39th

NORTH CAROLINA STATE UNIVERSITY - INDUSTRY COOPERATIVE TREE IMPROVEMENT PROGRAM

1 9 9 5
ANNUAL
REPORT

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

EXECUTIVE SUMMARY

PROGRESS REPORTS FOR RESEARCH:

Significant family differences for both net volume increment and light interception were detected and these measures were linearly and positively related.

Age six results from four Piedmont locations of the Inbreeding Study show a 4.5% reduction in height growth with each 0.1 increase in the inbreeding coefficient (F–value).

Computer modeling of breeding strategies concludes that large sublines maintain greater genetic diversity but at the expense of short–term gain.

Quantitative Trait Loci (QTLs) associated with early shoot elongation have been detected for loblolly pine.

Studies of phenological variation for growth and latewood formation confirm that southerly sources continue to grow later in the season, evaluation of the timing of latewood formation is underway.

BREEDING, TESTING AND SELECTION ACTIVITIES:

The last progeny tests for this cycle will be planted in 1996.

Third–cycle selection work intensifies.

Elite population breeding for the Piedmont and lower gulf regions are progressing well.

Analyses of 21 diallel test series at age six show several very informative trends. Efforts to establish tests on very uniform sites have resulted in higher selection efficiency and will produce more gain.

SEED PRODUCTION:

The 1994 seed harvest was one of the smallest in recent years because of damage to flower crops in the March 1993 "Storm of the Century".

Since 1969, Cooperative members have harvested enough genetically improved seed to reforest 20 million acres.

ASSOCIATED ACTIVITIES:

The Cooperative has had five graduate students working on degrees and conducting research important to the Cooperative during the past year.

We will miss the presence and contribution of Dr. Floyd Bridgwater as he relocates to Texas A & M University during the upcoming year.

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INTRODUCTION

The North Carolina State University – Industry Cooperative Tree Improvement Program has completed 39 years of continuous operation. The progeny test establishment activities of the Cooperative's current breeding and testing cycle are nearly complete. The final tests for this phase of the program will be established during the 1996 planting season. The progeny testing of 3300 plantation selections and 700 second generation selections represents a very large investment by Cooperative members. How do we best utilize the information and material produced from this effort? That question is the focus of much current activity as the Cooperative moves into the 40th year of operation.

During the past year, the forest industry has shown great interest in increasing the productivity of intensively managed timberlands. The reasons for this are several. The nearly 90% curtailment of harvesting on public lands in the northwest has shifted demand to the south with an associated rise in stumpage prices. Timberland assets are now more valuable than just a few years ago. Additionally, many companies are experiencing pressure from customers to demonstrate sustainable production and environmental stewardship on their timberlands. In some cases this is causing a change in management strategy on as much as 30 to 40 percent of their total land base. The change in management strategy may reduce to an extent the allowable cut on these acres. On forest land that will continue to be intensively managed, we must apply the best technology. Many questions are being asked, often by the highest level executives in industry, about the more aggressive use of advanced forest management technology. The forest genetics / tree improvement programs in the region have been focused on this issue for several decades, yet now the intensity of interest in new technology development is increasing.

Pressure to develop a reasonable cost source of hardwood fibers that can be logged in all weather conditions has once again surfaced. Juvenile wood of pine is again being investigated as a substitute for hardwood fibers. We know from past work that for some products, juvenile pine is a satisfactory substitute, however it has not been exploited in the past because the logging, transportation and processing costs for small trees were too high. With better genetics and silviculture we now routinely grow stands averaging 9 to 10 inches in breast height diameter in 15 to 17 years. This now makes the substitution of short fiber juvenile pine for hardwoods a real possibility.

Tree improvement must and is changing as we learn to extract more genetic gain from the breeding populations we are intensively developing. We have breeding strategies in place that will capture genetic gains at a faster rate and at a lower cost than previous efforts allowed. Our third–cycle breeding system, when aggressively implemented, will go far toward realizing the tremendous potential for accelerated improvement. Our continuing collaboration with biotechnology and vegetative propagation programs offers similar promise. It is a rewarding and challenging time to be involved with tree improvement !!

RESEARCH

Computer Modeling of Breeding Strategies

Evaluation of the breeding strategy adopted by the Cooperative members in 1992 for the third cycle of selection and breeding continues. Three alternatives were addressed and reported in the last annual report. These are:

- Selecting the best individual from the four best families (self or outcross) ranked on expected breeding values is an alternative that will give good genetic gains and result in relatively moderate rates of increase in coancestry within sublines.

- Assigning parents to sublines at random, or disassortatively, rather than by positive assortment will increase within-subline genetic variance and result in greater increases in breeding value for the first generation of selection and mating.

- It will be possible to enrich elite populations from the mainline population for 3–4 generations without reducing gains in the elite breeding program.

A fourth, important, alternative was the choice of small sublines, size 4. These very small sublines were adopted for three reasons:

- Smaller sublines reduce the chance that rare alleles included in the population will be lost.

- Small sublines can be combined in future cycles if necessary to create larger sublines while the converse is not possible.

- Smaller sublines help to maintain population variability (genetic diversity) in the long–term.

Figure 1 compares the population additive variance for 20 generations for subline sizes 4, 6, 8 & 12. With the model assumptions and subline size 4, population additive variance increases for 7 to 8 generations before slowly declining. Larger sublines decrease much more rapidly. Maintaining genetic diversity comes at the price of reduced genetic gains in the short–term (Figure 2). Trading short–term genetic gains to maintain genetic variability in the long–term means that the breeding population will remain viable for many generations.

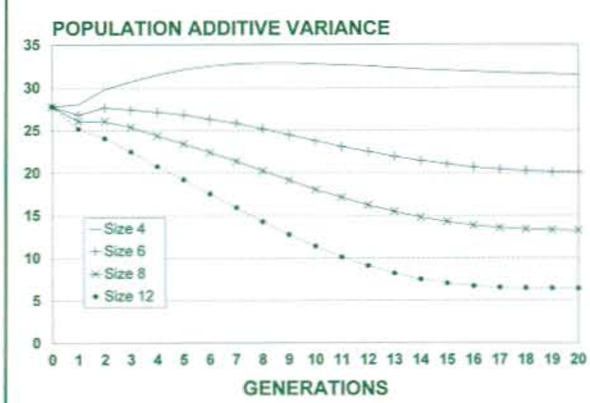


Figure 1. *Comparison of population additive variances for 20 generations for subline sizes 4, 6, 8, and 12.*

