Southern Pine Breeding and Genetic Resources

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The Southern Pines

The southern pines include four major and six minor species. Together, they make up much of the commercial wood production in the USA supplying approximately 56% of the overall wood consumed (**Table 1**). Southern pine is used for both solid-wood products such as dimensional lumber, plywood, and engineered structural beams and panels and for various pulp and paper products of which linerboard is a main application.

Loblolly pine (*Pinus taeda*) occurs throughout the South and ranges from Texas to Delaware, with only one major discontinuity, in the Mississippi River valley (**Figure 1**). It does not occur in the southern part of Florida. It has acceptable wood quality, is widely adapted and grows rapidly.

Loblolly pine seedlings account for over 80% of the annual nursery production in the South.

Slash pine (*P. elliottii* var. *elliottii*) occurs naturally only in the coastal plain east of the Mississippi River although it has also been widely planted as an exotic west of the Mississippi River in the coastal plains of Louisiana and Texas (**Figure 2**). It is popular for its rapid early growth, resistance to fire and tipmoth (*Rhyacionia frustrana*), and adaptability to phosphorus-deficient sites. Despite its rapid early growth and excellent form, it is ultimately outgrown by loblolly pine on most sites. However, its importance has declined primarily because of its susceptibility to fusiform rust (*Cronartium quercuum f. sp. fusiforme*) and its limited geographic range. Although rust-resistant varieties are now available, the species has not regained its former popularity.

Shortleaf pine (*P. echinata*) has the widest natural range of all southern pines. It occurs from New York to Texas, and is better adapted to heavy soils than some of the others. It also is well adapted to somewhat higher elevations, occurring in the Appalachian and Ozark Mountains as high as 1000 m. Very little shortleaf pine is planted commercially, because of its slow early growth and its susceptibility to tipmoth.

Longleaf pine (*P. palustris*) occurs in the coastal plain from Texas to Florida and north to Virginia. It forms a rosette, called the 'grass stage,' after germination. Under natural conditions, the grass stage will persist until a fire eliminates needles infected with brownspot disease (*Scirrhia acicola*), and reduces the surrounding competition and accumulated fuel. It will then grow very rapidly and become tall enough to be fairly resistant to the next fire. The species is difficult to plant, but is making an appreciable comeback with the use of containerized seedlings. It is prized for its straight stems and high-quality wood.

Southern pines are widely planted around the world as exotics. Many of the planting programs are supported by breeding efforts. Continents include South America (Argentina, Brazil), Australia, Asia (China), and Africa (South Africa, Zimbabwe, Swaziland, Malawi). The techniques used are similar to those described for the southern USA, but in slash pine somewhat more emphasis is placed on hybridization.

The minor southern pines include pitch pine (*P. rigida*), pond pine (*P. serotina*), sand pine (*P. clausa*), spruce pine (*P. glabra*), table mountain pine (*P. pungens*), and Virginia pine (*P. virginiana*). There are limited breeding programs to improve Virginia pine, which is widely planted for Christmas tree production. Most of the southern pines are closely related and belong to the subsection Australes

Table 1 Volume of roundwood products by southern pine species and type of product, 1996. Data from "National forest inventory and analysis," USFS.

Species group	*Saw logs*	*Veneer logs*	*Pulpwood*	*Composite products*	*Fuelwood*	*Post – poles – pilings*	*Other products*	*All products*
(a) Volume in millions of (m^3)								
Loblolly – shortleaf pine	56.5	17.5	45.4	2.2	2.3	0.9	0.1	125.0
Longleaf – slash pine	14.4	2.6	17.0	0.2	0.5	0.8	0.3	35.7
Major southern pines	70.9	20.1	62.4	2.4	2.8	1.7	0.4	160.7
Total US softwoods	146.1	31.8	80.7	3.2	14.0	4.7	3.7	284.2
(b) Volume as a percentage of total US grown softwoods								
Loblolly – shortleaf pine	38.7	54.9	56.2	67.7	16.3	20.5	2.9	44.0
Longleaf – slash pine	9.9	8.3	21.1	5.4	3.5	16.2	8.4	12.6
Major southern pines	48.6	63.2	77.3	73.1	19.8	36.6	11.2	56.5

