41st

NORTH CAROLINA STATE UNIVERSITY-INDUSTRY COOPERATIVE TREE IMPROVEMENT PROGRAM

1997 ANNUAL REPORT

Department of Forestry
College of Forest Resources
N.C. State University
Raleigh, North Carolina

EXECUTIVE SUMMARY

REPORTS OF RESEARCH:

Breeding values have been estimated and used to calculate genetic gain from 2nd-generation open pollinated test data. The best parents are providing a large amount of improvement.

The Early Selection Verification Trial has provided evidence for early culling of some poor half-sib families based on total height at age-two. Increased testing efficiency is possible.

Family means from seedling tests are highly correlated with rooted cutting family means.

Genetic variability in leaf area, photosynthetic capacity, and nutrient use contributes to genetic differences in loblolly pine volume production at age 11.

An association between later cessation of height growth, later transition to latewood formation and lower specific gravity (especially at the provenance level) has been found in young loblolly pine.

A negative genetic correlation between wood density and volume growth has been detected at the provenance level. There is a very slight similar effect for families within provenance.

BREEDING, TESTING AND SELECTION:

Piedmont Elite Population (PEP) breeding is complete. Sixteen pollen mix tests and 10 factorial mating tests will have been planted by this time next year.

Lower Gulf Elite Breeding was adversely impacted by a March 1996 freeze. Despite this setback, several PMX tests are scheduled for planting during 1997.

The 3rd-cycle selection system has been improved with 6-year volume, along with tree height, now being used to improve rotation volume. A combined family and within family selection index, weighted by family and individual tree heritabilities, has been field tested with great success.

Intensive selection for volume production in breeding populations should have little impact on adaptive traits associated with resource acquisition.

SEED ORCHARD PRODUCTION:

The 1996 seed harvest was the third largest in Program history. Most members harvested seed selectively from their genetically best parents in order to capture more genetic gain.

The program staff is evaluating alternatives for developing 3rd-cycle seed orchards. Members will begin establishing 3rd-cycle seed orchard acreage in the next year or two.

ASSOCIATED ACTIVITIES:

The Cooperative has nine graduate students working on degrees and conducting research important to the Cooperative.

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INTRODUCTION

The North Carolina State University - Industry Cooperative Tree Improvement Program has completed 41 years of continuous operation. Our mission, "To Economically Increase Forest Productivity Through Genetic Manipulation of Pine Populations", encompasses both forest genetics research and development of genetic resources for regeneration. As we complete the first year of the Cooperative's fifth decade, we continue to build on the strong foundation developed through 41 years of outstanding cooperation among program members in partnership with the Department of Forestry.

The members of the Cooperative have made a major investment in future forest productivity through their selection, breeding, and testing work. Collectively 3,834 plantation and second-generation loblolly pine selections have been bred in 639 six-parent disconnected half-diallels. The progeny grown from 9,585 controlled-pollinations have been planted in 1,278 progeny tests. We have conservatively estimated that this effort represents an investment of $38,000,000. The information being developed from this enormous testing program is starting to pay dividends as we implement strategies to effectively capture the gain from this effort.

Plantations grown from second-generation orchard seed have an estimated gain of 16% over the productivity of plantations grown from wild seed. Roguing these orchards intensively to the best 10 to 15 parents could boost the gain to as much as 20% to 24% improvement in height growth and an even larger improvement in volume production at harvest. A substantial number of second-generation parents have demonstrated outstanding growth characteristics as well as rust infection levels that are 20 to 25% below the unimproved checklots. The option to establish 2.5 generation seed orchards is now being implemented by several program members. Third-cycle seed orchard establishment will be a major activity for many in just 2 to 3 years. Selection of the best parents for these orchards will be based on breeding value estimates currently available and on those soon to be developed from the diallel testing program.

Continued support of The Cooperative's research program offers great promise. The Tree Improvement Cooperative has made long-term investments in forest genetics research which is today providing information to optimize the selection of outstanding parent trees. This vital research investment will also guide 3rd-cycle breeding work which will provide the foundation for yet another round of selection and gain. We have new breeding strategies in place to capture genetic gains at a faster rate and at a lower cost than previous efforts allowed. Investment in research to improve and implement new technologies for evaluating genetic test data, and for capturing more gain is intensifying.

Our efforts are expected to make a substantial difference in the trees we grow and in the way we grow trees in the next century. Our Cooperative Program has made a major impact in the past and is poised to continue this progress in the future.

RESEARCH

Breeding Values and Genetic Gains from Second Generation Selections

Data from 93 open-pollinated progeny tests of second-generation selections were analyzed to obtain genetic parameter estimates and breeding value predictions for height, volume and rust resistance. The selections were made from progenies of incomplete factorial matings of the first generation parents where each of 20 to 30 females was mated to four to six males. These selections were grafted to establish 2nd-generation seed orchards by each cooperative member. Open-pollinated seeds from each seed orchard were collected, and the 2nd-generation progeny tests were established by member organizations throughout the Southeast. The number of families in each test series ranged from 19 to 44, including several check seedlots. Each test series generally included 4 tests established over a two year period in two locations. The experimental design was a randomized complete block with six blocks

An outstanding progeny test site in eastern Virginia has been recycled by the Virginia Department of Forestry. In the background are first generation progeny tests (20+ years old). Similar tests were clearcut and replanted with advanced generation diallel tests in the foreground.

and 6-tree plots. All tests were measured for tree height, some were measured for DBH, stem straightness and rust infection. Most of the tests had 6-8 year measurements but a few had only 3-5 year measurements.

Since open-pollinated loblolly pine families generally show little genotype by environment interaction and high family stability in performance across a wide geographic area, the data are summarized for four major geographic regions: 1) Virginia and northern North Carolina with 124 families in 5 test series, 2) Atlantic Coastal Plains of North Carolina, South Carolina and Georgia with 131 families in 5 test series, 3) Piedmont regions of North Carolina, South Carolina and Georgia with 285 families in 12 test series, and 4) Lower Gulf region with 83 families in 3 test series. Several test series have been established in the upper gulf region of Alabama and Mississippi but are too young to be summarized at this time.

All data were adjusted for age and scale effects before estimating the genetic parameters and breeding values. Family-mean heritabilities ranged from 0.51 to 0.87 for height and from 0.43 to 0.87 for stem volume among test series. The family-mean heritabilities for rust infection varied with test infection levels and ranged from 0.01 to 0.86. Best linear unbiased predictions (BLUP) were used to estimate parental breeding values because the data are unbalanced with different numbers of parents, ages and variable test quality. The BLUP for parental general combining abilities (GCA) were estimated and then breeding values were estimated using the GCA estimates. Breeding value estimates were based on 8-year height and volume measurements. For ranking parents within a given geographic region, percent genetic gain over the local checklot was calculated from the predicted breeding value for height. Breeding values for rust infection at a 50% infection level (R-50) were also calculated for ranking parents for rust resistance.

Breeding value estimates are summarized by regions for percent gain over local checklots for height (Table 1). Only height gain is presented here since not all tests have DBH and rust measurements. It is evident from these

Table 1. Summary of genetic predictions for height (%) over local checklots by regions.

