TREE IMPROVEMENT AND SUSTAINABLE FORESTRY – IMPACT OF TWO CYCLES OF LOBLOLLY PINE BREEDING IN THE U. S.A.[1]

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Received February 8, 1999; accepted June 24, 1999

ABSTRACT

The N.C. State University-Industry Cooperative Tree Improvement Program has completed 43 years of genetic improvement for loblolly pine in the southern U.S. The impact of the tree improvement on forest productivity has been substantial through the two cycles of breeding, testing and selection. The southern U.S. plants more than one billion loblolly pine seedlings annually, all of which are genetically improved seedlings from seed orchards. Trees grown from seeds of first-generation seed orchards have produced 7–12% more volume per acre at harvest than trees grown from wild seed. Second-generation seed orchards are now producing more than 50% of the total seed harvest in the region with estimated gains ranging from 13% to 21% in rotation volume over unimproved seedlots. When second-generation seed orchards are rogued to the best 30% of the parents, gains of 26% to 35% in volume production at harvest should result. Gains over the first-generation are estimated to be 14 to 23% additional for rogued seed orchards. Genetically improved stock has not only demonstrated outstanding growth, but has also lower infection from fusiform rust, typically 20–25% below the unimproved seedlots. With additional improvements in value from quality traits (stem straightness and wood quality), the estimated genetic gains in value should be much greater. The intensively managed plantations of loblolly pine with genetically improved materials have had and will have significant impact on the sustained management of forest resources in the southern U.S. Although only 15 percent of the commercial forests are currently in plantations (11 million hectares), almost 50 percent of the South's timber supply will soon come from them. Improved wood production on limited commercial lands will reduce the logging pressures on natural forests, old-growth and ecologically sensitive forests. By increasing wood production per hectare in plantations, rather than by managing more hectares of forest, genetics, in combination with intensive silviculture, can and will provide better opportunities for the use of natural forests and forest lands for conservation and recreational purposes. Results from two-cycles of loblolly pine breeding strongly suggest that high-yield plantations by genetic improvement can contribute significantly to the conservation and sustained use of forest resources. The future impact will be even more dramatic as the tree improvement program moves to advanced generations. Together with intensive silvicultural practices, forest genetics and tree improvement will continue to contribute significantly to the sustained management of world forest resources.

Keywords: breeding, genetic gains, productivity, selection and sustainable forestry.

INTRODUCTION

Plantations of genetically improved forest trees are critical to maintaining sustainable wood supplies. Investment in genetic improvement has increased forest productivity and enhanced timber supply. Forest genetics has made significant contributions to forest productivity and plantation management throughout the world in the last 50 years. In the southern U.S., forests comprise more than 50% of the land cover and supply 53% of the timber harvested in the U.S. The southern pines are the most commonly planted species, with about 11 million hectares in plantations. The South plants approximately 1.2 billion seedlings annually, 80% of which are loblolly pine (*Pinus taeda* L.) seedlings and 20% are slash pine (*Pinus elliotti* var *elliottii* Engelm.) seedlings, and virtually all planting stocks are genetically improved seedlings from seed orchards. Productivity improvement from forest genetics has helped to provide a reliable, ecologically sustainable, and economically affordable supply of wood.

The N.C. State University-Industry Cooperative Tree Improvement Program (NCSU-ICTIP) has completed 43 years of genetic improvement for loblolly pine in the southeastern U.S. Members of the Cooperative, currently 16 industries and six states, annually plant more than 600,000,000 trees on 350,000 hectares, accounting for 37% of the annual tree planting in the

[1]) This paper was presented at the Third IUFRO-FAO Consultation on Forest Genetics and Tree Improvement August 22–28, 1998, Beijing, China

country. The first-cycle of loblolly pine breeding program started in the late 1950's and continued through the early 1970's. Seed orchards started to produce genetically improved seeds for reforestation in1969 and have provided sufficient seed needs for annual regeneration requirements since the early 1980's (Figure 1). The second-cycle breeding program began with selections from the first-generation progeny tests and additional plantation selections in the late 1970's. The second-generation seed orchards started to produce seeds in the late 1980's and now are producing more than 50% of the total annual seed harvest in the program. The hectares of loblolly pine plantations regenerated with the genetically improved seeds have been increased drastically since the 1980's (Figure 1). Up to 1997, a total of 9.6 million hectares of loblolly pine have been planted by the NCSU-ICTIP members.

