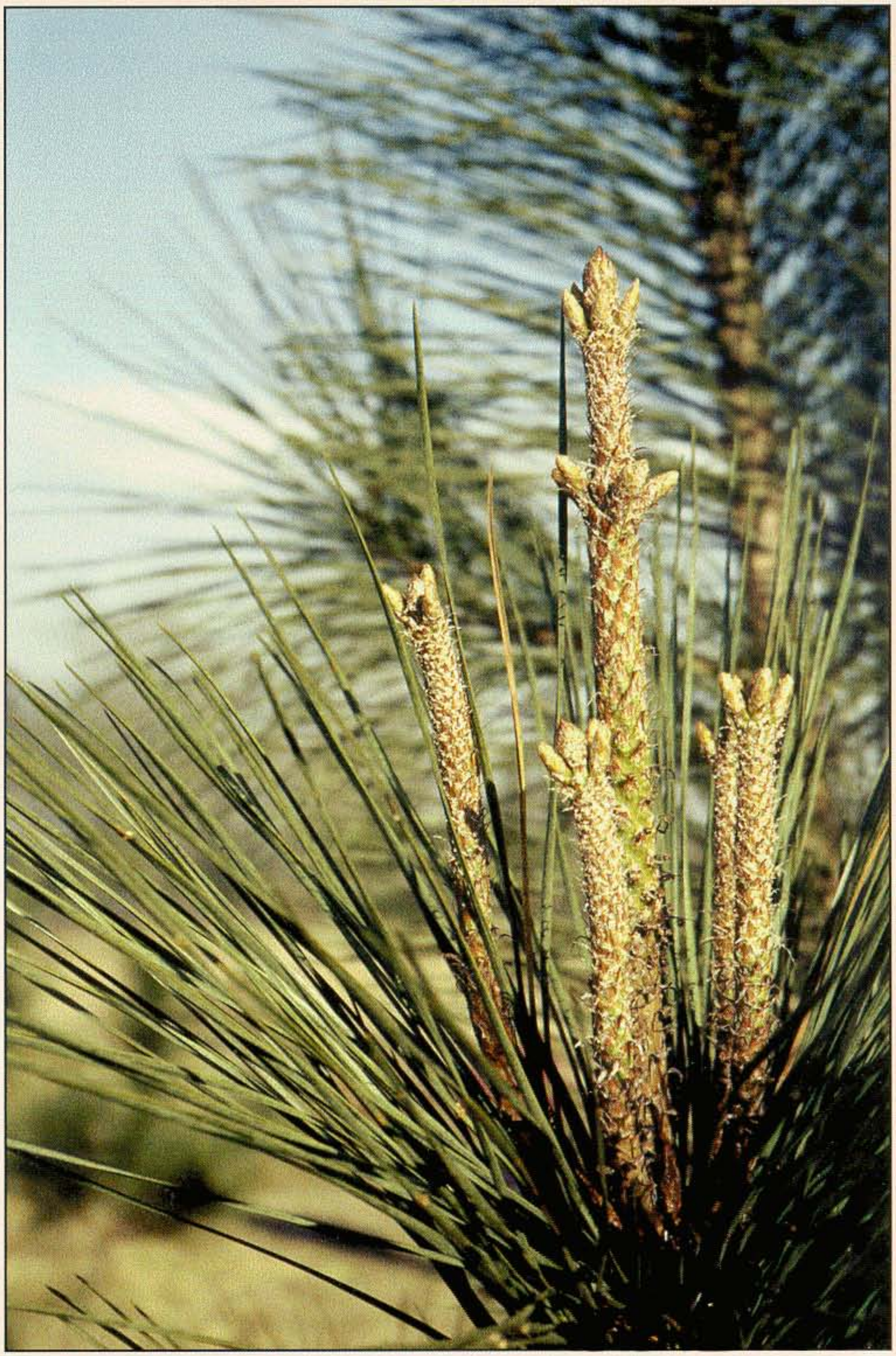
43rd ANNUAL REPORT

NORTH CAROLINA STATE UNIVERSITY - INDUSTRY COOPERATIVE TREE IMPROVEMENT PROGRAM



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Raleigh, North Carolina

1999

EXECUTIVE SUMMARY

REPORTS OF RESEARCH:

Analysis of Early Diallel Measurement Studies in one Cooperative breeding region indicates that selection for age-8 volume is more efficient using height or volume at earlier ages.

Research to develop an analytical model for choosing clones for a seed orchard showed that group merit selection could be used to maximize gain in orchards by balancing relatedness and genetic value.

An evaluation of coastal and piedmont sources of loblolly and their hybrids for growth and cold hardiness showed coastal x piedmont hybrids grew as well as pure coastal; and piedmont x coastal had superior height growth to pure piedmont. Differences in cold hardiness showed pure coastal sustaining more injury than the hybrids while the pure piedmont had the least injury.

Research shows that, while fertilization lowers wood density, the effect on overall wood production is more than offset by the increase in growth.

Results of a seed source study in region 1 showed Virginia, North Carolina and South Carolina provenances were essentially equal for growth with a slight advantage for straightness in the Virginia source.

BREEDING, TESTING AND SELECTION:

To date, members have collected data and screened candidates for the third-cycle in over 512 of the 1278 progeny tests. In 1998, candidates were screened in 200 tests and 149 new third-cycle selections were identified.

Research continued into utilizing topgrafting in the crowns of sexually mature ramets for stimulating both male and female flowers.

SEED ORCHARD PRODUCTION:

Coastal loblolly accounted for 67% of the cone collection in 1998. Of the seed collected in 1998, 56% was from second generation orchards.

Breeding values distributed to members in 1998 are useful for roguing second generation orchards, identifying half-sib families in second-generation orchards for deployment, selecting half-sib families for third-cycle orchards and selecting full-sib families for mass control-pollination programs and vegetative propagation programs.

ASSOCIATED ACTIVITIES:

The Cooperative has ten graduate students working on degrees and conducting research in support of the activities of the Cooperative.

The Tennessee Department of Agriculture, Forestry Division joined the Cooperative in January.

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INTRODUCTION

The North Carolina State University – Industry Cooperative Tree Improvement Program has completed 43-years of continuous operation. Our mission: "To Economically Increase Forest Productivity Through Genetic Manipulation of Pine Populations" encompasses both forest genetics research and development of genetic resources for use in intensive forest management programs. We have realized a very successful and productive year. Highlights of the activities and accomplishments of our 43rd year are presented in this annual progress report.

The recent technical accomplishment of the Cooperative has been outstanding. We have estimates of gain from rogued second-generation seed orchards that range from 14% to 23% over and above the gain from rogued first-generation seed orchards. Initial breeding values for parents mated in diallels and tested in the 2nd cycle of progeny tests are available and additional breeding value information is being developed each year as new progeny data are collected and analyzed. A Cooperative database system has been developed and is being distributed to members on CD-ROM along with comprehensive documentation. Essentially all the information ever developed from the Cooperative's selection, breeding, and testing investment is in an easily accessible format for use by program members. New 3rd cycle seed orchards are being established that are projected to provide genetic gain substantially above the gain realized from second-generation orchards. Additional 3rd cycle selections are being graded and accepted into the program each year. Breeding plans are being finalized, that when implemented, will provide the foundation genetic resources for the 4th cycle of improvement. Research on top grafting is providing a method to cost effectively and rapidly accelerate the breeding work for the next cycle of improvement. A three-year Department of Energy Grant for more than $420,000 has been received to support The Search for Major Genes research project and numerous other research initiatives are providing information that may be useful to future tree improvement.