Regions	Number of Families	Best Family	% of Families Below CC	Overall Mean	Mean of Top 30% of Families
Virginia/NC	124				
Over CC1		17.9	<1	8.1	12.7
Over CC2		12.2	30	2.9	7.2
Atlantic Coastal	131				
Over CC2		31.6	<1	13.2	19.9
Over CC3		17.1	44	0.67	6.7
Over CC4		21.4	24	4.4	10.6
Lower Gulf	83				
Over CC4		20.6	40	3.8	10.5
Over CC5		25.0	18	7.7	14.6
Over CC6		34.6	4	15.9	23.4
Piedmont	285				
Over CC6		23.5	4	15.5	15.5
Over CC7		29.3	<1	20.9	20.9
Over CC8		19.4	13	11.6	11.6

estimates that 2nd-generation selections have produced substantial gains over most of the checklots. The overall mean for families from Virginia/NC was 8.1% above the local checklots (CC1), and only one family had a breeding value below CC1. The relatively low gain over the North Carolina Coastal checklots (CC2) indicates that families from North Carolina sources may have potential in Virginia. For the Atlantic Coastal families, overall gains varied with different checklots, the greatest gain being over CC2 as expected and followed by gains over CC4 (coastal Georgia) and CC3 (coastal South Carolina). The superiority of South Carolina seed sources has been confirmed in other studies. The Lower Gulf families averaged 7.7% height gain over the local checklot, CC5, and the Atlantic Coastal families showed superior growth over local selections in this region. The overall gain for the Piedmont families ranged from 11.6% over CC8 (North Carolina Piedmont) to 20.9% over CC7 (Piedmont of South Carolina and Georgia), and very few families had height growth below the checklots.

These gains are in nearly all cases substantially higher than the height gain realized from first generation seed orchards. Published data from 16 first generation orchards indicated 3-4% height gain and 8-12% volume improvement. Volume gains of second generation orchards over unimproved checklots are expected to be much greater than those for height alone. These estimates indicate that in general, second generation breeding and selection has been effective for improving loblolly pine growth even with limited selection intensity resulting from the mating design used.

Much greater genetic gains can be expected from utilizing only the best families since large differences were observed among the 2nd-generation families (Table 1). The best family from each population was generally 10-20% above the 1st-generation seed orchard mix, indicating additional gains above the 1st generation selections. The best Atlantic Coastal family had 31.6% gain over CC2 and 17.1% over CC3, while the best Piedmont family had 29.3% gain over CC7 and 19.4% over CC8. The best performing families in the Lower Gulf region were from the Atlantic Coastal sources. Substantial genetic gains could be achieved by using these estimates to intensively rogue existing 2nd-generation seed orchards and establish new 2.5 generation seed orchards. The greatest gain could be made by selecting a few outstanding parents and making controlled mass pollinations, assuming that unfavorable specific combining ability is negligible for a full-sib cross. Genetic gain that could be achieved with different selection intensities is illustrated for the Atlantic Coastal (Figure 1a) and Piedmont populations (Figure 1b). By selecting the top 25 parents from each population, we could expect 8-21% and 14-24% height gains for the two populations respectively, depending on which checklots are used for comparison.

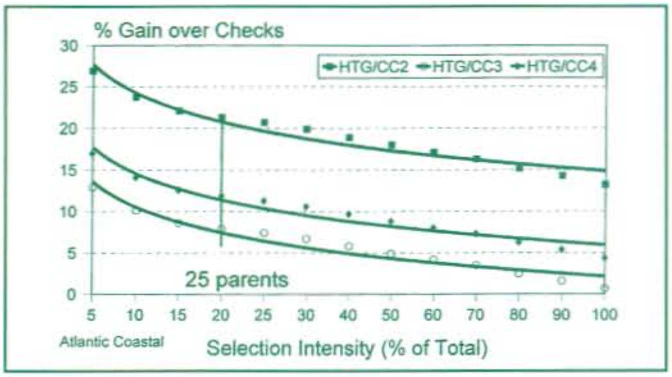


Figure 1a. Change in % gain in tree height over checklots CC2, CC3, and CC4 with varying selection intensities in the Second Generation Atlantic Coastal population.

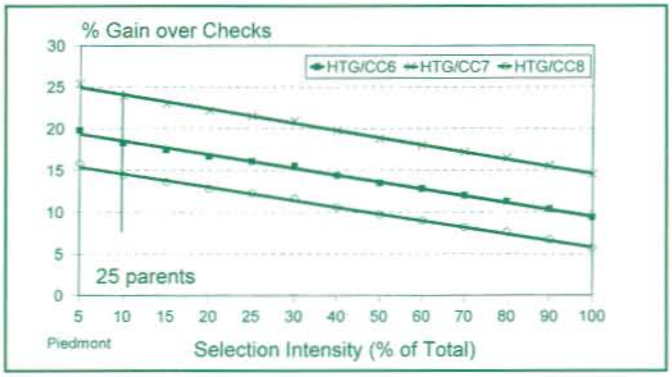


Figure 1b. Change in % gain in tree height over checklots CC6, CC7, and CC8 with varying selection intensities in the Second Generation Piedmont population.

Although genetic gain for stem straightness is difficult to quantify because of different ages and scoring systems in different tests, it is evident that most of the 2nd-generation families had a higher percentage of trees with above average straightness than did the checklots. In addition, rust infection (R-50) was generally lower for 2nd-generation families than the checklots. For example, in the Atlantic Coastal population, about 80% of the families had lower R-50 breeding values than all three checklots (CC2, CC3 and CC4). The top ranked 30% of families for rust in the Atlantic Coastal population had an R-50 of 29.6%, significantly lower than the three checklots (above 63%). Similar differences in R-50 values were observed for the Piedmont population, where the top ranked 30% of the families averaged 28% while the three checklots averaged 56%. No strong correlations were found between height growth and R-50 breeding values except in the Lower Gulf population. While rust infection was generally high for tests in the Lower Gulf, the R-50 was only moderately correlated (r = 0.48) with height growth (Figure 2). Because of this favorable correlation, it is possible to select fast growing families with relatively low R-50 values. Families with above 10% height gain and an R-50 less than 40% are identified in the Figure 2. To select for both fast-growing and rust resistant families in other populations, the combined index rankings of height gain and R-50 could be used. Different rust weightings could be utilized to select parents for deployment in different rust hazard zones.

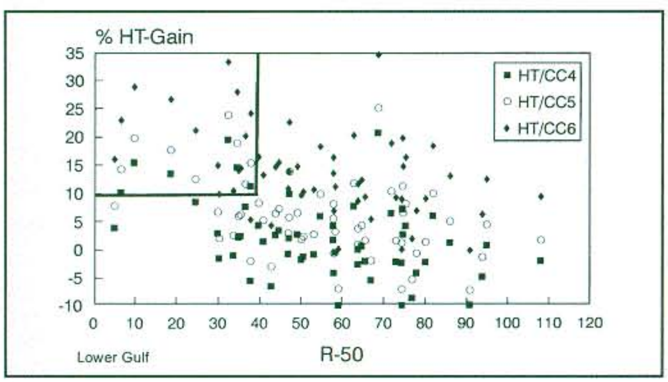


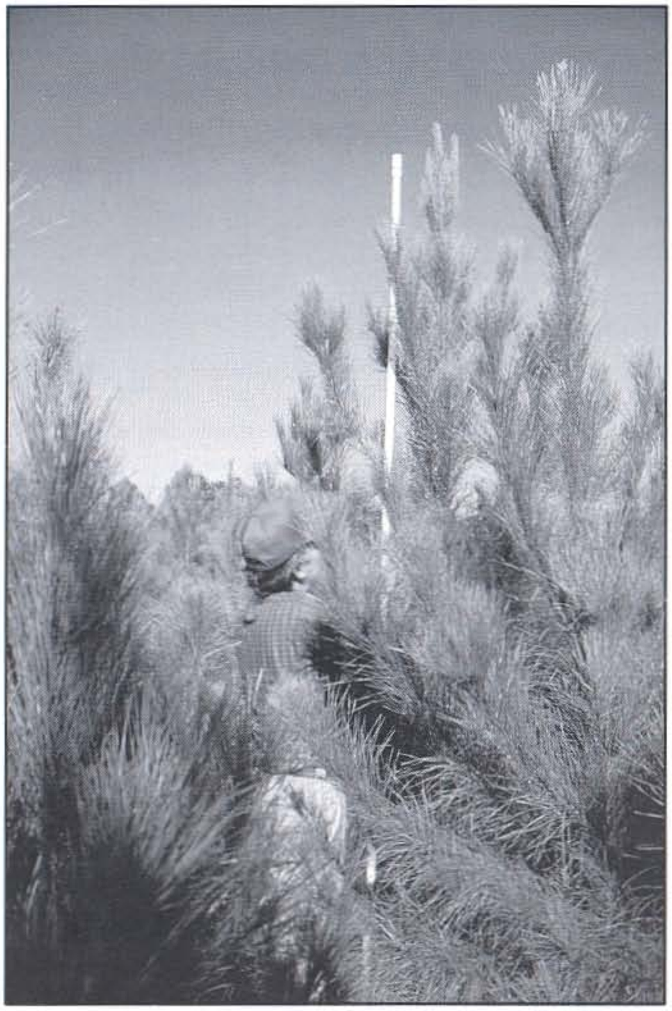
Figure 2. Scatter diagram depicting moderately favorable correlation between R50 and percent height gain over CC4, CC5, and CC6 in the lower gulf region.

