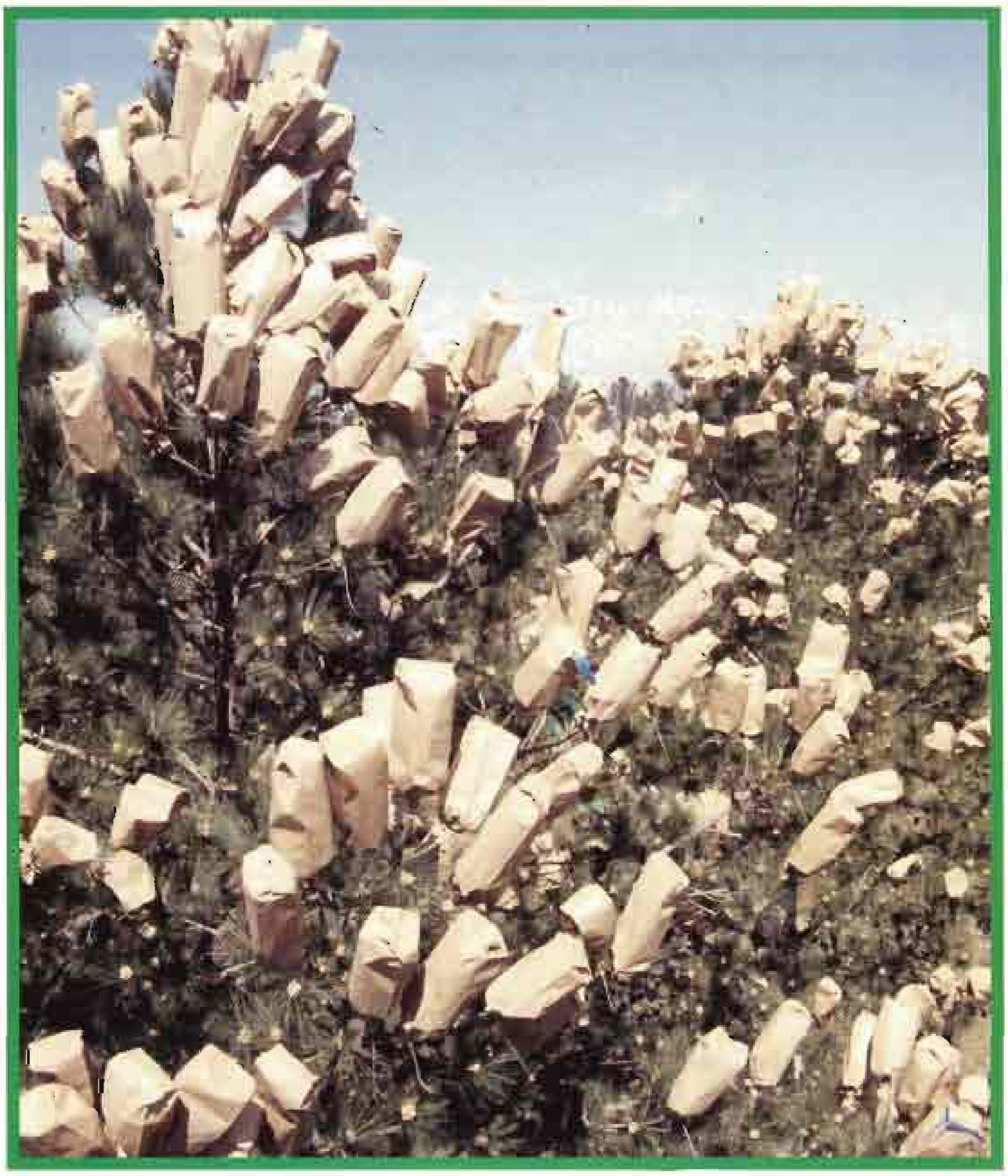
North Carolina State University — Industry Cooperative Tree Improvement Program

45TH ANNUAL REPORT



Department of Forestry
College of Natural Resources
North Carolina State University

May 2001

Front Cover

Mass Control Pollination is being used by many companies within the Cooperative to increase gain from deployment of the best full-sib families via seedlings or bulking up via vegetative propagation. Weyerhaeuser Company has invested in Control Mass Pollination for the past few years to increase the gain from their Lyons, GA seed orchard.

EXECUTIVE SUMMARY

BREEDING, TESTING, AND SELECTION

During this past year, Cooperative members screened another 158 tests, bringing the total number of tests screened to about 800. About 62% of the 1,278 progeny tests planted for second-cycle have been measured screened, and selections made. 141 new third-cycle selections this year brings the total to 778.

Pollen for polycross testing is now available for all three breeding programs (Northern, Coastal and Piedmont). The breeding priority this past year was to create the checklot seed needed for the next round of progeny testing. For those parents that had extra flowers, polycrossing with pollen mix and controlled crosses among parents within sublines were initiated. All in all, some 950 bags were pollinated this year.

PROGRESS REPORTS FOR RESEARCH

A new method was developed for the BLUP analysis of data from diallel mating designs. Checklot adjustment was shown to be critical to improve the prediction of genetic values. Analysis of the Early Diallel Measurement Study (EDMS) of second-generation disconnected diallels showed that earlier selection could be more efficient than direct selection on volume at age 8, although optimal selection ages varied for different breeding populations.

A test of seedlings and rooted cuttings from nine full-sib loblolly pine families made it possible to partition genetic variances for additive, dominance and epistasis effects. Epistasis and dominance had no significant role in growth traits at early ages; genetic effects for growth traits were essentially additive. Dominance variance for growth traits increased as the trees matured. Fusiform rust incidence appeared to be under both additive and epistatic genetic control.

Field tests demonstrated the potential for the Resistograph® to produce reliable, non-destructive estimates of wood specific gravity for large numbers of trees.

After two seasons, a clonal selection study established in collaboration with the NCSU Loblolly and Slash Pine

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INTRODUCTION

When Bob Weir retired last May, and I took over as Director, it was only the second time in the 45-year history of the NCSU-Industry Cooperative Tree Improvement Program that the directorship has changed hands. Add to that the retirements of long-standing staff members Alice Hatcher and Jerry Sprague, and ... well, it was bound to be a challenging year! If that wasn't enough, it quickly became apparent that the face of the forest industry was undergoing change at a head-spinning rate. Within weeks of my arrival, Champion International Corp. was purchased by International Paper Co., Fort James Corp. was swallowed up Georgia Pacific Corp, and The Timber Company signed a definitive agreement to merge with the Plum Creek Timber Company. WOW!! What had I gotten into here?

Fortunately, a few things DON'T change: the industry's appetite for high-quality wood fiber remains voracious; intensively managed, fast-growing plantations remain an ecologically and economically attractive way to meet that demand in the south; genetic gains in yield realized from today's seed orchards are in the order of 20% and improving all the time; and finally, trees continue to behave like trees, regardless of what the people and organizations around them are doing. As trivial as that final point may seem, it has been the basis for retention of my sanity throughout my professional career as a forester.

Despite all the upheaval in our industry, the collaborative approach to forest research remains an attractive model for many issues, including tree improvement. No one could tackle a loblolly pine breeding program at this scale on their own, and a ticket to ride on our cooperative tree improvement bus is still a mighty fine deal. I don't think charting the general direction of a breeding program is really all that difficult, but as with most roads leading into new territory, the surface may be a little bumpy and our bus may require a little maintenance and even some clever modification to face changing conditions. With some smart planning and good engineering, we can avoid having to push the road across swamps or deep gullies, and we might even find a few shortcuts.

