Chapter 2

Genetic Improvement of Forest Trees

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Introduction

In this chapter, readers can gain a basic understanding of why certain procedures are used to improve forest trees. The references listed can be used as a source for obtaining more detailed information, both historical background and technical details. Examples are frequently cited from operational tree improvement programs to focus the chapter on an applied level. Although many of the examples are taken from the author's professional focus of over 40 years in the southern United States, the principles they exemplify can be used world-wide.

Terminology

Many of the terms used in this chapter are listed in the Glossary; a more detailed glossary may be found in Snyder (1972) and Wright (1976). Comprehensive references on forest genetics include Dorman (1976), Wright (1976) and Zobel and Talbert (1984).

"Forest genetics" is the general term often used for the study of inheritance in forest trees, whereas "forest tree improvement" usually refers to the applied use of forest genetics to actually improve the quality of the trees. "Tree breeding" is often used as a synonym for tree improvement, but it also may be found referring to specific activities such as controlled pollination. Zobel and Talbert (1984) define forest tree breeding as "activities geared to solve some specific problem or to produce a specifically desired product." Tree improvement will be the term used most frequently in this chapter.

It is important to understand that tree improvement is an integral part of silviculture. Tree improvement provides the raw material for artificial regeneration, which is one of the most important weapons in the arsenal of the silviculturist. Tree improvement provides a direct avenue to introduce genetically improved seedlings (or cuttings) into the reforestation system with no additional "handling fees." It costs no more to plant a genetically improved seedling than a "woods-run" seedling. (Note that although the costs of producing genetically improved planting stock are not insignificant, they can be viewed as an investment in future increased productivity. Dividends accrue in terms of increased growth, better form and wood quality, and improved insect and disease resistance).

Allocation of Resources

One of the key elements of land management is allocation of resources. An ever-expanding world population demands an ever-increasing supply of wood products. These must be produced on both private and public lands. The most productive sites should be devoted to maximum timber production. Maximum wood production on these acres relieves the pressure on other acres, which can be devoted to native vegetation, wildlife production, aesthetic considerations, and other uses not compatible with maximum timber production.

Even those acres devoted to maximum wood production via artificial regeneration with genetically improved planting stock are not lost to most aspects of good forest management practices. These acres will support strong wildlife populations, preserve watersheds, and provide many recreational opportunities. All these are fully compatible with timber production.

Monoculture

Critics of plantation forestry programs often cite the dangers of monoculture as reasons to reject these programs. The reasons quoted range from disease outbreaks to site deterioration, but usually focus on lack of biodiversity. In point of fact, there are few documented cases of severe problems, even in clonal plantations. Where there have been losses from pathogens, the increased productivity of the plantations usually greatly overbalances the losses. [It should be noted that most Forest Service restoration plantings after fire and logging are not monocultures. Seedlings of the various species that are planted are grown from seeds collected from areas near the new site.]

There can be interactions between intensive culture and diseases, as in the case of fusiform rust—*Cronartium quercum* (Berk.) Miyabe ex *Shirai* f. sp. *fusiforme* (Hedgc. & Hunt) Burdsall & Snow—which may be increased by site preparation procedures and fertilization (Miller 1972). Some clonal plantations such as those of cottonwood and eucalyptus have encountered disease problems, but these are often due to "off-site planting" (that is, growing a species on a site for which it is poorly adapted) rather than the lack of genetic diversity. Even the fabled case of "Saxony spruce" in which pure stands of Norway spruce—*Picea abies* L.—were blamed for "site deterioration" was actually due to off-site planting. This, in conjunction with poor management and poor seed source selection, led to drastically decreased productivity of the plantations (Lutz and Chandler 1946).

Gene Conservation

The fundamental concepts of gene conservation are an integral part of the tree improvement process. In the preservation of selected trees in seed orchards, clonal banks and progeny tests, valuable germplasm is not only preserved but also replicated on different sites where it may enrich local tree populations via wind pollination. The planting of genetically improved seedlings on new sites likewise enriches the local gene pool of that species. Future populations of these trees can be expected to be more heterogeneous than the local stands as well as more productive (Namkoong 1974).

During the selection and breeding of forest trees, a tremendous volume of data is generated regarding species—site interactions, growth and tree quality information, and other physiological relationships. These data serve to increase our understanding of the importance of high-quality seedlings that are well-adapted to the planting site. Good forest stewardship requires vigorous, fast-growing trees as well as a diversity of flora and fauna.

The use of isozyme analysis has been adopted by many forest geneticists as a tool for estimating diversity in natural populations. For example, Shimizu and Adams (1993) used isozyme analysis in natural stands of Douglas-fir—*Pseudotsuga menziesii* (Mirbel) Franco—and found no evidence that planting nursery-grown seedlings contributed any less genetic diversity than natural regeneration.

Tree Improvement Versus Crop Improvement

The genetic improvement of forest trees has many similarities to the breeding of field crops. Most of the concepts are the same, namely the selection of above-average individuals from large populations, and subsequently breeding these individuals using a specified mating design. Following the breeding phase, the progeny must be tested on a variety of sites and under differing climatic conditions. Progeny tests are specially designed genetic tests that expose hereditary differences among trees, by bringing different genotypes together under a common set of environmental conditions.

When the progeny have developed sufficiently for a reliable assessment of their value, improved individuals or groups can be released for operational use and/or the breeding cycle can be repeated.

There are two major differences between working with field crops and forest trees. The first is time. Field crops such as corn and wheat reach reproductive maturity in a few months, while most trees require many years. Crop rotations with corn and wheat are also only a matter of a few months whereas trees may not produce a marketable crop for 25 to 100 years! Even in the tropics, it is rare to harvest a timber crop in less than 8 or 10 years. In practical terms, this means that a corn or wheat breeder can complete a breeding cycle in 2 or 3 years compared to the tree breeder's 8 to 10 years, at the very least (table 1).

Table 1—Chapter 2, Genetic Improvement of Forest Trees: the time factor

	Field crops	Trees
Reproductive maturity	1–2 months	5–20 years
Rotation length	4–6 months	10–100 years
Breeding cycle	1–2 years	8–20 years

The second major difference is that most field crop breeding is done with domesticated varieties that have been manipulated by humans for centuries and are often genetically homogeneous. Forest tree breeding, in contrast, usually starts with wild stands of trees that have been little-changed by humans. An exception here is "high-grading," the common logging practice of cutting the best quality trees and leaving the worst to regenerate the next generation. Unfortunately, tree improvement foresters are often forced to work with the results of one or more cycles of high-grading, namely trees of poor form and marginal value for breeding material. On the other hand, working with wild, unselected stands of trees does provide an opportunity to produce large gains in quality in the first few generations of breeding.