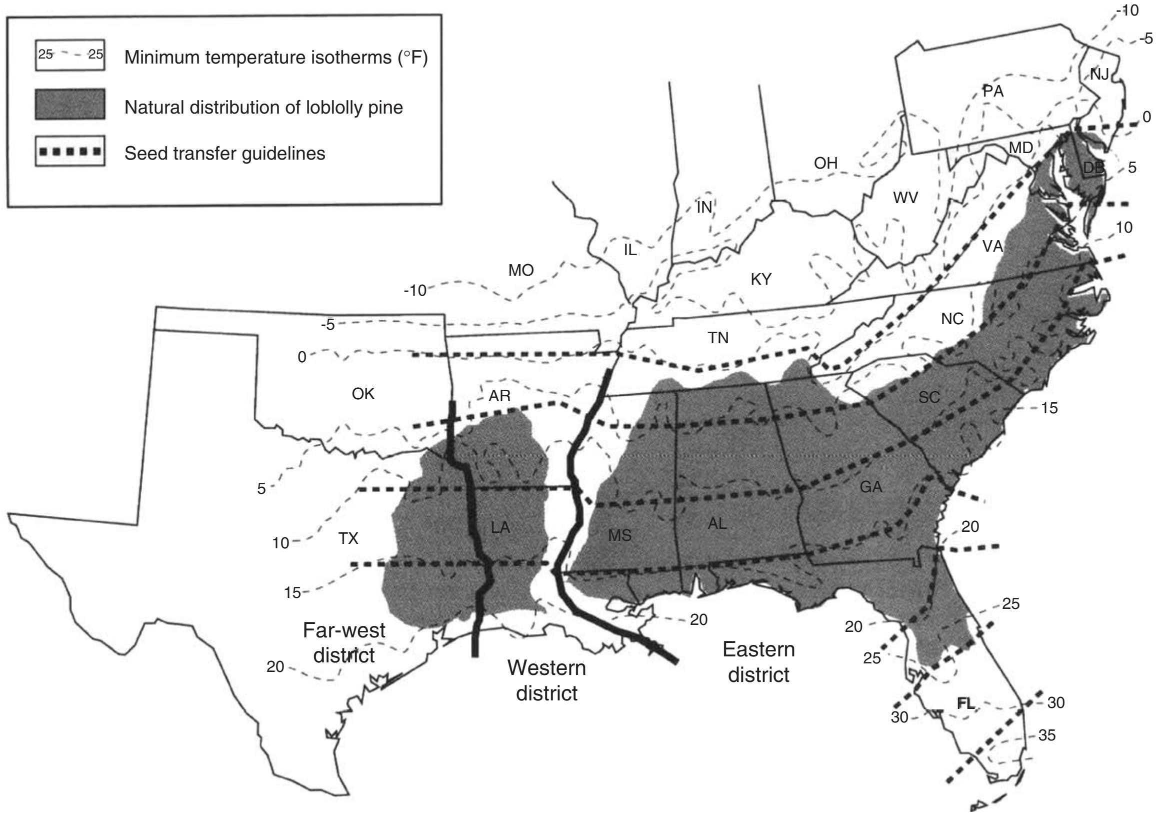

Figure 1 Natural range of loblolly pine with guidelines for the transfer of seed. From Schmidtling RC (2001) *Southern Pine Seed Sources*, General Technical Report no. SRS-44. Asheville, NC: USDA, Forest Service.

(southern yellow pines) of the genus *Pinus*. The exceptions are Virginia pine and sand pine, which belong to the subsection Contortae. As a result many of the southern pines can be crossed readily.