Despite this record of accomplishment we are being challenged by the most disruptive changes in membership in the 43-year history of the Cooperative. Mergers among industrial members are occurring frequently, with a commensurate loss of program financial resources. This has been offset to an extent by recruitment of new members, the most recent being the addition of the Tennessee Department of Agriculture, Division of Forestry, in January 1999. Additionally, several industrial members have announced intentions to sell all or a major portion of their southeastern timberlands, which complicates the completion of cooperative genetic resource development work. In short the wood using industry continues to consolidate and the ownership, control, and management of commercial forestland is increasingly being transferred to financial institutions and investment groups. The challenge of sustaining the program's effectiveness into the 21st century is substantial.

Through strong research and efficient development and deployment of superior genetic resources, we must and will find a way to realize the enormous potential of genetic improvement of loblolly pine, the most widely planted tree species in the United States.

RESEARCH

Genetic Parameters and Selection Efficiency Estimated from the Early Diallel Measurement Study

The analysis of data from first generation tests provided time trends in genetic parameters and suggested that height measured at age 6 and selection one year later would maximize gains per year (McKeand 1988, Balocchi et al. 1993). Annual data from well-balanced second-generation genetic tests established with crosses from a disconnected diallel mating design can be used to estimate genetic parameters through age eight more accurately and precisely. With better estimates of parameters over time, selection efficiency can be evaluated for different selection methods to get maximum genetic gain per unit of time.

Four test series from the Early Diallel Measurement Study (EDMS) from Virginia (region 1) were used for this analysis. Each test series included 4 tests (2 tests in 2 locations in each of 2 years). In each test, 30 crosses from two disconnected six-parent half-diallels were planted with 4 check seedlots. The experimental design was a randomized complete block with 6 replications and 6-tree row plots (Li et al. 1996). Trees were measured annually for height starting at age 1 and for DBH starting at age 4. Both traits were assessed through age 8.

To evaluate selection efficiency, tree volume at age 8 was used as the selection goal since volume is the most important trait at rotation age. Different selection methods at different ages were evaluated by comparing indirect selection at earlier ages for each trait with direct selection for volume at age 8.

Time Trends In Genetic Parameters

Time trends for genetic parameter estimates for tree height, DBH and volume were found to be similar. Unlike the results from Balocchi (1992), which showed that dominance variance exceeded additive variance at ages before 12, the percentage of dominance variance in the total genetic variance was found to vary from 10% to 40% for all traits, peaking at around age 6 or 7. This trend generally agrees with the results from earlier analysis on similar diallel tests (Li et al., 1996). In all three growth traits, the type B genetic correlation was consistently high across all ages, showing small genetic by environment effect within a test series. Heritability estimates did not vary much with increasing age for any of the three traits. In fact, they were all stable across ages except for a slight increase for broad sense individual heritability and broad sense within full-sib family heritability. The magnitude of family heritabilities always exceeded that of individual heritabilities, which in turn was larger than within family heritabilities.

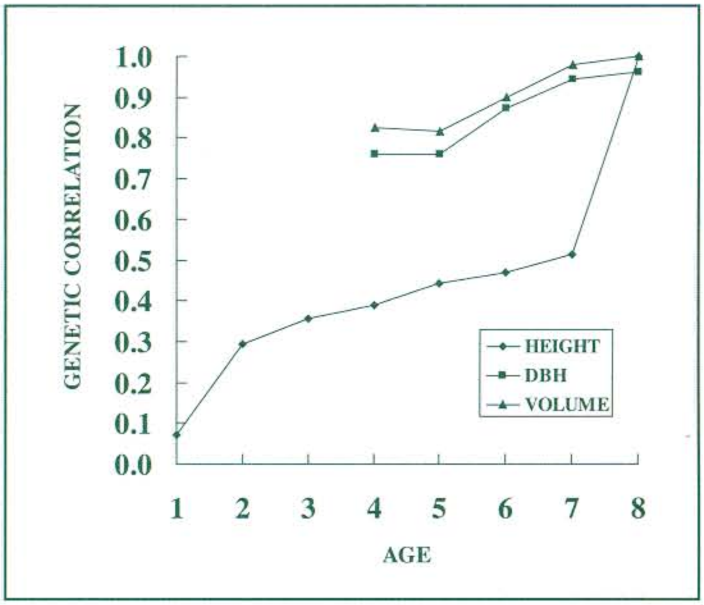


Figure 1. Genetic correlations between height, diameter, and volume at early ages and age-8 volume.

Age-Age Genetic Correlations

For tree height, the genetic correlation with 8-year height increased rapidly from age 1 to age 4. At age 4, the correlation exceeded 0.8. The age-age genetic correlation of DBH and volume was also high from age 4 to age7, though a bit lower than that for height. However, for predicting tree volume at age 8, DBH and volume had a higher correlation than height (Figure 1). These results indicate that selecting on height alone will not achieve maximum genetic gain for volume. DBH and volume must be considered to achieve maximum genetic gain.

Selection Efficiency

For indirect selection for tree height, the percent genetic gain was relatively low for all ages because of the relatively low genetic correlation between height and volume (Table 1). Even full-sib selection based on 8-year height only produced 50.6% of the gain possible from direct full-sib selection on 8-year volume. This was expected because of a low genetic correlation between height and volume. Among three selection methods, the combined selection of among full-sib families and within family resulted in the most genetic gain. Genetic gain from within family selection generally accounted for only half as much genetic gain as that from among family selection. This results from the fact that combined selection gives more weight to family deviation than to within family deviation.

Selection efficiencies for 8-year volume (gain per year), estimated as the ratio of the correlated gain per year expected from early height selection to the

Table 1. Results of indirect selections for 8-year volume based on early tree height (age 1-8) for within family selection (I=2.665), family selection (I=1.775) and combined selection of family and within family compared to direct full-sib family selection on age-8 volume.

	Genetic gain % (CG/G)			Selection efficiency (Q)		
Age	**FS family**	**Within family**	**Combined**	**FS family**	**Within family**	**Combined**
1	6.9%	2.7%	9.6%	55.4%	21.5%	76.9%
2	29.2%	13.2%	42.3%	116.6%	52.7%	169.3%
3	36.3%	16.9%	53.2%	96.8%	45.1%	142.0%
4	39.3%	19.0%	58.4%	78.7%	38.1%	116.7%
5	43.8%	21.9%	65.7%	70.0%	35.1%	105.1%
6	44.8%	22.6%	67.4%	59.7%	30.1%	89.8%
7	48.7%	25.0%	73.8%	55.7%	28.6%	84.3%
8	50.6%	25.2%	75.8%	50.6%	25.2%	75.8%

Table 2. Results of indirect selection for 8-year volume based on early tree volume (ages 4-8) for within family selection (I=2.665), family selection (I=1.775) and combined family and within family selection compared to direct full-sib family selection on year-8 volume.

	Genetic gain % (CG/G)			Selection efficiency (Q)		
Age	FS family	Within family	Combined	FS family	Within family	Combined
4	84.4%	41.9%	126.4%	168.9%	83.8%	252.7%
5	81.0%	38.3%	119.3%	129.6%	61.2%	190.8%
6	88.0%	44.2%	132.2%	117.3%	59.0%	176.3%
7	95.8%	50.2%	146.0%	109.5%	57.4%	166.9%
8	100%	53.4%	153.4%	100%	53.4%	153.4%

gain per year expected from direct selection of 8-year volume, showed 2-year height to be the most efficient age for selection in terms of genetic gain per year (Table 1). Efficiency values above 100% indicate that early selection based on height was more efficient than direct selection for volume at age 8 for genetic gain per year.

