. Variation of genetic origin is due to DNA polymorphisms as such (genes) but the genetic patterns of variation are also of major importance. Genetic variation can thus be seen as organized at different levels: variation between different species, between different populations (forests) within a given species, and between different individual trees of the same species within a given population. The idea of a genetic resource is that this genetic variation – in the broad sense stated above – is of potential value for humankind at present or in the future.

In addition to the genetic diversity as such, a subject of considerable interest is the evolutionary processes (e.g., natural selection in favor of healthy trees) that continuously work within and between populations, and assure continued adaptation to changing climatic conditions, competition with other species, or infections from new pests. This is based on the perception that populations need to be able to respond to changing environments and new competitors in order to maintain their relative fitness. It does hold true that most if not all tree species are exposed to constant competition from other species in a changing environment. Rapid coadaptation and development are thus believed to be necessary for any species in order to maintain fitness and ultimately to avoid extinction in the long run. This perception is sometimes referred to as the 'Red Queen hypothesis' after Van Valen, who chose the name from *Alice in Wonderland*, where the Red Queen tells Alice that 'she needs to run as fast as she can just to stay in the same place.' One can say that the genetic diversity is a dynamic feature of a species being constantly shaped by its environment through ongoing evolutionary forces. Therefore, management of genetic resources of tropical forest trees normally (although not always) aims at protection of the genetic processes as well as the resource itself.

The genetic resource of tropical hardwoods is considered to be especially valuable due to the vast array of potentially harvestable crops from the thousands of species. An important feature of many (although far from all) tropical trees is that they grow in very diverse ecosystems and therefore have a scattered distribution, and/or are found at low densities. This complicates large-scale harvest of the products and therefore in principle favors some kind of domestication of the species through planting activities. However, successful planting programs require planting material in sufficient amount and of high genetic quality. Aspects of characterization, identification, propagation, and breeding of tropical hardwood species have therefore been important research topics for many species for a number of decades.

Provenance Trials and Breeding Programs for Industrial Plantations of Tropical Hardwoods

For practical reasons, the initial focus was on breeding hardwood species with some kind of pioneer characteristics, i.e., shade-intolerant species with fast juvenile growth. Such species are easier to cultivate in plantation regimes compared to the more difficult shade-tolerant, mature-phase species that require shade and exhibit less vigorous juvenile growth. Some of the earliest tree improvement activities focussed on teak (*Tectona grandis*). Teak is considered to be one of the world's most prominent timber species due to its valuable wood but it is also easy to establish in plantation regimes. The juvenile growth rate is high but rapidly moderates with age and more than 50 years are in general required in order to obtain valuable teak logs. Selection and vegetative propagation of superior teak trees on a commercial scale in India, Indonesia, and Thailand go back to the 1950s. Large-scale international provenance tests were initiated in the 1960s as a joint effort between a number of teak growing countries in Africa, Asia, and Central and South America. This comprehensive series of trials has since shown that large differences exist between seed sources and that the selection of the best origin of the seed is therefore important in order to obtain vigorous growing trees (see **Table 1**). Variation in stem form was also found to be important.

Provenance trials have been established for a number of other tropical hardwoods including a number of widely planted species such as *Milicia excelsa*, *Dalbergia sissoo*, *Dalbergia* spp. (rosewoods), *Swietenia humilus* and *S. macrophylla* (mahoganies), *Gmelina arborea*, but also many lesser known species such as *Vochysia guatemalensis*, and *Zeyheria tuberculosa*. The general finding is that variation between populations is important for almost all investigated species.

Breeding in principle consists of continuous cycles of initial selection of superior trees according to their phenotypic performance, testing by growing the trees under relevant conditions in repeated field trials, analysis of the field trials and selection of superior trees or progenies of trees based on these results, crossing of the selected trees (formation of the next generation breeding population), and initiation of the next breeding cycle by selection in the progenies for second-generation testing. Breeding in terms of such selection and testing for tropical hardwoods have in general not progressed beyond the early stages (first generation). Experiences from fairly intensively bred *Gmelina arborea* and *Tectona grandis* have however indicated that at least selection for stem form and insect resistance are likely to provide good response (**Figure 1**). Breeding of rosewood (*Dalbergia sissoo*) in India and Nepal has also shown that a high level of genetic control exists for growth rate and that good response from selection can be obtained from breeding for both growth and especially stem form. This finding has been repeated in a number of species

Table 1 Relative growth rates (basal area at age 17 years) of 12 teak provenances grown in field trials at Aracruz, Brazil