The Southern Pines as a Genetic Resource

Natural Variation

The southern pines have much natural variability, which is basically intact because domestication has just begun. As a result both natural stands and current breeding programs are rich genetic resources. Genetic variation exists at various levels: regional, stand-to-stand, and among trees within stands. In natural stands, the tree-to-tree variation is most striking, while variation among stands is much less. Regional variation is also of major importance, particularly in species with large natural ranges. Elevational races are only important in species such as shortleaf pine whose range includes mountainous areas. Of the major species, loblolly pine and shortleaf pine are the most variable, while slash pine is most uniform. The variability (**Figure 3**) has been studied extensively, by means of *in situ* studies, geographic variation studies, heritability studies, and progeny tests done in the course of breeding programs.

Since natural regeneration is practiced on much of the public and nonindustrial private land, which comprises more than half of the forest land in the South, a major portion of the gene pool is preserved in its natural condition. In addition the breeding programs are making a concerted effort to preserve a large number of genotypes in test plantations and grafted scion banks.

Geographic Races

Loblolly pine and shortleaf pine, as discussed earlier, have very large ranges and the resulting geographic variation presents opportunities for spectacular successes and disasters. Loblolly pine from Livingston Parish, Louisiana, has done extremely well over a very large area, combining good growth rate with resistance to fusiform rust, while most southern pines from east of the Mississippi River do very poorly in East Texas. A major geographic variation study was undertaken to provide a scientific basis for the geographic movement of seed and seedlings.

The so-called Southwide Geographic Seed Source Study (SGSSS) was the first organized attempt to delineate these geographic trends. This study was