Field-crop breeding, therefore, usually involves working with well-known varieties that are often pure lines (genetically pure). With corn, for example, pure lines are crossed to produce heterozygous (genetically different) progeny that exhibit hybrid vigor (improved performance due to the interaction of different genotypes). Site considerations are also important here, as the corn will be planted on uniform, well-prepared sites while the trees may be planted on rough, cut-over sites with little or no site preparation. Adaptation is also a consideration as the corn is bred for a very narrow spectrum of soils, sites, and climatic zones. The trees, on the other hand, may be planted over a much wider range of soils, sites, and climatic zones.

The Biology of the Species

The genetic improvement of any crop will be effective only after a careful analysis of the biology of the species and how this influences the breeder's approach to the problem. For example, insect-pollinated species require special considerations from tree breeders. Genera such as maple (*Acer* L.), tuliptree (*Liriodendron* L.), magnolia (*Magnolia* L.), some species of willow (*Salix* L.), basswood (*Tilia* L.), and many tropical species are all insect-pollinated and, therefore, cannot be managed with the same techniques as wind-pollinated species. The majority of commercial timber species are both wind-pollinated and monoecious, producing both male and female "flowers" (cones or stroboli) on the same tree. The location of these stroboli usually favors cross-pollination. For example, most conifers bear female cones in the upper areas of the crown with the male cones below, usually favoring cross-pollination rather than self-pollination.

Cross-pollination, in most plants, is an adaptation designed to increase heterozygosity, which is usually linked to vigorous growth, high fertility, and strong resistance to attack by pathogens. Conversely, self-pollination often leads to poor growth, weakness, and reduced fertility. Most breeding programs are designed to favor cross-pollination for these reasons.

Some tree species are dioecious, with the sexes separated on different trees. Members of the following genera are dioecious: ash (*Fraxinus* L.); holly (*Ilex* L.); juniper (*Juniperus* L.); poplar, cottonwood, and aspen (*Populus* L.); willow (*Salix* L.); and yew (*Taxus* L.). Fortunately, many of these genera can be propagated vegetatively. Also, in the case of the poplars, cross-pollination can be accomplished very quickly on a greenhouse bench by simply brushing pollen onto the receptive female flowers (Miller 1970).

Precocious (early flowering) species are adaptable to seedling seed orchards because they produce flowers at a young age and their seed production is abundant. Examples include Virginia pine (*Pinus virginiana* P. Mill.), sand pine (*P. clausa* (Chapman ex Engelm.) Vasey ex Sarg.), lodgepole pine (*P. contorta* Dougl. ex Loud.), and European black alder *(Alnus glutinosa* (L.) Gaertn.). Species that can be vegetatively propagated present unique opportunities because sexual reproduction is not necessary, and, therefore, the recombination of parental characteristics can be avoided. Species such as eastern cottonwood (*Populus deltoides* Bartr. ex Marsh.) can be produced vegetatively with unrooted stem cuttings planted directly in the field (figure 1). Other species require rooting under special conditions before they can survive field planting. These include Monterey pine (*Pinus radiata* D. Don), Norway spruce (*Picea abies* (L.) Karst.), tsugi (*Cryptomeria japonica* (L.f.) D. Don), Alaska-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach), sweetgum (*Liquidambar styraciflua* L.), and sycamore (*Platanus occidentalis* L).

Figure 1—Chapter 2, Genetic Improvement of Forest Trees: hybrid poplar plantation in Oregon planted from unrooted cuttings.

Concepts of Genetic Improvement

Phenotype and Genotype

When we look at an individual Sitka spruce (*Picea sitchensis* (Bong.) Carr.), a cherrybark oak (*Quercus pagodafolia* Raf.), a Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), or even an Angus bull, for example, we see a phenotype, a living organism with its own unique genetic constitution, as modified by its environment. In contrast, the genotype of the organism is encoded in its DNA. Each tree, therefore, has its own individual set of genetic blueprints. These are the instructions that will determine the genetic potential of its progeny.

The formula that "phenotype is the product of the genotype as affected by its environment" is often written as $P = G + E$. The phenotype is the organism that we see, measure, and with which we work. Life would be much simpler if the genotype was as obvious! Geneticists spend a great deal of their time and energy working to ascertain the actual genotype of their target organism. A major reason for progeny testing is to gain a better understanding of the genotypes of the selections that we are breeding. Recent advances in gene mapping with loblolly pine (*Pinus taeda* L.) (Sewell and Neale 1995) indicate that real progress is being made with the description of the loblolly genome. Some day we will understand the genomes of important commercial conifers as well as we understand common research bacteria and the common fruit fly.

The Genetic Code

The physical basis of genetic information is the DNA molecule, a long double helix of base pairs. This molecule is sufficiently stable to provide for the continuity of the species, yet flexible enough to allow for periodic changes. DNA therefore serves as both the blueprint for cell structure and metabolism and also the template for replication of many exact duplicates. These unique properties enable evolution to proceed in a remarkably stable universe. The evolutionary forces of mutation, migration, hybridization, and natural selection are responsible for the great variety of life that exists today.

New genotypes that result from mutations may move about (migration) and interbreed with other genotypes (hybridization). The new gene combinations that result are then sorted out by the process of natural selection. If these new genotypes are able to survive, reproduce, and leave more progeny than their competitors, they are "well-adapted." Therefore the tree species, races, and stands with which we are working are well-adapted to a specific site by virtue of their survival and reproduction in that environment.

Chromosome numbers. Chromosome numbers can change as a result of mutations. Polyploidy has been an important evolutionary factor in the plant kingdom. In most of the commercially important conifers, chromosome numbers range from n = 11 to 23 (Saylor 1972)(table 2). A notable exception is redwood—*Sequoia sempervirens* (Lamb. ex D. Don) Endl.—which is hexaploid (6n = 66). In contrast, chromosome numbers in the commercially important broadleaved trees vary widely, from n = 7 to 19, with a number of polyploids, including the genus alder (*Alnus* P. Mill.), birch (*Betula* L.), several *Prunus* species, and magnolias. A comprehensive table of chromosome numbers is found in Wright (1976).

Selection. Almost every process of genetic improvement starts with selection. This is true regardless if we are working with dairy cattle, winter wheat, or forest trees. The concept of selection involves the selection of a very small proportion of a population for one or more desirable characteristics. The difference between the proportion selected and the population mean (average) is called the selection differential.