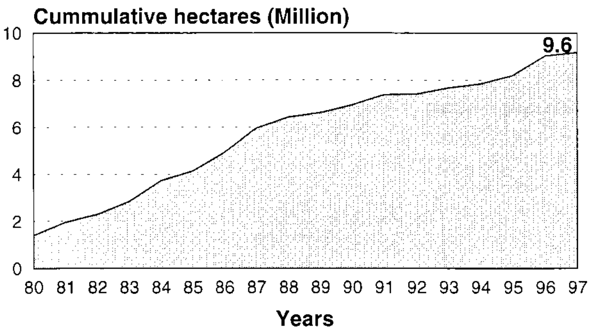

Figure 1. Cumulative hectares of loblolly pine plantations regenerated from seeds produced from seed orchards of the NCSU-ICTIP.

The impact of tree improvement on forest productivity was substantial through the first cycle of breeding, testing and selection completed by the NCSU-ICTIP (Figure 2). Trees grown from seeds of first-generation seed orchards have produced 7–12% more volume per hectare at harvest than trees grown from wild seed (TALBERT 1982). With additional improvement in value from quality traits (stem straightness, disease resistance, wood density), the estimated genetic gain in value from first-generation breeding is about 20% (TALBERT *et al.* 1985).

Second-generation seed orchards are now producing more than 50% of the total seed harvested in the region. Extensive progeny tests have been established across the regions to evaluate breeding values for those parents in seed orchards. Progeny test data from 2nd-generation seed orchards are now available to provide genetic gain estimates. In this paper we summarize the genetic gains from two cycles of loblolly pine breeding by the N. C. State Tree Improvement Program and discuss the impact on stand productivity and sustainable forestry.

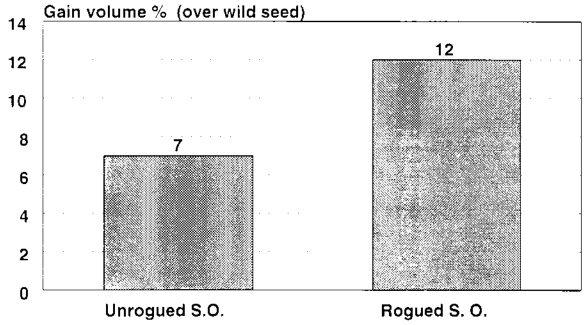

Figure 2. Twenty-five year volume gain estimates from unroqued and rogued seed orchards of the first-generation over unimproved checklots (from TALBERT *et al.* 1985).

METHODS

Phenotypically superior loblolly pine trees were selected from natural stands to form the first generation breeding population and production seed orchards (ZOBEL & TALBERT 1984). A tester mating scheme (an incomplete factorial mating design employing four or five tester clones which were mated to all other selections), was used to generate full-sib families for the progeny tests (TALBERT 1982, LI *et al.* 1996). Row plots were used to evaluate family variation and compare the selected stock with unimproved check lots. Tests were measured at age 4, 8 and 12 years of age to estimate average percentage gains in height growth over unimproved check lots (TALBERT *et al.* 1985). Ten of these first-generation tests were measured at the rotation ages of 25–28 years to verify the gain predictions based on the early ages by TALBERT *et al.* (1985).