With the loss of so many staff members in one year, there was really little choice but to slow down a bit while we took care of some essential program maintenance. At N.C. State, we reorganized staff duties and recruited some new people. Our Coop members participated in an exhaustive review of membership structure, hoping to find some stability for our critical programs in the face of industry consolidation. I had the good fortune to kick dirt in the field on a one-to-one basis with all of our cooperators. It was good time to establish personal relationships and to review the concerns and priorities of our members. At the end of the day, it might appear that rather few changes have been made, other than a couple of new faces in our office. As you'll see in this report, our breeding and research programs continued to make good progress. This has not been a time to introduce change for change's sake, but rather to prepare for what may lie in front of us.

Now, in the past few weeks, just when I thought things were calming down, Bowater has signed a definitive agreement to acquire Alliance Forest Products, and Georgia Pacific has put the former Fort James seed orchard and their Coop membership on the auction block. Oh dear, looks like things will stay interesting for a while yet!

Tim Mullin, Director

BREEDING, TESTING AND SELECTION

THIRD-CYCLE BREEDING UPDATE

With the third-cycle selection work past the 62% mark, more breeding sublines are being formed. Since 1999, Cooperative members have been busy collecting polycross pollen to be used for pollen mixes for the Northern, Coastal, and Piedmont breeding programs. Pollen from 20 parents in each program is to be mixed and used for polycross breeding in this next cycle. We have identified all of the pollen parents for each program and received enough pollen this spring to make a mix of 1800 cc's for the Coastal, 2100 cc's for the Piedmont and 200 cc's for the Northern programs.

The Cooperative's breeding activities in spring 2001 (similar to 2000) included:

1. Collection of more pollen from all pollen parents in each of the three breeding programs to store for breeding in 2002. The designated pollen parents have been assigned to backup organizations for grafting over the next couple of years, assuring that we will not lose the pollen parent if an organization is sold.

2. Third-cycle breeding continued this spring in a modest way. The breeding priority was to create the checklot seed needed for the next round of progeny testing. Ten parents were designated in each program as female parents for checklot seed production. These parents are being crossed with the pollen mix for that program to create sufficient checklot seed. The total checklot seed needs for the three programs are as follows: Northern, 14,000 seed; Coastal, 32,000; and Piedmont, 21,000. Several members have made controlled crosses for checklot seeds. We need to produce one-third of the checklot seeds before any progeny tests can be established. For those parents that have extra flowers, polycrossing with pollen mix and controlled crosses among parents within sublines were initiated this spring. All in all, some 950 bags were pollinated this year. The third-cycle breeding efforts will dramatically increase over the next couple of years.

Ben Morel and a visitor from India perform 3rd-cycle breeding at The Timber Company's Oliver Tree Improvement Center near Statesboro, GA. Isolation bags for operational Controlled Mass Pollination can be seen in the background

THIRD-CYCLE SELECTION PROGRESS

During this past year, Cooperative members screened another 158 tests, bringing the total number of tests screened to about 800. To date, about 62% of the 1,278 progeny tests planted for second-cycle breeding have been measured, screened, and selections made. This year's work has resulted in 141 new selections, bringing the total to 778 for the third-cycle selections. Of these, 343 selections are for the Coastal program, 311 for the Piedmont, and 124 for the Northern breeding program.

Several new sublines have been assigned and, in a few cases, previously formed sublines have been revised as conditions warrant. These assignments should accelerate third-cycle breeding and testing progress. The subline formation within the breeding programs is summarized in Table 1.

Third-cycle selection work will continue to be a high priority activity for the next two to three years. The data for the final diallel test series will be collected in 2003 and the last selections should be identified in 2004. All third-cycle selections are being grafted into breeding orchards and a few of the "truly elite" selections are being incorporated into new third-cycle seed orchards.

Tannis Danley (Mead Coated Board) and a third-cycle selection

Table 1. Summary of third-cycle breeding sublines for the Coastal, Piedmont, and Northern breeding programs

Program - region	Number of sublines	Number of cooperators	Number of selections	Total % gain in height	Total % gain in volume
Coastal- Atlantic Coastal	10	6	119	12	28
Coastal- Florida	2	2	27	18	60
Coastal- Lower Gulf	9	4	103	11	30
Piedmont- GA and SC	11	6	128	12	38
Piedmont- Upper Gulf	5	4	61	11	34
Northern zone	6	4	81	8	26
TOTALS	43		519		

THE COOPERATIVE'S ELITE BREEDING POPULATIONS

To realize the tremendous genetic and economic potential of breeding highly selected trees, several elite breeding populations have been formed by the Cooperative in recent years. The extra gain possible from breeding only the best trees for specific geographic regions, and possibly for different product goals, is the main benefit of including elite populations in the Cooperative's third-cycle breeding strategy. The second major advantage of elite populations is rapid generation turnover. Accelerated breeding and testing techniques have been developed that can reduce generation turnover from about 20 years to less than 10. In particular, breeding is much faster and less costly in elite populations because it is much quicker to breed a smaller number of entries (e.g., 20 to 40 in elite populations) as compared to 160+ entries in the mainline population, thus gain per year will be higher.

Numerous options are available for management of elite populations, and elite populations can be customized for each cooperator or groups of cooperators. The active elite populations for breeding in the Cooperative are the Piedmont Elite Population (PEP), the Lower Gulf Elite Population (LGEPop), and the 3 "Conventional" Elite populations.

For the PEP, results from Cooperative studies and other seed source trials indicate that across many sites in the Piedmont, loblolly pine from the Atlantic Coastal Plain grows 5-10% faster than trees indigenous to the Piedmont region. Unfortunately, the Coastal trees tend to be more susceptible to cold and have worse stem form than the Piedmont trees. The PEP breeding population is based on the production of hybrids between Coastal and Piedmont trees to incorporate the advantages of each population. Both industry and state organizations are willing to take the calculated risk that this approach will pay big dividends. If we find that these hybrids are not as superior as hoped for, other populations will be available for use. "Conventional" elite populations that will utilize the best genotypes from the local Piedmont source (e.g., lower risk, but probably lower benefit) are also being developed.

The 4-year measurements of the PEP Population II Pollen Mix tests were made this past winter and spring (data are just now coming in). The data from these 16 tests from the Fall Line, Middle Piedmont, Upper Piedmont, and Cold Regions will be analyzed to show the limitations of safe movement of the inter-provenance hybrids, as well as the within-provenance families. Results from the factorial and diallel breeding to generate hybrid families will not be available for 2 to 4 years.

The Lower Gulf Elite Population (LGEPop) is similar to the PEP in that genotypes from different geographic regions are being utilized. Cooperators in the N.C. State Coop, the Western Gulf Forest Tree Improvement Program, and the Cooperative Forest Genetics Research Program at the University of Florida are all collaborating to bring the best genetic material together for the Lower Gulf Region of the loblolly pine range. We know that the local provenance is much less productive than provenances from the South Atlantic Coastal Plain, Central and Northern Florida, and Livingston Parish, LA. By combining genotypes from these regions, we hope to dramatically increase the genetic potential of the new "land race" that will be developed for this region.

Pollen mix tests (16 total) were established throughout the region in 1998, and measurements are scheduled for age 6. The best parents and sources for use in the Lower Gulf will be identified based on these trials. A total of 8 diallel tests (mating was 8-parent disconnected diallels) were established this year and will be used both for identifying the best full-sib families for deployment and for within-family selection.

Second-cycle selection and breeding efforts have identified the best tree genotypes for "conventional" elite populations for the Coastal, Northern, and Piedmont zones. We consider these conventional in that only the best 20-30 parents from within each geographic region are being bred together; no inter-provenance hybrids are being used as in the PEP or

LGEPop. The first 8-parent diallel for the Coastal elite has been formed, and breeding should be complete in the next year or two. As the second-generation testing program nears completion and breeding values for more parents are available, additional elite diallels will be generated. We want to use only the best material in these populations.