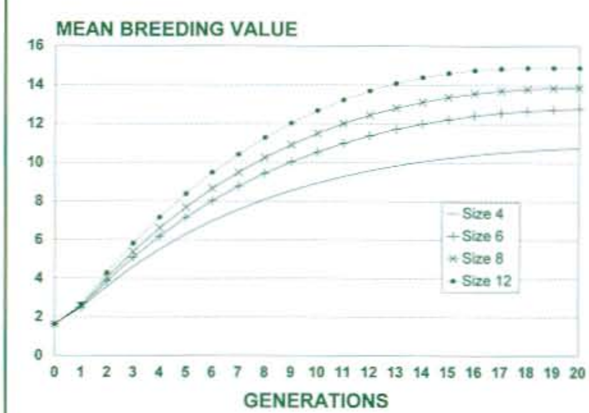


Figure 2. *Mean breeding values by subline size over 20 generations of breeding.*

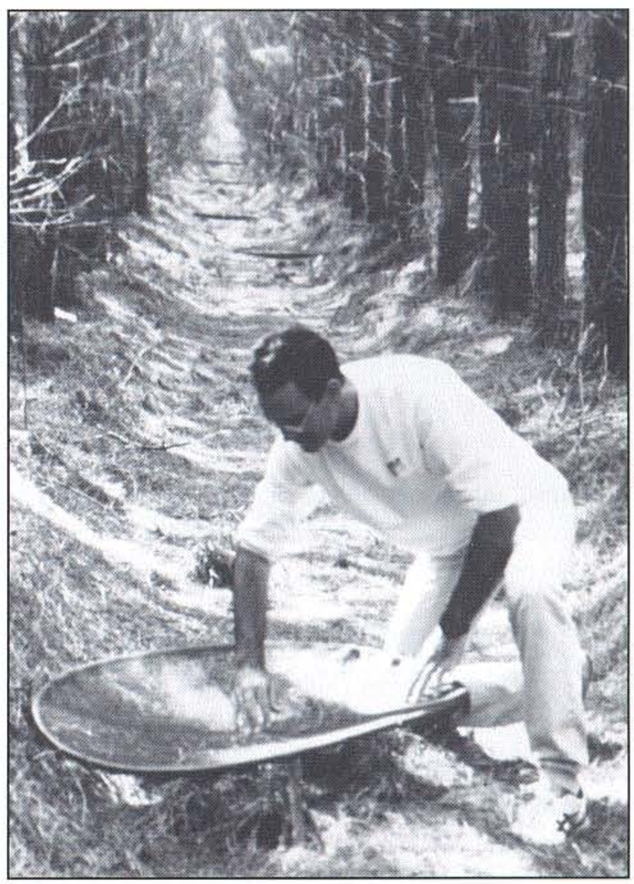
Genetic Variation in Light Interception and Its Relationship to Stand Productivity of Twelve Open–Pollinated Loblolly Pine Families

This project was conducted by graduate student Peter Althoff working jointly with the N. C. State University Forest Nutrition Cooperative and the Tree Improvement Cooperative. The study was designed to assess the genetic differences in canopy structural components affecting light interception and its relationship to stand productivity. 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. When assessments were made in 1992 and 1993, the canopies in the plots were closed. Significant family differences in cumulative growth existed when the measurements were initiated in 1992.

Results of the study include the following:

- Significant family differences were detected for both net volume increment and light interception. The relationship between the two traits was linear and positive with an R^2 of .47.
- Family variation in light interception capacity ranged from 84% to 90%.
- An analysis of canopy structural components showed leaf area index and total branch basal area to be the two most important traits in explaining variation in light interception. These two traits, leaf area index and total branch basal area were also highly correlated. Differences in leaf area index appear to be strongly related to number of needles per flush, number of needles per branch and number of flushes per branch, thus the high correlations to total branch basal area.
- Further analysis of the canopy structural components showed that 97% of the variability in light interception could be explained by leaf area index and the light extinction coefficient.
- Strong family differences existed in growth efficiency (net volume per unit leaf area). The differences showed clearly, however, that efficiency could not be assessed simply as the relationship between leaf area index and growth. Some families exhibited a linear response to increases in leaf area index while others exhibited a curvilinear response. Variations in growth efficiency may also be due to other physiological processes such as nutrient uptake and utilization.

Work is continuing in the same field planting to assess CO_2 exchange, nutrient uptake and utilization to determine their relationship to biomass production. This final phase of the research should be completed by the end of 1995.



Depicted is the closed canopy of the Jones County, NC stand where Peter Altoff collected litter-fall samples to use in estimating leaf area traits.

Piedmont Loblolly Inbreeding Study – Age Six Results

The Piedmont Loblolly Inbreeding Study was established in five field trials in the spring of 1988. The trials were established by Bowater(SDW), Procter & Gamble, Bowater(CWD), Federal and S.C. Commission of Forestry. The Procter & Gamble study was abandoned due to poor survival. The four remaining Piedmont trials were measured in 1994 at age six.

The objectives of the Inbreeding Study are:

- To determine the response to related matings in improved loblolly pine.
- To characterize family differences in sensitivity to inbreeding.

Parents used in the study were all second generation selections. Four levels of inbreeding were created from matings among selfs (F=.50), full–sibs (F=.25), half–sibs (F=.125) and unrelated selections (F=0). For all matings, except selfs, parents were mated to two individuals to reduce the bias caused by the breeding value of the other parent in the cross.

A preliminary analyses of age six data shows a significant reduction in growth from inbreeding. Results indicate that for every .1 increase in the inbreeding coefficient (F value) there is, on average, a 4.5% reduction in height growth. Figure 3 graphically displays the actual growth response and the predicted growth response. Parents differed significantly in their response to inbreeding. Figure 4 displays the response of six parents at each inbreeding level. Parent 1–1069 showed a positive response to inbreeding at all three levels. Parent 1–1310 performed very poorly at all three levels of inbreeding. These significant interactions suggest that no general prescription could be made for use of related individuals in seed orchards.

A more detailed analyses of the data is currently underway and should be completed by mid–summer.

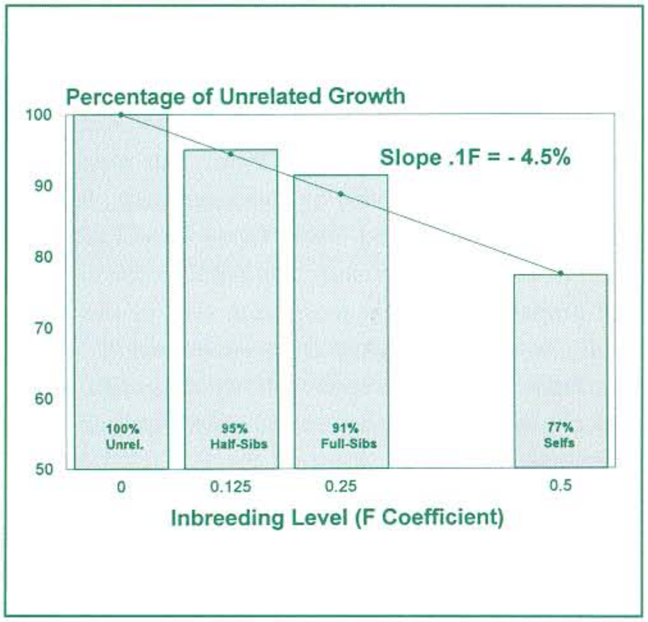


Figure 3. Actual growth response vs. predicted growth response for different levels of inbreeding.