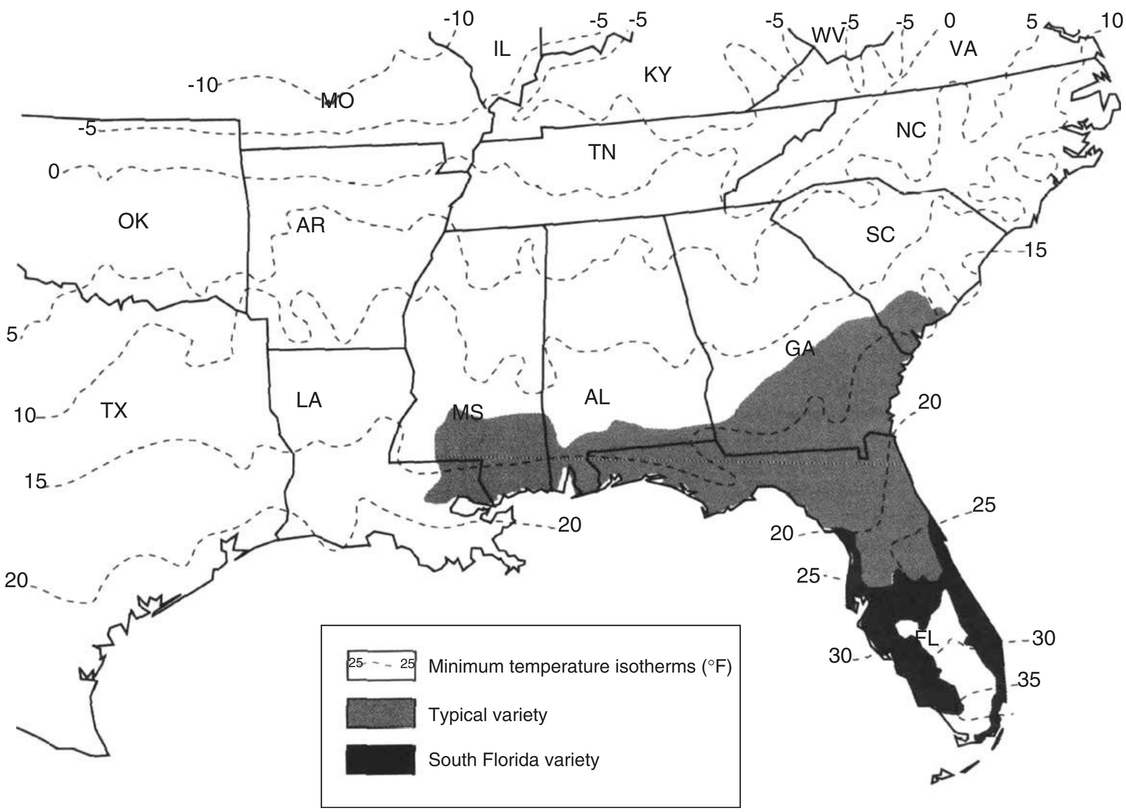

Figure 2 Natural range of slash pine with minimum temperature isotherms. From Schmidtling RC (2001) *Southern Pine Seed Sources*, General Technical Report no. SRS-44. Asheville, NC: USDA, Forest Service.

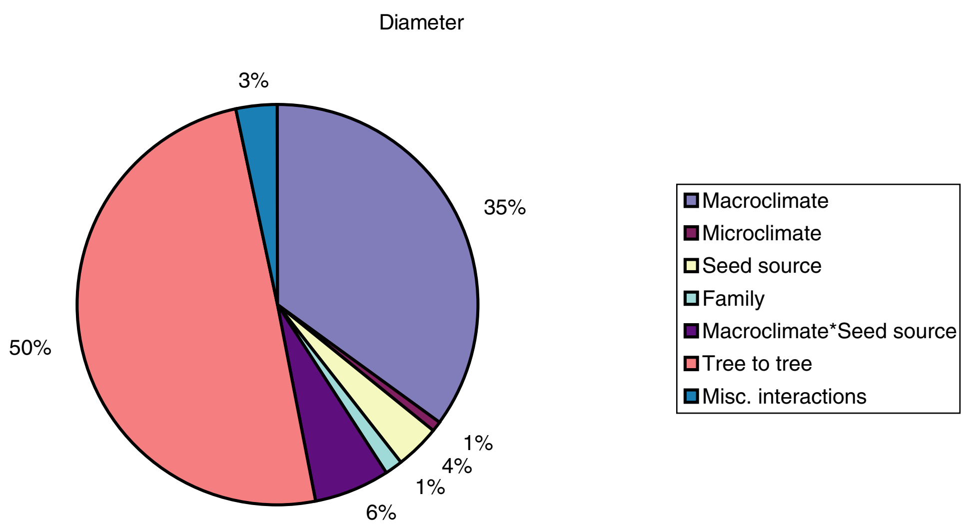

Figure 3 Breakdown of the total variation within the western part of the loblolly pine range into its variance components. Results are based on Western Gulf Forest Tree Improvement Program Geographic Variation Study Series 1.

undertaken in 1951 by the Southern Forest Tree Improvement Committee, with the Southern Experiment Station of the US Forest Service playing a major role. It was a truly cooperative effort with 17 organizations including industries, forestry schools, State agencies, and the US Forest Service participating. The study was nonintensive, with one or two seed collections and a similar number of plantings from each State, but it provided extremely important results that still provide the guidelines for the movement of southern pine germplasm throughout the South (**Figure 1**).

The SGSSS was followed up by individual studies using a finer grid. The most recent general guidelines provided on the basis of these studies are:

> Seedlings will survive and grow well if they come from any area having a minimum temperature within 5°F of the planting site's minimum temperature. Seedlings from an area with warmer winters will grow faster than seedlings from local sources; seedlings from an area with cooler winters will grow slower…. The difference in winter lows can be as much as 10°F, but with increased risk of damage at the cold end of the range and growth loss at the warm end. East–west transfers within districts are usually successful, and in some instances may be desirable if improved stock is available.

History of Southern Pine Tree Improvement

Several factors contributed to the establishment of large-scale breeding programs in the South. The virgin forest had largely been cut over by early in the twentieth century and large scale-planting programs had been undertaken partly in response to the Great Depression and the soil erosion that resulted from drought and poor farming practices. At the same time, research in Sweden, Denmark, and the USA was showing that choosing the right seed source was important for successful regeneration of forest stands.