Across all breeding regions, over 2,000 second-generation selections were made from 1st-generation progeny tests and grafted to establish 2nd-generation seed orchards. Open-pollinated progeny tests from those 2nd-generation seed orchards were established throughout the southeastern U.S. The number of families in each test series ranged from 19 to 44 including several unimproved check lots. Each test series generally included four tests established over a two-year period at two locations. The experimental design was a randomized complete block with six blocks and 6-tree row plots. All tests were measured for tree height, and some were measured for DBH, stem straightness and fusiform rust infection (LI *et al.* 1997). The tests were grouped into four general geographic regions for genetic gain estimates: Virginia and northern North Carolina, Atlantic Coastal Plain, Lower Gulf, and Piedmont. The numbers of families ranged from 83 to 285 per region.

Details of the data analysis and genetic gain estimates for those 2^{nd}-generation open-pollinated progeny tests were given by (LI *et al.* 1997). Briefly, a method of best linear unbiased predictions (BLUP) (HUBER 1993) was used to estimate parental breeding values for 8-year height, *i.e.*, they measured the amount of genetic superiority that can be inherited by progeny of parents. The expected genetic gain was then calculated from the predicted breeding values for height. Using unimproved checklots in progeny tests as the baseline, genetic gains were estimated as the percentage over local unimproved check lots. Breeding values for rust infection were calculated as the expected rust infection percentages for parents when the stand average would be 50% rust infection level (R–50).

Volume gains at rotation (age 25) were estimated from 8-year height gains using the methods described by (TALBERT 1982, TALBERT *et al.*1985). Briefly, percentage height gains at age eight years were assumed to equate to percentage gains at age 12, and the 8-year differences in height were assumed to equal site index value changes at stand age 12. The site index values were then used with the growth and yield model first developed by (HAFLEY *et al.* 1982) to estimate the volume in unthinned plantations at age 25 years. The simplifying assumption was that the shape of height over age curves is essentially equivalent for all families and that selection has little impact on other parameters of stand growth and yield such as mortality functions and height-diameter relationships, which were found to be reasonable assumptions in most situations (BUFORD & BURKHART 1987).

RESULTS

Genetic gain estimates directly from the 10 first-generation rotation tests, ranged from 5–13% for volume, were similar to those estimated by (TALBERT 1982) based on the early measurement. The predicted gains based on the early ages are generally reliable estimates for rotation gains. Over all regions, genetic gains for 25-year volume from an unthinned plantation are approximately 7% on average for unrogued 1st-generation seed orchards and 12% on average for rogued seed orchards (Figure 2).

Genetic gains over unimproved checklots (wild seeds) from 2nd-generation seed orchards for growth are substantially higher than those from the 1st-generation seed orchards (Figure 3). The genetic gains for all families in a region are representative of the gains from unrogued 2nd-generation seed orchards, while gains for the top 30% of families are representative of the gains from intensively rogued 2nd-generation seed orchards. Eight-year height gain averaged 8% above the local checklots for Virginia/North Carolina, 8% for the Lower Gulf, 6% for the Atlantic Coastal Plain, and 10% for the Piedmont region. The estimated rotation volume (25-year) gains over unimproved check lots ranged from 13% to 21% for unrogued orchards and 26% to 35% for the top 30% of families in rogued orchards (Figure 3).

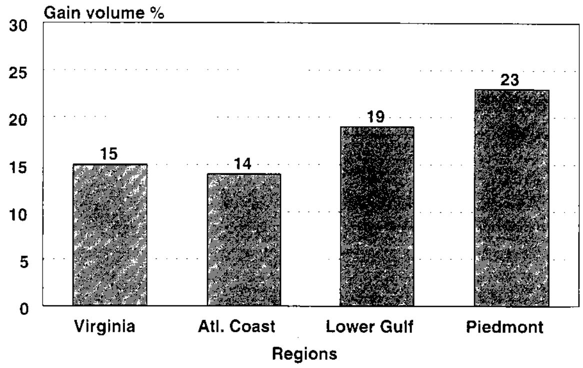

Figure 3. Twenty-five year volume gain estimates from unroqued and rogued seed orchards of the second-generation over unimproved checklots for the four geographic regions: Virginia, Atlantic coast plain, Lower Gulf, and Piedmont.

