Chapter 10.

The Role of Genetics and Tree Improvement in Southern Forest Productivity

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Abstract*—Because of space limitations, a thorough discussion of the rich history of tree improvement in the Southeastern United States cannot be totally accomplished in this forum. However, a synopsis of key program highlights and the people who forged and directed these programs is presented, together with a discussion of current and future work. This discussion covers improvement programs for both southern pines and hardwoods. Comparisons of and contrasts between these two types of programs are discussed and punctuated by the reasons for successes and failures. Today, southern pine tree improvement programs are on the cutting edge of genetic technology, moving from open-pollinated seed to clonal programs encompassing molecular genetic features. Programs for southern hardwoods generally are much less advanced, because there are several limiting factors unique to hardwoods and because hardwood fiber is available at low cost.*

INTRODUCTION

Consumption of forest products is expected to continue its rapid increase during the 21st century. In contrast, the land base used for wood production is expected to decline because of population pressures, environmental concerns, lack of adequate management by many landowners, and the divesture of lands deemed nonstrategic. Even today, removals equal or exceed growth rates in some areas (Wear and Greis 2002). However, models indicate that the potential productivity of forests in many regions can be much higher than is currently realized (Allen 2000, Bergh and others 1998, Sampson and Allen 1999). With investments in appropriate management systems, growth rates > 25 m^3/ha/year for pines are biologically possible and can be financially attractive for a broad range of site types in temperate, subtropical, and tropical regions.

In the early days of southern forestry, vast areas were clearcut with little or no regard for regeneration. Natural regeneration was satisfactory in some areas but totally lacking in others. Very little planting occurred before the Civilian Conservation Corps began wide-scale planting during the Great Depression. Wakeley (1944) estimated that < 500 acres of southern pines had been artificially regenerated successfully before 1920.

Historically, the practice of silviculture focused on controlling the composition, quantity, and structure of forest vegetation and the maintenance of site quality. As forest plantations have become important sources of fiber, fuel, and structural material, this custodial role has given way to active intervention to improve both plant and soil resources. Forest managers are recognizing that intensive plantation silviculture requires active management of both biotic and abiotic resources to optimize production. Silvicultural treatments including soil tillage, vegetation control, fertilization, fire, and thinning can dramatically affect soil resources. The key

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to optimizing fiber production is to deploy the best genetic material available and to provide sufficient resources to allow the full genetic potential to be realized.

SOUTHERN PINE TREE IMPROVEMENT

Early Work

Before 1920, little was known about how seed source might affect forest plantation productivity in the United States. Since well before the turn of the 20th century, the importance of geographic seed source was known for European species. In this country, native seed collections for an extensive study of Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] were initiated in 1912 (Kaufman 1961), and testing of ponderosa pine (*Pinus ponderosa* Laws.) seed sources in northern Idaho and Colorado began in 1916. Inspired by some of Luther Burbank's work with walnut (*Juglans* spp.) hybrids, James G. Eddy started the Eddy Tree Breeding Station (which later became the Institute of Forest Genetics) at Placerville, CA, in 1925.

Although Chapman (1922) identified the first natural southern pine hybrid [longleaf pine (*P. palustris* Mill.) x loblolly pine (*P. taeda* L.)], the history of southern tree improvement began with Phil Wakeley, who came into the region in 1924. His undaunted drive led him to complete a monumental amount of research in basic silviculture, and his manual "Planting the Southern Pines" (Wakeley 1954) is still in use. Although he had little training in genetics, he was aware of seed source effects and in 1926 installed an important loblolly pine provenance test near Bogalusa, LA. This test was one of the first to clearly demonstrate genetic differences in a southern pine. The magnitude of the seed-source effect in southern pines was unknown before Wakeley published age-15 data indicating that growth and disease resistance varied widely among geographic races of loblolly pine (Wakeley 1944). Wakeley is also credited with creating the first artificial southern pine hybrid in 1929, a cross between longleaf and slash (*P. elliottii* Engelm.) pines (Dorman 1951).