Genetic gain or progress is measured by the product of the selection differential and the heritability (degree of genetic control) of the trait in question (for example height, straightness, and volume). Therefore by selecting individuals that are well above average in height, and assuming that the heritability (h^2) of height growth is sufficiently high to show progress, some gain in height should be expressed in the next generation. On the other hand, if the population in question is extremely uniform in height, and/or the heritability of height growth is low, selection may not be an effective approach. In some species, for example red pine—*Pinus resinosa* Soland.—the population is so uniform that selection for many traits is not cost-effective (Fowler and Morris 1977).

Hybridization

When populations are uniform and selection is not likely to be effective, one possible technique of genetic improvement is hybridization. Most of the successful hybrids in forestry have been interspecific (between species) hybrids. Examples include hybrid larch (*Larix leptolepis* x *decidua*), hybrid poplars (*Populus* spp. widely hybridized with many cultivars), the *Pinus rigida* x *taeda* cross in Korea (Hyun (1976), and the eucalyptus hybrids (Campinos 1980).

Heterosis (hybrid vigor) is a controversial topic among tree breeders. Many interspecific hybrids grow better than their parental species when planted in transitional environments. The actual quantitative documentation of heterosis is seldom published however.

A great deal of effort has been expended to produce a hybrid chestnut resistant to the chestnut blight—*Cryphonectria parasitica* (Murr.) Barr. Unfortunately, the American chestnut—*Castanea dentata* (Marsh.) Borkh.—which was devastated by the disease in the early 1900's, has little resistance to the disease. It is possible to cross American chestnut with Chinese chestnut—*C. mollissima* Blume—which is resistant to the blight. The hybrids produced are resistant, but unfortunately their form is so poor

Table 2—Chapter 2, Genetic Improvement of Forest Trees: chromosome numbers for some commercially important genera

# chromosomes	Genus
11	*Juniperus, Nyssa, Sequoia, Thuja*
12	*Abies, Larix, Picea, Pinus, Quercus, Tsuga*
13	*Acer*
14	*Betula*
15	*Liquidambar*
16	*Carya, Juglans*
19	*Liriodendron, Populus, Salix*
21	*Platanus*
23	*Fraxinus*

that they have little value as timber trees. There are two possible approaches to this problem. One is genetic engineering; the other is back-crossing to pure American chestnut. The American Chestnut Foundation has produced many successful back-crosses with the potential of restoring this grand tree to its former dominance in the eastern hardwood forest.

Many tree species that coexist on the same sites maintain their status as separate species primarily by a separation of flowering time. On transitional sites (ecotones) when one species is accelerated or retarded in flowering time, hybrids often result as in the case of the Coulter pine (*Pinus coulteri* D. Don) x Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) hybrids in California (Zobel 1951) and the pond pine (*Pinus serotina* Michx.) x loblolly pine (*P. taeda* L.) mixtures in North Carolina (Saylor and Kang 1973). Hybridization often occurs near the edge of the range where the species is losing its adaptive advantage. In southeastern Oklahoma and northeastern Texas, shortleaf (*P. echinata* P. Mill.) and loblolly pines occupy many sites together and hybrids are not uncommon (Abbott 1974).

Natural hybridization is a common phenomenon among the oaks (*Quercus* L.) (Muller 1952), some birches (Barnes and others 1974), and aspens (Pauley 1956).

Testing for Breeding Value

After the elite, select, or superior individuals have been selected, some system of testing their genetic value must be used. We have identified these trees as good phenotypes but we do not know their genotypes and therefore we are uncertain as to their value as breeding stock. Sometimes the outstanding trees in a stand may be taller than their neighbors due to an environmental advantage such as better soil or more moisture. It is important to use only trees with better than average genetic characteristics, as the environmental differences will not be passed on to future generations. In natural stands, it is critical to determine the age of individual trees. Trees growing together may have a similar size, yet be quite different in age. Obviously we would prefer that our select trees not be outstanding merely based on the fact that they are older than their neighbors.

The usual way to test vegetatively propagated trees is to plant them in blocks and compare performance with a standard population. This may be a clone of known performance, or in some cases seedlings from a standard seedlot may be used. Tests that are designed to evaluate the relative performance of a specific clone are called clonal tests.

Trees propagated from seed are usually progeny tested with one or more test designs modified from crop breeding. Early work with trees involved open-pollinated tests in which cones or seeds were collected from select trees and the half-sib progeny (female parent known, males unknown) were evaluated in plantations. As technology evolved, control-pollinated tests were developed that provided much better estimates of breeding values.

Most progeny tests are designed with row plots in field plantations, although single-tree plots have some advantages over row plots. A technique developed by the Western Gulf Forest Tree Improvement Cooperative uses greenhouse testing (Lowe and van Buijtenen 1989). This technique culls the poorest 17 to 20% of the progeny at about 5 months, based on shoot dry weight. This system reduces both the time and the cost of testing greatly.

Screening for Fusiform Rust Resistance

Due to the economic importance of fusiform rust with the southern pines, the USDA Forest Service established the Rust Testing Center at Bent Creek, North Carolina, in 1976. Forest Service pathologists developed a standardized inoculation system to screen loblolly and slash pine seedlings for susceptibility to fusiform rust (Knighten 1988). The Resistance Screening Center inoculates an average of 40,000 seedlings annually (figure 2). The southern tree improvement cooperatives routinely screen all new selections by sending seeds to the Rust Testing Center for evaluation. This is an essential part of the progeny testing procedure.

Screening for White Pine Blister Rust Resistance

Cooperative programs designed to develop resistance to white pine blister rust—*Cronartium ribicola* J.C. Fisch.—

Figure 2—Chapter 2, Genetic Improvement of Forest Trees: fusiform rust inoculation chamber at USDA Forest Service, Southern Station, Resistance Screening Center in North Carolina.

have been operating for a number of years in California and Idaho. For example, the USDA Forest Service, Pacific Southwest Region's program has identified 985 rust-resistant sugar pines—*Pinus lambertiana* Dougl.—for future tree improvement use. Family selection has been used as a breeding strategy.

Advanced Generation Breeding

Advanced generation breeding is usually designed with a combination of selections from first generation progeny test plantations in conjunction with new selections from operational plantations or other sources. A major advantage of selection in plantations is that the environment is usually more uniform than in natural stands. Tree age, spacing, and soils are often relatively uniform, with the result that the phenotype more closely approaches the genotype. In this case, selection is more efficient and gain can be increased. In most advanced generation breeding plans the best individuals are selected from the best families. It is important, however, to separate the production population from the breeding population to minimize the effects of inbreeding (Lowe and van Buijtenen 1986).

Starting a Tree Improvement Program

Establishing Objectives

Before a tree improvement program is begun, the situation needs comprehensive analysis. Tree improvement is long-term work, and a great deal of time and energy can be saved with some careful planning. The following factors should be considered.