Since these estimates represent genetic gains from two cycles of breeding, by subtracting the average of 1st-generation gains, rogued second generation seed orchards produced additional 15% above the first-generation for Virginia/North Carolina, 14% for the Atlantic Coastal Plain,19% for the Lower Gulf, and 23% for the Piedmont region (Figure 4). On average over all regions, second-generation breeding and selection has produced additional 7% and 18% volume gains for unrogued and rogued seed orchards, respectively over the 1st-generation seed orchards (Figure 3 and Figure 4).

Improvement in resistance to fusiform rust is apparent based on the significantly lower R–50 for 2nd-generation families than for unimproved check lots. The R–50 measures the expected rust infection percentages for families when the average stand rust infection

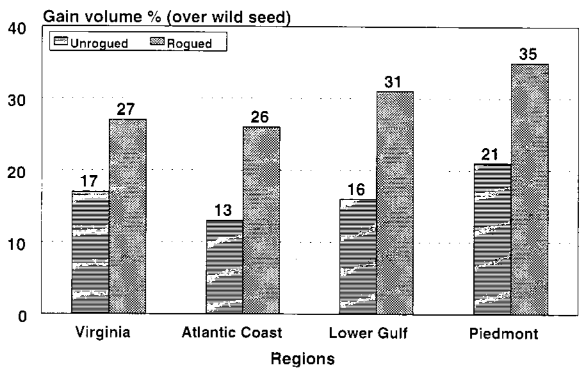

Figure 4. Twenty-five year volume gain estimates from rogued seed orchards of the second-generation over first-generation seed orchards for the four geographic regions: Virginia, Atlantic coast plain, Lower Gulf, and Piedmont.

would be at 50%. As shown in the example of the Atlantic Coastal plain (Figure 5), about 80% of the families had lower R–50 breeding values than the check lots. The top ranked 30% of families for rust in this region had an R–50 of 30% which is significantly lower than the checklot average (above 63%), more than a 30% reduction in rust infection. Similar differences in R–50 were observed for the Piedmont population which averaged 28% for the best 30% of the families and 56% for check lots.

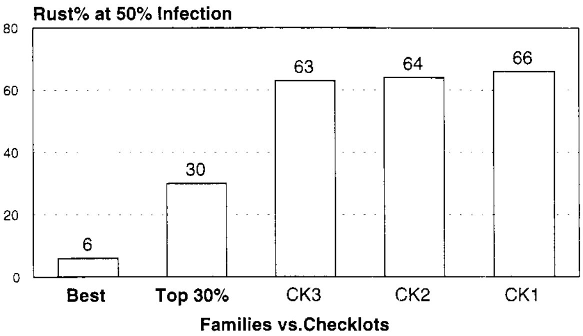

Figure 5. Percent rust infection (R–50) for the best family and the top 30% families compared to the three unimproved checklots (CK1, CK2 and CK3) in the Atlantic Coastal region.

Much greater genetic gain can be expected from utilizing the best families since large differences were observed among 2nd-generation families. The best Atlantic Coastal family had over 38% volume gain over the unimproved checks, while the best Piedmont family had 66% volume gain over the unimproved checks (LI *et al.* 1997). Although genetic gain for stem straightness is difficult to quantify based on subjective scoring systems, it is evident that most of the 2nd-generation families had much better stem/crown quality than the unimproved checks. The unimproved check lots are usually ranked at or near the bottom for stem straightness.

DISCUSSION

The Impact on Productivity

Loblolly pine, already the most significant commercial tree species in the U.S., will become an increasingly important source for softwood fiber for pulp and timber. To meet future demands without increasing pressures on old-growth and ecologically sensitive forests, timber productivity per hectare must increase (GLADSTONE & LEDIG 1990). Intensively managed plantations of loblolly pine, employing the best genetically improved planting stock and best silvicultual practices, are believed to be the most effective strategies to meet these demands, rather than managing more hectares of forest. With 7–12% more volume per hectare at harvest from the 1st-generation (Figure 2) and 17–30% more volume per hectare at harvest from the 2nd-generation than trees grown from wild seed (Figure 3), the impact of the tree improvement on forest productivity has been substantial through the two cycles of breeding by the NCSU-ICTIP. Considering the large scale planting program (Figure 1) and genetic gain estimates for the first generation (Figure2) and second-generation (Figure 3 and 4) seed orchards, it is estimated that additional 212 million m^3 of wood are being produced from these improved loblolly pine plantations, compared with the expected wood production from unimproved plantations. This enhanced wood production, using the current wood price in U.S., would translate into additional 4.3 billion US dollars of stumpage value.