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

Grafting the 141 new selections made this year was a big effort by cooperators. Jim DeWit (Molpus Timberlands – Joshua Land Management) is grafting one of the 3rd-cycle selections.

Bowater's second-generation loblolly pine orchard at Catawba, SC

RESEARCH

ANALYTICAL METHODS FOR DISCONNECTED DIALLEL PROGENY DATA

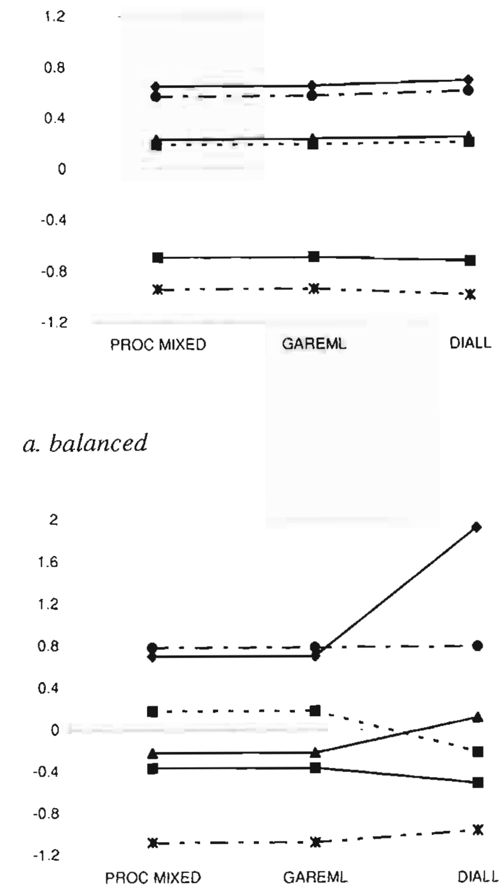
A New Mixed Analytical Method

Diallel mating is a popular mating design used for crop and tree breeding programs, but its unique feature of a single observation with two levels of the same main effect, general combining ability (GCA), makes it difficult to analyze with standard statistical programs.

A new approach using the SAS PROC MIXED procedure was developed in this study for analyzing genetic data from diallel mating. Dummy variables for GCA effects were first constructed with SAS PROC IML, then PROC MIXED was used to estimate variance components and to obtain BLUE (best linear unbiased estimators) of fixed effects and BLUP (best linear unbiased predictors) of random genetic effects (GCA and SCA effects) simultaneously.

The method was validated using computer-simulated data with different levels of data imbalance and was shown to produce accurate estimates of variance components for all random variables as compared with true values. The true genetic values (simulated) were strongly correlated with BLUP estimates of GCA, SCA and genetic values (GV) for both balanced and unbalanced data. The new method produced variance estimates similar to other variance-estimate procedures such as GAREML and DIALL under balanced situations, and was superior to DIALL with unbalanced data (Figure 1). The new method also simplifies the difficulty of diallel genetic analysis and provides more flexible options in the analysis.

The new method can also be used for predicting individual breeding values with BLUP methodology, applying SAS IML to the outputs provided by PROC MIXED to calculate breeding value for each individual in the progeny test, adjusted for the fixed effects of replicate and test location. Accurate BLUP prediction, the ability to estimate individual breeding values, and the ease of use makes this new method especially attractive for analyzing tree-breeding data.



b. 60% survival and 5 missing crosses

Note: Lines connecting like symbols represent GCA estimates for a given parent derived from each of the 3 methods

Figure 1. Comparison of GCA estimates for tree height, as the deviation from the population mean by SAS PROC MIXED, GAREML and DIALL for 6 parents in each of 2 data sets of different imbalance levels (a, b)

Optimal Analytical Method of Disconnected Diallel Data

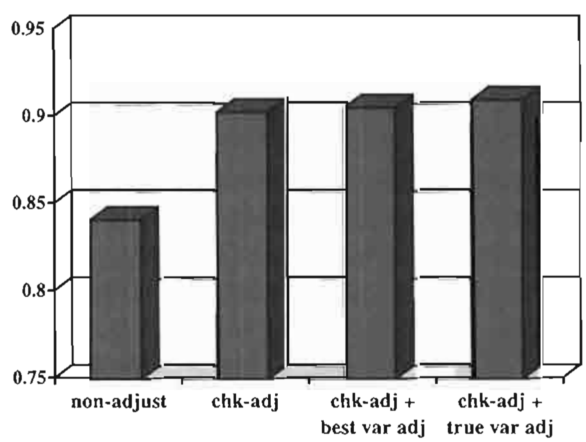
For disconnected diallels with different sets of parents, three analytical models can be considered with regard to the treatment of diallel effect in the model. The diallel effect can be included as a fixed effect (Model 1), a random effect (Model 2) or no diallel effect (Model 3). Simulated data generated with known parameters were analyzed using BLUP methodology to compare these three alternative models. Results indicated Model 1 and Model 3 produced unbiased GCA variance estimates. Model 2 resulted in a downward-biased estimate of the GCA variance component and occasionally produced unrealistically large diallel variance estimates. Model 3 was slightly better than other two models in accuracy of GCA variance estimates, while the difference in accuracy between Model 1 and Model 2 was rather trivial.

The accuracy of BLUP prediction for the three models, measured as correlation between true genetic value (GV) and prediction, was very close, with Model 3 slightly better than the other two. With a random selection of parents in diallels and random allocation of crosses in the field test design, the disconnected diallel mating can be efficiently analyzed using Model 3, where disconnected diallels are treated as a large incomplete diallel. When a complete model is warranted with non-random selection of parents into disconnected diallels or allocation of crosses in the field design, Model 1 may be preferred by considering diallel as fixed effect in the model. Model 2, which treats diallel as a random effect, may result in downward biased GCA variance estimates, and hence underestimate additive genetic variance and heritability.

Several statistical approaches were evaluated for combining multiple disconnected diallel test series within a given region. The best sample variance prediction in the class of linear combination of local variance estimates was developed. This improved local variance estimate can be utilized to adjust both parental GCA and full-sib GV prediction. Another simple adjustment is to use a common checklot to connect test series.

Results from simulation data showed that, for multiple disconnected diallel test series, checklot adjustment was critical to improve the prediction of genetic values obtained using BLUP analysis. It can significantly improve the chances of selecting best performers based on GCA or full-sib GV. The improvement of prediction by using checklot adjustment is surprising but has important implications for future progeny testing and data analysis. Checklot adjustment alone can increase correlation by more than 0.05 in GCA prediction, and almost 0.10 for full-sib GV over all parameter settings (Figure 2). Beyond checklot adjustment, additional improvement in accuracy by GCA sample variance prediction is limited, due to the fact that the accuracy of checklot-adjusted prediction alone is already close to the theoretical limit.

For practical reasons, BLUP analysis for single diallel test series using the fixed diallel effect model (Model 1), followed with checklot adjustment for GCA and breeding values over multiple test series, is the best way to analyze multi-disconnected diallel test series established within a breeding region. Results from this study confirmed the importance of using checklot for connecting disconnected test series. This method has now been used for breeding value estimates from Cooperative program data.



