Deployment of Genetically Improved Loblolly and Slash Pines in the South

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Above: **For this 15-year-old loblolly pine plantation, intensive silviculture was coupled with the best genetics to enhance growth.**

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ABSTRACT

Foresters in the southern United States are responsible for more than 75 percent of the nation's tree planting, and more than 95 percent of the seedlings are genetically improved loblolly and slash pines. Planting the best open-pollinated families on the best sites can dramatically increase productivity. However, such practices reduce genetic diversity in a plantation. Although a survey of state and industrial plantation managers reveals no problems thus far, as more homogeneous plantations are established on more acres, both gains and potential risks must be quantified so that landowners can make informed decisions about deployment options.

Keywords: genetics; industry; plantation forestry; silviculture

The South has truly become the "wood basket" for the United States. The recent Southern Forest Resource Assessment (Wear and Greis 2002) makes the trends very clear:

> Between 1953 and 1997, the South's timber production more than doubled, its share of US production increased from 41% to 58%, and its share of world production increased from 6.3% to 15.8%. The region now produces more timber than any other country in the world. …Timber market models forecast that timber production in the United States will increase by about a third between 1995 and 2040. Nearly all of this growth will come from the South, where production is forecast to increase 56% for softwoods and 47% for hardwoods. (www.srs.fs.fed.us/sustain/)

In 1998, 2.62 million acres and 1.6 billion seedlings were planted in the United States (Moulton and Hernandez 2000). The 12 southern states accounted for 78 percent of that, or 2.06 million acres. Available land, favorable political and social attitudes toward production forestry, productive soils, and a moderate climate all favor the growth of plantation forestry in the South. The trend is for these acres to be more intensively managed (Allen 2000; Prestemon and Abt 2002). With global demand for timber products increasing at 1.5 to 2 percent per year, even as the area of the world's forests is decreasing (FAO 1999), the productivity of southern plantations has local, regional, national, and global implications. By growing more wood on less area, these plantations can help provide timber to meet increasing demands while simultaneously reducing the environmental impact of industrial forestry (e.g., Sedjo 2001). A direct link between increased forest productivity in pine plantations and "saving" natural forests can also be made (Prestemon and Abt 2002).

Productivity increases in southern pine plantations have been dramatic over the past 30 to 50 years. If the best genetic material is planted with the best silvicultural inputs, mean annual increments of 300 $ft^3 a^{-1} yr^{-1}$ (21 $m^3 ha^{-1} yr^{-1}$) can be routinely obtained (Allen 2000). There are few other regions in the world where the combination of silviculture and genetics is having as big an impact on forest productivity. An integral part of the increase in plantation productivity and value has been the improvement in growth rates and wood quality from tree improvement programs in the South.

Virtually all forest products companies and all state forestry agencies in the South have active tree improvement programs, with some now entering their third generation of selection and breeding. Essentially all of the more than 1.2 billion loblolly pine and 150 million slash pine seedlings planted annually are the result of breeding, testing, and selection programs. Estimates of genetic gains from these improvement programs vary by geographic region, cycle of improvement, and degree of rouging, or culling, in seed orchards, but in general, gains in volume production per unit area average 10 to 30 percent over unimproved planting stock.

Genetic gains realized in the deployment population can be substantially larger than average gains from the breeding population. This is possible because plantations can be established with selected populations that range in selection intensities from orchard bulks with many parents to single clones. Different deployment strategies produce different levels of genetic gains but also result in different levels of genetic diversity. Four deployment strategies utilized to produce planting stock for plantations are listed in increasing order of genetic gain and decreasing order of genetic diversity:

1. Bulk mixes of seed collected from seed orchards: least genetic gain and most genetic diversity.
2. Single, well-tested open-pollinated families collected from wind-pollinated seed orchards (OP family forestry).
3. Single full-sib families created through breeding of well-tested parents, propagated from seed or bulked up through vegetative multiplication (full-sib family forestry).
4. Single, well-tested clones created through vegetative propagation (clonal forestry): most genetic gain, least genetic diversity.

Our objective in this article is not to evaluate the appropriate amount of diversity and gain in deployment populations but rather to summarize the deployment activities of the forest products industry and small landowners in the South. How are genetically improved genotypes being deployed, what are the levels of genetic diversity in operational plantations, and have foresters seen any problems from the various deployment strategies?