1. **Desired products**
   Wood properties necessary to produce the desired products
   Required volume of wood
2. **Possible species**
   Native or exotic (long-term consequences of using exotic species?)
   Rotation length (shorter rotations give major improvements in gain per unit time)
3. **Chosen reforestation system**
   Seed propagation or vegetative?
   Bareroot or container seedlings?
   Storage and distribution methods
   Planting techniques and cultural procedures
4. **Plantation evaluation/survival system**
   Required personnel
   Numbers and skill levels
   Required facilities and equipment
   Required long-term budgets

Identifying the Raw Material To Be Used

Native versus exotic species. Are there native species available that are well-adapted to the planting sites to be used or would exotic species be more productive? The temptation to introduce an exotic species may be strong but there are a number of advantages of native species.

- They have evolved in harmony with their environment and usually have developed a mutual tolerance with competitors and pathogens. Exotics, on the other hand, may not perform well in a new environment—they have not been exposed to the stresses of this new environment and often have not had sufficient time to adapt to local conditions.
- Native species have well-defined management regimes that have been tested over time. Reforestation personnel have learned how to grow, ship, store and plant the seedlings or cuttings.

An exotic species introduced into a new environment does not necessarily produce wood with the same characteristics as in its place of origin. Excessive amounts of juvenile wood are common, as are wide bands of earlywood and narrow bands of latewood. These growth patterns lead to low-density wood and drying defects (Zobel 1981). There are notable exceptions, such as Monterey pines grown in New Zealand, but in general the wood quality of native species is more desirable than that of exotics.

Public opinion is running strongly in favor of native species both in the United States and overseas. Plantation forestry with exotic species has encountered strong public resistance in a number of locations.

Successful introductions of exotics. There have been many successful introductions of exotic species world-wide (table 3). Native U.S. species have been introduced into other countries, especially Monterey pine, a minor species in coastal California that has become the backbone of the forest products industry in New Zealand, a country with few conifers of economic importance. Monterey pine has also done well in Australia, Chile, and South Africa. Douglas-fir and Sitka spruce, both native to the Pacific Northwest, have been widely planted in Great Britain and northern Europe. Several of the southern pines have been widely planted in Australia, South America, and South Africa.

Land races. When the decision has been made to use a given exotic species, the question arises as to the source of material to be used. Often it is more efficient to select within a land race of the species rather than the original population in its native environment. A land race has become adapted to its new environment by virtue of its survival there for a number of years. For example, Monterey pine has been growing in New Zealand for over 100 years. During that period, this species has weathered many storms and fought off many pathogens. Thus, natural selection has altered the population by gradually eliminating individuals not well adapted to their new environment. Selection of individual trees within this land race will be more cost-effective therefore than returning to the native populations in California.

Geographic variation. Philip Wakeley of the USDA Forest Service established one of the first definitive studies of geographic variation in the United States in 1926 and 1927. Wakeley collected loblolly pine seed from Arkansas, Georgia, Texas, and locally (Louisiana), grew the seedlings and planted them on a site near Bogalusa, Louisiana (table 4). This study was the first solid evidence that the source of seeds was important in the growth and rust resistance of loblolly pine. The trees grown from seeds collected locally produced almost twice the volume of wood as the other sources after 22 years. In addition, this was the first evidence that loblolly pine from Livingston Parish, Louisiana, had special merit as a rust-resistant source.

Following this test at Bogalusa, the Southwide Pine Seed Source Study was designed by Wakeley as a cooperative project involving 17 different agencies, with field plots established from Texas to the Atlantic coast. This study demonstrated that loblolly pines grown from sources west of the Mississippi River usually had better planting survival and greater rust resistance than those from eastern sources. On the other hand, seedlings grown from sources along the southern Atlantic coast had faster growth rates than those from western sources (Wells 1969; Wells and Wakeley 1966; Wells 1983).

The results of this study have led to widespread planting of Livingston Parish loblolly seedlings throughout the southeastern coastal plain, leading to major reductions in fusiform rust infection (Wells 1985). Likewise, forest industry has planted seeds from Atlantic coast sources of loblolly in Arkansas and Oklahoma with impressive gains in volume growth on the better sites (Lambeth and others 1984) (figure 3).

On the Pacific coast, the Eddy Tree Breeding Station was established in California in 1925. This later became the Western Institute of Forest Genetics and played a major role in the development of forest genetics in the West.

The 2 varieties of Douglas-fir (coastal and interior) (figure 4). have been studied extensively (Kung and Wright 1972). The coastal variety has been widely planted in Great Britain and northern Europe. Other western species with pronounced racial differentiation are ponderosa pine, and grand (*Abies grandis* (Dougl. ex D. Don) Lindl.) and white firs (*A. concolor* (Gord. & Glend.) Lindl. ex Hildebr.). In the Northern United States, white spruce (*Picea glauca* (Moench.) Voss) occupies an extensive east–west range with considerable racial variation (Nienstaedt 1968).

Table 3—Chapter 2, Genetic Improvement of Forest Trees: examples of exotic species used in plantation forestry

	Location of planting					
Origin	**North America**	**Central America**	**South America**	**Europe**	**Africa**	**Australia & New Zealand**
North America						
Picea sitchensis (Bong.) Carr.				X		
Pinus elliotti var. *elliotti* Engelm.		X	X		X	X
Pinus radiata D. Don			X			X
Pinus taeda L.		X	X		X	X
Populus L. spp.				X		
Pseudotsuga menziesii (Mirb.) Franco				X		X
Central America						
Pinus caribea Morelet			X			X
Pinus oocarpa Schiede ex. Schltdl.		X			X	
Europe						
Picea abies L.	X					
Populus L. spp.	X					
Asia						
Gmelina arborea Roxb.			X		X	
Tectona grandis L. f.		X	X		X	
Australia/New Zealand						
Eucalyptus L.Her. spp.	X	X	X		X	

Figure 3—Chapter 2, Genetic Improvement of Forest Trees: areas of major commercial use of non-local loblolly pine seedlings. Coastal North Carolina seeds were used in Arkasas and Oklahoma **(A)** for increased growth rate and Livingston Parish, Louisiana, seeds were used from Mississsippi to South Carolina **(B)** for improved rust resistance.