Other early work included a large open-pollinated progeny test of loblolly pine installed in 1934 by A.L. McKinney and L.E. Chaiken of the U.S. Department of Agriculture Forest Service, Appalachian Station [now part of the U.S. Department of Agriculture Forest Service (Forest Service), Southern Research Station]. Substantial inherent differences were noted before the planting was flooded by the Santee-Cooper Power Project (Kaufman 1961).

In 1941, Mitchell, Dorman, and Schopmeyer, working at the research station in Lake City, FL, started selecting slash and longleaf pine for high gum yield. Open- and controlled-pollinated seedlings from these selections were used to establish the first progeny tests in southern pines demonstrating the existence of individual tree genetic variation.

Around 1949, L.T. Easly (1953), a forester with Westvaco, gave some high school students permission to collect cones from one of his saw-log operations and sell them to the State nursery. The students later told him that they preferred short, scrubby trees with lots of cones on them, rather than the sawtimber he was cutting. Aware of Dorman's work, Easly concluded that the dysgenic selection would result in poor-quality trees because of the student's preferred collecting methods. This prompted him to establish the first seed production areas in loblolly pine, which he referred to as orchards.

In 1951, the Southern Forest Tree Improvement Committee was formed to foster research and development in forest genetics and tree improvement. It has continued to be a guiding force in forest genetics and tree improvement research and technology transfer to the present day. According to Kaufman (1961), two events provided the impetus for the rapid expansion of genetics and tree improvement in the 1950s. The first was the influence of several prominent foresters who attended the World Forestry Congress in Helsinki in 1949, where they became aware of the tremendous progress being made by tree breeders in Europe. The 1950 meeting of the Appalachian Section of the Society of American Foresters was devoted to tree improvement. The second event was an exchange of correspondence beginning in the fall of 1949 between the Forestry Relations Division of the Tennessee Valley Authority (TVA) and the Forest Service's Southern Forest Experiment Station on the possibility of establishing a regional seed-source research program. The result was the first Southern Forest Tree Improvement Conference held in Atlanta, GA, in January of 1951. The organizers were surprised when > 80 people attended. Since then, the conferences have been held every other year. The proceedings of the conferences are major sources of information in genetics and tree improvement, as is evident in the literature cited for the present chapter.[2]

One product of the first conference was the establishment of a subcommittee, headed by Phil Wakeley, to install the Southwide Southern Pine Seed Source Study (SSPSSS), one of the most comprehensive provenance tests ever established. The results from Wakeley's (1944) first test were dramatic, but the study was planted only at Bogalusa, LA. The local seed source from Livingston Parish, LA, was clearly the best not only for growth but also for disease resistance.

The SSPSSS, on the other hand, was much more comprehensive. It was a very large undertaking, involving many cooperators across the Southeastern United States who collected seed and provided planting sites. All four major southern pine species were included—loblolly, slash, longleaf, and shortleaf (*P. echinata* Mill.) pines. A total of 128 plantations were established, including seed from and plantations in 16 States, ranging from New Jersey and Pennsylvania south to Florida and west to Texas, Oklahoma, and Missouri (Wakeley 1961).

The results of the SSPSSS and some other more limited provenance tests showed that the local seed source was not always the best source. Seed sources from warmer climates tended to grow faster than local sources, if the warmer climate sources were not moved to areas with climates greatly unlike those where they originated. Unlike the other southern pines, loblolly has important east-west differences. Seed sources from west of the Mississippi River are slower growing but more resistant to disease and tolerant of drought than sources from east of the Mississippi. Sources from just east of the river, centered at Livingston Parish, LA, combine the rust resistance of the western sources with the faster growth of the eastern sources. Results of this study led to large-scale transfers of seed to increase productivity. Disease-resistant Livingston Parish, LA, seed was widely planted in locations to the east. For example, much of this seed was planted in Georgia, where disease had caused losses in productivity. Fast-growing coastal Carolina seed sources have been planted extensively in Arkansas, where they outgrow the local sources.

It was assumed, based on the loblolly results, that east-west differences would be important in longleaf and shortleaf pines, because they also occur on both sides of the Mississippi River. Recent analysis has shown that this is not so, and the latest seed-movement guidelines (Schmidtling 2001) stress the importance of minimum temperatures in seed transfer considerations for these two species.