Early Selection Verification Trial

As the Cooperative prepares to enter the third-generation of breeding and testing, the ability to identify selections which can be culled from the population before expensive control pollinations are initiated would be extremely valuable. To use early selection as a screening tool, a reliable and repeatable early selection system is required.

A Cooperative study, in conjunction with Dr. Floyd Bridgwater of the USFS, was established in 1989 in southwest Georgia at two locations – one established by International Paper Company and one by Georgia-Pacific. The objective of the study was to evaluate the use of stem elongation traits as a method of early selection. The study consisted of 13-16 OP families from each of the following five provenances: South Atlantic Coastal Plain; Marion County, FL; Gulf Hammock, FL; Lower Gulf Coastal Plain; Middle and Upper Gulf Coastal Plain. The first four provenances were also growing in the Florida Loblolly Provenance-Progeny Tests established in 1982-83 by members of the University of Florida and the NCSU Cooperatives. The Middle and Upper Gulf families were growing in the Cooperative's Intensive Culture Study planted in 1984.

Preliminary results from this study (reported in the 35th Annual Report) suggested that the utility of first and second year stem elongation for predicting sibling growth after five years in the field differed among provenances. Stem elongation after two years in the field was most strongly related to the fifth-year heights of half-sibs in the Atlantic Coastal Plain, Middle-Upper Gulf, and Marion County Florida regions. Stem elongation was only weakly related to the fifth-year heights in populations from the Lower Gulf and Gulf Hammock, FL regions. These preliminary results were not considered definitive since juvenile-mature family mean correlations have been shown to continue to increase after age five. The final determination, therefore, had to wait for the ten-year data from the Florida Loblolly Provenance-Progeny Trial.



The Early Selection Verification Trial has provided evidence for early culling of half-sib families based on total height of family means at age two.

When the ten-year data from the Florida Loblolly Provenance-Progeny Trial were analyzed, family means for total height after two years in the close-spaced Early Selection Verification Trial proved to be a useful tool for culling loblolly pine half-sib families from several regions of the southeastern United States. Culling the poorest 30% of families based on juvenile heights increased the expected average Performance Level for total height of older siblings by 0.3 to 0.5 standard deviations. There were no "Type A" errors among 38 families from three provenances. Type A errors result when families are culled on the basis of poor juvenile performance, but have good mature performance. Two families were "Type B" errors. Type B errors result when families are not culled at the juvenile stage, but do not perform well in older trials. Type B errors may not be as important as Type A errors because Type B errors can be revealed in subsequent long-term field tests.

Implementing the practice of culling half-sib families based on total height growth after two years in close-spaced tests could reduce the costs of a tree improvement program by reducing the number of families that must be included in long-term genetic tests. This should be an extremely valuable screening tool as we move into the third generation of breeding, especially for the accelerated breeding, testing and selection associated with elite population improvement strategies.

Field Comparison of Seedlings and Rooted Cuttings

As the Cooperative Program moves forward into the third-cycle of breeding and testing, there is an expanding investment in research focused on evaluation and development of promising technologies that could capture the gain possible from mass propagation of elite genotypes of loblolly pine on an operational scale. Rooted cutting technology is one potentially useful method that could substantially increase the genetic gain to be derived from past and future investments in breeding and testing. To do this practically, it is important to know that elite high value families, propagated as rooted cuttings, will grow as well or better than trees from those same families grown as seedlings. A field comparison of nine loblolly pine full-sib families grown at two locations as both rooted cuttings and seedlings has been maintained by the rooted cutting project and was recently summarized by the staff of the Tree Improvement Cooperative.

Data have been collected from two field locations following six growing seasons in the field. Field site one was established and maintained by Kimberly Clark Corp. in Monroe Co., AL and site two by Rayonier in Nassau Co., FL. The nine full-sib families used in the trial were developed from a 3 x 3 factorial mating design.

Seedlings and rooted cuttings from each of the nine families were grown in a greenhouse and then field planted. Data were collected annually on each site for height, fusiform rust, and DBH through age six (Table 2). No significant differences in height and DBH were found between rooted cuttings and seedlings on either site, although rooted cuttings had consistently larger height and DBH than seedlings on site two. Rooted cuttings had lower rust infection percentages than seedlings on both sites, although the differences were not significantly different except for the 4-year rust percentage on site one.

Growth performance and rust infection of rooted cuttings are strongly correlated with seedling performance of the same families at site one (Figure 3), where the family mean correlations increased over time and were highest at age six with correlations of 0.97, 0.98 and 0.84, respectively for height, DBH and rust infection. However, the correlations were low and nonsignificant between cuttings and seedlings among families for growth on site two due to two families that had different ranks when grown as cuttings and seedlings. After further examination of the data, seedlings of these two families were found to have much higher rust infection than their rooted cutting counterparts on this site. Family-mean correlations across the two sites were similar for rooted cuttings and seedlings, suggesting that rooted cuttings showed no greater interaction across the two sites than seedlings.

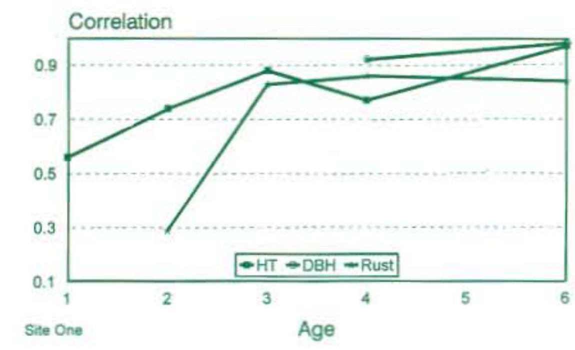


Figure 3. Family mean correlations of height, DBH, and rust infection between rooted cuttings and seedlings for 9 full-sib families – ages one through six.

Table 2. Mean height(feet), dbh(inches), and fusiform rust infection (%) of seedlings and rooted cuttings of nine loblolly pine families on two sites.

Trait	Site One Seedlings	Site One Cuttings	Site Two Seedlings	Site Two Cuttings
1-Yr Height	1.64	1.58	1.65	1.83
2-Yr Height	5.26	5.08	2.54	2.77
3-Yr Height	9.80	9.48	–	–
4-Yr Height	15.80	15.70	8.93	9.60
5-Yr Height	–	–	13.70	14.60
6-Yr Height	25.50	25.50	18.40	19.70
4-Yr DBH	3.09	3.02	1.54	1.72
5-Yr DBH	–	–	2.46	2.64
6-Yr DBH	5.39	5.23	3.36	3.52
3-Yr Rust %	29.4	26.3	–	–
4-Yr Rust %	45.7	37.9	25.6	19.0
5-Yr Rust %	–	–	26.9	19.1
6-Yr Rust %	50.2	44.7	22.2	15.6

In summary, rooted cuttings of loblolly pine can grow as well as and with slightly less rust infection than regular seedlings; seedling growth of loblolly pine families may be used for predicting growth of rooted cutting families; and rooted cuttings have similar stability across sites as seedlings. The results from this 6-year field study strongly support the use of rooted cuttings for operational deployment.