For indirect selection using juvenile volume, genetic gain was higher for all ages before year 8 in terms of absolute value (Table 2). This indicates that selection on volume at age 4 (the earliest estimate of volume), or perhaps even earlier, would provide good genetic gain for age 8 volume. Considering time, age 4 was the most efficient year for selection (253% for combined selection).

Two Stage Selection

Two-stage selection is of particular interest in a breeding program because it would allow selections to be established in breeding orchards at relatively

Table 3. Results of two stage family selection with the first selection on height and volume at 1-7 years of age followed by a second stage of selection based on age 8 volume. Shown are the family rank correlations between the two stages and the percentage of final selection gain obtained at the first stage of selection.

First stage selection age	2	3	4	5	6	7
Height –family rank correlation of two stages	.51	.70	.75	.78	.79	.79
Height –gain as % final selection	92%	95%	93%	99%	99%	99%
Volume- family rank correlation of two stages	-	-	.85	.90	.95	.98
Volume –gain as % final selection	-	-	100%	100%	100%	100%

young ages, providing adequate scion supply for orchard establishment when the final selections are identified and providing sufficient flowers to commence breeding immediately.

To investigate this selection strategy, five full-sib families within each test series were selected from the total of 30 families by first selecting 10 families at an early age and then selecting the final 5 families based on age 8 volume. Selection criterion was the breeding values (estimated with the BLUP) of full-sib families for either height or volume at the first stage and 8-year volume at the second stage. Selection strategies were compared based on genetic gain in age 8 volume. Results were averaged across 4 test series and are shown, together with the rank correlation between the selection criteria and breeding values for 8-year volume, in Table 3. Genetic gain was very comparable between one stage and two-stage selection, whether using early height or volume in stage one. Even using height at age 2, first stage selection was very efficient with genetic gain equal to 92% of that from direct selection at age 8. All of the final 5 families were selected correctly in the first stage when the criteria was early volume starting at age 4, and genetic gain was 100% of that achieved by direct selection on year 8 volume. Two-stage selection was very effective in this example, partly due to the fact that the rank correlation is higher than the true genetic correlation and also because the second stage selection secures good genetic return.

Maximize Seed Orchard Gain by Balancing Breeding Value and Relatedness of Selected Clones

Second-generation seed orchards of loblolly pine are now producing more than 50% of the total seed harvest in the Cooperative with substantial gain in rotation volume over 1st-generation seed orchards. Genetic roguing, based on progeny test data, can further increase gain in these seed orchards, but because each orchard does not include all of the good clones, the increase in gain from roguing would be limited. If the best 30% of the parents, based on breeding values from open pollinated progeny tests, were used to establish a new seed orchard, additional gain over unrogued 2nd-generation seed orchards (Li at al. 1999) would be available. This assumes that the top 30% of the clones are not related and thus no inbreeding depression would occur among these top ranked clones. In reality, there is considerable relatedness among the top ranked clones in this population.

It is generally well known that mating of related individuals results in inbreeding depression for growth for most outcrossing species. It has been reported that inbreeding in loblolly pine results in a height reduction of 4-5% per 0.1 increase in the inbreeding coefficient (Annual Report, 1998). Traditionally, to avoid related mating and inbreeding depression in a seed orchard, the number of related clones used for seed orchard establishment has been restricted to a number that would allow them to be spatially separated in the orchard. As tree breeding programs move into advanced generations, the number of related families will increase. Breeders are thus faced with a dilemma. Would the use of related selections in a seed orchard result in substantial genetic gain or in an intolerable amount of inbreeding depression? When establishing advanced generation seed orchards, a critical question is how to maximize seed orchard gains by balancing breeding values and relatedness of selected clones. The goal of this study was to develop an analytical model for choosing clones for a seed orchard considering both relatedness and the effects of the subsequent inbreeding so that the predicted genetic gain would be optimized.

Breeding values from open-pollinated progeny tests of 2nd-generation seed orchards in the Atlantic Coastal region were used for this study. Using parental breeding values for height, the top 50 clones with known pedigree were used for the genetic gain evaluations. It was assumed that mating in seed orchards is random, except selfing was disregarded (or considered constant under the conditions of this study). The selected clones were equally represented in the seed orchard.

When a fixed number of clones are chosen for a seed orchard, the expected gain for the orchard can be estimated as the average breeding value of the selected clones minus the inbreeding depression from the mating of related clones (penalty) times the group inbreeding coefficient. If the clones are completely unrelated, then genetic gain is equal to the average breeding value of the selected clones. Inbreeding depression in loblolly pine has been found to be proportional to the inbreeding coefficient and has been estimated as 4% in height reduction for each 0.1 increase in the inbreeding coefficient. The penalty factor is determined based on inbreeding depression, i.e., the amount of reduction in genetic gain when the materials are totally inbred. The penalty factor for an average loblolly pine population would be about 40% for height breeding value. If all clones contribute equally as mating partners to all other clones, the average coancestry among the clones will be the inbreeding coefficient of their seed.

Following modified algorithms by Lindgren & Mullin (1998), the genetic value, or what is referred to as group merit (GM), for a seed orchard of fixed size with a particular penalty factor for inbreeding can be calculated as: $GM = \overline{BV} - c\bar{f}$ where $\overline{BV}$ is the average breeding value of the group, $\bar{f}$ is the group coancestry without considering selfing, and c is the penalty factor, which measures the loss of genetic gain when the group is totally inbreed. Three levels of penalty factors, 0%, 40% and 80%, which represent no inbreeding depression, and a 4% and 8% reduction in height respectively, were used to examine the effects of inbreeding on the genetic value for group merit selection.

Genetic diversity of the selected clones can be calculated as the status number from information on group coancestry (Lindgren and Mullin,1997). The status number describes the population based on the actual gene pool and reflects the number of unrelated and non-inbred individuals. For a given number of selected clones, the genetic values for Group Merit selection were calculated using the three different levels of penalty factors (0, 40 and 80%). These values were compared with those from traditional restricted selection (RS), i.e., parent restricted selection in which a single individual from a given parent was allowed to be included in the group. A computer program was developed to calculate genetic gains from Group Merit and restricted selection.

Table 4. Expected gains from restricted selection (RS) and group merit (GM) selection with three penalty factors (0, 40, 80). The number of clones selected ranged from 2 to 20 from a deployment population of 50.

No of Selections	RS	GM		
		0	40	80
2	28.10	28.65	28.10	28.10
4	24.01	26.99	25.48	24.65
6	21.39	24.64	23.64	22.64
8	19.96	22.51	21.97	21.44
10	18.94	21.20	20.10	20.48
12	18.21	20.22	19.91	19.65
14	17.57	19.45	19.18	18.97
16	16.93	18.84	18.58	18.37
18	16.39	18.30	18.01	17.81
20	15.80	17.76	17.48	17.27

Genetic gains were greater from Group Merit selection than from the restricted selection of one clone per parent at all penalty levels (Table 4). The difference was smaller at the high penalty level of 80% than at the low penalty level of 40%. The difference in Group Merit selection with different penalties was due to different inbreeding levels of related clones in the selection group. In general, the effect of inbreeding decreased with increasing census number and penalty factors.