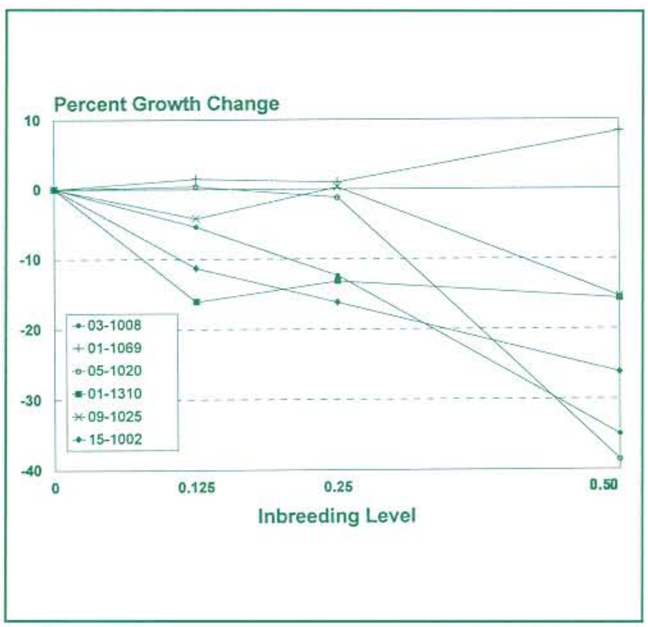


Figure 4. Growth response of six clones at each inbreeding level.

Research Study Updates

Provenance and Family Variation in Wood Properties in Loblolly Pine

This study is a supplement to the research study "Phenological Variation in Shoot Elongation and Diameter Growth and Their Relationships to Latewood Formation and Wood Specific Gravity in Loblolly Pine." This supplemental study is being jointly funded by Container Corp., Rayonier, Scott Paper Company and Union Camp Corporation. This study will evaluate provenance and family variation in the wood properties of older trees from four of the Florida Loblolly Provenance/Progeny Trials established in 1982 and 1983. Traits being assessed include wood specific gravity, within ring and between ring specific gravity, tracheid lengths and percent extractives.

Bark to bark increment cores were taken from trees in all four trials in the spring of 1994. Graduate student Paul Belonger will assess specific gravity variation and variation in tracheid characteristics for his Master's thesis research.

Phenological Variation in Shoot Elongation and Diameter Growth and Their Relationship to Latewood Formation and Wood Specific Gravity in Loblolly Pine

Graduate student, Keith Jayawickrama continues work on this project supported by Georgia–Pacific with in–kind support from International Paper Company. The study intensively sampled 8 five–year–old families from each of the following four provenances:

Atlantic Coastal Plain (ACP)
Gulf Hammock, Florida (GH)
Lower Gulf Coastal Plain (LG)
Upper Gulf Coastal Plain (UG)

The study will determine how the timing of initiation and cessation of height and diameter growth affect wood properties. The trees were measured through the summers of 1993 and 1994 and the cambium (wood forming tissue) of each tree was marked weekly using a wounding technique applied during late summer and early fall.

Collecting wood samples for the phenological evaluation of growth and latewood formation study – subtitle "Associate Dean Jett returns to the field".

There was little difference between provenances as to when height growth started in the spring, but significant differences existed for the date of growth cessation in the fall. The fast growing Gulf Hammock provenance grew the longest (well into September), while the slowest growing source (Upper Gulf) was first to stop growing (early August at the International Paper site and late August at the Georgia–Pacific site) (Figure 5). Families within provenance were not significantly different for the date of growth cessation. The trees were cut and wood samples were taken in January 1995. Microscopic evaluation of the wood samples is in progress to determine the timing of transition from early to latewood and the cessation of seasonal wood formation.

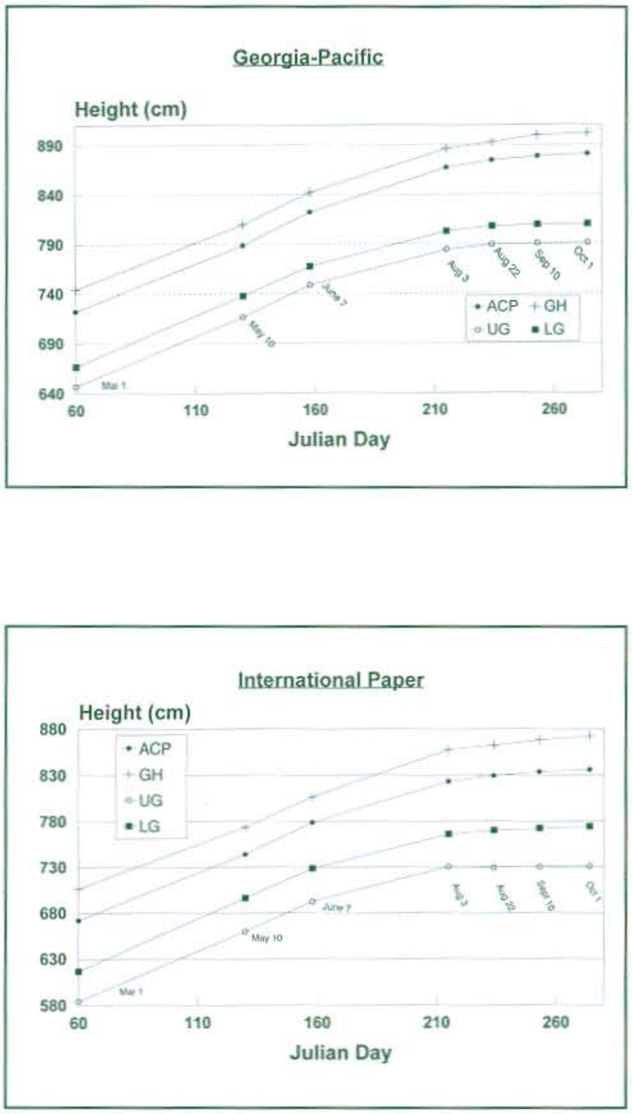


Figure 5. Height growth in 1994 for trees from four different provenances in the Wood Phenology Study planted at Cedar Springs, GA (Georgia-Pacific) and Bainbridge, GA (International Paper Company).