Genetic Differences in Carbon Dioxide Assimilation, Nutrition and Biomass Production in a 10-Year-Old Loblolly Pine Plantation

This project was conducted by graduate student Jan Svensson working jointly with the North Carolina State University Forest Nutrition Cooperative and Tree Improvement Cooperative. The study was established by Weyerhaeuser in Jones County, North Carolina in 1985 to quantify growth differences among 12 open-pollinated loblolly pine families. Each family was planted in a 100-tree block replicated four times in a randomized complete block design. The twelve open-pollinated families were analyzed for differences in height and volume growth from 1988 to 1995. Leaf area indices for six families which represented the range in height growth were assessed monthly for three years. Five of these families were also measured monthly for seasonal variation in foliar nutrient concentrations and light saturated photosynthetic rates from November 1993 to October 1994.

Family differences were found for height and volume production. Family heritabilities ranged from .32 to .52. The genetic correlation between height at age 4 and height and volume at age 11 was greater than 0.9. Only minor family rank changes occurred during this period. The differences in growth rates show that families differed in the utilization of the site's resources for stemwood growth. Leaf area index derived from litter fall showed no significant family differences, but optical estimates of leaf area index (using the LI-COR LAI-2000 PCA) did show family differences. One family differed by having lower leaf area index and higher growth efficiency based on LAI-2000 estimates. This was interpreted as a very efficient family, having low light interception while still having the highest growth rates.

Of the nutrients analyzed, P and Mg differed by family and two families had higher P contents. Differences among families in green needle retranslocation of Mg were significant and green needle retranslocation of N did show a weak family effect.

Light saturated photosynthetic rates (A_{sat}) when averaged across all months, differed significantly among families. Foliar nitrogen was positively correlated with A_{sat} when the winter months were excluded. Family differences in A_{sat} still existed when N was included in the model. No clear relationship was found between photosynthetic capacity and growth or between foliar nutrition and growth. In summary, the results of this work suggest that genetic variability in leaf area, phosphorus, magnesium and to some extent nitrogen and photosynthetic capacity could, over time, contribute to genetic growth differences.

Date of Earlywood-Latewood Transition in Provenances and Families of Loblolly Pine, and Its Relationship to Growth Phenology and Juvenile Wood Specific Gravity

There are several recent reports that fast-growing southern and coastal sources of loblolly pine have lower wood specific gravity than northern and inland sources when grown together in plantations. In this study, conducted by Keith Jayawickrama and supported by Georgia-Pacific, growth phenology, date of latewood transition and juvenile wood specific gravity of 5 and 6 year old trees were studied during two growing seasons

(1993 and 1994) in southwest Georgia. The trees were from 7-9 open-pollinated families from each of four provenances in tests at two locations. The four provenances were: Atlantic Coastal Plain, Gulf Hammock, Lower Gulf Coast and Upper Gulf Coast.

Provenances did not vary as to when height growth started in the spring, but showed significant differences for the date of cessation of growth in the fall. The Gulf Hammock source had the longest height growth period (until the end of August) and was a close second for height increment. The Upper Gulf source was the first to cease height growth (early August) and had the least annual height increment. Provenances also differed significantly for the date of cessation of diameter growth (with 22 days between the Gulf Hammock source and the Upper Gulf source in 1994). The order of the cessation of diameter growth was the same as for the cessation of height growth. The order of growth cessation was the same in both years. Families within provenances were significantly different for date of cessation of both height growth (maximum range of 20 days) and diameter growth (maximum range of 17 days). When least squares family means were calculated across provenances, there was a correlation of .69 between annual height increment and date of height growth cessation. There was a weaker association between faster growth and a longer growing season within provenances.

Provenances were significantly different for the date of latewood initiation in 1994, with a range of 22 days between the earliest and the latest. There were also significant differences among families within provenances for that year. Significant correlations existed between the date of latewood transition and the date of height growth cessation (r = 0.74 in 1993 and 0.67 in 1994), and with specific gravity (r = -0.43 and -0.45). These trends were even stronger based on provenance means. There was a strong, negative correlation between percent latewood and the date of latewood transition in 1994. Juvenile specific gravity had a weak negative correlation with annual height increment (r = -0.33 (93) and -0.22 (94)) and a stronger negative with diameter increment (r = -0.63 (93) and -0.34 (94)). This study provided evidence of an association (especially at the provenance level) between a later cessation of height growth, a later transition to latewood and lower wood specific gravity in five- and six-year-old trees.

Genetic and Environmental Effects on Biomass Production and Wood Density in Loblolly Pine

The objectives of this study, conducted by graduate student Paul Belonger, are to quantify family variation and covariation of wood density and stem volume, and to determine the environmental effects on wood density and volume. The source of the material for this study was six loblolly pine provenance progeny trials established jointly by members of the North Carolina State University Cooperative and the University of Florida Cooperative Forest Genetics Research Program. The trials were planted in 1982 and 1983 and included open-pollinated families from the following four geographic provenances: 1) Georgia-South Carolina Atlantic Coastal Plain, 2) Marion County, Florida, 3) Gulf Hammock area of Florida located in Levy and Dixie Counties, and 4) Lower Gulf region of Mississippi and Alabama. This study is being jointly funded by Georgia-Pacific, Kimberly Clark, Jefferson Smurfit, Rayonier and Union Camp.

Bark-to-bark 12 mm increment cores were taken from up to 5 dominant and codominant trees from each family in the three most uniform blocks from each location. Tree height and diameter at breast height were assessed for the same trees sampled for wood density. Stem dry weight was estimated as the product of volume (m^3) and wood density (kg m^{-3}) assessed at breast height.

Large family differences were found for stem volume and wood density. Family means ranged from 0.078 to 0.123 m^3 for individual tree stem volume and 410 to 458 kg m^{-3} for wood density. Family performance was stable across test locations with the family x site interaction accounting for less than 1% of the total variation for both stem volume and wood density (one-seventh the family variance). Further evidence of large family variation is provided by the individual tree heritabilities (Table 3) for the traits of interest. The heritabilities may be inflated by provenance effects but reflect the amount of variation available to tree breeders within southern sources of loblolly pine.

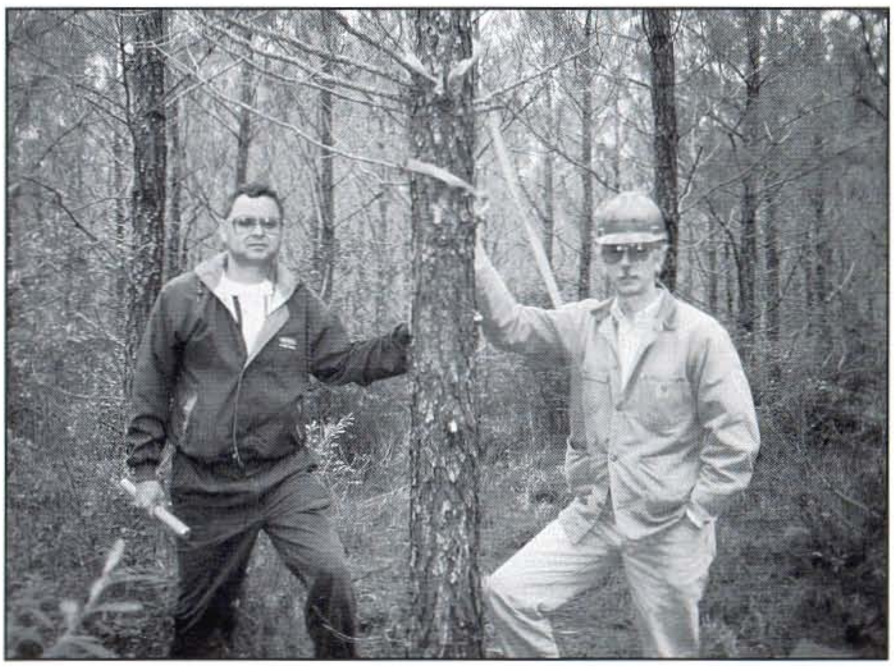
Table 3. Genetic (above diagonal) and family mean (below diagonal) correlations among traits of interest. Individual tree heritabilities are along the diagonal. Standard errors for heritability and genetic correlation estimates are in parentheses.