Genetically improved stock has not only demonstrated outstanding growth, but has also lower infection from fusiform rust, typically 20–25% below the unimproved check lots (Figure 5). With additional improvements in value from quality traits (stem straightness and wood quality), the realized genetic gains in value should be much greater.

With the continued large scale planting program (Figure 1), these fast-growing plantations of loblolly pine will have much more significant impact on the future wood supply and the sustained management of forest resources in the southern U.S. Although only 15 percent of the commercial forests are currently in plantations (11 million hectares), almost 50 percent of the South's timber supply will soon come from them (KELLISON 1997). Improved wood production on limited commercial lands will reduce the logging pressures on natural forests and provide better opportunities for the use of natural forests and forest lands for conservation and recreational purposes. Clearly, results from two-cycles of loblolly pine breeding strongly suggest that genetic improvement, as an integrated part of intensively managed plantations, can contribute significantly to the sustained use of forest resources.

Maximizing Genetic Gains with New Technologies

The low efficiency of wind-pollinated seed orchards remains a significant barrier to realizing the genetic gain possible from the Cooperative's breeding, testing, and selection investments. The loss of potential gain increases in absolute value with each advanced cycle of improvement (*i.e.* pollen contamination) will be more detrimental to realized gain from third-cycle seed orchards than it was from first-cycle orchards. Research work is underway to improved technologies for capturing more gain from our breeding and testing investments. Technologies being developed include: Controlled Mass Pollination (CMP); Vegetative Propagation, both rooted cuttings and tissue culture (somatic embryogenesis); and molecular biology methods that could lead to marker aided selection and eventually genetically engineered forest trees.

Using the operational CMP (BRAMLETT 1997) and vegetative propagation techniques, we can maximize genetic gains by increasing the selection intensity of the production population, capturing the non-additive genetic variance, eliminating pollen contamination and selecting crosses or clones that have the most desirable trait combinations. An example is illustrated for genetic gain on 25-year rotation volume from second-cycle seed orchard bulk seed mixes, and the best three specific crosses, and the best clone selected from the best cross (Figure 6). These differences are supported by the papers by (TODD *et al.* 1995) and Frampton and HUBER 1995). Second-cycle seed orchard mixes are expected to produce 28 percent more wood per hectare than would be expected from plantations grown from wild seed. If CMP was used, for the best three full-sib crosses, gain could be as high as 40%. If rooted cutting or other vegetative propagation methods could be used for the mass production of the best individual tree in the best cross, it would yield as much as 60% more wood per hectare at harvest.

Biotechnology research has the potential to further enhance the benefits of genetic improvement through marker-aided breeding, selection and gene transformation. Progress is being made in describing the underlying genetic control of important traits and searching for genes that control growth, disease resistance and wood quality. The ultimate goal is to produce genetically engineered seedlings with desirable genetic makeup, but there are still many hurdles to cross before these techniques will be viable for the production of commercial seedlings for reforestation programs.

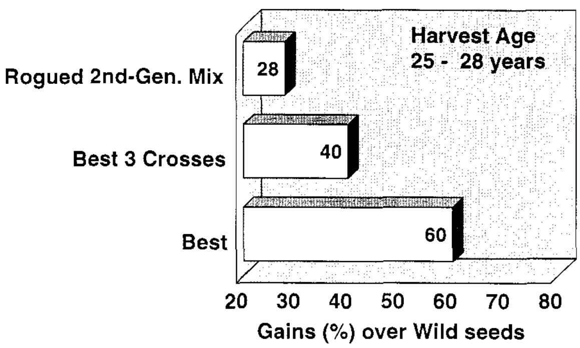

Figure 6. Expected gains of loblolly pine plantation harvested at rotation (25–28 years) from several genetic improvement – deployment alternatives.