Mapping Quantitative Trait Loci (QTLs) Controlling Juvenile Shoot Growth of Loblolly Pine

Genetic dissection of quantitative traits such as early height growth is the primary objective of a project being conducted by The Tree Improvement Cooperative and The Forest Biotechnology Program in cooperation with Federal Paper Board Company. If major gene effects or quantitative trait loci (QTLs) can be found and tagged with markers, they could possibly provide the basis for marker–aided selection.

In loblolly pine, early height growth has been shown to be a quantitative trait with moderate heritability and has a strong correlation with height growth at a later age. A RAPD genomic map was constructed for loblolly second generation selection 9–1020. A sample of loci from the map was used to develop a marker / trait association on 288 progeny in the field planting at Lumberton, NC. Height growth was analyzed as three components: initial planting height, shoot elongation for year–one in the field, and shoot elongation for year–two in the field. Height growth QTLs were detected, however, they mapped to different map locations for the three different growth components. The magnitude and number of QTLs detected in this half–sib family were smaller than expected. The differences in map location for the three growth components could be due to changes in genetic control of physiological development (different genes being turned on or off at different stages of early growth) or it is possible that environmental variations were a dominant influence on growth during this early period. The study trees will be thinned (original planting density was over 4000 trees per acre) to allow field measurement to continue for several more years with a sample size of 250 trees per family.

BREEDING, TESTING, AND SELECTION

Status of Progeny Testing

Establishment of the Cooperative's 1200+ plantation and second generation progeny tests is approaching its final year. The last tests will go out in the 1996 establishment year. The peak year was 1994 when 179 tests were established and 126 tests are being planted during the current year (Figure 6). In 1996, there should only be about 68 tests to put in the ground. Of the 38 breeding programs in the Cooperative, about half have completed test establishment as of spring, 1995. The balance will be completed in 1996.

Progeny test measurements are continuing to increase as 201 tests were measured in 1995. The measurement load will continue to increase and peak in the year 2000 when a projected 260 tests will be measured. So, as the test establishment draws to a close, activity in measurement and third generation selection work moves to the forefront for the next several years.

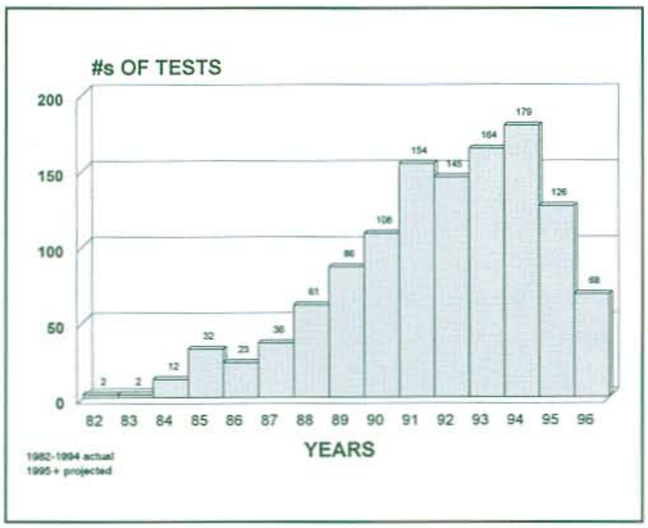


Figure 6. Distribution of progeny test establishment.

Piedmont Elite Population – A Progress Report

Breeding for the Piedmont Elite Population (see the 1993 Annual Report for details of the breeding plan) has progressed well since its initiation in 1993. To briefly review, the Piedmont Elite Breeding Program consists of the following two populations:

> **Population I** consists of 27 Piedmont X Coastal Plain Hybrid parents to be bred in four–parent diallels to produce elite outcrossed progeny, and selfed to produce S_1 offspring. Each parent will also be crossed with a Piedmont pollen mix to generate material for the polymix tests which will be used to determine parental values.
>
> **Population II** consists of approximately sixty 2.5 generation selections from the Atlantic Coastal Plain and Piedmont provenances. Each of the parents in Population II was to be crossed with two pollen mixes—a Piedmont pollen mix and a Coastal pollen mix. Each parent was also to be crossed in a 4 X 4 factorial to generate outcrosses to produce a base for selection.

To date, most of the breeding effort has been concentrated in Population II. Approximately 77% of the polymix crosses and 94% of the outcrosses are complete. With the excellent flower crop this spring, all breeding in Population II should now be complete. The first of the full–sib block–plots (for within family selection) will be established this year, only three years after the elite breeding program was initiated. All twenty–seven selections in Population I have been grafted by Bowater. All twenty–seven polymix crosses were made this spring.

The aggressiveness with which members have completed the breeding is indicative of the value they place on elite population breeding. Development of this elite population is an effort on the part of industries and state organizations to maximize productivity on forest lands by capturing additional gain at a faster rate with minimal costs.

Barbara McCutchan extracts a 12mm increment core from a new third-cycle selection graded in one of Westvaco's progeny tests.

Third Cycle Selections

Selection of third–cycle selections from 6–year–old progeny tests is progressing well. Last fall (1994), selections were made from 34 tests and during 1995, another 80 tests will be examined. To date, there have been 157 third–cycle selections made.

Lower Gulf Elite Breeding Population

Plans were initiated in August, 1994 for establishment of an elite breeding population for the Lower Gulf region of AL, FL, GA, and MS. Cooperators participating in development of this elite population believe the potential for increased genetic gain will be worth the additional investment in breeding, testing and selection of another population hierarchy.

While most elite populations will be formed from local mainline populations, it would be premature to select an elite population from the Lower Gulf mainline population at this time. An elite population using the best third–generation clones could not be initiated much before 1999 when 45–50 percent of the third–generation selections will be available. There is, however, an opportunity to utilize non–local selections for the Lower Gulf Region. Recent results from provenance tests and open–pollinated tests of 2nd–generation seed orchards have confirmed the superiority of many non–local sources over the Lower Gulf source. The ten–year results of the Florida Loblolly pine Provenance/Progeny Trial indicate that growth and rust resistance can be significantly improved if Atlantic Coastal (ACP) and two sources from Florida, Gulf Hammock (GH), and Marion County (MC) families, are used rather than Lower Gulf families (Table 1). Similarly, in open–pollinated tests of seed orchards in the Lower Gulf region, Atlantic Coastal families routinely are superior to local families. Other long–term trials such as the Cooperative's GGC trials, have demonstrated the value of the Livingston Parish (LP) seed source across a broad range of sites.

Table 1. Provenance means for different traits at age 10 years for the Florida Loblolly Pine Provenance/Progeny Trial. Means are combined over 6 test locations.