Trait	Density	Stem Volume	Dry Weight
Wood Density	0.66 (.124)	-0.31 (.145)	-0.07 (.150)
Stem Volume	-0.25+	0.32 (.075)	0.97 (.010)
Dry Weight	-0.03	0.97	0.29 (.069)

Selection of families for deployment or breeding is slightly constrained since the genetic correlation, although moderate to low, is negative between stem volume and wood density. Selection of families for volume would result in a slightly negative correlated response in wood density. The trend in the negative correlations is dominated by provenance effects with little influence by families within provenance. There was a strong positive family-mean and genetic correlation between stem volume and dry weight. It is apparent that fast growing trees are needed to maximize dry weight yield regardless of their wood density. Such a strategy may however trend toward lower quality of the wood produced, especially with respect to strength properties in solid wood.

Sites differed dramatically for both wood density and volume and were by far the most important effects in the study. Site effects accounted for 56% of the total variation for wood density and 67% of the total variation for volume. There was a strong negative correlation between wood density and stem volume for the four study site means. The most likely reason why such a strong negative environmental correlation exists among these sites is the availability of water late in the growing season. Water is rarely limiting on the flatwoods soils that exist at the Georgia and Florida sites, but late-season water stress is common in the well-drained soils at the Alabama and Mississippi sites.

Work is continuing on this project to determine within ring and between ring specific gravity, tracheid lengths and percent extractives. This phase of the project should be finished within the next year.



Maxie Maynor and Richard Bryant are justifiably pleased with an outstanding 3rd-cycle selection graded in an International Paper diallel test in the Coastal Plain of South Carolina.

BREEDING, TESTING , SELECTION

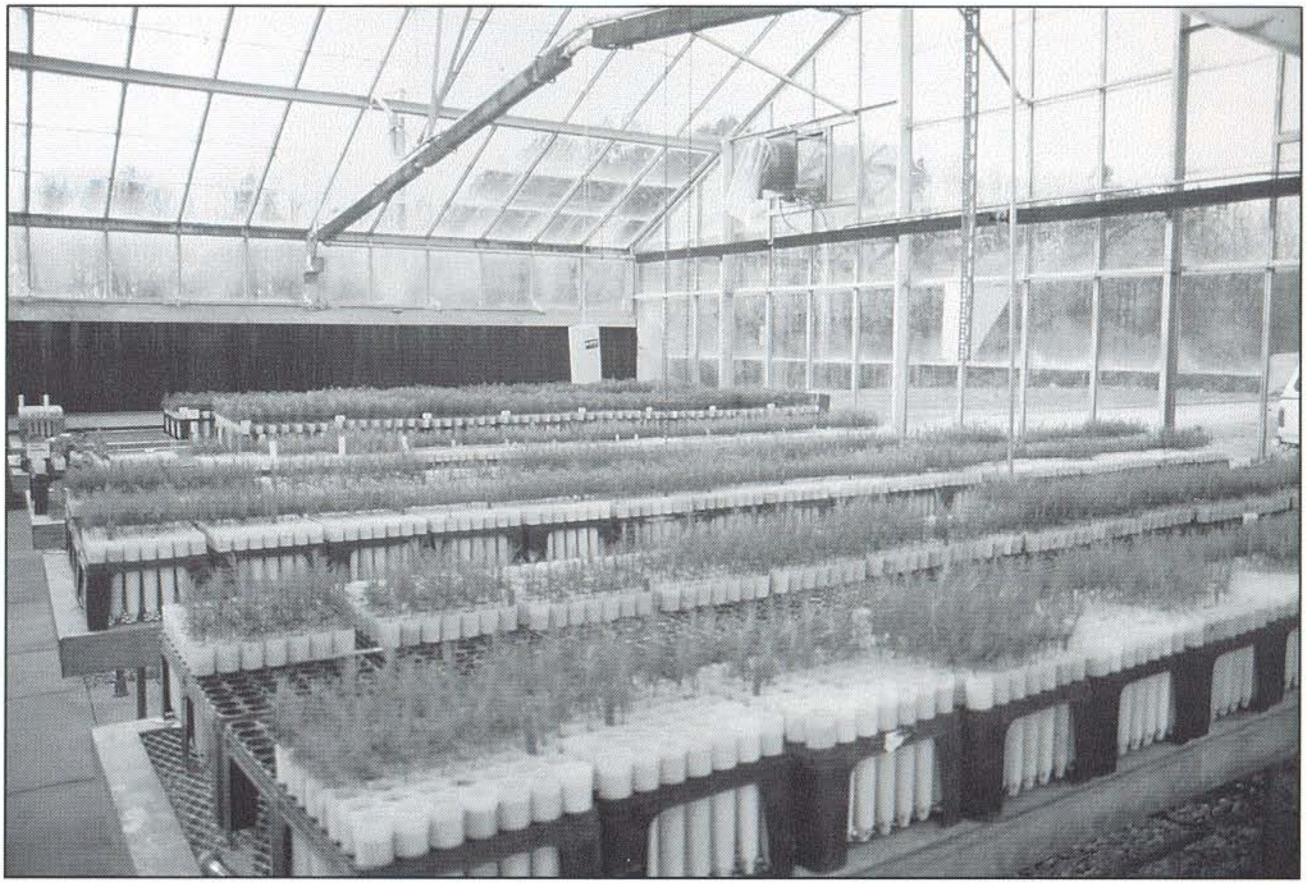
Piedmont Elite Population

Breeding for the Piedmont Elite Population (PEP) is essentially complete. The pollen mix (PMX) breeding of the 2.5 generation Piedmont and Atlantic Coastal Plain parents has been completed. Sixteen pollen mix tests were established this year in the fall-line, middle Piedmont, upper Piedmont and cold areas of the Cooperative. These PMX tests will provide information on the growth and adaptability of the Piedmont, Atlantic Coastal Plain, and Piedmont x Atlantic Coastal Plain hybrids across a range of sites.

The factorial mating of the 2.5 generation selections has also been completed. Two replicated tests with 116 full-sib hybrid families were established this year. Another eight tests will be established with 137 families next year. An increased interest in deployment of full-sibs necessitated the establishment of replicated tests to determine full-sib performance.

Breeding of the 27 Piedmont x coastal hybrids has also progressed well. We anticipate planting these PMX and diallel tests in the next two years.

Development of the Piedmont Elite Population began a mere five years ago. Cooperators participating in development of this Population are to be commended for their aggressiveness in completing the work for this Population so rapidly. Their efforts will yield valuable results in the next few years – results that should significantly impact the productivity of Piedmont forests in this region.



Test seedlings derived from pollen mix (PMX) breeding in the Piedmont Elite Population (PEP) were outplanted in sixteen tests during the past year.

Lower Gulf Elite Population

Breeding for the Lower Gulf Elite Population was adversely impacted by the freeze in early March 1996. Most of the female strobili were frozen along the Gulf Coast and South Atlantic Coast regions, thus very little breeding was accomplished last year. Diallel breeding was continued this year by members of the NCSU Cooperative, the University of Florida Cooperative Forest Genetics Research Program, and the Western Gulf Forest Tree Improvement Program.