Origin	*Provenance (location of collection site)*	*Estimated annual rainfall*	*Average growth relative to the fastest growing (%)*
Southern India	Mount Start, Tamil Nadu	2032 mm	100
Southern India	Nilambur, Kerala	2565 mm	96
Southern India	Konni, Kerala	2540 mm	91
Indonesia	Ngliron, Java	1200 mm	86
Ghana (African landrace)	Jema	Not available	69
Laos	Khong Island	1925 mm	58
Northern India	Purunakote, Orissa	1350 mm	58
Laos	Vientienne Town	1570 mm	55
Thailand	Ban Pha Lai	1100 mm	54
Thailand	Ban Mae Pam	1200 mm	47
Northern India	Munda Reserve Forest	1350 mm	47
Laos	Savannakhet	1300 mm	44

Note: The trial site at Aracruz in Brazil has an annual rainfall of approximately 1400 mm. Still, the most vigorous provenances at this planting site come from parts of Southern India, where the rainfall is substantially higher. It is a general observation that the genetic patterns of variation often are difficult to predict without proper testing in field trials. Use of planting material from healthy stands of local origin is therefore often preferred when results from provenance trials are lacking. Adapted from Kjær, E.D., E. Lauridsen & H. Wellendorf 1995. *Second Evaluation of an International series of Teak Provenance Trials*. Danida Forest Seed Centre, Humlebaek, Denmark, 117p.

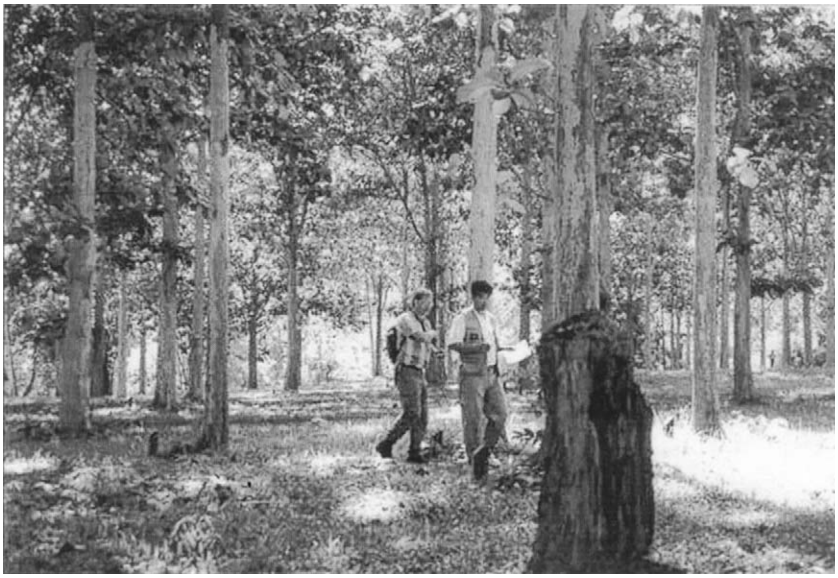

Figure 1 Clonal seed orchard in Northern Thailand. These trees are vegetatively propagated graftings (clones) from so-called plus-trees (very straight trees identified and selected in natural forests in Thailand during the 1960's), and established in order to collect improved seed for planting programs. In front Verapong Suangtho of the Royal Forest Department, Bangkok.

and revealed a pattern that indicates that gains from selection in the early stages are often surprisingly high in many tropical and subtropical species compared to similar findings in temperate species. Over the years, breeding has therefore been accepted as an important means to improve the productivity of plantation species (**Figure 2**).

Propagation

Large-scale propagation of the selected and improved genetic material has proved to be a severe obstacle for large-scale application of many tropical hardwoods. Technically successful breeding programs have in many cases not led to the expected increase in productivity in the plantations, simply because the improved planting material has not been applied at any substantial scale. The problem of effective multiplication is most complicated for species with large fruits, moderate seed, and/or seed that are sensitive to desiccation and therefore difficult to handle and transport. One or more of these features unfortunately characterizes the seed biology of many valuable hardwood species from moist or semimoist tropical conditions, and has by itself limited large-scale application of such species altogether for large-scale planting purposes.

The traditional propagation of improved genetic material is in seed orchards based on seed collection from graftings of the superior trees. However this approach has proven to be much more difficult for many tropical hardwoods compared to the experience from temperate conifers. Thousands of hectares of seed orchards of teak have been established in India, Indonesia, and Thailand, but they have produced only limited commercial seed.

Much research has therefore focused on development of alternative propagation methods to seed. Development of rooted cuttings through application of growth hormones has proven to be a feasible option for a large number of species including several of the difficult dipterocarp species. Development of tissue culture has also been successful for a number of species. Although important findings and important tools for breeding, the vegetative propagation techniques have in general proven to be associated with additional costs that have limited their commercial-scale application with only a few exceptions.