Table 5. Selection of the 20 best clones using restricted selection (one clone per parent, RS) and group merit selection (GM) with penalties of 40% and 80%. Clones are sorted by breeding value (percent gain) for tree height for a deployment population of 50 clones. Selected individuals for each set are marked by "x"

Clone ID	Parent 1 ID	Parent 2 ID	Breeding Values	RS	GM 40	GM 80
1	A	B	30.44	x	x	x
2	C	B	26.86		x	x
3	D	A	25.76	x	x	x
4	E	B	24.90		x	x
5	F	G	22.19	x	x	x
6	H	I	17.67	x	x	x
7	-	-	16.25	x	x	x
8	J	-	16.01	x	x	x
9	K	L	15.96	x	x	x
10	M	I	15.92		x	x
11	-	-	15.42	x	x	x
12	N	B	15.22		x	
13	P	R	15.18	x	x	x
14	-	-	14.56	x	x	x
15	S	T	14.54	x	x	x
16	-	-	14.51	x	x	x
17	C	U	14.43	x	x	x
18	C	L	13.55			
19	-	-	13.10	x	x	x
20	-	-	12.80	x	x	x
21	C	V	12.60			
22	W	-	12.14	x	x	x
23	-	-	12.10	x		x
24	M	-	12.01	x		
25	X	M	11.33			
26	H	Y	10.86			
27	-	-	10.53	x		
28	-	-	10.43	x		
Group coancestry				**0.025**	**0.03**	**0.028**
Group inbreeding				**0.5**	**0.5**	**0.5**
Average cross coancestry				**0**	**0.005**	**0.003**
Genetic value of seed orchard				**15.80**	**17.48**	**17.26**
Average breeding value				**15.80**	**17.69**	**17.54**
Number of clones selected				**20**	**20**	**20**
Number of parents				**40**	**35**	**36**
Status number				**20**	**16.7**	**17.8**

The increase in inbreeding was reflected in the reduction of status number using Group Merit selections (Table 5). The status numbers using restricted selection of one selection per parent was equal to the census number, while group merit selection reduced the status numbers to 17 and 18 respectively for penalty levels of 40% and 80%. This reduction is relatively small and may be acceptable for a loblolly pine seed orchard. To compare genetic gains at the same diversity levels, genetic gain was plotted against the status number (Figure 2). Even after adjusting the gains by the slightly reduced status numbers, genetic gain from group merit selection was consistently higher at a given status number than that from restricted selection.

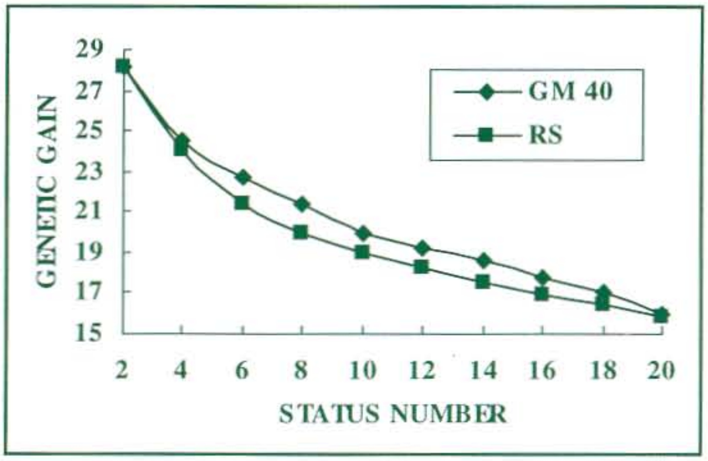


Figure 2. Genetic gains adjusted for inbreeding effect, i.e., at the same status levels for restricted selection (one clone per parent, RS) and group merit selection with the penalty 40% (GM 40) from a loblolly pine deployment population of 50 clones.

The results from this study support the use of the group merit selection model to maximize gain in a seed orchard by balancing relatedness and genetic value. The increase in genetic gain is substantial even after adjusting for the inbreeding effect. The use of related but highly ranked clones in a seed orchard should result in greater genetic gain from loblolly pine seed orchards.

Evaluation of Coastal and Piedmont Sources of Loblolly Pine Seedlings and their Hybrids for Growth and Cold Hardiness

Hybridization between diverse provenances of forest trees may provide opportunities to combine the desirable growth and adaptive traits of the parental populations. Hybrids between Atlantic Coastal and Piedmont sources of loblolly pine have the potential to combine the faster growth of the Coastal source with the cold hardiness and straightness of the Piedmont source. An elite breeding program has been developed to integrate loblolly pine sources of Atlantic Coastal with Piedmont for planting in Piedmont regions. As part of this breeding program, a study with seedlings was conducted to examine the early growth of Coastal, Piedmont, and Coastal x Piedmont hybrids in an outdoor environment and to examine their cold hardiness in controlled environments.

Twenty clones from the Piedmont region of GA, SC and NC and 20 clones from the Coastal Plains of NC and SC were used as female parents for polycrosses. Pollen from 20-30 average clones of Piedmont and Coastal sources was collected and bulked to form pollen mixes for the Piedmont and Coastal Plain. With these two pollen mixes, twenty polycross families were generated for each of the two hybrid combinations, i.e., Piedmont x Coastal and Coastal x Piedmont. Long-term field tests have been established in each of four regions 1) Fall Line, 2) Central Piedmont, 3) Inland or Northern Piedmont, and 4) Cold Areas.

Using the same genetic material, seedlings of 59 polycross families representing 4 populations, the Atlantic Coastal Plain (C x C), Piedmont (P x P), Piedmont x Coastal (P x C), and Coastal x Piedmont (C x P) were used in this study. An unimproved check from the Piedmont region of GA and SC were also included in the study. Seed was sown in a greenhouse and transplanted into big pots, and seedlings were then grown outside in Raleigh, NC using a randomized complete block design with 10 blocks in single tree plots per set. Height was measured from the soil line to the top of the terminal shoot at three-week intervals. Root collar diameter was measured at the soil line at 6-week intervals. Volume index was calculated as the product of height and diameter squared. Budset was estimated retrospectively for the last three measuring periods.

A subset of the loblolly pine seedlings from the growth study was used for examination of cold hardiness. The preconditioning treatments consisted of three acclimation regimes designed to reflect climatic conditions in three of the four deployment regions: fall Line, middle Piedmont and cold areas. Seedlings were acclimated for six-weeks in a phytotron with a 9 hour photoperiod for all three treatments and then subjected to a freezing treatment with temperature drop at a rate of 3-5°C per hour until the target -15°C was reached. Seedlings were maintained at the target temperature for 3 hours, before removal to a walk-in cooler to thaw at 4.5°C for 24 hours. After thawing, seedlings were removed to an outdoor facility for symptoms to develop.

Freezing injury of the entire seedling, measured as percent dead foliage, was subjectively scored on

Table 6. Population means for the Coastal(C x C), Coastal x Piedmont(C x P), Piedmont x Coastal(P x C), and Piedmont (P x P) populations for total stem height, root collar diameter, volume index, injury I percent, injury II percent, and percent mortality.*

Population	Total Ht(cm)	Diameter(mm)	Volume(cm^3)	Injury I(%)	Injury II(%)	Mortality(%)
C x C	59.3 a	6.6 a	25.57 a	65.8 a	66.3 a	50.2 a
C x P	57.6 ab	6.7 a	24.87 a	55.5 b	71.7 a	57.3 a
P x C	55.6 bc	6.7 a	24.66 a	41.0 c	52.2 b	31.2 b
P x P	53.1 c	6.7 a	23.82 ab	39.7 c	51.3 b	32.5 b
Checklot	50.1 d	6.6 a	21.48 b	67.9 a	58.8 a	58.8 a

**Differences followed by the same letter are not significantly different*

a scale of 0-100% in increments of 10, with 0 indicating little or no foliar browning, and 100 indicating all foliage brown. A second injury of browning assessment was made after the trees began flushing.