Wise use of information about geographic variation has resulted in large increases in southern pine productivity. Further increases have been realized through breeding. Forest tree breeding in the South started in earnest with the formation of the tree improvement cooperatives in the 1950s, with the main emphasis on pines. The first cooperatives evolved in the early 1950s out of research programs at the University of Florida (headed by T.O. Perry) and at the Texas Forest Service (headed by Bruce Zobel). Zobel moved to North Carolina State University in 1956 to form the third and the largest of the tree improvement cooperatives that exist today.

Current Status

Productivity improvements from genetics have helped to make investments in intensive forestry very profitable throughout the world. In regions such as the Southeastern United States, managers of facilities for wood-based manufacturing facilities have realized that their future depends upon a reliable, ecologically sustainable, and economically affordable supply of wood. Plantations of genetically improved forest trees are critical to maintaining this supply. In the South, > 1 billion loblolly pine seedlings are planted each year, and nearly every seedling is a product of a tree improvement program. Because of the economies of scale, even modest genetic gains are worth millions of dollars to industrial landowners, and the small landowner benefits as well. Even through only one generation of improvement, gains have been substantial. For first-generation loblolly pine and slash pine, volume, stem quality, and disease resistance have been improved, and the gain in harvest value is estimated to be 15 to 20 percent over unimproved trees (Hodge and others 1989, Talbert and others 1985). Estimates from the second generation of improvement in loblolly pine are even more encouraging. Additional

[2] Copies of proceedings of the Southern Forest Tree Improvement Conferences are available from the National Technical Information Service, 5285 Port Royal Rd., Springfield, VA 22161, 800-553-6847 or 703-605-6000, fax 703-605-6900, orders@ntis.gov.

productivity gains over the first generation average 7 percent for unrogued orchards to 18 percent for rogued orchards, and improvement in quality should dramatically exceed what was seen in the first generation (Li and others 1999).

Because of the substantial improvements in forest productivity from both genetics and silvicultural manipulation (Allen 2000, McKeand and others 1997), the options available to foresters have increased greatly. Combining a thorough knowledge of soil productivity and optimal silvicultural techniques with use of the most advanced genetic material will dramatically increase productivity. It is estimated that 20 to 30 percent more wood can be produced per hectare by utilizing the most responsive families from the first-generation programs in conjunction with the best site preparation and nutrition management practices (McKeand and others 1997). Even greater gains are expected when the best second-generation families are deployed to the best sites (Li and others 1999).

Deployment options for further increasing the genetic quality of planting stock are also being pursued. Mass production of selected full-sib families (Bramlett 1997) will have significant impact on forest productivity, especially in areas where additional selection intensity for environmental concerns such as cold tolerance is necessary. Because more genetic gain can be realized if the best full-sib families are used for regeneration (Li and others 1999), foresters will have more options for increasing productivity and profitability. Limitations to utilizing the best full-sib families are the cost-efficient production of seed and the bulking of these families with vegetative propagation. Pollination methods for mass-producing full-sib seedlings are being developed in the South (Bramlett 1997, Goldfarb and others 1997) and have been used successfully in other pine regeneration programs around the world (Balocchi 1997, Carson 1996, Walker and others 1996).

A breeding program is the backbone of any deployment program, and to sustain genetic gains through time, the breeding program must be of sufficient size and diversity to provide new and improved genotypes. A general trend has been to supplement traditional mainline breeding populations with intensively managed and selected elite breeding populations (Cotterill 1989, McKeand and Bridgwater 1998, White 1993, White and others 1993). In the elite populations, financial benefits can be realized in the short term by breeding only the very best genotypes. Fewer trees are bred, so breeding generations cycle faster, and the gain per year is dramatically increased.

These elite, intensively managed breeding populations are complements to, and not replacements for, larger breeding populations where the long-term management of genetic resources is a primary objective. Tree breeders have a unique responsibility and opportunity compared to other plant and animal breeders. Most forest tree species remain as wild undomesticated populations, and those few species that are being bred have only been domesticated in the past few years. Forest trees generally have very high levels of genetic variation compared to other plants and animals (Hamrick and others 1992), and this variation is the foundation of the successful efforts to improve productivity through genetics.