Fortunately, seed yields from the 1995 pollen mix breeding were very good and the first pollen mix tests will be sown this summer. Plans are to establish a total of sixteen pollen mix tests across the southern part of the loblolly pine range ----- 12 tests east of the Mississippi River and four tests west of the Mississippi River. These tests will provide information on the relative value of trees from the South Carolina and Georgia coastal plain, Florida, and Livingston Parish/ Southeast Texas. Approximately 65 families will be established in this first series of tests.

Optimizing Selection Methods for the Third-cycle Breeding

Although large genetic gains have been achieved through the first two cycles of breeding, testing and selection by the cooperative members, additional gains

Grafts of 3rd-cycle selections made by the Virginia Department of Forestry will be transplanted into their breeding orchard during 1997.

can be achieved through advanced generation breeding. A third-cycle breeding strategy for the Cooperative has been outlined to provide accelerated gains for short- and long-term programs. To implement the third-cycle breeding plan, an efficient selection system has been developed to maximize gain from selection in the diallel progeny tests established during the current breeding cycle.

Early tree height has been used as the selection criterion for loblolly pine volume at rotation age. This trait was chosen because it was reported to have higher heritability than diameter or volume at early ages and was a good predictor of stand volume at rotation based on earlier studies. However, most of these studies were based on generalized prediction models with a few tests younger than rotation age, and data on other traits such as diameter or volume was not always available for estimating selection efficiency. A recent analysis of first generation rotation test data has been completed to obtain more accurate genetic parameters to predict rotation age volume and to obtain more accurate juvenile-mature correlations for diameter and volume. Juvenile DBH and volume had heritabilities similar to height, but were significantly better predictors than height for tree volume at rotation. Thus, the selection efficiencies for rotation volume (gain per year) were much higher using volume than using only height.

Based on these results, tree-volume has been added, along with height, in third-cycle selection. In general, tree height is strongly correlated with DBH, but the correlation is not perfect, family-mean correlations ranged from 0.75 to 0.90 depending on the diallel test series. This indicates that there is variation in DBH for families with a similar height. This is illustrated in Figure 4 using a 2nd-generation progeny test series with 12 parents in two diallels and several checklots. There is a generally strong positive correlation between mid-parent height and mid-parent volume for 30 full-sib crosses, but at a given tree height, i.e., around 19 feet, there is important variation in individual-tree volume, ranging from 0.5 to 0.57 cubic feet per tree. Selection of the tallest tree based on height could result in only intermediate volume among full-sib families in this case. By considering volume, it is possible to select "tall and fat" trees from this test series. It is also interesting to note the relative rankings of checklots in this test, "short and skinny" as marked in Figure 4, indicating the effectiveness of 2nd-generation breeding and genetic gains.

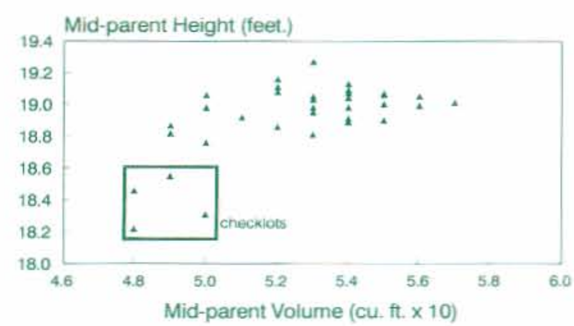


Figure 4. Variation in volume (resulting from DBH variation) for trees of similar height in a 2nd-generation diallel test series. Note the "short-skinny" checklots in the box.

Based on the genetic parameter estimates and least square means generated from the diallel analysis, a combined family and within family selection index has been developed to select the best individuals from the best families. Data are standardized to remove the scale and environment effects and then a combined index is calculated with both family and individual within family performance for height and volume, using family-mean heritability and within family heritability as weights. This combined index allows for selection of the best individuals from the families with highest mid-parent breeding values, not the best trees from average families. In addition, with both height and volume index information, it is possible to avoid open-grown candidate trees and to avoid "tall and skinny" trees in the field. A candidate tree list is generated according to the combined index and followed by a pre-screening to eliminate those undesirable trees based on rust infection and quality traits. A final decision (after field selection) is made after examining the co-ancestry information among parents and the relative comparison of parental breeding values among different diallel test series.

Genetic Diversity of Adaptive Traits

The major concern in deployment of intensively selected families is the increased risk of susceptibility to pests or other stress factors due to a reduction in genetic variation. Breeders are constantly concerned about reducing the genetic variation below "acceptable" levels. Unfortunately, there is no clear definition of what is or is not acceptable.

Currently, a typical industrial regeneration program in the South would utilize between 5 and 20 open-pollinated families in any given year. A different set of families may be utilized by each organization and state agency. Diversity among and within families is tremendous since numerous parents are contributing to the pollen mix. As propagation methods are refined to capture more of the potential gain through use of mass control pollinations or rooted cuttings, the genetic base of the deployed propagules could be further reduced. Care must be taken to guard against deploying only the very best genotypes to the point where the level of vulnerability to pathogens is unacceptably high.

To date, the level of genetic variability for adaptive traits among genotypes intensively selected for the economically important traits is still quite high. Breeders have long recognized that intensive selection for quality traits such as stem straightness and wood specific gravity have little impact on adaptive traits since these traits are most often genetically independent. A recent evaluation of the genetic associations among traits that have strong adaptive significance and stem volume was completed. Results showed that adaptive traits related to the acquisition of light, water, and nutrients were not strongly associated with volume production. That is, genotypes with high stem volume production grow fast for different reasons. One genotype may be very efficient at nitrogen or phosphorus uptake while another is more efficient at water use or photosynthesis, but generally any one adaptive trait or suite of adaptive traits was genetically independent of volume production. Therefore, intensive selection for volume production in breeding populations should have little impact on adaptive traits associated with resource acquisition.

With second generation orchards in full production, plans are being initiated for establishment of third-cycle seed orchards.

SEED ORCHARD PRODUCTION

Establishment of Third Cycle Seed Orchards

During the past year, several members have expressed an interest in exploring opportunities for capturing additional gain based on information coming out of the second breeding and testing cycle. After considerable discussion, it has become apparent that there are numerous factors to consider before embarking on a new cycle of orchard establishment.

First, a determination must be made as to when a sufficient level of gain is available to warrant the cost of establishing a new seed orchard block. The first step in making this determination is to calculate the gain being realized from your current orchard blocks as they are currently constituted and their potential gain when rogued based on Open Pollinated Test data. A new orchard block should only be established when it can provide gain over and above that currently available or available after roguing existing orchards.

Once it has been determined that sufficient gain exists to warrant establishment of a new orchard block, a number of questions must be answered prior to establishment. What kind of orchard should be established? What size block will be established? What is the optimum orchard spacing?

Type of Orchard – Should the new orchards be 2.5 generation orchards (parental), 3.0 generation orchards (offspring) or a combination of parental and offspring. Thinking is currently on the side of 2.5 generation parental orchards. While we believe the gain from the two orchard types may be equivalent, the parental orchards offer several advantages: 1) Family selection intensity is higher in parental orchards since two parents are involved in each selection in an offspring orchard, and in many cases the best parents were never mated to each other, thus no offspring selection exists, 2) Orchards are developed with proven winners, 3) Only clones with acceptable flower production need be established, and 4) Clones which have demonstrated a significant level of graft incompatibility can be avoided. While the orchard may be predominantly a parental orchard, a few exceptional third generation selections could be included. Selections considered for inclusion would be from full-sib families where both parents are of high enough quality that they would have been included in the parental orchard. Offspring selections from such families would have almost no adverse impact on the selection intensity, yet would have the potential for some added gain from within family selection. Whether or not it will be possible to include both selection types in the same orchard will depend on results from the Scion Maturation Study. If selected trees from different generations (ages) develop at vastly different rates, inclusion of selections from different genererations may be unwise since the slower growing material could well end up as suppressed trees. Results of the Scion Maturation Study will provide information on how fast grafts from selections of different ages develop. The study is scheduled for measurement this spring and results should be available by the end of the summer.