As told by Zobel and Sprague, one crucial event galvanized the forestry community of the South into action. At that time the Swedes were most advanced in the study of forest genetics. In 1950, Dr Åke Gustafsson gave an inspiring lecture on his accomplishments as a crop breeder, which was attended by the State Governor of Texas, the director of the Texas Forest Service, and a number of forest industry leaders. As a result the Texas Forest Service started a cooperative tree improvement program in 1951, hiring Bruce Zobel to lead the effort, and as they say: the rest is history. About that time, the University of Florida Cooperative Forest Genetics Research Program was started under the direction of Tom Perry. In 1956, Bruce Zobel moved to North Carolina, starting the cooperative at North Carolina State University. At the time, the model of a cooperative tree improvement program was novel, based on some very good biological, economic, and psychological reasons. It allowed the participants to pool their genetic and financial resources and their technical expertise. The free exchange of genetic material and information among the members was crucial to the success of the individual programs. The cooperative spirit of those early days was very different from the competitiveness frequently fostered by the current research and economic climate. Genetic expertise was scarce, the task was too large for the resources of one organization, forests were not seen as profit centers, and the critical mass achieved in the early cooperative programs generated a spirit of enthusiasm.

Approach to Breeding

The Seed Orchard Approach

Most tree improvement programs for the southern pines followed the seed orchard approach to forest tree breeding (*see* **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement). This consisted of mass selection of superior phenotypes in natural stands, followed by the concurrent establishment of seed orchards for the production of commercial seed and progeny tests to determine the genetic value of the selected parents. When results of the progeny tests became available, these data were used to 'rogue' the seed orchards (i.e., remove clones of poor genetic value). With this genetic base established, the breeding programs continued as recurrent selection programs.

Major Phases of the Breeding Programs

Initially, a major effort was expended in locating superior trees in natural stands. The selection criteria reflected the breeding objectives with the relative merit of the candidate trees judged by an elaborate grading system that compared their performance to that of their neighbors. Selection efforts were eventually extended to locating candidate trees in unimproved plantations to serve both as infusions and expansions of the original breeding populations.

The breeding objectives differed somewhat depending on the species, the intended deployment zone, and the desired product. Initially, there was great emphasis, particularly in loblolly pine, on the improvement of stem straightness. Rust resistance was a major criterion in areas where rust was a major problem. This was the case for loblolly pine for planting in Georgia, and for slash pine in some parts of its natural range and in all the areas where it was planted as an exotic. Of course, height and volume growth were of major importance in all programs and for all species. In some programs, great effort was also expended on wood quality research, although the selection pressure exerted to improve wood quality was actually very mild.

The grading systems were basically a form of index selection, rating the merits of various traits, but without the benefit of known heritabilities or genetic correlations between traits. The candidate tree was compared to a number of check trees in the immediate neighborhood and given points according to its degree of superiority. After a candidate was identified, a grader employed by one of the tree improvement cooperatives would evaluate the tree to make the final judgment as to whether it should be included in the breeding population. A great many trees were rejected in the process. In any case, hundreds of thousands if not millions of trees were screened to identify the individuals that were ultimately included in the breeding population.

Plantation selections were depended on heavily for the base populations, which caused some concern because the geographic origin of many of the plantations was not known. Fortunately the results of extensive geographic seed source studies of plantation selections have paralleled those of seed source studies from natural stands.