Provenance	Height (ft)	Volume (cubic ft)	Strt. Score	% Rust	% Survival
Atlantic Coastal	39.5[b]	3.2[b]	3.0[b]	45[b]	79[a]
Gulf Hammock, FL	40.9[a]	3.6[a]	3.3[a]	46[b]	75[a]
Marion County, FL	40.1[b]	3.4[a]	3.5[b]	43[b]	75[a]
Lower Gulf	36.7[c]	2.7[b]	3.1[b]	54[a]	77[a]

Note: Means within a column followed by the same letter are not significantly different at $p<0.05$.

While the growth potential of the Florida sources and the Livingston Parish source is tremendous, there is a risk from cold damage as these sources are moved north. A marked decline in survival has been observed from south to north when LP, MC and GH sources were planted in the Lower Gulf, Middle Gulf, and Upper Gulf regions. To determine the range of movement possible, selections in the elite population will be tested at the northern limits of the Lower Gulf area.

To capture the potential benefits of using ACP, MC, GH, and LP trees in the Lower Gulf region, a plan has been developed to:

- Directly compare the best selections available from each of these provenances through pollen mix testing, and

- Interbreed the best of these trees in a diallel mating design to make both inter– and intra–racial crosses.

The elite population will consist of 40–80 selections. The population will be composed of the best parents available for breeding in 1995 from the following sources:

- Atlantic Coastal Plain:
  (20–40 selections consisting predominately of tested second–generation parents tested in open–pollinated tests).

- Marion County and Gulf Hammock
  (15–30 tested first–generation parents)

- Livingston Parish
  (5–10 tested first–generation parents)

Each of the selections were bred in the spring of 1995 using a pollen mix of Atlantic Coastal plain selections. The top 40 clones based on current data will be bred in five, 8–parent diallels. Each diallel will consist of one Livingston Parish, three Florida and four Atlantic Coastal Plain parents.

A chapter of history closes!! *Pictured is the clearcut of the NCSU-International Paper Co. Heritability Study. For 30 years this pioneering project contributed to our fundamental knowledge of genetic variation and control of economic traits in loblolly pine.*

The polymix crosses will be planted in replicated field tests throughout the Lower Gulf region. The full–sib seedlots will be established in non–replicated block plots to maximize the efficiency of within–family selection. A subset of the full sib crosses will be established in replicated tests to assess inter–source heterotic effects and SCA effects.

Establishment and development of the Lower Gulf elite population is the combined effort of the members and staffs of the North Carolina State University–Industry Cooperative Tree Improvement Program, the Cooperative Forest Genetics Research Program, and the Western Gulf Forest Tree Improvement Program.

Analyses of Diallel Tests At Selection Age

The Cooperative has for the last decade been actively breeding and testing some 3300 plantation selections and over 700 second generation selections. The breeding is complete and by 1996 all progeny tests will be planted. Selections have been bred in 6–parent disconnected half–diallels and the resulting progeny have been planted in balanced test series (4 tests per series) each comprised of progeny from two, or on occasion three diallels. As of March 1995, measurement and analyses were complete in 21 test series at age 6 years, with 44 separate diallels represented (Table 2).

With the database derived from these 21 test series we have initiated the third–cycle selection effort employing a new multi–trait selection index. We have recently completed a thorough evaluation of the selection process and have been very pleased with how well the new selection index, developed under the leadership of Floyd Bridgwater, seems to be working. The trees we select on paper are for the most part the ones we want to select in the field. This is the best measure of how well a selection index works. As the analyses of the diallel tests has proceeded and we gained some experience with the selection index some interesting and useful trends and relationships have developed. Highlights of these analyses and interpretations are summarized on the following pages.

Table 2. Measurement and Analyses Summary for 21 Test Series (age 6) representing 44 separate diallels

Test Area	# Series	# Diallels	Averages			Individual tree Heritabilities for Height		Family Mean Heritabilities		
			Ht.	Rust	Surv.	h^2_{ns}	h^2_{bs}	Ht.	Rust	Surv.
1	3	6	17.9	1.7	95	0.31	0.38	0.85		0.84
2	0	0								
3	4	9	20.8	12.7	82	0.08	0.12	0.46	0.72	0.58
4	4	8	19.6	31.9	88	0.22	0.34	0.72	0.81	0.89
5	6	13	21.3	23.3	93	0.31	0.39	0.85	0.87	0.76
6	2	4	17.4	3.1	87	0.12	0.25	0.57		0.49
7	2	4	17.5	44.2	81	0.18	0.24	0.84	0.85	0.76
8	0	0								
Total	21	44	19.7	19.8	89	0.22	0.31	0.72	0.73	0.78

Relationships Between Genetic Parameters and Test Characteristics

Several informative relationships among progeny test characteristics and estimates of genetic parameters have been identified. The estimates of individual–tree heritabilities (both narrow–sense due to additive genetic variance and broad–sense due to both additive and non–additive genetic variance) appear to be in line with other estimates for height. The average narrow sense heritability (individual basis) is .22, while the comparable broad sense heritability average is .30. The average narrow–sense family mean heritability estimates for height, rust infection, and straightness score are 0.72, 0.73 and 0.78 respectively (Table 2).

The estimates for narrow sense heritability (individual basis) range between 0 and 0.93. Reasons for this large range of estimates include: 1) Genetic sampling, there are apparently real differences in the genetic variance included in the 44 small samples of six parents comprising the diallel mating groups. 2) The variation in heritability estimates were at least partially explained by variation in test precision (as measured by the coefficient of variation (CV) based on rep x family effects) and by average test survival. If test precision was relatively low (CV > 8%) then the likelihood of having a high heritability was relatively low (Figure 7). Likewise, if survival was below 85%, there were very few estimates of heritability greater than .20 (Figure 8).

Although these relationships are not extremely strong, they illustrate the value of maintaining minimum standards for survival and environmental uniformity in a progeny testing program. While high survival and good test precision do not guarantee that heritability estimates will be high, (the effect of genetic sampling in the small diallels can always be influential), in tests that have large environmental variance and/or poor survival, genetic effects will often be masked, and heritability will be low.