SOUTHERN HARDWOOD TREE IMPROVEMENT

Early Work

Early studies in the South concentrated on establishing geographic variation patterns in growth and wood properties by means of provenance trials and sample collections from widely distributed natural stands. The earliest studies in the South date from the spring of 1936, when the forestry division of the TVA became involved in this work. This program included the breeding of walnuts (*Juglans* spp.), hickories (*Carya* spp.), chestnuts (*Castanea* spp.), oaks (*Quercus* spp.), honey locust (*Gleditsia triacanthos* L.), black locust (*Robinia pseudoacacia* L.), and persimmon (*Diospyros virginiana* L.) as a means of combining high productivity and quality of nuts, acorns, or other fruits with desirable timber quality (Schreiner 1938, Wakeley 1975). In the 1950s and early 1960s, trials of yellow-poplar (*Liriodendron tulipifera* L.) (Farmer and others 1967, Kellison 1965, Lotti 1955, Thorbjornsen 1961), sweetgum (*Liquidambar styraciflua* L.) (Webb 1964), and eastern cottonwood (*Populus deltoides* Bartr. ex Marsh.) (Farmer and Wilcox 1966, Maisenhelder 1961) were established. At this time, the Forest Service initiated a tree improvement program to help mitigate a shortage in timber resources in the United States expected in the mid-1980s (Tibbs and Windham 1999). Studies soon followed for other hardwood species, including northern red oak (*Q. rubra* L.) (Gall and Taft 1973), cherrybark oak (*Q. falcata* var. *pagodifolia* Ell.) (Randall 1973), and sycamore (*Platanus occidentalis* L.)

(Land 1981, Webb and others 1973). By 1983 at least 27 hardwood species had been considered for tree improvement, and collections had been made for most of these (Purnell and Kellison 1983). Unlike southern pines, no one species or small group of species is suited to the various site types throughout the South, because hardwoods are very site specific. Understanding site specificity is essential to understanding and realizing genetic gain in hardwoods. However, the absence of economy of scale greatly limits the ability to develop a viable genetic program for most hardwood species.

Three early programs stood out for their longevity and contributions to hardwood genetics. These programs were established by the Forest Service, Southern Forest Experiment Station; the North Carolina State University Hardwood Research Cooperative (HRC); and the Texas Forest Service. The Southern Forest Experiment Station's program of hardwood tree improvement began in the early 1960s at the Southern Hardwoods Laboratory located in Stoneville, MS. Sweetgum, cherrybark oak, sycamore, and eastern cottonwood were studied initially, and other species added in the late 1970s and early 1980s just prior to the closing of the hardwood project in 1982 (Ferguson and others 1977, Mohn and others 1970). Eastern cottonwood, probably the most intensively studied hardwood species in the South, was the subject of testing from 1965 through 1980. Early tests indicated that local sources were superior to earlier introductions of European hybrids (Maisenhelder 1970). Testing eventually resulted in the release of the first and only certified genetically superior cottonwood clones in the country (Land 1974). Subsequently, collections were made from natural stands throughout the lower Mississippi River Valley, from coastal areas from North Carolina to Texas, and from other programs as far north as Minnesota. Large clonal tests were established with industry and university cooperators in Arkansas, Illinois, Kentucky, Louisiana, and Mississippi. Clones suitable for use in various portions of the Mississippi River Valley were identified, and data collected on vegetative propagation, controlled pollination, disease resistance, crown architecture, and selection strategies provided excellent information for industry and university programs to build upon (Cooper and Ferguson 1979; Cooper and Filer 1976, 1977; McKnight 1970). In general, clones originating up to 200 miles south of the plantation sites grew faster and had greater leaf rust resistance than local clones. Many of the cottonwood clones developed at Stoneville remain the backbone of plantation and breeding programs today.