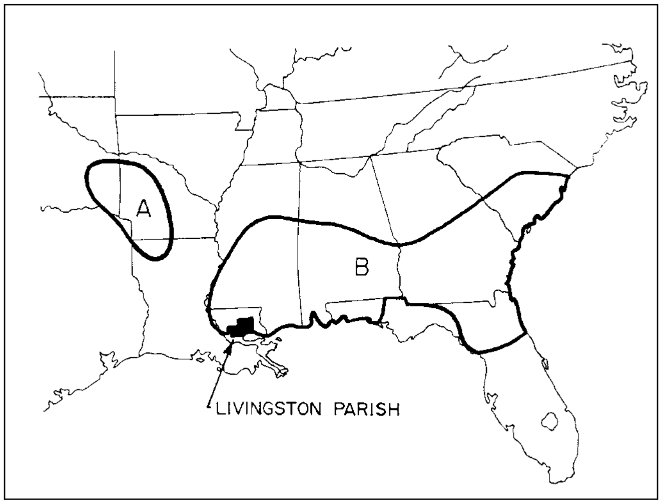
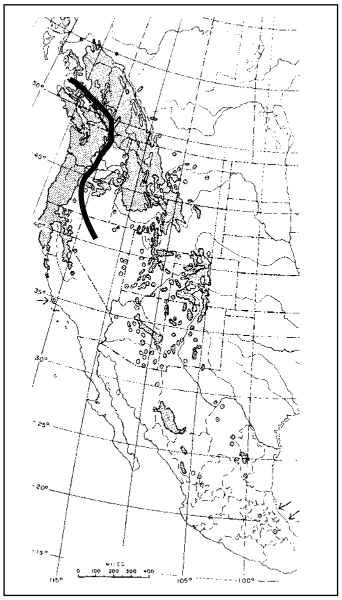


Figure 4—Chapter 2, Genetic Improvement of Forest Trees: the range of Douglas-fir, with the 2 varieties separated by a black line.



Utilizing the Raw Material

Seed production areas. Time is a critical factor in determining the route to follow in a tree improvement program. A useful expedient is the seed production area (seed stand). This is a high-quality stand that can be thinned to remove the lower quality individuals and then managed for seed production (Cole 1963; Rudolf 1959). Although the gain from these stands is not high, (Easley 1963), the time saved can be more important than the degree of improvement. These stands can be managed by prescribed burning, fertilized, and sprayed for insect control. Seeds can be collected by climbing, shaking, tarping, or felling trees. An efficient seed collection system can be designed where the felling of trees is planned to coincide with good seedcrops.

Although natural stands are preferred sources for seed production areas (figure 5), plantations are often used where the seed source can be verified. In these cases, the plantation is treated like a land race, and good performance over a

Figure 5—Chapter 2, Genetic Improvement of Forest Trees: longleaf pine seed production area in Georgia.

Table 4—Chapter 2, Genetic Improvement of Forest Trees: loblolly pine (*Pinus taeda* L.) plantation* performance illustrates the importance of geographic sources of seed

Source	Survival (%)	Height		dbh		Volume		Rust infection (%)
		m	ft	cm	in	m^2/ha	cords/ac	
Louisiana (Livingston Co.)	82	14	46	12	6.7	265	42	4
Texas (Montgomery Co.)	83	12	41	13	5.2	145	23	6
Georgia (Clarke Co.)	77	11.5	38	13	5.2	113	18	37
Arkansas (Howard Co.)	84	11	36	12	4.7	94	15	5

Source: Wakeley (1954).

* Located in Bogalusa, Louisiana.

given time is evidence that this plantation has adaptive value on this site.

Clonal seed orchards. The most common tree improvement system is the clonal seed orchard (figure 6). These have been established for many outcrossing species worldwide. The procedures used involve selection of individual trees, progeny testing to determine their breeding value, and replication of the ortets (selections) in an orchard environment. In actual practice, the orchard is usually established by grafting and the progeny testing is done by controlled pollinations within the orchard or in clonal banks.

Seed production usually begins before progeny testing is completed, resulting in the production of improved seeds that cannot be certified as genetically superior (seed certification is covered in chapter 6) until progeny testing is completed and the orchard can be rogued (that is, trees with low breeding value are removed).

Selecting Plus Trees

Selection of plus trees from wild stands that are pure (single species) and relatively even-aged usually involves grading candidate trees in comparison with the best adjacent crop trees (of similar age) in the stand. Characteristics compared with southern pine (for timber) are straightness, height, DBH, volume, form class, crown size, branch diameter, branch angle, natural pruning and wood quality. Any evidence of insect or disease susceptibility usually calls for rejection of the candidate. Acceptance of the candidate tree depends on the numerical rating of the tree, its wood quality, age class, geographic location, and any special attributes.

Figure 6—Chapter 2, Genetic Improvement of Forest Trees: loblolly pine clonal seed orchard in Arkansas.

Selecting Orchard Sites

All seed orchards require good access, level topography, and well-drained soils. Because vehicular traffic is essential in the management and harvesting of orchards, a coarse-textured soil is mandatory. Subsoiling is practiced in many seed orchards to fracture any hardpans formed from compaction by vehicles. Even in sandy soils, compaction can seriously reduce root growth of the trees. Establishment of a year-round ground cover is important to stabilize the soil and prevent or reduce erosion (Jett 1986).

Establishment

Most clonal orchards are established by grafting, although at least one slash pine orchard has been planted with cuttings (Bengston 1969). Rootstock planted in the field can be grafted in-place (field-grafting) or potted stock grown in a greenhouse, lath-house, or nursery bed can be grafted. Grafting on potted stock is more cost-effective, but field-grafting is preferred by some orchard managers because of the often shorter time to reach commercial cone production.

Graft incompatibility occurs in many species, including most conifers. This is a problem in roughly 22% of southern pine clones (Lantz 1973) and it is particularly serious in Douglas-fir, where up to 67% of the clones may be affected (Wheat 1967). There is some evidence that clonal root stocks from related material may reduce incompatibility rates (Bower and McKinley 1987) but the data are not conclusive. Copes (1967) has developed a tissue sampling technique that can be used to predict incompatibility in Douglas-fir.

Management

Most seed orchards are fertilized to promote flowering and some are irrigated to reduce the impact of moisture stress. Insect control is essential for maximum seed production. In the absence of cone and seed insect control, Belcher and DeBarr (1975) have estimated that 11% of the loblolly cones were attacked by cone worms (*Dioryctria* spp.). In their report on 26 seed orchards surveyed over 3 years, an average of 9.9% of the collected seeds were damaged by insects. There was a large amount of clonal variation, as the range of cone worm attack was from 0 to 67%, depending on clonal susceptibility.

More recently, Jett and Hatcher (1987) reported that cone worms can cause losses exceeding 90% of loblolly cones when pesticides are not used.