Note: **chk-adj**: checklot adjustment; **best var adj**: adjustment using best GCA variance prediction; **true var adj**: adjustment using true GCA sample variance (theoretical limit)

Figure 2. Comparison of adjustment methods applied to GCA prediction from multiple 4-test series (for parameter setting: h^2=.2, =.3, rB=.8)

GENETIC GAIN AND SELECTION EFFICIENCY FOR EACH BREEDING PROGRAM

Genetic parameter estimates for loblolly pine have been well studied in the past. Early selection studies on loblolly pine indicated that selection on growth traits at early ages could be effective. From a study of unimproved population of loblolly pine, Balocchi et al. (1993) suggested that measurement of height at age 6 and selection one year later would maximize the genetic gains per year. However, genetic parameters and trends over time may be different with the improved loblolly pine population that has been generated using different mating designs and field-test layouts.

Using the new mixed analytical method, the well-balanced data from the Early Diallel Measurement Study (EDMS) of second-generation disconnected diallels were analyzed to obtain more accurate and precise estimates of genetic parameters of both height and volume at early ages. With better estimates of parameters, time trends of selection efficiency were re-evaluated for different selection methods, and the impacts of non-additive variance on genetic gain were examined.

Genetic parameters were examined for Northern, Coastal, and Piedmont populations from analyses of 23 disconnected half-diallel progeny test series, with 275 parents or 690 full-sib families. The genetic gains in age-8 volume predicted by various selection methods at age 6 revealed that selection on volume yielded more gain than selection on height. Among breeding programs, the Coastal population had the greatest correlated response, followed by the Piedmont and the Northern populations. Family plus within-family selection was the most effective way to achieve genetic gain for early selection on both height and volume. Additional gain (10-40%) can be achieved by capturing the non-additive genetic component through mass-producing full-sib crosses and/or vegetative propagation.

The criterion of selection efficiency was formulated as the ratio of gain per year (SE1) or present value (SE2) between indirect selection and direct selection. Optimal selection ages were determined for various selection methods. The analysis of selection efficiency (Figure 3) showed that earlier selection could be more efficient than direct selection on volume at age 8. Family selection can be performed as early as age 3 for height and at age 4 for volume, which is the earliest measurement age in this study. Family plus within-family selection was optimal at age 3 or age 4. Optimal selection ages also varied for different breeding populations.

Due to the non-availability of genetic information from rotation age, year 8 (one third of rotation age) was used as the response trait in this selection efficiency study. Assuming that age-age genetic correlation follows a log:age ratio (LAR) regression model (Lambeth 1980), the regression slope *b* turned out to be a key factor in the ratio of age correlation (Eq. 1), which is the appropriate criterion to assess the accuracy of using earlier age rather than rotation age as the response trait.

$$\begin{aligned}\frac{r_{j\cdot 25}}{r_{j\cdot 8}} &= 1 - b \cdot \ln\left(\frac{25}{8}\right) / r_{j\cdot 8} \\ &= 1 - 1.139 \cdot b / r_{j\cdot 8}\end{aligned} \qquad [1]$$

Age-to-age correlations up to age 8 for traits height and volume were used to fit the LAR model. Within the estimated range of slope *b* (0.1~0.3), changes in the ratio age correlation were minimal after age 4 for volume and after age 2 for height. Thus, based on a comparison with the rotation age gain formula via Eq. [1], the selection efficiency criteria used in this study were appropriate for most early ages except for age 1 and 2. Optimal ages for volume and height at age 3 or later remained the same. However, caution must be taken for selection at early ages because of planting shock and other adaptive environmental effects in the field.

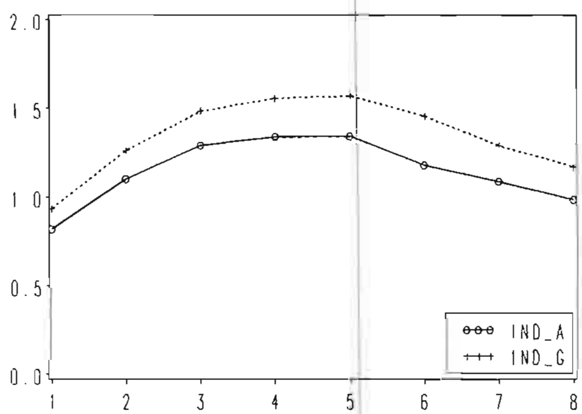
While substantial gain can be achieved for height selection at previous optimal age 6, selection at earlier age (e.g. 3 or 4) and volume selection should be considered in early selection of loblolly pine in order to achieve the maximum gain per unit of time, especially for family selection. Due to the regional differences with regard to the optimal age and selection efficiency level, separate considerations should be applied to each region.

References:

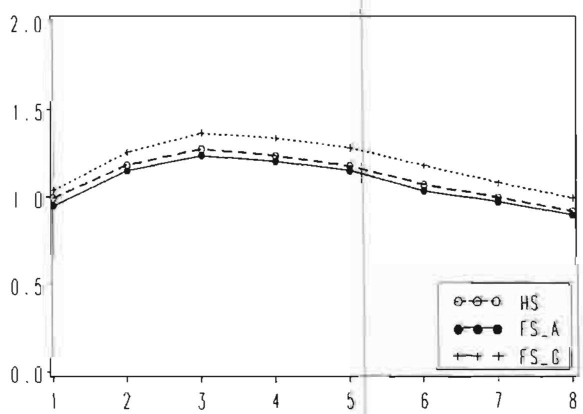
Balocchi, C.E., Bridgwater, F.E., and Bryant, R. 1993. Age trends in genetic parameters for tree height in a nonselected popultaion of loblolly pine. For. Sci. 39: 231-251.

Lambeth, C.C. 1980. Juvenile-mature correlations in Pinaceae and implications for early selection. For. Sci. 26: 571-580.

Individual selection



Family selection



Family plus within-family combined Selection

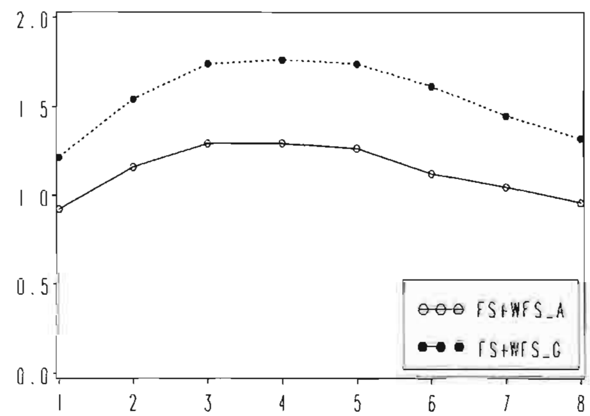


Figure 3. Comparison of selection efficiencies (based on SE1) of early height on 8-yr volume of Coastal population for individual (IND) selections, half-sib (HS) and full-sib (FS) family selections, and combined (FS+WFS) selections, based on either only additive (A) or total genetic variance (G)

GENETIC PARAMETER ESTIMATES FROM A LOBLOLLY PINE CLONAL TRIAL

Genetic variance can be partitioned into additive, dominance and epistatic variances using clonally replicated progeny tests. Very little is known about the contribution of epistatic variance to total genetic variance and its effect on growth of loblolly pine. Estimation of non-additive genetic variances for loblolly pine will give further insight into the genetic control of growth and incidence of fusiform rust. It may help to develop more efficient breeding deployment strategies to maximize gain.

For this study, nine full-sib loblolly pine families were generated by crossing three individuals as females in a factorial mating design with three others as males. Families were cloned and seedlings and rooted cuttings of the same families were deployed at two sites, one in Alabama and one in Florida, using a split-plot experimental design with six replications. Height at ages 1, 2, 4, 6; Diameter, volume and fusiform rust disease at age 4 and 6 were measured. Additive, dominance and epistatic genetic variances for each trait were estimated according to the Foster and Shaw (1988) model.