While it is expected that traditional wind-pollinated seed orchards will continue to supply the bulk of the seed needed for regeneration in the near future, members may wish to consider establishment of at least a few clonal blocks to facilitate mass control pollinations. Seed generated from mass control pollinations allow additional gain resulting from the mass production of a cross with exceptional mid-parent values and positive specific combining ability to be captured. Mass control-pollination also eliminates the problems of pollen contamination experienced in traditional seed orchards. Pairs of clonal rows or blocks of the parents of full-sibs with exceptional performance can be established as they are identified from the breeding program. Information on flowering should also be available from the breeding program, allowing selection based on good flowering as well as on performance. The ability to select for flowering (both male and female) is critical if this technology is to be economically feasible. Establishment of clonal rows or blocks is an ongoing process. Whenever a full-sib with exceptional performance is identified and both parents have acceptable flowering levels, a block or row of the two parents can be established.

Analyses are currently underway to quantify the potential gains from the different orchard types and to further define the pros and cons of alternative orchard types. We are also gathering available information on mass control pollinations and defining research needs to optimize the technology.

Block Size – Will the entire orchard be established at one point in time or will the total acreage needed to meet seed requirements be divided into a couple of blocks and established at different points in time? Each year the percent of gain possible from the current breeding and testing cycle increases. A hundred percent of the possible gain will not be available until the year 2003. A substantial portion of the gain, however, will be available in the next year or two. While the gain from a block of orchard established now will be somewhat less than what will be available at the end of the current cycle, it is captured five to six years earlier. A practical approach may be to establish a block of the orchard now and the remainder at or near the end of the breeding and testing cycle.

Orchard Spacing – It is still recommended that orchards be established at an initial stocking level of approximately 100 trees per acre. At higher stocking levels, significant thinning is required prior to the availability of information from open-pollinated seed orchard tests and prior to any significant level of seed production. Initial stocking levels that are lower than 100 trees per acre result in too few ramets per clone per acre and a reduction in early per acre seed production .

Any number of spatial arrangements (15' x 30', 18' x '25', 21' x 21') will yield approximately 100 trees per acre. Square arrangements are advantageous for crown development and will slightly delay the time of the initial roguing which can provide additional time in which to obtain results from open-pollinated tests.

The economic value of any tree improvement investment is derived from translating genetic gain from breeding, testing and selection into improved forest plantations. The Cooperative has excelled in the past in producing large quantities of open-pollinated seed from orchards for their regeneration programs. We not only need to continue to excel in this area, but also need to initiate developmental work to optimize the techniques needed to mass produce the best specific crosses from this and future breeding cycles.

Cone and Seed Yields

The 1996 loblolly pine seed harvest was the third largest in the history of the N.C. State Tree Improvement Cooperative. A total of 75.8 tons of genetically improved seed was harvested, which is sufficient to plant over 2.5 million acres of forest land. The size of this harvest was exceeded by only the 1987 and 1984 seed crops of 93.3 and 80.1 tons, respectively. The 1996 harvest was more than double the crop harvested in 1995 (Table 4). Of the 75.8 tons harvested, 22.7 tons were from Piedmont orchards and 53.1 tons from Coastal orchards. The Piedmont second-generation orchards more than tripled

Table 4. Comparison of 1996 and 1995 loblolly seed orchard harvests in the N. C. State Tree Improvement Cooperative.

	BUSHELS OF CONES		POUNDS OF SEED		POUNDS OF SEED/BUSHEL OF CONES	
SOURCE	1996	1995	1996	1995	1996	1995
Coastal 1.0	40,285	13,494	66,073	22,641	1.64	1.68
Piedmont 1.0	15,345	8,118	22,350	12,595	1.52	1.55
Coastal 2.0	25,897	14,744	40,177	22,424	1.55	1.52
Piedmont 2.0	15,209	4,250	22,027	6,207	1.45	1.46
TOTALS	**96,735**	**40,606**	**151,867**	**63,867**	**1.57**	**1.57**

production, increasing from 3.1 tons in 1995 to 11 tons in 1996. Overall, second generation Piedmont orchards provided about 50% of the total Piedmont seed harvest. A measure of seed orchard management efficiency is the yield of seed in pounds per bushel of cones harvested. In 1996 all Cooperative seed orchards averaged 1.57 lbs. of seed per bushel of cones. This was exactly the same as 1995, and remains the third highest in Cooperative history; only the 1986 and 1987 crops had higher pounds per bushel yields, at 1.65 .

When favorable environmental conditions (warm temperatures, ample rainfall and sunlight that occur late in the growing season of the year flowers are initiated) are joined with effective management of seed orchards (namely, nutrition amendments, stocking control and most importantly effective insect control) then "bumper" seed crops can result. In 1996 this happened and most seed orchard managers were able to meet seed production targets while harvesting only from the genetically best parents. Many seed orchard managers collected cones and seed from only the best 6-10 parents in each seed orchard. Many of these parents produced more than 2.0 lbs. of seed per bushel of cones. Three parents produced more than 3.0 lbs. of seed per bushel; 8-120 and 10-5 in Champion International orchards, and parent 9-17 in a Rayonier seed orchard. We have observed several parents that are highly efficient seed producers regardless of where they are growing; for example, in 1996 parent 10-5, known to produce seed which is very rust resistant, produced well above the orchard average in four different seed orchards, located in three states (Table 5).

Table 5. Some parents, such as 10-5, tend to produce higher lbs./bushel yields than the orchard average regardless of where they are growing.

Orchard	Parent 10-5 Lbs./bushel	Orchard Ave. in Lbs./bushel
Jefferson Smurfit	2.24	1.87
MacMillan Bloedel	2.55	1.74
Rayonier	2.68	2.19
Champion	3.38	2.13

For the first time in many years, production efficiency leaders were all above the 2.0 lbs. of seed per bushel mark. Seed orchards of Champion International Corporation once again lead the way with 7 orchards ranked in the top ten for production efficiency (Table 6). Rayonier had two orchards producing above the 2.0 mark and Georgia Pacific had one. The very best seed orchard in 1996, rated on seed production efficiency, was a repeat from last year. It was Champion International's 1.5 generation Alabama orchard, located in Newberry, SC and managed by George Oxner and associates. Table 6 shows the top ten orchards for seed production efficiency and their managers. Congratulations to all of these organizations and their seed orchard managers for a job well done!

Table 6. Seed orchard production efficiency leaders for 1996.

Organization	Orchard Type	Age	Lbs./ Bushel	No. of Parents	Orchard Manager
Champion, SC	1.5 Alabama	21	2.66	3	George Oxner
Champion, NC	1.0 Coastal	34	2.40	4	George Brantley
Rayonier	1.5 Coastal	20	2.19	5	Randall Driggers
Champion, SC	1.5 Piedmont	30	2.18	5	George Oxner
Champion, SC	2.0 Piedmont	20	2.15	12	George Oxner
Champion, FL	1.5 Coastal	19	2.13	16	Homer Gresham
Champion, SC	Rust Resistant	27	2.07	5	George Oxner
Champion, NC	2.0 Piedmont	16	2.07	11	George Brantley
Georgia Pacific	1.5 Coastal	17	2.04	18	Keith Palmer
Rayonier	2.0 Coastal	16	2.03	10	Randall Driggers

ASSOCIATED ACTIVITIES

Graduate Student Research and Education

The education of graduate students and the research they conduct as part of their degree programs continues to be an important activity of the Cooperative. During the past year, nine graduate programs have been developing in association with the Tree Improvement Cooperative. Four were directed towards a Masters degree and five were involved in Ph.D. programs.