Hardwood cooperatives were organized somewhat later than the pine cooperatives. The HRC began in 1963 with a combined program of intensive tree improvement and less intensive management of natural stands (Young 1996). Sweetgum, sycamore, yellow-poplar, green ash (*Fraxinus pennsylvanica* Marsh.), and water oak/willow oak (*Q. nigra* L./*Q. phellos* L.) received most of the attention during the early years because of their commercial importance across a majority of the Southern United States. Initially, a selection index was used to identify phenotypically superior trees, which were then grafted into clone banks and seed orchards with the oaks established in seedling seed orchards. In 1972, region-wide progeny testing was initiated by the HRC (Anon. 1999). Open-pollinated seed from phenotypically average or better than average sweetgum, sycamore, water oak, willow oak, and black walnut (*J. nigra* L.) were collected from natural stands throughout the South. The modified selection scheme was used because the index system proved inadequate for identifying genotypically superior southern hardwoods in natural stands (Purnell and Kellison 1983).

In 1971, the Texas Forest Service's Western Gulf Forest Tree Improvement Program formally added the Hardwood Cooperative Tree Improvement Program to their existing pine program (Byram and Lowe 1995). To date, 17 species-site trials and 188 open-pollinated progeny tests have been established with nearly 1,500 families (Byram and others 2000). After 20 years, sycamore, sweetgum, and green ash tests indicated that family differences were significant, but there were neither consistent provenance effects nor any meaningful genotype x environment interactions for hardwood species in the southern Coastal Plain (Byram and others 1998). A slight indication was found that sources from the western edge of the species range are slower growing. Families that performed well across the region could be identified as early as age 5 or 10.

Current Status

A survey of State tree improvement personnel indicated that most Southern States currently have hardwood tree improvement programs, and almost half are active members of one of the two hardwood cooperatives. Arkansas, Louisiana, Mississippi, and Texas benefit from their affiliation with the Western Gulf Forest Tree Improvement Program. North Carolina and South Carolina are currently members of the HRC. Sycamore and sweetgum are of primary importance in both programs, but other species have been added. Justification for research on a particular species sometimes results more from its importance to wildlife than from its importance to fiber production. Federal cost-sharing programs, e.g., the Conservation Reserve Program, drive planting of southern bottomland hardwoods on nonindustrial private land almost entirely. Demand is high now for hardwood seed to support Federal cost-share programs (Byram and others 2000), and if these programs are expanded through the extension of eligibility to additional lands, hardwood planting could increase substantially, and demand for improved seedlings would correspondingly increase.

Tree improvement efforts on Federal land in the South have shifted dramatically over the last 15 years. This is mainly because new laws have reduced the number of acres harvested and have subsequently reduced the number of acres planted annually. As rotations have lengthened and management programs have become less intensive, pine improvement programs are no longer justified for Federal lands (Tibbs and Windham 1999). Under current policy, only northern red oak and white oak (*Q. alba* L.) will have artificial regeneration programs, and these will rely on seedling seed orchards. Hardwood species that are difficult to maintain or are threatened by introduced pests such as American chestnut [*Castanea dentata* (Marsh.) Borkh.], butternut (*J. cinerea* L.), and dogwood (*Cornus florida* L.) receive special attention (Tibbs and Windham 1999) as gene conservation becomes a major focus of more programs (McCutchan 1999). The University of Tennessee and the Georgia Forestry Commission are partners with the Forest Service in these projects.

Genetic improvement of eastern cottonwood is probably more advanced than that of any species in the South. Ease of vegetative propagation, abundant seed production, and established techniques for controlled pollination have enabled programs to make significant advancements. Clones developed by the Southern Forest Experiment Station and the Texas Forest Service form the basis for several current programs, including the interspecific hybridization programs in the Pacific Northwest and around the world. Westvaco (now MeadWestvaco) probably has had the most consistent cottonwood program since the closure of the Stoneville project. Both clone and progeny tests were established throughout the 1980s. These were aimed at increasing realized gains, establishing a genetically diverse deployment population, and constructing a viable breeding population. Today, fiber farms (irrigated and fertilized plantation systems) are being investigated as a source of hardwood fiber for various southern mills. Improvement programs are targeting these sites for their specific needs.