Breeding a Wider Range of Tropical Hardwood Species

Given the thousands of valuable tropical hardwoods, breeding has until recently focused on surprisingly few species. This is probably due to a combination of lack of resources, the partly mythical view that most tropical hardwoods are slow growing (this is often not the case), the preference for growing plantations as monocultures without nurse species, and the fact that many of the species have complicated breeding systems.

Research into Genetics and Population Dynamics of Tropical Hardwood Species

Basic research into the often complicated breeding systems of tropical hardwoods has over the last three decades generated important knowledge for a much larger number of tropical hardwood species. Understanding of pollination ecology is often an important

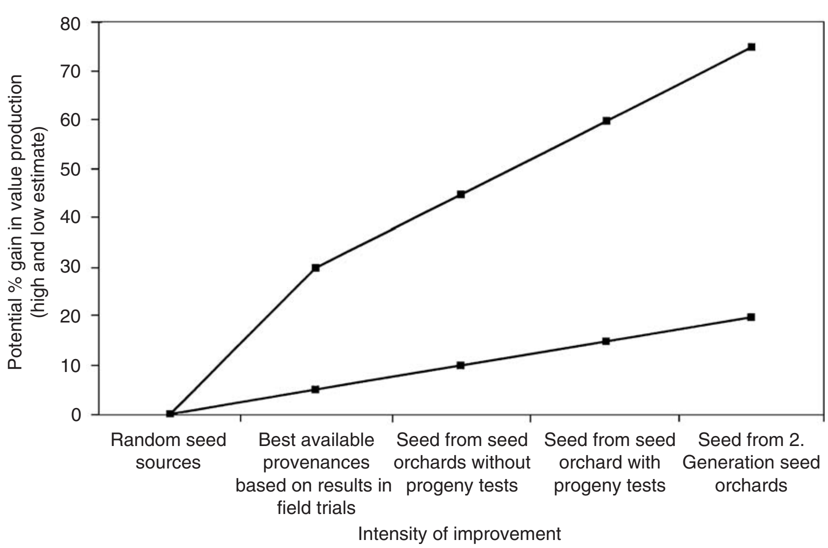

Figure 2 Expected gains from tree breeding. Based on estimates in Foster GS, Jones N, and Kjaer ED (1995) *Economics of Tree Improvement in Development Projects in the Tropics*. In: Environmental and Economic Issues in Forestry: Selected Case Studies in Asia. Edited by Shen S and Converas-Hermosilla A. World Bank Technical Paper no. 281. The World Bank, Washington D.C.

prerequisite for effective breeding programs, and for good management of the genetic resource as such. Formal studies of pollinators and estimation of selling rates and gene flow are time consuming, but results from a number of tropical hardwood species with different pollination syndromes has allowed some important generalizations to be drawn that are valuable for practical management of the genetic resources of tropical hardwoods. These include the recognition that most species are predominately outcrossing and pollen is often dispersed over large distances depending on the pollinators. For example, fig wasps have been found in general to have a pollination radius on the scale of several kilometers whereas beetles often move pollen less than 100 meters. For some species such as some understory woody species, the average pollen movement distance has been found to be only a few meters. The research programs into genetic processes and population dynamics of tropical hardwoods have in most cases been initiated based on concern for their conservation status, where increasing fragmentation of natural habitats is a major concern. However, the findings have also proven very useful for practical breeding and domestication because a basic understanding of the reproductive ecology is important in order to develop effective propagation and genetic management programs.

Breeding of Hardwoods for On-Farm Plantings in Heterogeneous Environments

The large number of potentially important species, combined with the general development towards joint forest management of tropical forest, has in recent years challenged traditional breeding techniques. Further, focus in many forestry programs has moved from industrial plantations to support farmers planting on their own farms in wood lots and agroforestry systems.

Large-scale international provenance trials of dry zone acacias were initiated in the 1980s and these trials have revealed substantial differences in survival and biomass growth according to the origin of the seeds. They indicate that choice of the right seed source is even more important for species growing under dry or semi-dry conditions. Results from domestication of species grown for fodder and fallow (e.g., *Bauhinia* sp. *Sesbaria sesbar*, and *Gliricidia sepium*), gum arabic (*Acacia senegal*), oils (e.g., *Melaleucas*), and other non-wood products (e.g., *Azadirachta indica*) have also proven that these characteristics are often under as high genetic control as growth and stem form. Breeding for non-timber forest products thus seems to be an important option, although often more difficult to select for in practice. On-going research into this issue will contribute important information in the coming years.