Pollen Contamination

Most seed orchards are located with some consideration for pollen contamination. Unfortunately economics often dictates locations that cause a major problem with pollen contamination. Early seed orchard establishment in the South carried a recommendation of at least 122-m (400-ft) isolation zones surrounding the orchard (Squillace 1967). Later studies indicated that vegetation formed a more effective barrier than either soil or sod.

Pollen contamination in seed orchards was estimated by Adams and Birkes (1989) using isozyme analysis. In seed orchards of Douglas-fir, loblolly pine, and Scots pine (*Pinus sylvestris* L.), they estimated that as much as 50% of the pollination within the orchards was due to outside pollen. The amount of self-fertilization within the orchards was estimated as less than 10%, with considerable variation by clone.

An additional study by Smith and Adams (1983) also indicated that pollen contamination was in the 40 to 52% range for 2 Douglas-fir seed orchards in Oregon. Suggestions for reducing contamination included more complete geographic isolation, water spraying to retard flower development, and supplemental mass pollination.

Supplemental Mass Pollination

Supplemental mass pollination (SMP) has been used effectively in southern pines, Douglas-fir, and Scots pine (Bridgwater and others 1993). The authors have summarized their recommendations for success with SMP:

1. The goals of SMP must be clear.
2. Orchard phenology must be monitored in order to apply SMP prior to maximum pollen flight in the orchard.
3. Fresh pollen or high viability stored pollen must be used.
4. The pollen application system must be effective.
5. The success of the SMP can be monitored with isozymes or other procedures.

Harvesting

Cones, seeds, and fruits may be harvested by climbing or with bucket trucks, aerial lifts (figure 7), tree shakers, or seed collection nets. Seed collection nets as developed by the Georgia Forestry Commission are effective when bulk collections are harvested from the orchard (figure 8). When individual tree (or clonal) collections are needed, the other systems must be used. The USDA Forest Service Missoula Technology Development Center refined the net retrieval system concept (McConnell and Edwards 1984), which has been widely copied and modified. This system is an effective method of harvesting southern pine seeds on nets when orchard mix collections can be used.

Figure 7—Chapter 2, Genetic Improvement of Forest Trees: cone collection with JLG lift in South Carolina.

Genetic Gains

Realized genetic gains in volume growth from first generation southern pine clonal seed orchards have ranged from 6% with un-rogued loblolly and slash pine orchards to 17% for rogued orchards of these species (Squillace 1989). The gains from advanced generation loblolly orchards have been predicted at 25% greater volume than unimproved material for the second generation, 35% for the third generation, and 45% for the fourth generation (Zobel and Talbert 1984).

Advanced-Generation Breeding

Advanced-generation breeding often is designed to combine the best individuals from the best families in the first generation with unrelated individuals from a separate breeding population. The Western Gulf Forest Tree Improvement Program has developed a sub-line system separating the breeding population into breeding groups that are crossed to produce seeds only when a production orchard is established (Lowe and van Buijtenen 1986). With this system, inbreeding is restricted to the breeding populations and the production populations are not affected.

A similar system has been used with northern red oak—*Quercus rubra* L.—in Indiana. Coggeshall and Beineke (1986) have designed 6 sub-lines with 30 clones in each for a total of 180 clones. These sub-lines will be crossed only when the production seed orchard is established.

Figure 8—Chapter 2, Genetic Improvement of Forest Trees: seed collection nets deployed on floor of Georgia Forestry Commission seed orchard.

Figure 9—Chapter 2, Genetic Improvement of Forest Trees: accelerratedd breeding orchard in North Carolina.

Seedling Seed Orchards

When working with precocious species, considerable time can be saved by collecting open-pollinated seed from select trees, growing the half-sib progeny in a nursery, and establishing a progeny test/seed orchard with the seedlings. A major problem with this system is designing a plantation that is effective for progeny testing and will also permit effective seed production after the poor performers are removed. Effective designs have been developed by Wright (1976) and Hodge and others (1995).

A recent report by Hodge and others (1995) indicated a gain of 10.7% in volume for a seedling seed orchard of longleaf pine (*Pinus palustris* Mill.) at 8 years. In this case the heritability of volume growth was calculated at 0.21 and there was a moderate genotype × environment interaction related to geographic regions.

Accelerated Breeding

Accelerated breeding techniques developed in recent years can substantially reduce the breeding cycle. One of the most direct methods is selection at younger ages. A pilot-scale accelerated breeding study was developed by van Buijtenen and others (1986). This study used a 3-phase procedure with half of the loblolly pine families eliminated in each test. The tests measured dry weight, root growth potential, and resistance to heat stress. The survivors of these tests were then subjected to flower-induction techniques.

Potted seed orchards growing in greenhouses can reduce the length of the breeding cycle by at least 20% (Zobel and Talbert 1984) (figure 9). In this case, a 20-year cycle can be reduced to 16 years by accelerating flowering in the greenhouse as compared to a conventional outdoor seed orchard. The trees can be maintained in 20- to 40-gallon tubs with a drip irrigation system. McKeand and Weir (1983) calculated that a reduction of 6 years in the breeding cycle with a 30,000 seedlings per year regeneration program would amount to a savings of $2 million. A similar system has been reported for western hemlock (Bower and others 1986). In this case, potted ramets produced about 10 times the amount of seeds as field-grown trees.

With a potted orchard, several techniques can be utilized to increase both male and female flowers. Water stress and applications of gibberelic acid ($GA_{4/7}$) will promote early female flowers (Todhunter 1988), whereas out-of-phase dormancy (Greenwood 1981) will speed up the development of male flowers. Wire girdling is also an effective way to promote male flowering.

Top-working grafted loblolly ramets has also accelerated flower production (Bramlett and Burris 1995). In this case, both male and female flowers were produced in the year following grafting.

Deployment of Genetically Improved Material

Seed Zones

Seed zones have been established for most of the major commercial forest species. These are areas that are environmentally similar and within which a given source can be expected to perform uniformly. When reforestation is needed within the zone, seeds should be collected from that zone. In some cases, when seeds are not available from that zone, seeds from an adjacent zone may be substituted.

In the Western United States, seed zones can be quite narrow, depending on the topography. For example, seed zones for Douglas-fir in Oregon are delineated on 152-m (500-ft) elevation intervals (Ching 1978). Restricted zones have also been recommended in the northern Rocky Mountains for western white—*Pinus monticola* Dougl. ex D. Don—and ponderosa pines (Rehfeldt and Hoff 1976).