Additive genetic effects were the major source of genetic variance for growth traits. Epistatic gene effects seemed to have no significant role, except a slight increase for height at age six (Figure 4 and 5). Coefficients of additive genetic variance (CVA) ranged from 4.0 to 11.0 for height, 5.6 to 11.4 for diameter and 10.0 to 23.0 for volume. CVAs estimated from rooted cuttings were up to 2.8% greater than the CVAs estimated from seedlings for height. Similarly greater (up to two times) additive genetic variances were estimated from rooted cuttings for diameter and volume.

Dominance effects were negligible both for growth and disease resistance. However, a slight increase was observed for height and diameter at age six (Figures 4 and 5). The coefficients of dominance genetic variance (CVD) for height and diameter were 1.3 and 1.9, respectively. However, dominance genetic variance was considerably higher for volume, 4.8 and 8.8 at ages four and six.

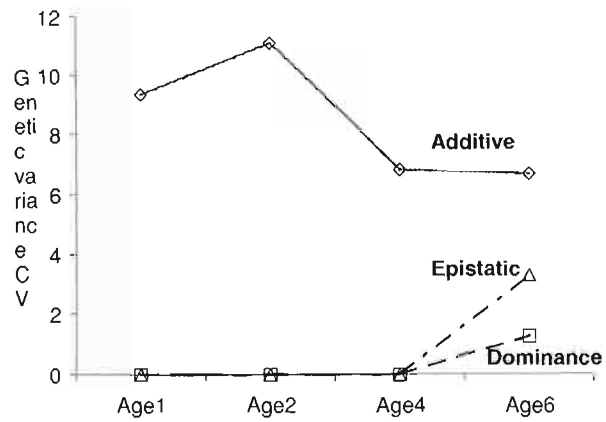


Figure 4. Genetic variances for height based on rooted cuttings.

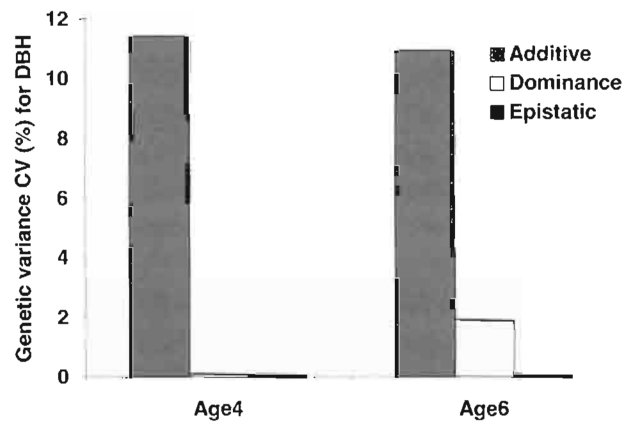


Figure 5. Genetic variances for diameter, estimated from rooted cuttings.

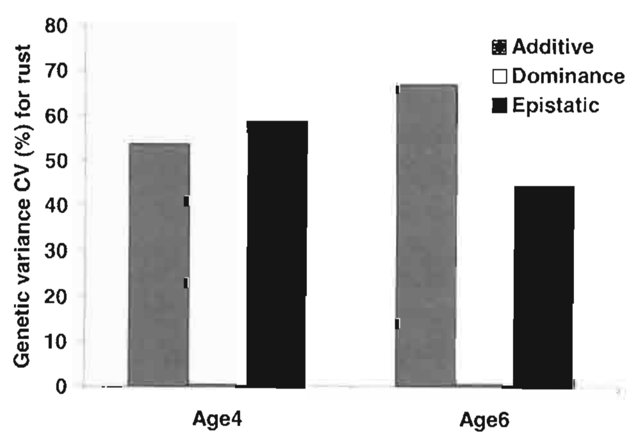


Figure 6. Additive, dominance and epistatic genetic variances for fusiform rust disease

Genetic differences among the clones within families accounted for 48.6% of the total variance for disease resistance. In contrast to growth traits, epistatic gene effects were as important as additive genetic effects for fusiform rust incidence (Figure 6). Coefficients of epistatic genetic variance (CVI) were 58.9 at age four and 44.5 at age six.

Additive genetic correlations between the growth traits and fusiform rust incidence were generally negative and ranged from 0.29 to –0.47 (Table 2). Similarly, non-additive genetic correlations were also generally negative between growth traits and fusiform rust incidence, and varied between 0.02 to –0.65.

Conclusions

The results in this study here revealed certain important points for loblolly pine tree improvement strategies. First, epistatic and dominant gene interaction seemed to have no significant role in growth traits at early ages; additive genetic effects are the major source of genetic variance for growth traits in loblolly pine. Second, dominance variance for growth traits tends to increase as the trees mature. Third, fusiform rust incidence appeared to be under both additive and epistatic genetic control.

Genetic differences among clones within families accounted for 50% of the total variance for disease incidence. A tree improvement strategy based on selection for general combining ability of parent trees based on clone means within families might substantially increase genetic gain both in growth and especially in fusiform rust incidence. Also, using clonally replicated trials would increase selection efficiency and gain substantially, since environmental noise is better controlled by the clones within families (Libby 1962). Negative additive and non-additive genetic correlations between the growth traits and fusiform rust incidence are also encouraging for rapid simultaneous genetic improvement of these traits during the same cycle of selection.

References:

Foster, G.S., and D.V. Shaw. 1988. Using clonal replicates to explore genetic variation in a perennial plant species. Theo. Appl. Genet. 76:788-794.

Libby, W.J. 1962. Estimation of variance components of internode length in a cloned population of *Mimulus guttatus*. Genetics, 47:769-777.

Table 2. Additive and non-additive genetic correlations between fusiform rust incidence and growth traits (height, diameter and volume) at age four and six in loblolly pine.

	Additive Genetic Correlations		**Non-additive Genetic Correlations**	
	Rust at age 4	**Rust at age 6**	**Rust at age 4**	**Rust at age 6**
Height (rc)[1]	0.29±.09	-0.08±.22	-[3]	-
Height (s)[2]	0.07±.65	-0.07±.78	0.02±.09	0.04±.09
DBH (rc)	-0.31±.08	-0.35±.15	-	-
DBH (s)	-0.25±.54	-0.47±.56	0.07±.09	-0.43±.07
Volume (rc)	-0.24±.08	-0.29±.16	-	-
Volume (s)	-0.13±.63	-0.28±.63	-0.36±.08	-0.65±.05

[1] (rc) Estimation was based on rooted cuttings
[2] (s) Estimation was based on seedlings
[3] Dominance or epistatic genetic variances were not estimated due to zero or negative estimates.

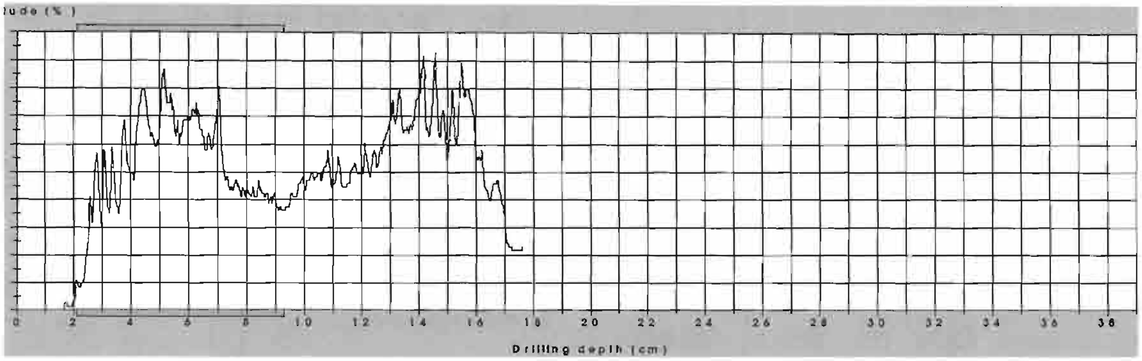
USE OF RESISTOGRAPH TO MEASURE WOOD DENSITY

Specific gravity (density) is one of the most important characteristics of wood. It affects various wood properties, i.e., lignin and cellulose contents, wood strength, structural wood quality, paper strength, paper tear resistance and sheet density. The industry is increasingly relying on fast-growing pine plantations in the southern US for pulp and paper material, and more organizations are interested in using wood density as a selection criterion. An efficient, reliable and affordable wood-density assessment is thus becoming an increasingly important issue for members of the Cooperative, because a large number of trees would need to be assessed at each cycle for wood quality.