There was no relationship between average height and any estimate of heritability (r = 0.08 for mean height and narrow sense heritability, and r = 0.05 between mean height and broad sense heritability). This is an important "non–relationship"! From this, one can conclude that we are just as likely to see strong genetic effects on low site index sites as on high site index sites. The average height for a test series varied by

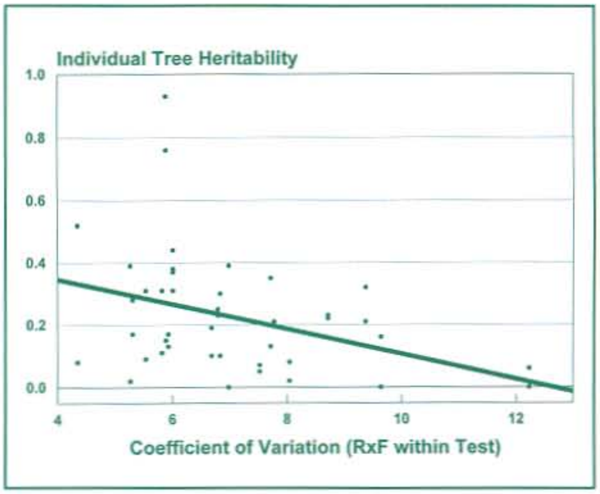


Figure 7. Impact of test precision on estimates of heritability for height.

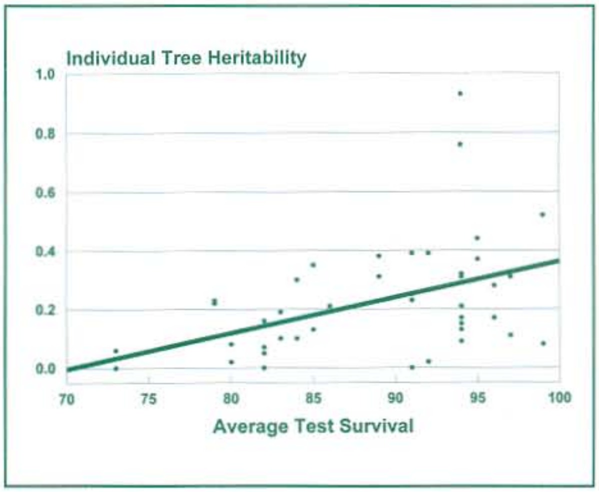


Figure 8. Impact of test survival on estimates of heritability for height.

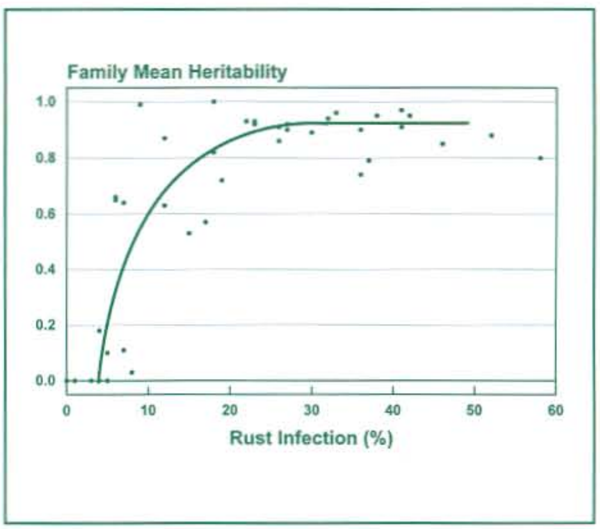


Figure 9. Impact of rust infection on estimates of heritability for rust.

almost 25% (from 15.6 feet to 19.2 feet) at age 6 years. When establishing our progeny tests, the use of agricultural fields was encouraged, not because of the potential for fast growth, but because in general the site uniformity on agricultural fields is much better than what is routinely encountered on cut over sites.

The most useful relationship between heritability and site factors is for rust infection (Figure 9). When rust levels are very low (< 5%) there is very little chance of detecting significant family differences (h^2 based on family means is usually near 0). With rust levels of 5% – 20%, the estimates of h^2 are much more variable than at levels of rust above 20%. The consistency of heritability estimates when rust is above 20% is cause for confidence in these estimates. For routine analyses of diallel tests and OP tests in the N.C. State Tree Improvement Cooperative, rust performance is estimated only when average rust infection equals or exceeds 20%.

Genetic Correlations Among Traits

In a multi–trait selection index, the relationships or associations among the traits included in the index have a major impact on the gains for any individual trait of interest. For example if there is a strong, unfavorable relationship between height and straightness, selecting for height would degrade stem quality. Across the different diallels, the genetic correlations vary widely:

Genetic Correlation for:	Low	High	Average
Height - Rust Infection	-0.93	0.96	-0.20
Height - Straightness	-1.08	0.98	0.05
Rust - Straightness	-0.93	0.93	0.08

When there is a favorable correlation between height and rust infection or between height and straightness (i.e., negative correlation is favorable since high values for rust and straightness score are bad), selecting trees is relatively easy. When there is a strong unfavorable genetic correlation, it has been difficult to find good trees in tall, straight, rust–free families. Fortunately the average genetic correlations are either slightly favorable (i.e., r = –0.20 for height and rust infection) or are essentially zero for height and straightness. Again, with the small genetic samples included in each diallel, the correlation can vary widely, but the expectation for the average of all correlations is about zero.

Genotype by Environment Interactions

In past studies, we have seen very little evidence for important genotype by environment interaction (GxE) at the half–sib family level. For example, in the Good General Combiner Trial, half–sib families were remarkably stable across a wide range of sites that encompass large differences in site productivity. In the diallel tests, we have the opportunity to assess GxE for both half–sib and full–sib families. Full–sib families might be expected to display a higher degree of interaction with the environment than half–sib families, since there is less genetic variance within each family (ie, a lower level of buffering to environmental variations) and more of the genetic variance is distributed among families. Additionally, GxE at the full–sib family level is caused by both additive and non–additive effects:

For half-sibs: Family Variance $= 1/4\ \sigma^2_{A}$

G x E Variance $= 1/4\ \sigma^2_{AxE}$

For full-sibs: Family Variance $= 1/2\ \sigma^2_{A} + 1/4\ \sigma^2_{NA}$

G x E Variance $= 1/2\ \sigma^2_{AxE} + 1/4\ \sigma^2_{NAxE}$

One way to evaluate the importance of G x E is to relate its magnitude to the magnitude of genetic variance. The ratio of the genotype x environment variance over the genetic variance may be referred to as the K–statistic. This is a useful measure of genotype by environment interaction when the environments are considered to be a random sample from a larger set. For this case, the K–statistic may be interpreted as the proportional amount by which the expected genetic variance within environments exceeds the genetic variance measured over environments.

For half-sib families

$$K = 1/4\,\sigma^2_{AxE} \;/\; 1/4\,\sigma^2_{A}$$

For full-sib families

$$K = (1/2\,\sigma^2_{AxE} + 1/4\,\sigma^2_{NAxE}) \;/\; (1/2\,\sigma^2_{A} + 1/4\,\sigma^2_{NA})$$

The average K–statistic for half–sibs was 0.31 meaning that the GxE variance was only about one–third the genetic variance. As we have found in other trials, the family by environment or specifically the additive genetic by environment variance is of little practical concern. On the other hand, the GxE for full–sibs is higher (K = .54), apparently this is because of the contribution of non–additive effects to the GxE. Nevertheless, the magnitude of GxE variance for full–sibs is still only about half the magnitude of the genetic variance, thus it appears to be of small practical importance.