In the South, seed zones for most species are much broader, reflecting the larger geographic provinces and more uniform topography (Lantz and Kraus 1987)(figure 10). The Western Gulf Forest Tree Improvement Program has defined specific seed deployment zones for areas west of the Mississippi River (Byram and others, 1988), and the North Carolina State University—Industry Cooperative Tree Improvement Program has adopted a more flexible approach for areas to the east (McKeand and others 1992)

Genotype x Environment Interactions

Progeny tests of the first and second generation select trees have highlighted some outstanding families in the southern pines. Some of these families perform well on dry sites, some on wet sites, and some do well across-the-board. The famous International Paper clone 7-56, for example, seems to be a top performer wherever it is planted.

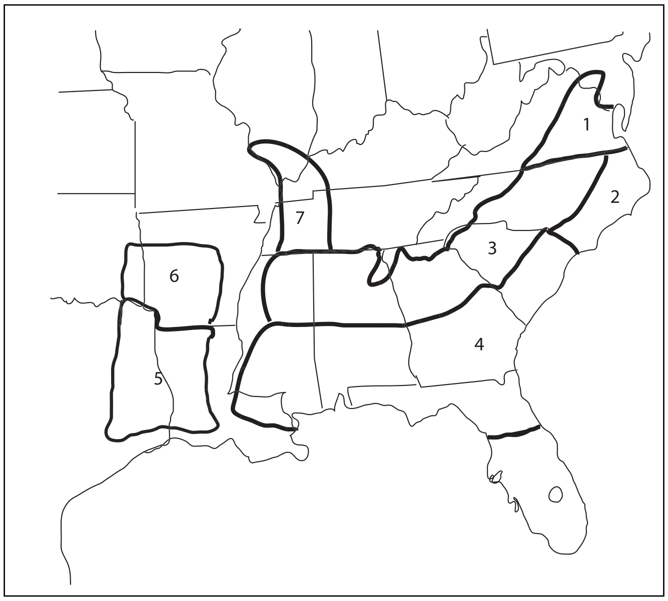
In general the genotype × environment interaction (change in relative rank among tested families) of most improved material has been unimportant. However, the University of Florida Cooperative Forest Genetics Research Program has reported a strong genotype x environment interaction for growth with some recent loblolly pine tests (Hodge and others 1995).

Single-Family Block Plantations

Many forest industries in the South routinely establish single-family block plantations and often record a growth advantage compared to mixed family blocks (Williams and others 1983). Using block plantings rather than progeny tests, Gladstone and others (1987) recorded 16% greater stand volumes for single-family plantings than for woods-run material. Mixed family blocks had only 11% greater volume than the checks.

Although single-family blocks may perform well on company land for short rotations, few non-industrial private forest landowners understand the risks involved. When a single family is planted on private land where long rotations are used and where natural regeneration may be employed, genetic diversity can be reduced to a low level. In only 1 or 2 cycles of natural regeneration, inbreeding could seriously reduce growth and productivity.

Figure 10—Chapter 2, Genetic Improvement of Forest Trees: seed zones for loplolly pine.



Molecular Biology

Isozymes

Brewbaker (1967) was one of the first scientists to propose the study and use of isozymes in forestry. Since then, isozymes have been widely used for taxonomic work, pollen contamination estimates, heterozygosity estimates, and a number of other uses. In isozyme analysis, a single gene codes for production of a single protein that can be visually distinguished as one band on an electrophoretic gel. The band pattern on a stained gel may be interpreted as a direct reflection of the genotype of the tree. Cotyledons, needles, or embryos (all diploid tissues) may be used or pollen grains and female gametophytes (haploid tissues) may be used.

Isozymes have been used to compare the rates of heterozygosity and outcrossing (El-Kassaby and others 1986) with Douglas-fir. These authors found no significant differences between clonal and seedling seed orchards in outcrossing rates. There were, however, significantly greater proportions of homozygous progeny from the seedling orchard.

Although isozyme analysis has been an effective tool for many forest genetics studies, Libby and others (1997), summarizing a southern meeting on genetic diversity, found that isozyme data have a number of limitations when used to estimate the genetic variation within a single species. However, isozyme analysis has been widely used to estimate the amount of pollen contamination in seed orchards (Adams and Birkes 1989).

The USDA Forest Service has established a National Forest Genetics Electrophoresis Laboratory in Camino, California, where genetic variation studies, taxonomic determinations, "DNA fingerprinting," and the effect of silvicultural and management procedures can be evaluated. This laboratory served an important role after Hurricane Hugo demolished the longleaf pine seed orchard on the Francis Marion National Forest in coastal South Carolina. Isozyme and DNA analyses were used to identify the surviving ramets in the orchard and facilitate reconstruction of the orchard.

Gene Mapping

New techniques such as RFLPs (restriction fragment length polymorphisms) (Nance and Nelson 1989) and RAPDs (random amplification of polymorphic DNA) (Sewell and Neale 1995) have paved the way for significant advances in gene mapping of QTLs (quantitative trait loci). Conkle (1981) produced linkage maps for several *Pinaceae* species and Sewell and Neale (1995) constructed a "consensus" map for loblolly pine. Another technique for mapping genes using PCR (polymerase chain reaction) markers has been developed for pines by Harry and Neale (1993). Other mapping work has been done with *Eucalyptus* spp. and *Populus* spp. These mapping techniques are resulting in a great deal of data on the genome of loblolly pine. This information will allow more efficient selection procedures (marker-assisted selection) to be employed in the future.

In addition to the work done on pollen contamination and heterozygosity using isozymes, RAPD markers have been used to assess genetic variation in aspen following the 1988 Yellowstone fires (Tuskan 1995).

Fingerprinting

Electrophoresis has been used for a number of years to "fingerprint" clonal material in seed orchards. Now PCR techniques have been used to identify Douglas-fir seedlots produced in a seed orchard in British Columbia and RAPD markers have been used to identify Norway spruce clones in Austria (Neale 1995).

Genetic Engineering

Genetic engineering has received a considerable amount of attention from the media, but few examples of forest tree applications are available. There has been a case of gene transfer in hybrid poplar that conferred resistance to glyphosate (herbicide). There is also interest in transfer of DNA with resistance to chestnut blight (Carraway and others 1993). In this case, somatic embryogenesis could be used to establish ovules and zygotic embryos on culture media. Transfer of this material would be accomplished by bombardment with plasmid DNA containing the resistant gene or genes.

Tree Improvement Cooperatives

Tree improvement cooperatives have been established in the major timber-growing regions of the United States and Canada, including California, the Pacific Northwest, the Inland Empire (also known as the intermountain region or the Great Basin), the Great Lakes region, and the South. Advantages of these cooperatives include a long-term breeding plan, often developed by forest geneticists at a land grant university, statistical support for progeny test design and analysis, laboratory facilities for wood-quality determinations and soil tests, and pollen and seed processing facilities. Technology transfer of new developments in the field of tree improvement and training is also an important function of these cooperatives.