The U.S. Department of Energy (DOE) is currently sponsoring research to develop *Populus* clones for the Southeast as part of their Biomass Fuels Program (Land and others 2000). Breeding and testing programs are active at Mississippi State University. New seed collections have been made from throughout Southeastern United States and clone tests have been established in Missouri (MeadWestvaco), Florida (University of Florida), Alabama (Boise Cascade), and North Carolina (International Paper).

Venture companies are exploring the possibilities for commercializing transformation products in a number of species. The Southeast will also benefit from work being accomplished at the Tree Genetic Engineering Research Cooperative at Oregon State University and the Poplar Molecular Genetics Cooperative at the University of Washington, especially in the genus *Populus*. The most exciting effort to date is the genomic sequencing work that is being done with *Populus*, which is being funded through the DOE (Anon. 2002). This effort is already developing projects aimed at increasing production of hemicellulose and auxin.

Unlike southern pine tree improvement, hardwood tree improvement has generally lacked a unified approach or the benefits of having a single-species focus. McKnight recognized this in 1975 when he characterized hardwood tree improvement as a "haphazard thing, a searching for meaning and direction." These words are still accurate when summarizing hardwood tree improvement efforts in not only the Southeast but throughout the United States. Numerous programs have been intensive at times only to be closed when demand lessens, when research dollars tighten, when raw material costs decrease, or when the perception of a hardwood shortage is replaced by problems of greater importance. This wavering has limited gains, mainly because it has necessitated the rebuilding of testing and breeding populations, something that has been avoided in

the continuous pine tree improvement programs of the South. Several major factors contribute to the unique aspects of hardwood tree improvement; these include the number of species, their site sensitivity, and their infrequent occurrence in even-aged monospecific stands (Land 1975).

As with past programs, current hardwood programs face a lack of long-term funding because hardwood furnish is perceived to be low in cost and accessible even though numerous southern mills are reaching further for their hardwood fiber supply. Even though large amounts of hardwood fiber are needed to sustain these mills, little has been invested in research to develop low-cost hardwood fiber sources that would provide substantially higher yields than natural stands do, and in less time. Industry funding has become even more restricted with the recent downturn in the paper industry. The funding crunch is also affecting long-term cooperatives through mergers and the capitalization of the supporting land base that is thought to be nonstrategic to a specific mill. Today's industrial programs are faced with a need to develop plantation schemes that will meet return-on-investment demands and build programs focused on one or two species that are adapted over a range of sites throughout the South.

THE FUTURE OF TREE IMPROVEMENT IN THE SOUTH

Many new tools are available to aid in efficiently manipulating the genes of forest trees. While traditional methods of quantitative genetics have been very effective, they can be enhanced with emerging technologies. There are exciting new possibilities for improvement through advances in biotechnology that allow incorporation of genes for traits such as herbicide resistance, insect resistance, increased cold tolerance, modified lignin, and growth. A requisite first step to applying biotechnology to plantations is the ability to vegetatively propagate selected clones. Rooted cuttings of many hardwood species and fewer conifers have been used in intensive forestry practices for decades and in a few situations for centuries. Classic examples include willows (*Salix* spp.), poplars, and sugi (*Cryptomeria japonica* D. Don), which has been clonally propagated for > 1,000 years and used in plantation forestry in Japan since around A.D. 1400 (Toda 1974). Unfortunately, most conifers and certain recalcitrant hardwoods have not been clonally propagated successfully. The primary obstacle to success is maturation. As seedlings of these species that are difficult to root mature, they undergo many morphological and physiological changes. One important trait that changes is the ability of severed stems to form adventitious roots. For these species, rooting of cuttings collected from very juvenile seedlings will often be high (> 80 percent), but rooting success of cuttings from open-grown trees typically drops to almost zero over a period of 2 to 10 years.

In many species, juvenility (the ability to form adventitious roots and rapid growth of rooted cuttings) can be maintained for several years through severe pruning (hedging) of stock plants to produce cuttings for rooting (Goldfarb and others 1997, Rowe and others 2002). Cuttings can be rooted at high frequencies even when taken from hedged loblolly pine that is several years old (Cooney and Goldfarb 1999). Rooted cuttings of this type grow as rapidly as seedlings from the same families (Frampton and others 2000, Stelzer and others 1998).