Of special note is the completion of degree programs by two students in 1996: Keith Jayawickrama and Jan Svensson. The graduate students working in association with the Cooperative, the degree to which each aspires and the subject of their research project are listed in the highlighted box below:

Student, Degree, Research Project

Paul Belonger, M.S.
Provenance and family variation in specific gravity and trachieds of loblolly pine.

Jim Grissom, M.S.
Genotypic variation and genetic control of above-ground yield for loblolly pine families growing in contrasting environments.

Keith Jayawickrama, Ph.D.
Phenological variation in shoot elongation and diameter growth and their relationships to latewood formation and wood specific gravity in loblolly pine. (Completed in 1996)

Angela Kegley, M.S.
Seedling study of Coastal and Piedmont loblolly pine families and their hybrids for growth and cold-hardiness.

Zhigang Lian, Ph.D.
QTL dissection of productivity variation in loblolly pine.

John Mann, M.S.
The influence of water and nutrient availability on the transition from earlywood to latewood.

Jan Svensson, Ph.D.
Ecophysiological bases for genetic differences in growth of loblolly pine stands. Joint project with Forest Nutrition Cooperative. (Completed in 1996).

Bin Xiang, Ph.D.
Genetic parameter estimation and development of optimum selection strategies for advanced generation breeding.

Wen Zeng, Ph.D.
Identification of major genes with biometrical methods.

We currently have two special students from India studying for three months under the guidance of Bailian Li and in close association with the Tree Improvement Cooperative staff. The students, Jagdish Pvesad Sharma and Buddhafal P. Nonhare, are not working toward a degree, but are studying a wide range of topics related to the genetic improvement of forest trees. The strong recognition of our program continues to draw interest for programs of special study from tree improvement professionals around the world. Five of the nine students working on graduate degrees are from foreign nations.

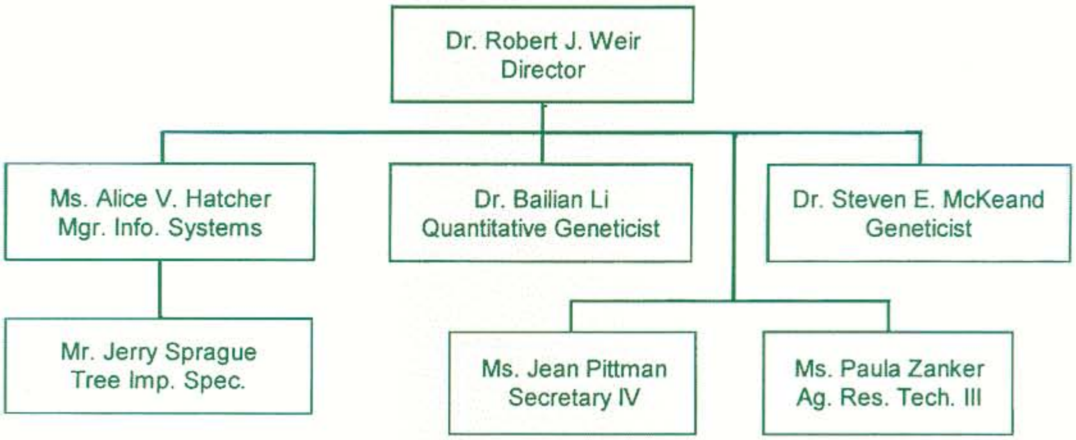
Our successful graduate education program is an accomplishment for which we are proud, and one for which the Cooperative membership deserves much credit. Members of the Cooperative routinely contribute to graduate research projects by contributing land, equipment, manpower resources and genetic test data for the conduct of research. We wish to recognize this outstanding contribution, for without it our graduate research and education program would be substantially reduced in scope and accomplishment.

Program Staff

Current program staff and areas of responsibility are depicted in the Cooperative Tree Improvement Program Organizational Chart. During the past year, Chris Hunt resigned to accept a position with the Christmas Tree Genetics Project in the Department of Forestry. We would like to thank Chris for his numerous contributions to the program. We would like to wish Chris the very best in his new position.

After assessing the needs of the Program, the position vacated by Chris will not be filled. Paula Zanker has assumed all responsibilities for laboratory and field research support. Temporary labor will be used when activities deem it necessary.

Cooperative Tree Improvement Program Organizational Chart - May, 1997



MEMBERSHIP OF THE TREE IMPROVEMENT COOPERATIVE

Alabama Forestry Commission

Bowater, Inc.

Champion International Corp.

Chesapeake Forest Products

Georgia Forestry Commission

Georgia-Pacific Corp.

International Paper Company

James River Corp.

Jefferson Smurfit Corp.

Kimberly Clark Corp.

MacMillan Bloedel, Inc.

Mead Coated Board

N. C. Division of Forest Resources

Rayonier, Inc.

S. C. Commission of Forestry

Tenneco Packaging Corp.

Union Camp Corp.

U.S. Alliance Coosa Pines Corp.

Virginia Department of Forestry

Westvaco Corp.

PUBLICATIONS OF SPECIAL INTEREST TO MEMBERS OF THE COOPERATIVE

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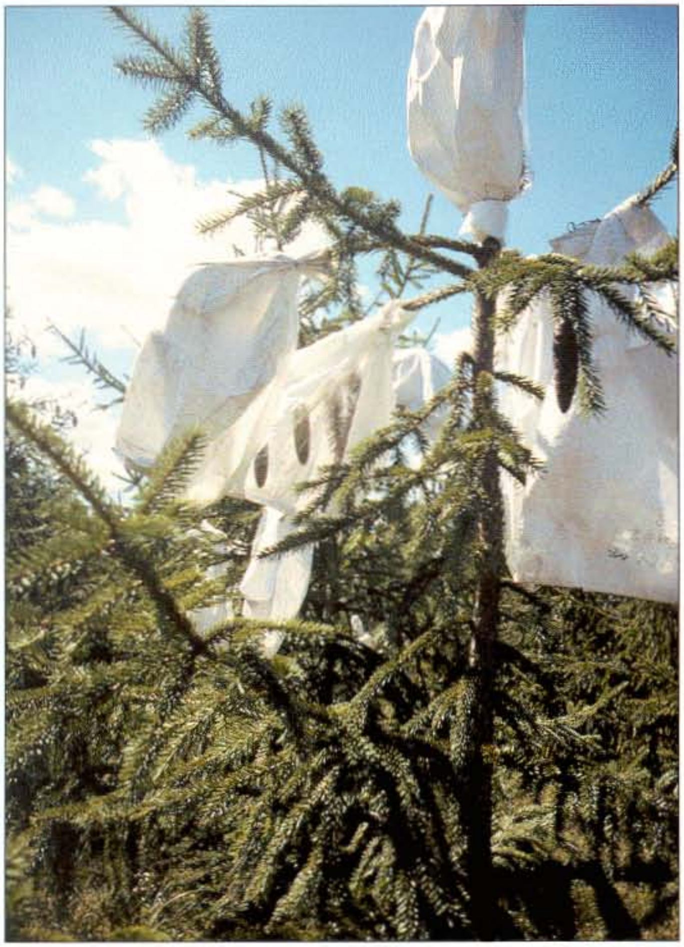

Photo highlights from the 1996 Contact Meeting in New Brunswick, Canada include (l to r):

Greenhouse Breeding of Jack Pine
White Spruce from Embryogenesis
Norway Spruce Breeding Orchard
A Balsam Fir Seed Orchard
A Water Powered Sawmill *circa* 1880