Often select trees, pollen, seed, and grafting material are shared among members of the cooperative. Some cooperatives share orchards and even nursery sites. Duplication of effort is minimized and cooperative members gain significant economies of scale as they share breeding and testing workloads. Separate staffs are not needed by the individual organizations as the scientists and support personnel employed by the cooperatives are shared by all member organizations.

The South

Bruce Zobel started tree improvement cooperatives in the United States in 1951 at Texas A&M University. A few years later, Tom Perry began the University of Florida Cooperative Forest Genetics Research Program. Zobel later moved to the North Carolina State University and organized the NC State University Industry Cooperative Tree Improvement Program. J.P. van Buijtnen reorganized the Texas A&M Cooperative as the Western Gulf Forest Tree Improvement Coop in 1969. In the Spring 1988 Society of American Foresters Tree Genetics and Improvement Working Group newsletter, Tim White reported that in 1987 these 3 cooperatives involved 28 forest industries, 12 State forestry agencies, and 3 seed companies. Average annual seed production over all members at that time ranged from 60,000 to 90,000 kg (70 to 100 tons) of pine seed and the average annual hectares planted with seedlings was 728,000 (1.8 million acres). Recent divestitures of industrial forest land dramatically decreased cooperative membership. This may seriously and negatively impact future seed production.

The Pacific Northwest

Tree improvement activities began in the Pacific Northwest in the 1950's when the Industrial Forestry Association coordinated the establishment of clonal seed orchards for coastal Douglas-fir. In the 1960's, forest industry started hiring forest geneticists and individual programs were started by several companies. About this time, the USDA Forest Service started a tree improvement program for Douglas-fir; western hemlock (*Tsuga occidentalis* (Raf.) Sarg.); and ponderosa, western white, and sugar pines on national forest lands in Oregon and Washington (Daniels 1994). The Forest Service program was followed in the 1970's by the USDI Bureau of Land Management's tree improvement program for Douglas-fir in western Oregon.

From 1967 to 1985, Roy Silen at the USDA Forest Service's Pacific Northwest Forest and Range Experiment Station and Joe Wheat of the Industrial Forestry Association developed 20 cooperatives for Douglas-fir and 2 for western hemlock. These "progressive tree improvement programs" featured low-intensity selection of large numbers of roadside trees followed by open-pollinated progeny tests (in contrast to the high-intensity selection practiced in most of the southern pine programs). In 1986, the Industrial Forestry Association's Pacific Northwest Program was reorganized and named the Northwest Tree Improvement Cooperative of the Western Forestry and Conservation Association. This organization currently has 37 members, with a land base of 2.8 million hectares (6.9 million acres) and more than 80 breeding zones (Daniels 1994).

The overall Pacific Northwest region had a total of 282 seed orchards with a total of 1,389 ha (3,473 ac) in western Washington, western Oregon, and northern California in 1994 (Daniels 1994). Federal agencies manage 64% of this area; industry, 30%; and States and other cooperative groups, 6%.

The Inland Empire

The Inland Empire Tree Improvement Cooperative membership has 20 separate organizations, including forest industry, State forestry agencies, tribal councils, Federal agencies, universities, and other private organizations. Lauren Fins established the cooperative in 1978 at the University of Idaho to serve Idaho, western Montana, and eastern Washington. The cooperative has established 16.8 ha (42 ac) of western white pine and ponderosa pine orchards which have produced an average of 322 kg (710 lb) of seed annually. In addition to these cooperative orchards, many member organizations have established their own orchards.

California

The California Tree Improvement Association, organized in 1978 with 26 members, manages over 9 million acres of forestland. Ponderosa pine was the first species selected, followed by Douglas-fir and sugar pine. Members include forest industry, the State of California, and the USDA Forest Service. Local tree improvement associations were formed to focus on one or more of the California tree seed zones. The main objectives of the association are the selection of superior trees, the establishment of clone banks, the establishment of progeny test sites, and the establishment of a ponderosa pine seed orchard.

The Great Lakes Region

The Minnesota Tree Improvement Cooperative was established in 1980 and currently has 18 full members and 7 supporting members. The cooperative is working with black (*Picea mariana* (Mill.) B.S.P) and white spruces, and jack, red, and white pines. There are 35 seed orchards occupying about 50 ha (125 ac). In 1995, about 30 hl (84 bu) of cones were collected from 3 of these orchards. Six orchards were approved for production of certified seed in 1995. Gains in height growth have ranged from 3 to 9%.

The Future

The demand for wood products will continue to increase worldwide. Computer and printing paper will be in great demand, particularly in Southeast Asia where population growth is expanding exponentially (Kellison 1997).

In the United States, timber harvesting on the forest land base is being progressively restricted, which dictates that wood production be concentrated on less land area each year. This requires management for maximum wood growth on our most productive sites. Fortunately this will result in reduced pressure on average and marginal sites which often have high value for recreation and aesthetic pursuits.

Tree improvement programs, combined with intensive management, have dramatically increased wood yields. In the Southeastern United States, genetically improved loblolly pine on good sites, under maximum cultural care, can be expected to yield 10.8 to 14.4 m^3 (3 to 4 cords) per 0.4 ha (1 ac) per year. On the Pacific Coast, vegetatively propagated hybrid cottonwood grown under maximum culture on 6- to 7-year rotations is producing 25.2 m^3 (7 cords) per 0.4 ha (1 ac) per year (Kellison 1997). In South America, southeast Asia, and South Africa, plantations of acacia, eucalyptus, and Gmelina from genetically improved sources are expected to yield about 25.2 m^3 (7 cords) per 0.4 ha (1 ac) per year. Many of these plantations can be managed with coppice rotations to further increase their economic value.

Tree breeding techniques must be fine-tuned in order to provide these increased yields of wood. Vegetative propagation procedures can be improved to provide more propagules at lower cost. Accelerated breeding will shorten generation intervals. Marker-assisted selection using molecular biology technology will result in both more efficient selection and shorter breeding cycles.

Continued research is needed to identify those parameters that predict the performance of specific genotypes on specific sites and work is needed to quantify genotype × environment interactions over a wide range of sites.

Public education will assume even greater importance in the future as competition for land increases. Engagement with many diverse groups will be required for making progress based on sound scientific principles. Many different approaches and mixes of objectives are possible and the consequences, both positive and negative, will have to be weighed in the balance of public opinion. Topics such as the long-term effects of using biotechnology in the forest, planting selected families on large land areas, and preservation of non-commercial species must be openly discussed.

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