Other strategies exist for maintaining juvenility until clones can be selected and multiplied. One strategy employs establishing clone trials from stock plants while maintaining juvenility of the stock plants through selection age. A possible modification could include establishment of clones as axillary shoot cultures and maintaining the cultures at temperatures that are low but above freezing to delay maturation.

A second strategy being pursued consists of initiating somatic embryogenic cultures from candidate seeds. The cultures would be divided to generate somatic seedlings for clonal field tests while the remaining portions of the culture would be placed in liquid nitrogen for cryopreservation. When superior clones have been selected, preserved cultures could be recovered, multiplied, and used to generate somatic seedlings for reforestation. For the southern pines, all of these steps have been achieved, but there are limitations in the efficiencies of each step in the process. Also at this time, only a relatively low percentage of genotypes (families and clones) can be successfully propagated through all the steps.

Ultimately, the strategy most likely to be employed widely will be the one with the lowest cost per genetic gain delivered. Both technologies, though possible on a research scale, still require further development on an operational scale, so it is difficult to precisely predict gains and costs. Perhaps the ideal system would comprise elements of both technologies. That is, clones would be started as embryogenic cultures, cryopreserved, and clonally tested with somatic seedlings. Once selected, a moderate number of somatic seedlings could be turned into stock plants for large-scale, low-cost production of rooted cuttings for reforestation stock. Despite technological and strategic uncertainties, it appears likely that research advances in recent years, together with the potential genetic gains available and the widespread interest of many industrial landowners, will result in the development of some clonal system for the southern pines in the near future.

A third strategy, which may only be applicable to certain species, utilizes alternative explant sources from mature trees to initiate cultures. Pioneering work at the University of Georgia (Sommer and Brown 1980, Sommer and others 1985) has led to the propagation of mature trees via staminate inflorescence tissues (Merkle and others 1997). Sweetgum propagation has been an ongoing project at the University of Georgia since the mid-1970s. The development and refinement of asexual propagation techniques for sweetgum has been ongoing at North Carolina State University since the mid-1990s. Efforts have focused on optimizing the collection of cuttings, storage methods, basal auxin treatments, and transplanting times (Anon. 1998, 1999, 2000; Rieckermann 1995; Robison and others 1999). Recent success in both rooting and survival of sweetgum, however, has been tempered by poor shoot growth following rooting (Anon. 2001, Gocke and others 2001). Sweetgum would be more widely adaptable for use on southern sites than more easily propagated *Populus*, *Salix,* or *Eucalyptus* species.

True clonal forestry as is practiced with *Eucalyptus* species in many tropical countries (Zobel and others 1987), and with *Populus* species in temperate regions (e.g., Li and Wyckoff 1993, Stettler and others 1988), provides additional gains not possible through conventional breeding. When specific clones of any age tree can be propagated, the full genetic potential of the population can be utilized. Because no sexual recombination occurs when clones are propagated, there is no opportunity for specific gene combinations to be lost. If maturation can be reversed or at least arrested, clonal forestry for southern pines and recalcitrant hardwoods will likely become a reality.

Productivity increases from clonal forestry have often been dramatic. The best clones of *E. grandis* (Hill ex Maiden) in Brazil produce 70 m^3/ha/year, whereas unimproved seedlings produce only half this much volume (Zobel and others 1987). Similar benefits for hybrid poplars in the Pacific Northwest of the United States have also been realized. The best clones from hybrid crosses of *P. trichocarpa* x *P. deltoides* produce yields that are > 100 percent better than those produced by average seedlings (Stettler and others 1988). As clonal forestry becomes practical in more species, breeding will adapt from a population improvement approach to one that will capture heterosis by producing individual elite genotypes (Tuskan 1997).

Multiplication of specific full-sib families that have demonstrated proven performance has become operational with *Pinus radiata* D. Don and has had major economic impact on plantation programs in New Zealand, Australia, and Chile (Balocchi 1997). Several companies in the Southeastern United States are actively pursuing a similar strategy for the southern pines.