Wood specific gravity is typically determined by volumetric measurement and x-ray density profiles. Tree-ring density charts produced by the x-ray densitometry and variation between and within tree rings give important detailed information on wood properties. These reliable and high-precision methods are time consuming and expensive to use on a large scale. An efficient and cheaper method to determine the wood specific gravity of the trees is badly needed.

A new device known as the Resistograph® is being used to study the wood characteristics of tree stems. When a tree is drilled with the Resistograph, the resistance is recorded according to penetration depth. The Resistograph charts reveal the variation in the density of early and late wood. The Resistograph has been widely used to detect decay in standing trees and for wood quality evaluation to determine relative density of various boards. But to our knowledge, there has been no study on the determination of standing-tree wood density. If the Resistograph method yields a reliable sound-wood density estimate of standing trees, then it will be a fairly easy, affordable method to estimate wood density of large number of trees.

A large-scale sampling was carried out from four diallel genetic tests in the South Carolina



Resistograph profile from a standing tree

Piedmont. Altogether, 2,016 trees were selected, and 12-mm increment cores were collected. Wood specific gravity was determined for each by the standard volumetric method.

These same trees were drilled in the field with the Resistograph. For each drilled tree, the average of the drilling amplitude (%), average of the amplitude for the first half of the tree (from the bark to the pith), and drilling depths were calculated. The increment cores were then prepared for the x-ray densitometry following the procedure given by Harding (1995). The cores were scanned and data were produced from the x-ray profiles.

Correlation and regression analyses were conducted to determine relationships between the gravimetric wood density and Resistograph-generated data. Families having high wood density tend to have higher amplitude percentages (Figure 7). On the other hand, families having low wood density tend to have smaller amplitude average percentages. This is expected since resistance to the needle is higher when the wood is denser.

Wood density was moderately correlated (r=0.631) with Resistograph average amplitude (Figure 7). A regression model was developed to predict wood density using the Resistograph variables. Average amplitude of the profiles explained about 40% of the variation in wood density.

The preliminary results showed that average amplitude of the Resistograph could be employed to predict wood density. The method is promising to perform large numbers of green-wood density measurements. However, further research is needed to improve the relationships between the actual wood density and Resistograph profiles. The comparison of Resistograph and x-ray profiles will produce more detailed information. If the research proves strong relationships, then the Resistograph can replace expensive and time-consuming wood density measurement methods.

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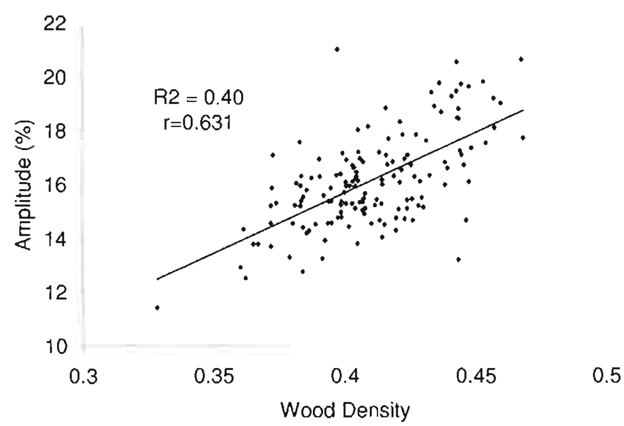


Figure 7. Relationship between Resistograph average amplitude and actual wood density for 2,016 sample trees.

CLONAL SELECTION STUDY

A clonal selection study has been established in collaboration with the NCSU Loblolly and Slash Pine Rooted Cutting Program. The study is to develop information that will enable individual organizations to efficiently select and propagate superior clones. The study began in October 1996 with the germination of seeds from eight full-sib loblolly pine crosses from the South Atlantic Coastal Plain region. The crosses were chosen from the Tree Improvement Program's diallel tests on the basis of rapid growth, good rust resistance, acceptable form, availability of seed, and non-relatedness. Results from this study may provide useful information on: (1) the ideal number of clones per cross to begin selection; (2) number of ramets per cross necessary to characterize growth on one site; (3) efficiency of selection at different ages; (4) multiplication rates for a large number of clones; and (5) magnitude of predicted genetic gain for the best clones in each cross.

The study began with approximately 100 clones of each cross. After hedge production from the seedlings, rooting and sorting, 450 clones were planted in two field tests: 168 clones from four crosses on International Paper land near Jay, Florida in December 1998; and 282 clones from the other four crosses on Westvaco land in South Carolina in November 1998. The experimental design was a randomized complete block, with 9 blocks and one ramet per clone per block.

Survival and height were measured after the first two growing seasons. Survival after two seasons was 93% on the FL site and 95% on the SC site. The mean height of all the clones after two seasons was 5.5 ft. in FL and 6.0 ft. in SC. First-year Clone x Block CV (coefficient of variation) was high at approximately 35%, but dropped to 25% after two seasons. Although Clone x Block CVs are expected to be higher than that of Family x Block CV in seedling progeny tests, some of the variation could be due to uneven stock quality at the planting time.

The percent differences in 2^{nd}-year mean height between select groups of clones and the mean of all the clones in each test are summarized in Table 5. The clone mean heritabilities and the juvenile-mature correlations, which are necessary to convert these differences to genetic gain, will be calculated after future measurements. Nevertheless, these differences suggest the magnitude of differences among clones. The best clone in each test was 38% taller than the test mean. The best 8 clones, irrespective of which cross they came from, were 29% (FL) and 33% (SC) taller than the test means. The best two clones from each of the four crosses in the test were 24% (FL) and 30% (SC) taller than the mean. Interestingly, even if one only chose the best 25% of the clones, they were 21% (FL) and 20% (SC) taller than the test mean. The test mean, of course, represents the gain that could be achieved from planting full-sib seedlings or rooted cuttings of outstanding crosses.

Annual measurements will be taken with rust infection and diameter scored at the appropriate times. The information coming from this study over the next few years should help organizations as they develop and implement their advanced-generation regeneration strategies.

Table 3. Percent differences of various clone means (2-year height) from the test means in the two test locations, Florida and South Carolina.

	% difference from test mean	
	Florida	**South Carolina**
Top clone	+38	+38
Top 8 clones	+29	+33
Top 2 clones/cross	+24	+30
Top 25% of all clones	+21	+20

GENOTYPE RESPONSE TO INTENSIVE CULTURAL TREATMENTS

In the last few years, several related investigations have aimed to further our understanding of genetic and physiological controls of productivity variation in loblolly pine. The coordinated field studies have utilized the same maternal pine families of two contrasting provenances (see 44th Annual Report, pages 17-21 for background info).

The study utilized genetic material of the same loblolly pine families planted at the SETRES-2 Study in Scotland County, NC. The overall purpose was to evaluate effects of root and shoot genotypes on productivity and physiology of loblolly pine seedlings grown in contrasting nutrient regimes. As presented in last year's report, it was found that root genotypes of the mesic Atlantic Coastal Plain (ACP) provenance were associated with greater aboveground biomass, compared to root genotypes of the xeric Lost Pines Texas (LPT) provenance.