Growth Differences

The Coastal x Piedmont hybrids (C x P) grew as well as the pure Coastal loblolly source, and the Piedmont x Coastal (P x C) hybrids were taller than the pure Piedmont population (Table 6). The hybrid populations exhibited heterosis, defined in this instance as superiority over the pure Piedmont source; they were 4-10% taller than the Piedmont population. The difference in root collar diameter among populations was small, and the differences in volume index were mainly due to seedling height differences. There seems to be an advantage for early seedling height growth in having at least one parent from the Coastal plain. These early results for seedling growth are similar to results of other studies where Atlantic Coastal Plain loblolly has exhibited superior height growth.

The growth difference between pure Coastal and pure Piedmont seedlings was expected since these seedlings were grown in an outdoor environment at a Piedmont site. Coastal loblolly pine populations were found to be less responsive to changing environmental conditions (e.g. decreasing photoperiod) than more inland sources of loblolly pine. This is probably due to adaptive strategies; trees from the Piedmont must enter dormancy sooner than Coastal families to ensure that they are hardy for the fall. Evidence of this is supported by the fact that the Piedmont families set buds sooner than the other improved sources. (Figure 3).

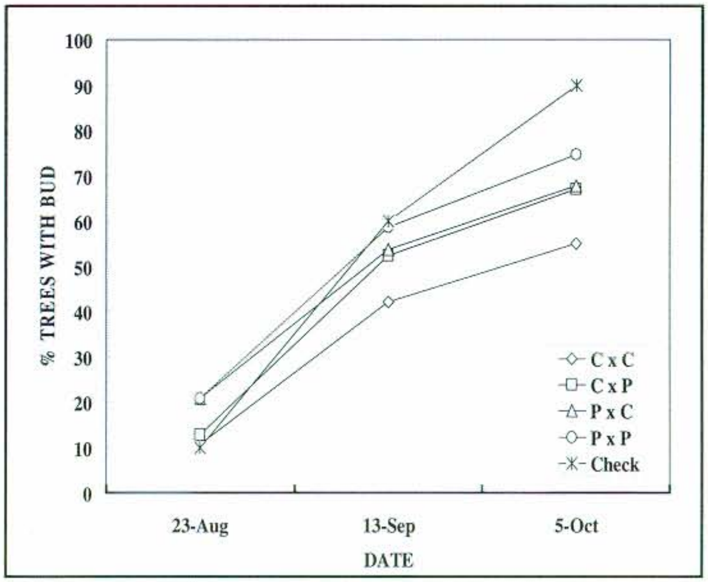


Figure 3. Mean bud set of pure Atlantic Coastal (C x P), Piedmont (P x P) loblolly pine seedlings and their hybrids (C x P and P x C) and unimproved checklot for each measuring date.

Superior height growth may be related to longer growing season. Typically, more inland sources of loblolly have a shorter growing season than Coastal sources. Loblolly pine from coastal North and South Carolina has about 225-270 frost-free days; western Kentucky (although outside the natural range, loblolly pine is deployed there) has a freeze-free period of about 180 days, while the Fall Line in Georgia has about 230 frost free days. Thus, Coastal sources of loblolly have adapted to receiving 40 to 90 more growing days than more inland sources.

Timing of bud set may explain the height differences between the pure Coastal and the pure Piedmont populations, but does not explain the difference in height growth between the two hybrid populations. The differences in height between the C x P and P x C populations appear to be due to variation in flush length. The C x P population may be growing more or longer stem units than the P x C population. Both the C x P and P x C populations had a significant height advantage over the P x P population.

Cold Hardiness Differences

Preconditioning treatments had no significant effects on cold hardiness of the seedlings, indicating that freezing injury would be the same regardless of preconditioning regimes. The implication is that a single preconditioning treatment could be applied to all families regardless of origin.

Differences in cold hardiness were as expected with C x C sustaining more injury than the hybrids of C x P and P x C and the Piedmont source sustaining the least injury (Table 6). The seedlings with a Piedmont maternal parent had increased hardiness (less injury) and higher survival relative to the three other populations. All the families in the bottom third for injury (e.g. most injured) had a Coastal parent. The greater cold hardiness of the P x C hybrids relative to C x P crosses could be reflective of maternal effects impacting growth and bud set (Figure 4). Trees that had set a terminal bud tended to be less injured than trees that had not set a terminal bud.

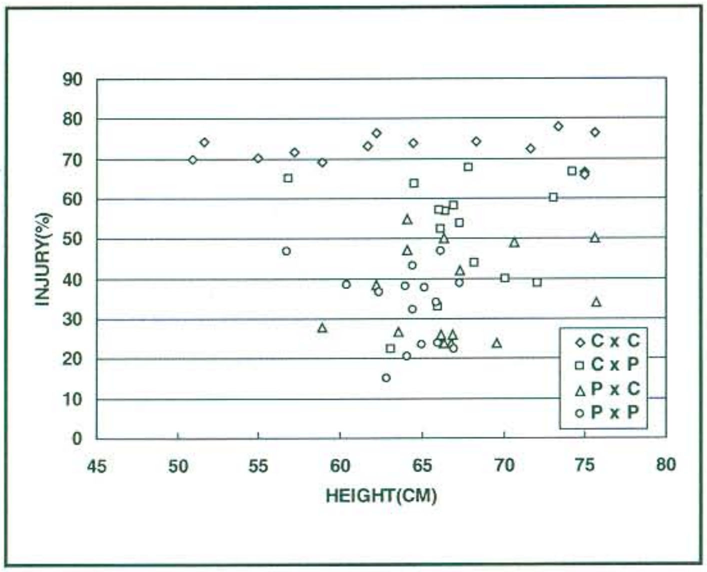


Figure 4. Plot of mean Injury I (% foliar brown) vs. height before treatment of Atlantic Coastal (C x C), Piedmont (P x P) loblolly pine seedlings and their hybrids (C x P and P x C).

In general, there was a slightly negative correlation between height and cold injury, but it was not statistically significant. It appears that intraspecific hybridization between the two sources of loblolly pine can provide taller trees similar to Coastal parents and with cold hardiness similar to the Piedmont parents. There could be an advantage to deploying Piedmont x Coastal hybrids on the more adverse (e.g. colder Piedmont, cold area) sites and deploying Coastal x Piedmont or hardy Coastal families on the milder sites.

The Effects of Fertilization and Irrigation on Wood Quality of Loblolly Pine

While numerous studies have reported the effect of water and nutrient availability on growth and specific gravity of southern pines, results are to some extent conflicting. To better understand how irrigation and fertilization affect wood properties of loblolly pine, John Mann (a Masters student in forestry) examined the affect of irrigation and fertilization on radial growth, the transition date (between earlywood and latewood), the proportion of earlywood and latewood formed in each annual ring, the specific gravity of each annual ring, and the dry weight of wood produced in an eight foot basal stem section.

The Southeast Tree Research and Education Site (SETRES) located in Scotland County, North Carolina was used for the study. The study was established in 1992 on a site with limited nutrient availability, low water holding capacity and an eight-year old loblolly pine stand. A randomized complete block 2 x 2 factorial treatment design replicated 4 times was installed in the loblolly stand during the spring of 1992. Fertilization treatments began in the spring of 1992 and irrigation treatments began in the spring of 1993. Irrigation was applied to maintain full field capacity in the top 50cm of soil, while the nutrient application was targeted to maintain foliar nitrogen concentration at 1.4% (optimal) while applying other major and minor elements to achieve proper ratios for balanced nutrition.

Wood cores were taken and analyzed using a direct scanning X-ray densitometer to provide average density and width of three successive annual rings as well as the earlywood and latewood fractions of each respective annual ring. Dendrometer bands were placed on randomly selected trees within each treatment plot (25 trees/plot) at breast height for one growing season. Band readings were recorded weekly through August and bi-weekly beginning in September until cessation of radial growth occurred. Following cessation of radial growth, twenty of the 25 banded trees were bored from bark to bark with a 12-millimeter increment borer. The band readings, along with the densitometer analysis, were used to determine the treatment effect on the transition date between earlywood and latewood. The volume response was integrated with the specific gravity estimates to determine the amount (dry weight in pounds) of wood assimilated for the basal stem section (8 feet) during the 1996 growing year.