Deployment of genetically improved planting stock is the only opportunity breeders have to directly impact forest productivity. The number of methods to affect the type of propagule that will be deployed has increased and will continue to increase with the help of molecular genetics. Already molecular geneticists and breeders have collaborated to identify genes that are important in controlling economically important traits. In loblolly pine, for example, major genes for disease resistance (Wilcox and others 1996), specific gravity of wood (Groover and others 1994), and volume production (Kaya and others 1996) have been identified using DNA markers that are associated with the locus or loci controlling the economic trait.

Using marker-trait associations effectively is not straightforward (Bradshaw 1996, Johnson and others 2000, O'Malley and McKeand 1994, Williams and Byram 2001, Wu and others 2000). Marker-assisted selection will likely supplement traditional selection methods in some elite breeding programs. However, molecular markers are expensive, and determining the marker-trait association with field trials is even more expensive. It is very likely that markers associated with desirable traits in one parent will have different associations in other parents. Only if linkage disequilibrium is common in a population will marker-trait association be the same in each member of the population (O'Malley and McKeand 1994), and it is unlikely that this situation is common (Strauss and others 1992). In the future, if the investment is made to map genotypes of all parents in an elite breeding program, the incremental cost of using the markers for selection in both breeding and deployment populations could be reduced. Again this promising technology awaits improvement in cost efficiency (Johnson and others 2000).

Molecular geneticists' greatest contribution to tree improvement may be a better understanding of the processes of wood formation and growth. With knowledge about processes such as lignin biosynthesis (e.g., MacKay and others 1997), molecular geneticists hope to manipulate the process to make pulping more efficient (e.g., Dimmel and others 2001). Genetic engineering, or the insertion of foreign genes into the genome of a desirable clone, has been realized in forestry. In species in which tissue culture via organogenesis or embryogenesis is feasible, insertion of genes has great potential. One of the major factors that will hamper hardwood molecular biology programs is the lack of highly sophisticated conventional breeding programs for most species.

Advances in mapping and transformation have been more rapid in hardwoods than in the pines because of their relative ease of culture and manipulation. Indeed, various *Populus* species and sweetgum have become model species for industrial and cooperative biotechnology programs. This is even more evident with the recent announcement of a project to sequence a *Populus* clone (Anon. 2002). Development of molecular resistance to more environmentally friendly herbicides would reduce establishment and early rotation maintenance costs that have plagued hardwood plantations. This possibility has tremendous potential, and transgenic tests throughout the United States are providing insights into it. While this trait alone would allow for a tremendous increase in hardwood plantation acreage in the South, the addition of other characteristics, such as reduced lignin content, would provide even more impetus.

It is unlikely that transformed [genetically modified (GM)] trees will be widely deployed until the negative public perception of their use can be changed. This issue is likely to be a serious impediment to tree improvement in general. Recent attacks by bioterrorists have resulted in the destruction of transformed trees, vehicles, laboratory buildings, and ordinary selected trees in a tree improvement program (Kaiser 2001, Service 2001). Most of the June 2002 issue of "Nature Biotechnology" (volume 20, number 6) was devoted to various aspects of the use of GM crops.

CONCLUSIONS

Genetic tree improvement and plantation management has had and will continue to have a positive impact on forestry and forest management worldwide. The demand for forest products will continue to increase, and intensive management will be needed to meet this demand. Plantation management of fiber farms can also alleviate pressure on ecologically sensitive forests and provide year-round accessibility to wood. Tree improvement can best promote the conservation of forest ecosystems by providing high-yielding, adaptable planting stock for these fiber farms.

Tree breeders must be cautious in the use of the genetic resources in breeding populations. The rich genetic variation in most tree improvement programs is an endowment that must be skillfully managed. Fortunately, breeders have learned to manage populations both for short-term financial benefit and long-term conservation of genetic variation. The future of tree improvement for both pines and hardwoods is bright, with more challenges, more available tools, and more opportunities for gain than ever before.

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