Clonal *seed orchards,* in which selected material is grafted into a single location and allowed to intermate to produce genetically improved seed, have been used for nearly half a century. Roguing seed orchards of undesirable clones, based on the poor performance of their offspring in field progeny tests, has long been the most common method used to enhance the genetic quality of plantations derived from tree-breeding programs. Historically, most orchards have been established with 25 to 50 phenotypically superior selections. These parent clones are multiplied by grafting many ramets of the same parent tree, then rogued to, say, the top 50 percent of those clones based on progeny test values. Roguing of orchards often increases the genetic gains by 40 to 50 percent over the initial mean.

Additional gains can be realized when single, well-tested *open-pollinated (OP) families* are deployed. Family block planting has become a common practice over the past 30 years (e.g., Duzan and Williams 1988; McKeand et al. 1997). Generally, these OP families are created by collecting seed from specific clones growing in wind-pollinated seed orchards. The mother of the family is well tested, and there are many pollen parents. Often the best families are planted on the best sites to maximize wood production, but average to above-average families are also deployed as blocks in plantations. Collecting OP families offers numerous advantages for improving production efficiency, such as maximizing seed-to-seedling conversion ratios in the nursery. Because family rank changes tend to be modest across most sites, there is little to be gained from matching specific families to specific site types (Duzan and Williams 1988). In addition, because there is typically a limit to the number of acres on which the best families can be planted each year, wood production is maximized if the best families are planted on the best sites. Similarly, if management inputs such as fertilization are limited, production gains are maximized if the best genotypes are treated first (McKeand et al. 1997).

Some companies are now deploying *full-sib families* (controlled crosses between two parent trees) in operational plantations (Bramlett 1997). Use of

Table 1. Results of a survey of 31 state and industry members of tree improvement cooperatives (100% response).

Annual seedling production (average annual number of seedlings the last 3 years)
- Loblolly: 1,137 million
- Slash: 150 million
- Longleaf: 32 million
- Other: 28 million

Number of seedlings deployed on your own lands (average the last 3 years)
- Loblolly: 427 million
- Slash: 73 million
- Longleaf: 6 million
- Other: 3 million

Number of seedlings for market sales and/or contracts (average the last 3 years)
- Loblolly: 697 million
- Slash: 86 million
- Longleaf: 28 million
- Other: 25 million

Number of seedlings deployed as open-pollinated family blocks (average the last 3 years)
- Loblolly: Company lands: 340 million
  - Market sales and/or contracts: 332 million
- Slash: Company lands: 37 million
  - Market sales and/or contracts: 28 million

Percentage of regeneration with 1st-generation seedlings (including 1½-generation): 46%
Percentage of regeneration with 2nd-generation seedlings: 54%
Percentage of regeneration with 3rd-generation seedlings (including 2½-generation): 0

Number of open-pollinated families deployed as family blocks (average the last 3 years)
- Loblolly: Company lands: 47 (average for each company)
  - Market sales and/or contracts: 66
- Slash: Company lands: 11
  - Market sales and/or contracts: 5

Average size of family blocks in plantations (on your own lands)
- Loblolly: 77 acres
- Slash: 82 acres

Number of parent clones in the seed orchards that supply your seed:

Loblolly: Rough average: 24	Fewest: 14	Most: 36
Slash: Rough average: 42	Fewest: 25	Most: 55

Note: Some numbers may not sum to expected totals because of some slight double counting and estimation of seedlings being planted.

families created by crossing well-tested parents on an operational scale allows for even more intensive selection of genotypes from the tree improvement program. Unlike OP families, both the female and the male parents are highly superior based on progeny test results, and potential gains and financial benefits can be extremely high (Bridgwater et al. 1998). These families are sometimes multiplied or bulked up through vegetative propagation. Although the expected genetic gain and the genetic diversity are very similar for both full-sib families and for rooted cuttings from full-sib seed of the same family, the number of genotypes (unique individuals) deployed with rooted cuttings is reduced slightly, as not all genotypes will root successfully.

Although only in its operational infancy with southern pines, *clonal forestry* has the potential to take productivity gains to very high levels. The process includes field-testing large numbers (hundreds or thousands) of individual genotypes, followed by mass multiplication of the few top clones (say 20 or 30) for operational plantations, generally established in monoclonal blocks. When the best individual genotypes are mass-produced and sexual recombination is avoided, then all the genetic potential from the tree improvement program can be exploited. This deployment strategy maximizes genetic gain but reduces genetic diversity in operational plantations.