Simultaneously with this tree selection effort a great deal of time was devoted to developing grafting techniques. Grafting the southern pines was not easy, and it took several years before a high success rate was obtained. The most successful types of grafts today are cleft grafts, side grafts and side-veneer grafts. Using these techniques thousands of hectares of seed orchards were established (**Figure 4**). Progeny test procedures also went through a long period of evolution. Initially, mostly open-pollinated or wind-pollinated progeny tests were established as this could be done quickly and cheaply. Gradually these were replaced by control-pollinated tests, as pollination procedures were developed (**Figure 5**). The most popular scheme in the early days was the four-tester scheme in which all clones in an orchard were pollinated with the same four 'males'. This scheme accurately evaluated the genetic quality of the female parents, but it soon became clear that advanced-generation selections from this scheme would be highly interrelated and that inbreeding would be a serious problem in the next cycle of orchards. As a result most organizations shifted to various types of diallel schemes. A complete diallel is the set of all possible crosses among the parents to be evaluated. Since the number of crosses goes up as the square of the number of parents it rapidly becomes unwieldy. A 30-clone orchard, for example, would require 900 controlled crosses. Various types of partial diallel are obtained by systematically sampling the complete diallel to get a good representation of all parents, while keeping the number of crosses within reason.

The field layout of the progeny tests also changed dramatically over the years. Row-plots and block-plots of as many as 100 trees were popular in the 1950s, but it soon became apparent that these tests were statistically inefficient. Also, they took up excessive land, since trees cannot be spaced anywhere near as closely as agricultural crops. The scheme evolved to short rows repeated many times and the whole test repeated at three to four different locations. Currently, many tests are laid out as single tree plots, where each cross in a block is represented by one individual. Randomized complete blocks are commonly used but incomplete blocks where entries are randomized with some restrictions are also used by some programs.

Advanced-generation breeding presented some new hurdles. The age of selection was the first. Ideally, one should select trees at maturity, when all harvest-age characteristics are known. However, this would be an extremely slow process. Theoretical considerations based on available progeny test data showed that genetic gain per year could be maximized by making selections much earlier. The consensus was that selection some time between ages 5 and 10 would be optimal. Considerable research was done to move the selection age even earlier by selecting families based on seedling measurements. At this time it would be very risky to select individual trees on this basis. However, some traits can be measured quite early on seedlings, and

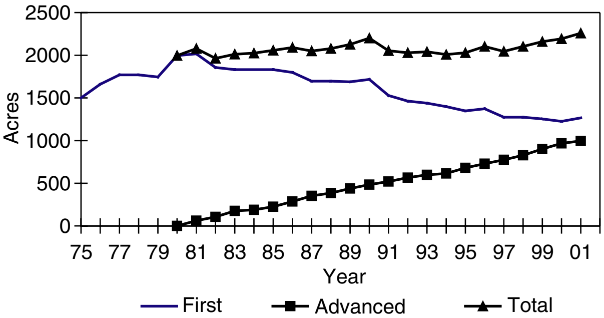

Figure 4 Western Gulf Forest Tree Improvement Program seed orchard acreage from 1975 through 2001.

Figure 5 Bucket trucks are widely used in southern pine seed orchards for pollination (shown here) and cone collection. Photograph courtesy of Texas Forest Service.

one can eliminate some families based on early testing data. Some cooperatives adopted stepwise screening, whereby measurements on greenhouse grown seedlings are used to eliminate poorly performing families before field testing. This resulted in considerable cost savings. Traits that have proven amenable to this procedure include rust resistance in loblolly and slash pine, and growth rate in some provenances of loblolly pine.

Inbreeding and potential inbreeding depression also presented a major problem. This is being managed by subdividing the population into smaller populations called breeding groups or sublines. By limiting crosses made for breeding purposes to matings among members of breeding groups, but designing the orchards so that mating would occur between individuals from different groups, one could confine inbreeding to the breeding population and ensure that seed produced in seed orchards would be largely outcrossed. The approach is somewhat similar to the use of inbred lines in corn, but in corn the lines are purposely inbred and specific crosses are made to combine hybrid vigor (heterosis) with crop uniformity. In southern pines, inbreeding is still avoided as much as possible, even within sublines, while the seed orchards are composed of the best available parents arranged in unrelated groups.

Several organizations have initiated elite breeding populations, or super breeding groups, consisting of only the very best individuals from all the sublines or combinations of breeding groups. These populations are generally a supplement to the mainstream breeding program, being intended to capture additional genetic gain for use in the production population.