New Concepts for Breeding Tropical Hardwoods

The introduction of two important concepts – (1) multiple population breeding and (2) breeding seed orchards – has been an important contribution to development of low-input, genetically diverse breeding programs. The point of departure in multiple population breeding is that a number of smaller, low-input, breeding programs are run in each separate ecologically based breeding zone. This supports local adaptation to ecological conditions and thereby manages the genetic diversity in the breeding program without a number of expensive, repeated tests. The breeding seed orchard is a special planting that serves multiple purposes: it produces seed (seed orchard), tests the genetic entries (progeny trial), and provides the base population of next generation selection (breeding population). This is obtained by establishing a seed orchard based on progenies from selected trees in a repeated block design. The design in terms of plot size, number of progenies and replications, are chosen in breeding seed orchards in ways that accommodate the combined requirements (**Figure 2**).

Interdisciplinary Approaches and Farmer-Based Domestication

Many programs have proven that breeding of tropical hardwoods cannot be done in isolation from the plantation technology and indeed not in isolation from the socioeconomic context. Genetic improvement and propagation remains an academic exercise unless the improved germplasm is distributed and applied by the tree planters. Tree improvement of tropical tree species has therefore gained much in recent years from an interdisciplinary approach that include institutional aspects and participatory methods. Participatory breeding and gene resource management programs for tropical hardwoods enables practical schemes to build on the local knowledge that are essential for breeding for number of non-wood products. Also, participatory breeding is required in order to deal with species cultivated through natural regeneration rather than plantings as is the case in the West African parkland, or species management by farmers at landscape level as is the case with many fodder species in the Nepali middlehills.

See also: **Genetics and Genetic Resources**: Propagation Technology for Forest Trees. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance; Breeding Theory and Genetic Testing; Economic Returns from Tree Breeding.

Further Reading

Bawa KS (1990) Plant-Pollinator Interactions in Tropical Rain Forests. *Annual Review of Ecology and Systematics* 21: 399–422.

Dieters MJ, Matheson AC, Nikles DC, Harwood CE, and Walker SM (eds) (1996) *Tree Improvement for Sustainable Tropical Forestry*. Caloundra, Australia: International Union of Forest Research Organizations.

FAO (2002) *Proceedings from the South Asian Moving Workshop on Conservation, Management and Utilization of Forest Genetic Resources*. Forspa Publication no. 31. Bangkok, Thailand: Food and Agriculture Organization.

Foster GS, Jones N, and Kjaer ED (1995) *Economics of Tree Improvement in Development Projects in the Tropics*. In: Environmental and Economic Issues in Forestry: Selected Case Studies in Asia. Edited by Shen S and Converas-Hermosilla A. World Bank Technical Paper no. 281. The World Bank, Washington D.C.

Gibson GL, Griffin AR, and Matheson AC (1989) *Breeding Tropical Trees: Population Structure and Genetic Improvement Strategies in Clonal and Seedling Forestry.* Oxford, UK: Oxford Forestry Institute.

Leakey RRB and Newton AC (1994) *Tropical Trees: The Potential for Domestication and the Rebuilding of Forest Resources*. London, UK: HMSO.

TREE BREEDING, PRINCIPLES

Contents

A Historical Overview of Forest Tree Improvement

J Burley, University of Oxford, Oxford, UK

© 2004, Elsevier Ltd. All Rights Reserved.

Introduction

Genetic principles have been applied widely in the practice of forest management within the last 100 years although elements of breeding operations were practiced earlier. Various terms have been used to describe the discipline, particularly forest genetics and tree breeding, but a collective term, tree improvement, is useful since it incorporates genetic change, silvicultural improvement, and better use of the end products and services derived from trees.

The twentieth century saw changes in the objectives of forest management and hence of tree improvement, in the species of interest, in the benefits sought, in the nature and number of individual characteristics improved, and in the techniques used. Recently emerging issues include the concept, conservation, and control of the genetic resources that underlie tree improvement, and the application of modern techniques of biotechnology. A number of contributions to this Encyclopedia summarize the state of knowledge of these issues and the progress in genetic understanding and practical improvement of many species.

Concepts of Forest Genetics, Tree Breeding, and Tree Improvement

Forest genetics is generally considered to include Mendelian (traditional) genetics, population genetics and quantitative genetics. Gregor Mendel, an Austrian monk, established the basis for traditional genetics in 1866 with his famous experiments on peas in a monastery at Brno (now in the Czech Republic); these led to his famous laws of heredity (segregation and independent assortment of discrete genes), dealing with the inheritance of traits in relatively small groups of individuals over short periods of time. They concern descendant generation segregation, progeny–parent relationships, linkage of genes and characteristics, and individual gene action (additive, dominance, and epistatic effects).

The implications of Mendel's results were not appreciated by the scientific community until the early 1900s but then agricultural plant and animal breeders effected rapid advances in productivity by the application of these principles. However, they were not applied to forest trees on a significant scale because of the long generation intervals of most trees, especially in commercial rotations; it proved difficult to determine these genetic controls without long-lasting field trials until the development of biochemical methods allowed the identification and tracking of individual genes and character controls. Although some efforts were made earlier, it is