In summary, the analyses of 44 diallels in 21 test series and the initial third–cycle selection work has led to several conclusions:

- Planting tests on uniform sites is essential if reasonable levels of heritability and genetic gains are to be achieved.
- Test survival below 85% usually results in low heritability estimates.
- Genetic differences in height are not related to site index, but genetic differences in rust resistance can only be detected if rust infection exceeds 20%.
- Genetic correlations among traits vary because of the sampling effect with small diallels, however, on average the correlations are near zero, which indicates that the traits are inherited independently.
- Genotype by environment interaction effects are inconsequential.

SEED ORCHARD PRODUCTION

Cone and Seed Yields

The 1994 collection of seed from Cooperative loblolly pine seed orchards was the lowest in 15 years. There were 15.6 tons of seed collected; the previous low was the 1980 crop of 7.9 tons of seed. The small amount collected in 1994 is due to several factors, partially to the surplus of seed on hand, but also due to the "storm of the century" in the spring of 1993, when many orchard flower crops in the cooperative were damaged by cold and snow. Due to the surplus and the small crop left by the storm, several cooperators chose not to collect or to collect very selectively. In years of surplus seed and small crops, there is a tendency not to invest in insect control and consequently, the pounds per bushel yield are low. The 1994 crop produced 1.22 lbs./bushel, one of the lowest yields in the past ten years. Based on records kept since 1969,

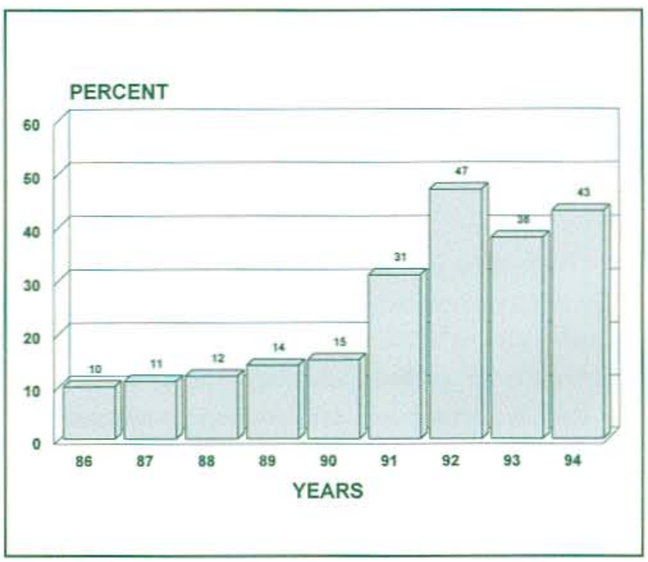


Figure 10. *Percent of total crop represented by second generation seed collections from 1986-1994.*

Table 3. Top ten production orchards for the 1994 cone crop.

Organization	Orchard Type	Age	Lbs./ Bushel	No. of Clones	Orchard Manager
Champion, SC	1.5 Alabama	19	2.36	5	George Oxner
Champion, SC	1.5 Piedmont	28	2.13	9	George Oxner
Champion, SC	2.0 Piedmont	18	2.11	6+	George Oxner
Champion, SC	Rust Resistant	25	2.09	5	George Oxner
Bowater (CWD)	1.5 Piedmont	20	1.81	6	Jake Clark
Westvaco, SC	1.0 Va. Pied.	23	1.79	6	Dave Gerwig
Evergreen	2.0 Piedmont	12	1.65	18+	Tom Kirby
Kimberly Clark	1.5 Piedmont	14	1.59	12+	Al Lyons
Va. Dept. of For.	2.0 Coastal	15	1.55	40	Billy Barber
Bowater (CWD)	2.0 Piedmont	17	1.49	8	Jake Clark

the Cooperative orchards in 1994 exceeded 1 million bushels of cones harvested. About 1.5 million pounds of seed were produced in the same time period. This production level is sufficient to regenerate 20 million acres.

A total of 25,529 bushels of cones were collected in 1994 for a total of 31,104 pounds of seed (1.22 lbs./bushel). Seed from second generation orchards totaled 6.6 tons and represented 43 percent of the total collection (Figure 10). Since 1991, the Cooperative members have produced approximately 40% of their seed from the second generation orchards. In the very near future, at least half of the seed is expected to come from the second generation orchards.

Seed Production Leaders

Table 3 shows production efficiency leaders in the Cooperative for the 1994 crop. Perhaps as no real surprise, Champion International tops the list with four of its orchards claiming the first four places. Four of the orchards produced over 2.0 lbs./bushel and were the only orchards in the Cooperative exceeding the 2.0 lbs./bushel mark in 1994. Coming in fifth place at 1.81 lbs./bushel was Bowater's(CWD) 1.5 Piedmont orchard in Rock Hill, SC. Rounding out the top ten are: Westvaco, SC, Virginia loblolly orchard producing at 1.79 lbs./bushel; Kimberly Clark's 1.5 Piedmont orchard producing 1.59 lbs./bushel; Evergreen's 2.0 Piedmont orchard at 1.65 lbs./bushel; Virginia Dept. of Forestry's 2.0 Coastal orchard, 1.55 lbs./bushel; and finally, Bowater's (CWD) 2.0 Piedmont orchard at 1.49 lbs./bushel. Note from Table 3 that members continue to collect from fewer parents but are selecting the very best in the orchards. Congratulations go to these orchard managers for a job well done.

Though yields were down this year, several parents produced very high yields. Sixteen of the 25 parents collected from several Champion, SC orchards produced in excess of 2.0 lbs./bushel. Clone 8–120 produced a high 3.19 lbs./bushel and has historically had high yields. However, this year a new record was set by two parents in Evergreen's Coastal and Piedmont orchards managed by Tom Kirby. Parent 5–1056 from the Piedmont orchard, produced 3.73 lbs./bushel and 18–1213 from the Coastal orchard produced 3.37 lbs/bushel. The previous high had been parent 8–73 at 3.3 lbs./bushel in 1989 from a Champion, NC orchard. Special congratulations to Tom Kirby and Amy Floyd for their excellent seed orchard management!

From reports around the Cooperative, the 1995 seed crop will be something to look forward to as most everyone is reporting a very large conelet crop.

ASSOCIATED ACTIVITIES

Graduate Student Research and Education

The education of graduate students and the research they conduct as part of their degree program continues as an important activity of the Cooperative. During the past year five graduate students have been working in association with the Tree Improvement Cooperative. The efforts of two were directed toward a Masters degree and three were involved with Ph.D. programs of study. During the year one student, Peter Altoff, completed his degree requirements.