The tradeoff of gain versus risk has long been recognized as an issue in tree improvement programs (Zobel and Talbert 1984). Genetic gain can be achieved only by eliminating undesirable genotypes from the breeding population, but if too few genotypes remain, the risk from narrowing the genetic base becomes unacceptable. This "breeder's dilemma" has been particularly important in tree improvement programs, where the results of genetic manipulation are evident for many years or even decades. The theoretical maximum gain would come from deploying the single most productive clone across all planted acres. For a landowner willing to take risks, especially on relatively few acres, the risk from deploying a single clone may well be offset by the potential gain and financial returns from harvesting more wood at rotation. Landowners who are risk averse may prefer to deploy more genotypes, despite the opportunity for dramatic increases in productivity.

Survey Data

In summer 2002, we conducted a survey of all companies and state forestry agencies that belong to one or more of the South's three cooperative tree improvement programs—the Cooperative Forest Genetics Research Program at the University of Florida, the Western Gulf Forest Tree Improvement Program at the Texas Forest Service, and the North Carolina State University–Industry Cooperative Tree Improvement Program. The objective was to determine how genetically improved seedlings were being deployed in the region.

We received a 100 percent response from all 31 state and industry members. These companies and states plant more than 1.3 billion pine seedlings annually in the South, or about 80 percent of the trees in the entire nation. Although there are other nurseries and organizations that plant trees in the South, we estimate that this survey represents at least 90 percent of the region's annual regeneration. Results of the first eight survey questions are given in *table 1.*

The vast majority (84 percent) of the seedlings being planted in the South are loblolly pine. Of the more than 1.1 billion loblolly seedlings planted each year, about 40 percent are planted on lands owned or managed by the organizations in the survey. The remaining 60 percent are for market sales and are planted by other industry landowners and nonindustrial private forest (NIPF) landowners. NIPF landowners purchase the large majority of their seedlings from private or state nurseries that participate in one of the three tree improvement cooperatives. Thus they, too, realize the benefit of the cooperatives' breeding efforts.

Just over half (54 percent) of the loblolly and slash pine seedlings being deployed come from second-generation seed orchards. No third-generation pines are currently being deployed, but the first seeds from such parents will be harvested in the next five years. Although not quantified, most of the remaining plantations using first-generation planting stock have originated from heavily rogued seed orchards or are only the very best families from these orchards.

On average, there are 24 clones in loblolly seed orchards and 42 clones in slash seed orchards, but the number of clones in orchards varies tremendously (see averages in *table 1*). The average least number of clones in an orchard was 10, but there were six orchards with only five to 10 clones. The greatest number of clones in an orchard was 70.

Overall, 59 percent of the loblolly pine plantations are established as single open-pollinated family blocks. About 80 percent of the regeneration on company lands is with OP families, compared with 48 percent of seedlings used for market sales. This represents a major shift in deployment strategy from 30 years ago, when virtually all plantations were established with mixed seedlots.

For slash pine, 43 percent of plantations are established as single OP family blocks. Compared with loblolly, a lower percentage (51 percent) of the regeneration on company lands is with OP families. The percentage of market sales seedlings (32 percent) is also lower for slash pine than for loblolly pine.

The relatively small regeneration programs with longleaf pine and other conifers and hardwoods (60 million seedlings annually) are with bulked seedlots. Some of the seeds come from seed orchards, some from seed production areas, and some from wild collections. We made no effort in this survey to determine the genetic quality of these propagules.

There are 14 companies using family blocks for deployment of loblolly pine, and on average they deploy 47 families on their own land. Six organizations grow and sell seedlings as specific families, and on average they sell 69 families. The number of loblolly families deployed as OP family blocks by a single company in a given year varies dramatically—from as few as four families in a single subregion to up to 90 families across the South.

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A researcher stands beside a superior individual tree for the third-generation improvement program.

The number of loblolly families being planted by a company represents what is deployed across all southern landholdings. A large company may plant a few families in a given subregion but numerous families across the South. We did not ask organizations to summarize by subregion. If the companies with geographically diverse landholdings are excluded, the average number of families deployed on company lands within a geographic province is 13.

For slash pine, there are six companies using family blocks for deployment, and on average a company deploys 11 families on its own land. Two organizations grow and sell seedlings as specific families, and on average they sell five families. The number of slash families being deployed as family blocks in a given year varied somewhat, from as few as three families to up to 22 families.