Here, we highlight major findings which may help to explain different growth patterns of these loblolly pine provenances, under intensive culture. Emphasis is placed on evaluating genotypic differences in terms of stemwood biomass relative to foliage and root biomass. Stem production relative to foliage mass, often termed stem growth efficiency (GE), is considered important since it indicates how much wood is being produced per unit of photosynthetic leaf area.

Stem Growth Efficiency

The mesic ACP trees achieved greater stem growth efficiency (GE) compared to xeric sources, when fertilized. This finding is consistent with many other studies, in that mesic plant ecotypes generally respond more to high fertility than ecotypes adapted to harsher environments. It is consistent with an independent study of the same open-pollinated families at the SETRES-2 site, where the mesic sources attained higher GE than the xeric sources at age five (Handest, MS Thesis).

Root systems of the drought-hardy LPT seedlings are typically more compact, with less biomass, yet have high proportion of fine roots, compared to the ACP trees which feature more root biomass, more woody roots, and a more widespread root system (c.f. Wu et al. 2000). For uptake of water and nutrients, the ACP root system might be characterized as an "exploitative" design, whereas the LPT root system may be of more "efficient" design.

The roots of the LPT genotypes are associated with a slightly higher stem GE (Figure 8), which may be partly facilitated by the smaller root system of the LPT genotypes. The subtle advantage in GE could, over a number of years, accrue to large gain in stemwood production.

Our results support the notion of a trade-off in allocation of biomass between stems and roots within the tree, a finding of many other studies. What factors determine how the trade-off between stems and roots is resolved? While it is widely recognized that environmental factors such as soil fertility are important, this study demonstrates that genetic factors also play a part. Further, this experiment suggests that inherent properties of root genotypes can contribute substantially to how the stem:root allocation is resolved.

In the case of xeric roots combined with mesic scions, increased allocation to stem mass was coupled with decreased allocation to root mass, with essentially no change in allocation to foliage mass. Hence, an increase in stem growth efficiency resulted, compared to the other grafted combinations (Figure 8). When combined as a grafted entity, the mesic-shoot with xeric-root trees exhibit the highest GE among the four combinations (Figure 8).

Leaf Physiology

Observed productivity differences between these provenances are only partially explained by biomass allocation patterns. Differences in physiological attributes such as leaf gas exchange and leaf nutrient content provide additional explanatory power.

On the dry sandy site of this field study, differences between the provenances were evident in water use characteristics, such as transpiration and leaf water conductance rates. Like other studies comparing loblolly pine sources, no substantial differences were found in photosynthetic rates. This points out the importance of considering parameters other than photosynthetic rates in examining leaf gas exchange properties which may differ among genotypes.

An important lesson of this study is: The observed differences in leaf physiology among genotypes translate into differences in efficiency of water use, and which correspond to differences in efficiency of stemwood production. This study shows how structural/ morphological characteristics of trees can be associated with physiological characteristics, which can be utilized to predict productivity of characteristic genotypes.

Reference:

Wu R., J.E. Grissom, D.M. O'Malley, and S.E. McKeand. 2000. Root architectural plasticity to nutrient stress in two contrasting ecotypes of loblolly pine. J. Sustainable For. 10: 307-317.

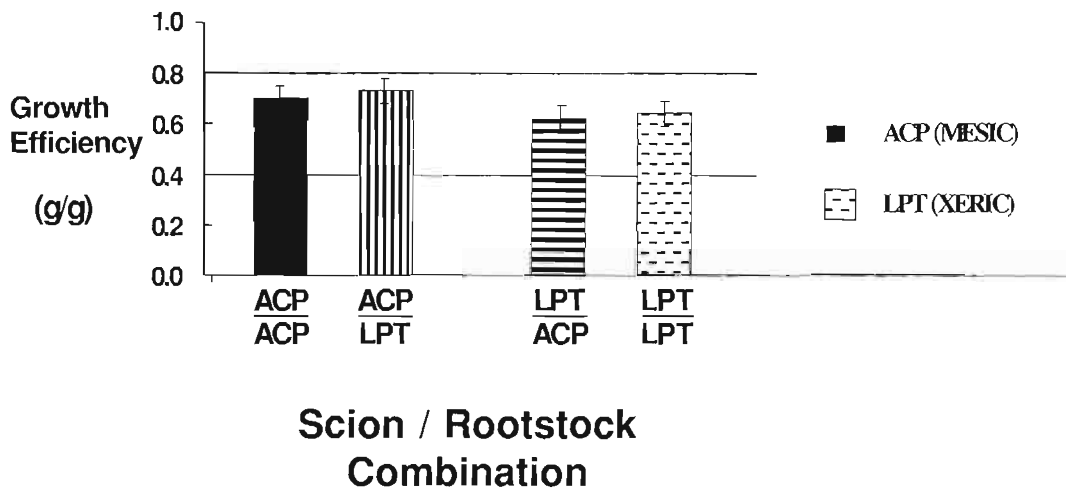


Figure 8. Stem growth efficiencies (stem biomass produced per unit leaf biomass) of grafted seedlings from the Atlantic Coastal Plain (ACP) and Lost Pines, TX (LPT) provenances, in fertilized field plots. Each bar depicts about 110 trees. The scion effect was highly significant ($p<0.01$) and the rootstock effect was marginally significant ($p<0.10$).

SEED AND CONE YIELDS

The fall 2000 seed collection for the Cooperative provided 36.9 tons of loblolly pine seed, slightly more than last year's crop of 35.9 tons and the largest collection since 1996 (75.8 tons).

Seed yields in pounds per bushel were also slightly less than last year (1.34 in 1999 vs. 1.43 in 2000). About 76% of the total seed came from second generation orchards and about 72% of the collection was from the Coastal source (Table 6).

Only one orchard produced above the 2.0 lbs./bushel mark this year; Westvaco, SC 2.0 Coastal orchard yielded 2.17 lbs./bushel. Westvaco, 2.0 Virginia orchard followed with 1.98 lbs./bushel and in third place was the Georgia Forestry Commission 1.5 Coastal orchard at 1.97 lbs./bushel. The remainder of the top ten producers are shown in Table 7.

Table 4. Comparison of 2000 seed and cone yields with previous year's.

Provenance	Bushels of Cones		Pounds of Seed		Pounds per Bushel	
	2000	1999	2000	1999	2000	1999
Coastal 1.0	13,249	13,138	18,305	18,286	1.38	1.39
Coastal 2.0	29,798	18,526	40,732	28,508	1.37	1.54
Piedmont 1.0	859	9,047	1,155	13,418	1.35	1.48
Piedmont 2.0	17,832	9,500	22,409	11,627	1.26	1.22
Totals	61,738	50,211	82,601	71,839	1.34	1.43

Table 5. Top ten production loblolly orchards in 2000.

Organization	Orchard Type	Age	Lbs./Bushel	Orchard Manager
Westvaco, SC	2.0 Coastal	26	2.17	Dave Gerwig
Westvaco, SC	2.0 Virginia		1.98	Dave Gerwig
Georgia Forestry Comm.	1.5 Coastal	14	1.97	Russ Pohl
The Timber Company	1.5 Coastal		1.91	Lorin Clark
Weyerhaeuser Co.	1.0 Coastal		1.85	Drew Dunnam
The Timber Company	1.5 Coastal	30	1.82	Keith Palmer
International Paper	2.0 Coastal	19	1.82	Maxie Maynor
International Paper	2.0 Piedmont	19	1.78	Maxie Maynor
Weyerhaeuser Co.	2.0 Coastal		1.76	Franklin Brantley
International Paper	2.0 Coastal	23	1.71	Tim Slichter

ASSOCIATED ACTIVITIES

GRADUATE STUDENT RESEARCH & 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 or were completed in association with the Tree Improvement Cooperative. Three were directed toward a Masters degree and six were involved in Ph.D. programs. Of special note is the completion of Ph.D. degree programs by Adolfo Bila (in collaboration with the Swedish University of Agricultural Sciences, Umeå), Wen Zeng and Bin Xiang during the past year. The graduate students working in association with the Cooperative, the degree to which each aspires, and the subject of their research project are listed below.