During the past year we have had two special students from the Peoples Republic of China studying for six months under the guidance of Floyd Bridgwater and in close association with the Tree Improvement Cooperative staff. The students, Shi Bin and Xianghui Wu, are not working toward a degree per se, but are studying a broad range of topics related to genetic improvement of forest trees and are especially interested in applied tree improvement methods and genetic analyses methods. The strong international recognition of our tree breeding research and development success continues to draw interest for programs of special study from tree improvement professionals around the world. We are negotiating at this time for a possible program of special study for six tree improvement specialists from Indonesia. Four of the five graduate students working on 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 have routinely contributed to graduate student research projects by contributing land, equipment, and manpower resources for the conduct of the research. We wish to recognize these contributions, for without it our graduate research and education program would not be nearly as successful.

STUDENT, DEGREE RESEARCH PROJECT

Peter Altoff, M.S.
Genetic Variation in leaf area / production stand level measures - Completed 1994 (Joint Project with Forest Nutrition Coop.)

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

Kevin Harding, Ph.D.
Age trends in genetic parameters for wood properties of loblolly pine.

Keith Jaywickrama, Ph.D.
Phenological variation in shoot elongation and diameter growth and their relationships to late wood formation and wood specific gravity in loblolly pine.

Jan Svenson, Ph.D.
Ecophysiological bases for genetic differences in growth of lobololly pine stands (Joint Project with Forest Nutrition Coop.)

Program Staff

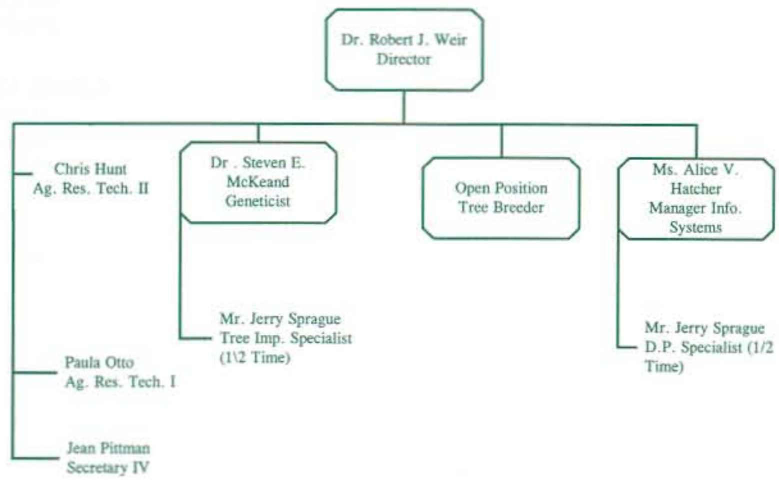
Not shown on the following organizational chart, but a highly productive member of the Tree Improvement Cooperative Program "Team" has been Dr. Floyd Bridgwater, Research Geneticist and Team Leader for the Forest Genetics Project of the Southern Station, U.S. Department of Agriculture, Forest Service. For the past 15 years virtually all of the research conducted or administrated by Floyd has been complementary to the Cooperative Program. Numerous outstanding tree improvement graduate students have completed their degree program under Floyd's direction and he teaches a course in genetic analyses of tree improvement experiments that is well received by our graduate students.

A substantial change in the association we have enjoyed with Floyd Bridgwater will take place in the next few months. As a result of his spouse taking employment on the faculty of the Forest Science Department, Texas A & M University, Floyd will also be relocating to College Station, Texas. It will be more challenging for all parties to continue the productive association and research collaboration that the Cooperative staff and members have enjoyed with Floyd over the past 15 years, yet we are determined to maintain an effective working relationship. The opportunities for continued collaborative research are many, particularly in the area of population genetics as it relates to breeding programs and issues of bio–diversity in managed forests.

Floyd, we wish you the very best in your new location. We will miss your presence, especially your ability to interject a note of humor at times when we seem to be getting much too serious for our own good. Most importantly we thank you for the many valuable contributions you have made to our Program and to tree improvement in the region. We hope to continue a productive association despite the many miles of separation. **Good luck to you Floyd,** any loss we experience from your move will clearly be a gain for our colleagues in the Western Gulf Forest Tree Improvement Program.

Cooperative Tree Improvement Program

Organizational Chart - May 1995



MEMBERSHIP OF THE TREE IMPROVEMENT COOPERATIVE

Alabama Forestry Commission
Bowater, Inc.
Champion International Corp.
Chesapeake Forest Products
Container Corp. of America
Evergreen Corp.
Federal Paper Board
Georgia Forestry Commission
Georgia–Pacific Corp.
International Paper Co.
James River Corp.
Kimberly–Clark Corp.
MacMillan Bloedel, Inc.
Mead Coated Board
N.C. Div. of Forest Resources
Packaging Corp. of America
Rayonier
Scott Paper Co.
S.C. State Commission of Forestry
Union Camp Corp.
Virginia Department of Forestry
Westvaco Corp.

PUBLICATIONS OF SPECIAL INTEREST TO MEMBERS OF THE COOPERATIVE

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Balocchi, C. E., F. E. Bridgwater, B. J. Zobel, and S.Jahromi. 1993. Age trends in genetic parameters for tree height in a non–selected population of loblolly pine. For. Sci. 39(2).

Bridgwater, F.E. 1993. Supplemental mass pollination. P. 69–77. In: Advances in Pollen Management. USDA Agricultural Handbook 698.

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Grattapaglia, D., J. Chaparro, P. Wilcox, S. McCord, B. Crane, H. Amerson, D. Werner, B.H. Liu, D. O'Malley, R. Whetten, S. McKeand, B. Goldfarb, M. Greenwood, G. Kuhlman, F. Bridgwater, and R. Sederoff. 1993. Application of genetic markers to tree breeding. P. 452–463. In: Proc. 22nd South. For. Tree Impr. Conf., Atlanta, GA.

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Wilcox, Phillip L. 1995. Genetic Dissection of Fusiform Rust Resistance in Loblolly Pine. Ph.D. Thesis, Dept. of Forestry, N.C. State University. Raleigh, NC, 125 pp.

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We note the retirement of three men that have contributed much to the success of the Cooperative. We praise their accomplishment and regret that this chapter of our enjoyable association is closing. We wish each of these long time friends and associates the very best in their retirement.

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Top Left : Bill Arnold
Mead Coated Board

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Bottom Left: Tom Dierauf
Virginia Dept. of Forestry

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Bottom Right: Grady Harris
North Carolina Division
of Forest Resources