The irrigation and fertilization treatment effects on the transition date between earlywood and latewood formation were significant (Figure 5). The fertilization treatment moved the transition date 16 days later than the control, while the irrigation treatment moved the date 7 days earlier. The combined treatments (fertilization + irrigation) resulted in the transition date occurring 7 days later than the control.

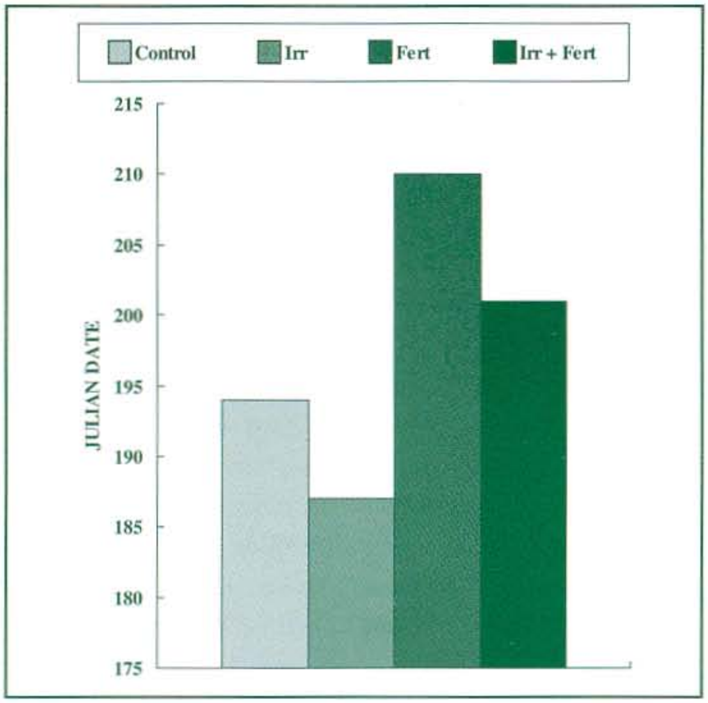


Figure 5. Effect of irrigation and fertilization treatments on transition date from earlywood to latewood.

The results for the irrigation treatment were not consistent with most of the literature which associated moisture stress with an earlier transition date. This study showed the opposite effect. Despite the earlywood-latewood transition occurring one week earlier in the irrigation blocks, there was no significant or direct increase in the amount of latewood grown and no significant effect on earlywood or latewood specific gravity and therefore no effect on the whole ring specific gravity. Other studies conducted at this site indicate that it may not be as severely moisture stressed as first indicated. Soil moisture levels, even on this deep sand series, may have been sufficient during the juvenile period of the stand's development to result in the irrigation treatments not showing any significant effect on specific gravity.

The response to the fertilization treatment delayed the transition date over two weeks. Fertilization treatments were associated with a 12 % decrease in latewood percent in the 1994 and 1995 growing season, but had no effect on latewood percent for the 1996 growing year. The stand was transitioning from juvenile to mature wood during the study and this may have played a role in the fertilization treatment not effecting the 1996 latewood percent, even though the fertilization treatment delayed the transition date by two weeks.

The fertilization treatments had a significant impact on earlywood, latewood, and whole ring specific gravity. The fertilization treatment resulted in lower earlywood specific gravity, by 1% in 1994, 5% in 1995, and 3% in 1996, and lower latewood specific gravity, by 10% in 1994, 3% in 1995, and 9% in 1996. As expected, with the decrease in the earlywood and latewood specific gravity, the whole ring specific gravity was decreased by 10% in 1994, 8% in 1995, and 7% in 1996 (Figure 6).

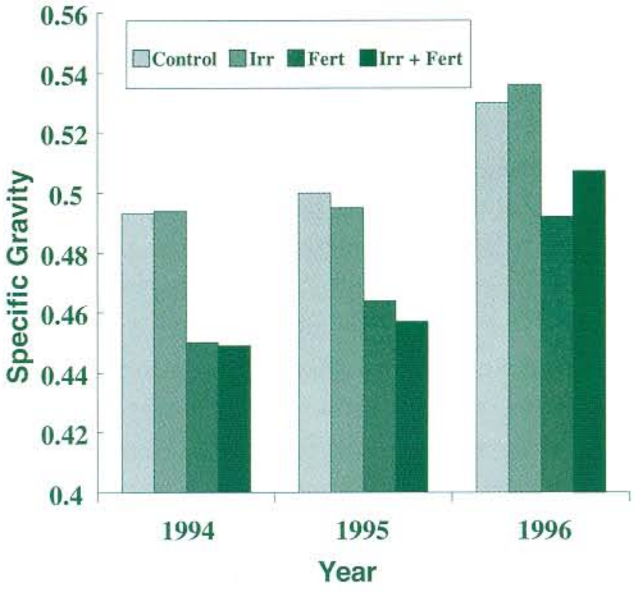


Figure 6. Effect of treatments on whole ring specific gravity.

In summary, fertilization was associated with a significant adverse impact on wood density. Fertilization treatments lowered the average specific gravity by 7.5% over the 3 years of the study. This was principally due to fertilization decreasing the specific gravity of the latewood by an average of 7% and also reducing the amount of latewood by an average of 7%.

It was subsequently of interest to determine if the increase in diameter growth associated with the fertilization treatment was sufficient to offset the loss in specific gravity. To determine this, an estimate of the dry weight (pounds) of wood produced in the bottom eight feet of the stem was made for the three years evaluated. This was done using breast height (4.5') as the center measurement for an eight-foot bolt length. In other words the 8-foot long bolt extended 4 feet above breast height and 4 feet below. An assumption was made that this bolt approximated a cylinder whereby the taper from 4 feet below breast height was equivalent to and offset the taper to 4 feet above. In a basal 8-foot bolt from trees of the size measured in this study, the assumption is believed to be reasonable.

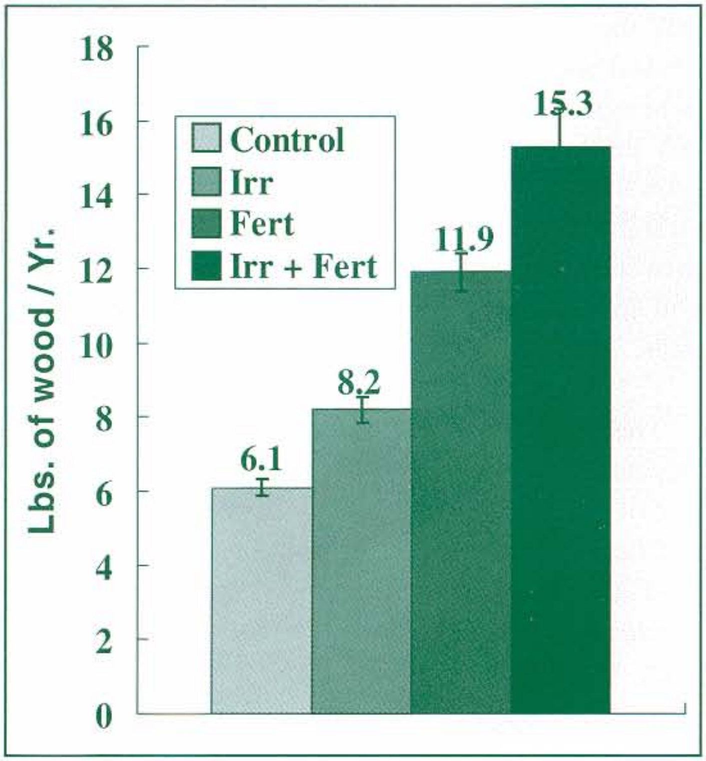


Figure 7. Dry weight of wood grown each season for the bottom eight foot stem section.