Maximizing Genetic Benefits with Intensive Silviculture

To realize the full benefits of genetically improved planting stock, intensive forest management must be practiced. Additional gains can be achieved by planting seedlings by family blocks, rather than mixing the seed from a given orchard. Volume yields from such a family-block planting system are projected as much as 70% higher than unimproved checklots (MCKEAND *et al.* 1997). Family-block plantings offer additional opportunities to take advantage of intensive cultural practices, such as good site preparation, fertilization, and weed control. Families of highest genetic quality generally show an even greater response to intensive culture than do average families. For example, on a very good site at 8 years, the highest genetic quality families were projected to produce about 75 $m^3 \cdot ha^{-1}$ of volume with intensive cultural treatments, while the low genetic quality families (similar to unimproved) should produce about 45 $m^3 \cdot ha^{-1}$ (MCKEAND *et al.* 1997).

The performance of genetically improved loblolly pine families is generally stable and predictable for growth and rust resistance (LI & MCKEAND 1989, MCKEAND *et al.* 1990) and for wood quality (JETT *et al.* 1991) across a wide range of sites in the South. It has been shown that across a wide range of sites varying from very fast growth to poor growth, the relative performance of the families does not change. When the top ranked families are deployed, the better the site and/or the more intensive the culture, the greater the volume response. Thus, the best families should always be planted on the best sites. When intensive silvicultural treatments are being considered, sites that have the best families planted on them should likewise receive the highest priority for treatment since the growth response will be the greatest.

Potential Benefits for Small Forest Landowners

Genetic improvement has had the greatest impact on lands managed by forest industries, who own or lease about 20% of the southern forest land base and produce about 37% of the softwood timber through intensive forest practices. Intensive forestry practices have been adopted by only a fraction of the 4.9 million nonindustrial private forest (NIPF) landowners in the South. To date, small forest landowners who own 70% of the region's forest land, have not fully explored the potential of genetic improvement because they have too often elected low-cost natural regeneration methods over plantation establishment. Timber products can be grown intensively on productive NIPF lands and

Timber prices are near record highs, and are projected to increase even further in real terms in the future. With the phase out of crop subsidies, high-intensity short-rotation wood fiber crops on marginal agricultural lands can become very attractive financially for domestic production and for wood exports.

The southern forest resource is becoming much more important as a sound economic base for rural development (CUBBAGE & ARUNA 1996). Investing in the best available genetic material can provide the opportunity to grow more volume per hectare at a modest cost and thus increase benefits to small forest landowners. Genetically improved stock provides better adaptability, better growth potential, disease resistance, and higher wood quality than unimproved stock.

CONCLUSIONS

Considering the large scale tree planting program in southern U.S., the impact of the tree improvement on forest productivity has been and will be substantial through the two cycles of breeding by the N. C. State University-Industry Cooperative Tree Improvement Program:

- 7% volume gain over unimproved stock from unrogued 1st-generation seed orchards
- 12% volume gain over unimproved stock from rogued 1st-generation seed orchards
- 17% volume gain over unimproved stock from unrogued 2nd-generation seed orchards
- 30% volume gain over unimproved stock from rogued 2nd-generation seed orchards
- additional 14–23% volume gain over first-cycle for rogued 2nd-generation seed orchards
- significantly reduced fusiform rust infection and improved stem quality
- greater gains with controlled mass pollination and vegetative propagation
- much greater gains when combined with intensive silviculture

The future impact will be even more dramatic as the tree improvement program moves to advanced generations (MCKEAND & BRIDGWATER 1998). Together with intensive silvicultural practices, forest genetics and tree improvement will continue to contribute significantly to the sustained management of world forest resources.

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