Recently increased emphasis is being placed on genetic conservation as an integral part of long-range breeding. The preferred method of conserving genotypes is through grafting into scion banks: a strategy of *ex situ* conservation. Long-term seed storage, commonly used in agriculture, is not very practical for the southern pines. It is not very reliable and would require that stands of trees would be established periodically to replenish the seed. In the absence of inbred lines there is a substantial risk that rare genes would be lost in the process. This approach complements *in situ* conservation through natural regeneration, which is still widely practiced in the South particularly on public and nonindustrial private land.

Accomplishments

The scale at which the tree improvement programs operate is truly staggering. Loblolly pine serves as a good example, since it is the most important species and figures are most readily available. In the initial phase, thousands of selections were made. Over 10 000 have now entered the breeding population (**Table 2**). Individual breeding populations are of course smaller, since breeding is a localized effort, but they are generally of the order of 1000 trees per population (**Figure 6**). Seed orchard acreage increased rapidly in the early years and reached a maximum of about 3900 ha (10 000 acres), leveling off and decreasing after that time because of increased efficiency of seed production as orchards aged. The initial orchards have now largely been replaced by newer selections. Many cooperative member organizations are operating on the advancing-front concept, where every few years an old section is replaced with the best selections currently available.

Southwide, over 1 billion improved seedlings are produced annually. These are sufficient to regenerate about 800 000 ha (2 million acres) per year (**Figure 7**). The genetic gains reported for volume growth range from 10% to 35%. The combined

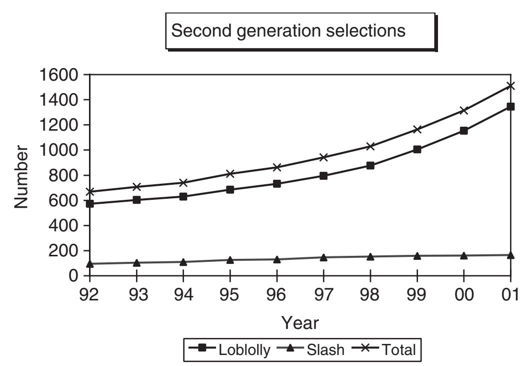

Figure 6 Western Gulf Forest Tree Improvement Program second generation selections from 1992 through 2001.

Table 2 Loblolly selections forming genetic base of North Carolina State and Western Gulf Forest Tree Improvement Program Cooperatives

	1st generation	*Plantation selections*	*2nd generation*	*3rd generation*	*Total*
Western Gulf Forest Tree Improvement Program	3350		1345		4695
North Carolina State	580	3120	680	778	4578
Total	3350	3120	2025	778	9273

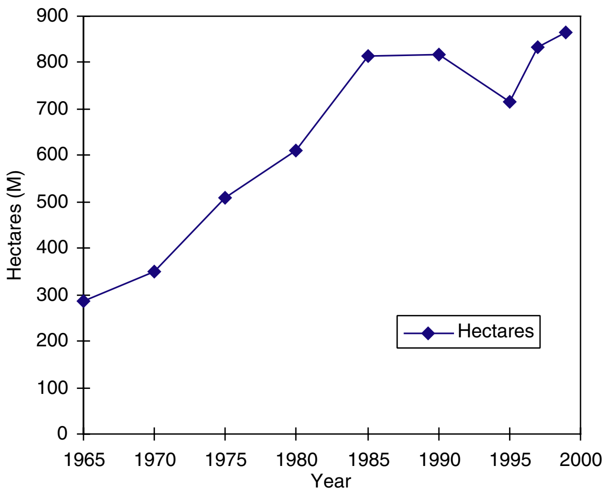

Figure 7 Area planted annually in the southern USA from 1965 through 2000. Based on data in Southern Forest Resources Assessment Draft Report. Data from USDA Forest Service, Southern Research Station.

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

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Tropical Hardwoods Breeding and Genetic Resources

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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