The effect of the decrease in specific gravity was minor when compared to the increased growth. The fertilizer treatment nearly doubled the dry weight of wood grown each season for the bottom eight-foot stem section (Figure 7). This indicates that fertilizer treatments can be applied to forest stands without worrying about a negative impact on overall wood production. The tremendous increase in growth more than offsets the decrease in specific gravity. Fertilization on this nutrient poor site can be expected to produce a lot more wood with slightly lower density.

Seed Source Study of Atlantic Coastal Plain Loblolly Pine in Virginia

As cooperators in the northeastern corner of the loblolly pine range begin to establish 3rd-cycle seed orchards, there is a large number of potential selections available from the local breeding region of Coastal and Piedmont Virginia as well as from the northern half of North Carolina (breeding regions 2 and 8). In addition to this large pool of genetic resources at the northern end of the range, more selections exist from further south. The question is how far south can cooperators reach to take advantage of well-documented seed source effects without incurring undue risks in long-term adaptability and stability?

It is generally accepted that seed source movements of 200 miles or less in a northerly direction in the Coastal Plain of the Southeast do not present significant risks. Indeed, most 1.5- and 2.0-generation Coastal loblolly orchards in VA include many parents from the northern half of North Carolina. The growth performance of the NC checklots in the diallel tests has been exceptional and dramatically demonstrates the <u>potential</u> genetic gains achievable from use of southerly seed sources. Results of the Good General Combiner tests have demonstrated that selected families of loblolly pine from coastal South Carolina and northeast coastal Georgia perform very well in many areas of the South. The potential for increased genetic gains would be expanded if the more southerly selections could be used since selection intensity would be increased.

In 1992, Chesapeake Corporation began a series of seed source trials with the following objectives:

- To compare growth and wood properties (not yet assessed) of SC and NC Coastal Plain loblolly pine to local material from Coastal Virginia in side-by-side comparisons in the VA Coastal Plain and Piedmont.
- To examine the stability of families within seed source.

Sixteen open-pollinated seedlots were used for each seed source: SC Coastal, NC Coastal, and VA Coastal. Half-sib family seedlots were collected from 2nd-generation orchards within each provenance to be tested. Three trials were established, two in 1992 (Piedmont and Coastal Plain) and one in 1994 (Eastern Shore). The field design was a randomized complete block with 10 replications per trial. Each replication was a split plot with each of the three sources planted in 100 tree block plots (main plots), with the 16 families/provenance as sub-plots. The measurement plot consisted of the interior 64 seedlings with four individuals from each family randomly located within the measurement plot. The two 1992 tests were measured for height, diameter, and straightness in 1998, and results are presented here.

At age six years, there were no seed source effects for any trait when data were combined across two sites. The average growth (height=16.4'), survival (94%), and uniformity (average Rep x Family CV for height = 6.6%) of the trials were superb. At both sites volume differences among sources were less than 0.05 cubic feet per tree. While the SC coastal source had the lowest mean volume on the piedmont site – the differences were not significant. All three provenances were essentially equal for growth. There was a very slight advantage for straightness in the VA source. For families within provenance, there were large differences for height and straightness, but not for volume across the two sites.

These results are unusual in that provenance effects are typically very large in most trials. This test of seed source and family variation in this more northern natural range of loblolly pine indicates equivalent performance among southern and northern sources. These trials will be followed through at least half rotation to see if these early trends in growth and form are maintained.

Research continues in topgrafting as a method to accelerate male and female flower production for breeding.

BREEDING, TESTING AND SELECTION

Third Generation Selection - A Progress Report

Members of the Cooperative have made a major investment in future forest productivity through their breeding, testing and selection work. Collectively, the Cooperative's members have bred 3,834 plantation and second-generation loblolly pine selections in 639 disconnected 6-parent half-diallels. Over 1,300,000 progeny test seedlings have been grown from 9,585 controlled-pollinations and these seedlings have been planted in 1,278 progeny tests. It has been estimated that this effort represents an investment by the membership of over 35 million dollars during the past 20 years. While this is a substantial investment, the projected value of the "extra" wood to be produced in the resulting managed plantations grown from this genetic material is expected to exceed 2 billion dollars over 20 years. This has clearly been an investment worth making.

To date, members have collected data and screened candidates for selection in over 512 of the 1278 progeny tests established. This work has resulted in 566 third-cycle selections graded for use in the third cycle breeding program. The breeding of these third cycle selections will provide the foundation for the fourth cycle of genetic improvement. During 1998 Cooperative staff working with program members graded 149 new third-cycle selections in 200 individual progeny tests. Third-cycle selection work will continue to be a high priority activity for the next four to five 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.

An outstanding 3rd-cycle selection graded in Kimberly Clark's progeny test near Monroeville, AL.

Accelerating Breeding by Topgrafting In Loblolly Pine

Grafting scions of new selections of loblolly pine (Pinus taeda L.) into the crowns of sexually mature seed orchard ramets has been a very effective tool for stimulating both male and female flowers. Two years after grafting, an average of 9 females per scion was stimulated on the new grafts in the upper crown and 11 pollen clusters per graft in the lower crown. With relatively little effort, breeding could be completed on these selections in only two or three years (Research by Dave Bramlett and Leon Burris). Many members of the Cooperative have experimented with topgrafting, and in general have had success with the methods. The opportunity to shorten the breeding cycle in the third generation to less than five years is a very strong incentive to utilize this technique.

In 1996, a study was initiated at the Smurfit-Stone Container Corporation (S-SCC) Escambia Research Station Seed Orchard in Brewton, AL to evaluate various aspects of topgrafting. The primary objective was to assess the impact of grafting on different seed orchard clones; is there a strong influence of the interstock clone on the number of flowers produced by the topgrafts? In horticultural orchard crops, the influence of rootstocks and interstocks on growth and reproduction is well documented. In general, the influence of rootstock on reproduction has not been great in most forest trees, but little information is available on the influence of interstocks.

The study was conducted in the S-SCC location of the Dwarf Rootstock Study which was grafted in 1988. Six second-generation clones were grafted in that trial. Although rootstock effects were negligible for growth and reproduction (flower counts or cone counts), there were large scion clone differences in the trial. For cone production, the six clones ranged from extremely high to almost sterile over the eight years of assessment.

Topgrafting was carried out over a two-year period. The 1996 study utilized the same six clones in the trial both as topgrafts and interstocks, and clones were grafted in all possible combinations. In 1997, ten third-generation selections from Champion International's breeding program were used as the topgraft clones. Standard dormant-season grafting procedures for loblolly pine were used with a few modifications. Cleft grafts were made in dominant branches in the upper quarter of the crowns. Rather than cover the graft union and scion bud with wax (the standard procedure), prior to grafting, scions were dipped in paraffin at 190∞F to cover the bud. After grafting, the graft union was covered with ParafilmR to prevent dessication.

Each scion clone was grafted into the crown of three different ramets of the six interstock clones. In addition, large seedlings (left in the Rootstock Study to minimize the influence of differential spacing on crown development) were also used as "interstocks". This would allow evaluation of large ungrafted seedlings for topgrafting; i.e., is it necessary to utilize grafted trees? A total of 126 grafts (6 scion clones x 7 interstocks x 3 grafts) were made in 1996, and 210 grafts (10 scion clones x 7 interstocks x 3 grafts) were made in 1997. In addition to the topgrafts, each scion clone was also grafted on to two or three one-year-old rootstocks. Female flower counts were made each spring from 1997 to 1999. The number of male pollen clusters was counted only in 1999.