VISITING SCIENTISTS

Dr. Fikret Isik, a research scientist in forest genetics from the Turkish Forestry Research Institute has joined us as a visiting scholar since September, 1999. His visit was supported by a NATO scholarship for scientific exchange. Dr. Isik worked on several research projects related to provenance variation, genetic variation in shoot morphology and wood quality.

Dr. Heidi Dungey, a forest quantitative geneticist with Queensland Forestry Research Institute, visited Raleigh for one month (September, 2000). Her study trip was supported by the CRC for Sustainable Production Forestry, Australia. Dr. Dungey worked on a project involved in the quantitative genetic analysis of hybrid pines.

Student, Degree, Research Project

Adolfo Bila, Ph.D. (In association with Swedish University of Agricultural Sciences, Umeå)
Fertility variation and its effects on gene diversity in forest tree populations. ***Completed 2000.***

Pat Cumbie, M.S. (In association with Rooted Cutting Program, NCSU).
Genetic variation in wood properties in clonal and seedling loblolly pine.

James Grissom, Ph.D.
Growth and physiology of loblolly pine seedlings as affected by genetics of the root system.

John Handest, M.S. (In association with the Nutrition Coop, NCSU).
Influence of nutrition and genetics on leaf area / stem wood production.

Dominic Kain, Ph.D. (With Australia National University).
Inheritance of wood properties in slash by Caribbean pine hybrids.

Hua, Li, Ph.D.
Major gene resistance in fusiform rust.

Paul Shannon, M.S.
An evaluation of the financial returns for different seed orchard establishment options.

Bin Xiang, Ph.D.
Genetic analysis of diallel tests of loblolly pine. ***Completed 2001.***

Wen Zeng, Ph.D.
Detection of major genes using phenotypic data. ***Completed 2001.***

PROGRAM STAFF

Dr. Tim Mullin began his duties as Director of the Cooperative in June 2000, literally the day after out-going Director Bob Weir entered his retirement. Tim spent a hectic year moving family and belongings from both North Africa and Canada, while visiting with all cooperators and completing his initiation as a new member of faculty at NCSU.

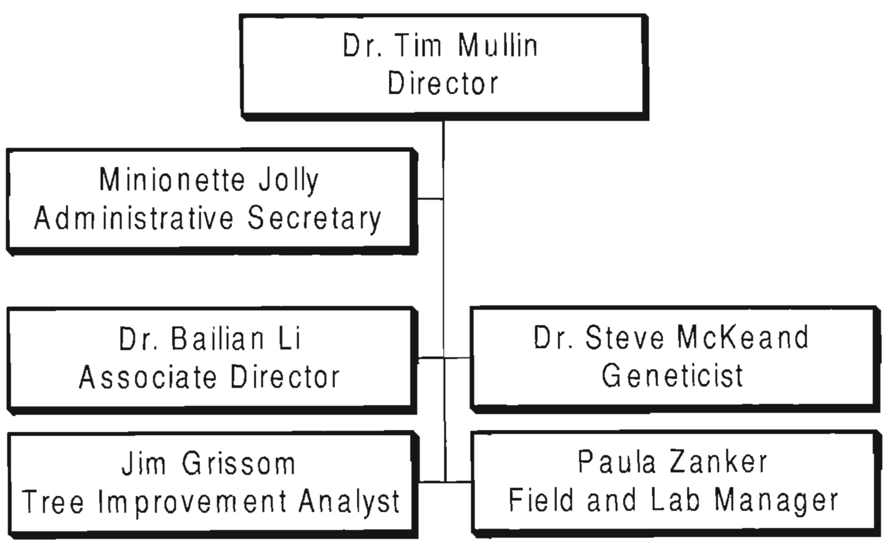
Heriberto "Eddie" Vélez left the tree improvement program in August 2000 to begin graduate studies in the Department of Plant Pathology at NCSU. Eddie was our able Office Assistant for 3 years and will be sorely missed. With Eddie's departure and the retirements of Bob Weir, Alice Hatcher and Jerry Sprague at the end of last year, we were left with some big holes to fill.

The decision was made to redistribute some of the duties among existing staff, and to describe two new positions, those of Tree Improvement Analyst and Administrative Secretary. Samantha Skillen filled our Administrative Secretary slot for just over 4 months, but left in February. Effective May 2001, Minionette "Mini" Jolly comes to join us from the Georgia Institute of Technology, as our new Administrative Secretary.

James "Jim" Grissom joined us in January as our Tree Improvement Analyst. Jim is no stranger to our program, having worked on his PhD under the supervision of Dr. Steve McKeand (waiting only to finish those corrections to the thesis – right, Jim?). On his arrival in January, Jim faced a backlog of updates to our Cooperative database, but is rapidly bringing the shared data up-to-date.

Our own Dr. Steve McKeand took on an additional role this year as Director of Graduate Programs for the Department of Forestry. This is one of those circulating tasks that require an experienced member of faculty and Steve agreed to find room for it on his plate. Brave man!

NCSU-Industry Cooperative Tree Improvement Program Staffing Chart - May 2001



MEMBERSHIP OF THE TREE IMPROVEMENT COOPERATIVE

The trend of industry consolidation and restructuring continued this past year with some impacts on our membership. Champion International Corp. was purchased by International Paper Co., who had just before acquired Union Camp Corp. Fort James Corp. became the target of an acquisition by Georgia Pacific Corp., who maintained their membership in FY2001, but announced late in the year that their tree improvement assets would be offered for sale. Two other members were targets of proposed acquisitions that were still pending at the time of writing: Plum Creek has announced plans to purchase The Timber Company, and Bowater has announced a planned acquisition of Alliance Forest Products. So, the face of our membership continues to change with head-spinning rapidity! As of May 2001, membership in the Coop stood at 19, with 6 state agencies and 13 private corporations:

Alabama Forestry Commission
Alliance Forest Products Inc.
Bowater, Inc.
Georgia Forestry Commission
Georgia Pacific, Corp.
Gulf-States Paper Corp.
International Paper Company
Joshua Land Management L.L.C.
Mead Coated Board Corp.
N.C. Division of Forest Resources
Rayonier, Inc.
S.C. Commission of Forestry
Smurfit-Stone Container Corp.
Tennessee Forestry Division
Temple Inland Forest, Inc.
The Timber Company
Virginia Department of Forestry
Westvāco Corp.
Weyerhaueser Corp.

PUBLICATIONS OF SPECIAL INTEREST TO MEMBERS

Research and the dissemination of those findings continue to be a critical component of the Cooperative program. Over the past 3 years, program staff members have made a major scholarly contribution in refereed, peer-reviewed journals (17 articles) as well as in conference proceedings and other technical publications (20 papers). The support from Cooperative members allows the staff to maintain the highest scholarship expected of university faculty, while also directing the research effort towards today's questions and tomorrow's challenges.

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Back Cover

A total of 141 3rd-cycle selections were made during the last year. The best individuals from the best full-sibs are what we are after — some are just better than others and deserve that "killer" status. Paul Belonger with The Timber Company was particularly proud of this selection in South Carolina.


KILLER TREE