In recent years, deployment of specific crosses and even some clones of loblolly and slash pines has become feasible. About 4.3 million loblolly (0.4 percent of annual southwide planting) and 2.5 million slash pines (1.7 percent) are planted as full-sib families, either as mass control-pollinated seedlings or as bulked-up full-sib rooted cuttings. On average these are deployed in plantations of 46 acres.

To date there are no operational plantations with selected, individual clones being deployed either as rooted cuttings or somatic embryos produced via tissue culture techniques. Only a few experimental plots and pilot-scale plantations have been established.

The average size of OP family blocks is 80 acres for loblolly and 131 acres for slash pine. Block size ranged from 50 to 200 acres for loblolly and from 50 to 300 acres for slash pine. Most land-

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A typical second-generation seed orchard.

owners limit their clearcut size to meet certification or industry standards (e.g., the Sustainable Forestry Initiative standards of American Forest & Paper Association call for clearcuts that average no more than 120 acres).

The survey also yielded valuable information from cooperators concerning the risk of deploying pine seedlings as OP family blocks. Are genetically more homogeneous stands more vulnerable to pests and climatic extremes than plantations established with very diverse genetic entries? To date, respondents have not experienced any serious environmental or pest problems—diseases, insects, cold, storm damage—in family block plantings. Some have noticed families that were not as adapted as advertised—trees that had been tested for cold or drought tolerance, but not as well tested as they should have been. If severe cold or drought affects a family, the breeder can identify the problem and stop deployment of that family. Once deployed in a bulk mix, however, the problem family cannot be practically identified. Family blocks thus give the forester more control and can provide additional information with which to modify deployment decisions. Respondents have observed no outright plantation failures due to the use of family blocks.

Discussion

Landowners in the South have benefited tremendously from the work of the tree improvement cooperatives and the intensive tree-breeding efforts of the past 50 years. For loblolly and slash pine, we are not aware of any plantations that are currently being established with unimproved or wild seedlings. Even the most modest genetic improvement available raises productivity by about 10 percent. If the best full-sibs or clones are planted, gains of 35 to 50 percent are possible.

With relatively little additional cost, many forest landowners are aggressively trying to increase the genetic gain captured from tree improvement programs in the South. The best available OP families from intensively rogued orchards are being planted, presumably on the best possible sites. Some companies are willing to plant all or the vast majority of their lands with as few as four OP families. Although the average number of families being planted by any one company in a region is 13, there were five companies that planted between four and nine OP families each year. These families change from year to year according to the availability of seedlings, but only the most productive families are being utilized.

The conflict arising from the desire to maximize genetic gain from selection while minimizing risk from decreased genetic diversity has long been a critical issue in tree breeding. Loblolly and slash pine breeding programs were initiated with large numbers of selections from wild stands and unimproved plantations (White 1992). After only two cycles of selection, breeding populations and seed orchards remain relatively undomesticated, retaining much of the genetic diversity found in natural stands (Williams and Hamrick 1996). When OP families from selected seed-orchard clones are deployed, the resulting plantations have relatively high genetic diversity, because (1) the seed-orchard genotypes are not inbred; (2) there is a very low degree of relatedness among orchard parents contributing pollen; and (3) rates of pollination by nonorchard parents are probably 50 percent, or perhaps even higher (Adams and Birkes 1989).

Nevertheless, like their agricultural counterparts, tree breeders must be vigilant and monitor plantations to assess the risk of deploying certain genotype mixtures (e.g., Bridgwater et al., in review). Given the experiences to date from deploying OP family blocks, the risk from narrowing the genetic base in these plantations appears to be minimal. That said, our experience is limited to the past 30 years, and breeders must not become overconfident that risks do not exist.

Tree breeders have emphasized the need to deploy heterogeneous populations, at least at the landscape level. These landscapes may vary from many thousands of acres of plantations that are intensively managed to small plantations that are intermixed with natural pine stands, upland and bottomland hardwood stands, and agricultural fields. Even though only 15 percent of commercial forestland is in pine plantations in the South (Wear and Greis 2002), in some regions, pine plantations are extensive.

Of some concern is the desire of some foresters to plant only the best OP family on almost all acres. If the best family is substantially better than the second-best family, it is difficult to discourage foresters from using it exclusively. Breeders can quantify the gain for each family relatively easily, but it has been impossible to quantify the risk from using individual families or clones. A challenge for tree improvement research in the coming years will be to quantify acceptable levels of risk for plantations established across a range of landscapes. As more homogeneous plantations are established on more acres, both gains and risks must be quantified so that landowners can make informed decisions about deployment options.

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