Flowers were counted on two "check" branches in each crown and were used as ungrafted controls. These counts and the flower and cone counts from the Rootstock Study data were combined into an index of the flowering tendency of each clone. This index of a clone's flowering tendency was then correlated with the clonal means when the clone was used as an interstock.

In both the 1996 and 1997 studies, there were strong topgraft clonal effects and interstock clonal effects for number of flowers. The total number of females over the 2 or 3 years of each study and the number of males in 1999 are presented in Table 7. As in other trials, topgrafting was very effective at stimulating both female and male flowers two and three years after grafting. In the conventional grafts made on young seedlings, there were very few flowers produced. The effect of grafting into crowns of different clones was generally significant and important (Table 7).

While differences exist between the two trials, some general trends are apparent. When used as interstocks, clones 071095, 111154, and 181210 appear to be very effective at stimulating female flowers. Clones 081166 and 111135 tend to be poor clones to use as interstocks, but the effect in the 1997 trial was not as large. The effect on male flowers was not as great as for females; there were no clonal effects in the 1996 trial, and the significant differences in the 1997 trial were not very large. Fortunately, there was no significant interaction between the interstock clonal effect and the topgraft clonal effect for any of the flower counts. Interstocks that are effective at stimulating flowers on one clone tended to be effective at stimulating flowers on all clones.

Although there were strong clonal effects, unfortunately, the flowering tendency of the clone was not related to its flower stimulation capacity as an interstock. This indicates that choosing good flowering clones to use as interstocks will not necessarily result in the best flowering in the topgrafts. Another concern is the impact of the interstock clone on survival. While clone 071095 was very effective at stimulating female flowers, the survival of topgrafts made on ramets of 071095 in the 1997 trial was only 67% compared to ≥80% for all the other clones. While clone 111154 is itself a very poor cone producer, it would be an excellent choice to use as an interstock. Survival of topgrafts on 111154 was 100%, and it was very effective at stimulating female flowers (Table 7).

Although the topgrafts made on the large seedlings did not produce many flowers, there were enough females and males to be useful for breeding. Not all cooperators have excess seed orchards or clone banks that can be used as topgrafting orchards, but existing plantations could be thinned to wide spacings and used as topgrafting orchards in the future.

Table 7. Clonal means for flowering tendency (combination of branch counts in current study and flower and cone counts from the Rootstock Study) and for the number of female and male flowers for each clone when used as an interstock.*

Clone	Flowering Tendency Index	1996 Study Total Number Female (3 yr)	1996 Study # Males in 1999	1997 Study Total Number Females (2 yr)	1997 Study # Males in 1999
071095	177.8	23.7^{ab}	33.9^{a}	29.5^{a}	15.7^{a}
081166	72.0	7.9^{b}	26.0^{a}	13.1^{b}	9.0^{bc}
081218	93.7	24.1^{ab}	29.8^{a}	13.4^{b}	8.3^{bc}
111135	298.1	8.8^{b}	24.9^{a}	14.6^{b}	10.0^{b}
111154	8.7	38.6^{a}	31.3^{a}	16.2^{b}	12.3^{ab}
181210	466.9	38.7^{a}	35.8^{a}	21.1^{ab}	10.6^{b}
Large Seedling	–	18.7^{ab}	20.8^{a}	12.4^{b}	5.1^{c}

**Flower counts within a column followed by the same letter are not significantly different at p≤05.*

SEED ORCHARDS

1998 Seed Orchard Production

The 1998 collection totaled 27.2 tons (see Table 8). As expected the 1998 cone collection was much larger than the 1997 crop of 12.9 tons when many cooperators chose not to collect due to the poor crop. Coastal loblolly made up 67% of the collection with Piedmont loblolly accounting for 33% of the collection. Of the seed collected in 1998, 56% was from second generation orchards. The average yield was 1.22 pounds per bushel, down from last year's figure of 1.35 lbs./bushel. Most organizations collected clonally and as usual there were clones which yielded above 2.0 pounds per bushel. For example, International Paper Co. had 6 clones yielding above 2.0 pounds per bushel with a high of 2.74 pounds per bushel for clone 7-1111.

As for overall orchard production, Table 9 shows the production leaders for 1998. Four orchards topped 2.0 pounds per bushel --- three Champion International orchards in South Carolina and North Carolina Forest Service's 2.0 Piedmont orchard in Goldsboro, North Carolina. The top producing orchard, Champion's 1.5 Alabama Loblolly orchard, yielded 2.65 pounds per bushel. This orchard has always produced well and has produced the three highest yields in Cooperative history. In 1995 it produced a Cooperative record high of 2.95 pounds per bushel and in 1996, 2.66 pounds per bushel. Westvaco also had three orchards in the top ten for 1998. Champion and Westvaco consistently have high yielding orchards due to their superb orchard management programs.

Table 8. Comparison of 1998 and 1997 loblolly seed orchard harvests from Cooperative orchards.

	Bushels of Cones		Pounds of Seed		Pounds of Seed/Bushel of Cone	
Source	**1998**	**1997**	**1998**	**1997**	**1998**	**1997**
Coastal 1.0	13,354	8,541	15,787	11,358	1.18	1.33
Piedmont 1.0	6,636	5,546	8,250	7,895	1.24	1.42
Coastal 2.0	16,947	1,505	20,590	2,019	1.24	1.34
Piedmont 2.0	7,606	3,591	9,482	4,618	1.25	1.29
Totals	**44,543**	**19,183**	**54,469**	**25,890**	**1.22**	**1.35**

Table 9. Top ten production orchards in 1998.

Organization	Orchard Type	Age	Lbs./Bushel	Orchard Manager
Champion, SC	1.5 Alabama	22	2.65	Steve Parker
Champion, SC	2.0 Piedmont	22	2.12	Steve Parker
Champion, SC	Rust Resistant	29	2.00	Steve Parker
NCFS	2.0 Piedmont	18	2.00	Cullen Swain
Westvaco, SC	2.0 Virginia	27	1.90	Dave Gerwig
Westvaco, SC	Central	27	1.84	Dave Gerwig
Rayonier	1.5 Coastal	18	1.75	Early McCall
Union Camp	2.0 Piedmont	16	1.74	George Lowerts
Westvaco, SC	1.0 Coastal	31	1.72	Dave Gerwig
Champion, FL	1.5 Coastal	21	1.72	Donnie Fleming

Use of Breeding Values in Production Populations

Breeding value estimates generated from diallel tests and open-pollinated tests of second-generation seed orchards were distributed to Cooperative members this past year and will be updated annually as additional test data becomes available. Breeding values are expressed as percent genetic gain over wild seed at measurement age-6. The breeding values are useful for ranking parents, roguing second generation seed orchards, identifying half-sib families in second-generation orchards for operational deployment, selecting half-sib families for third-cycle orchards, and for selecting full-sib families for mass control-pollination programs and vegetative propagation programs. The question becomes how and when to use which breeding values to accomplish each task.

Breeding Values and Second-Generation Orchards

Breeding values are useful for roguing second-generation seed orchards and for identifying half-sib families in the orchard for specific deployment goals.

The breeding values from the second-generation open-pollinated tests are the appropriate values for both purposes.

Based on the breeding value, the expected genetic gain for progeny from an open-pollinated family, a group of families, or a particular seed orchard mix can be calculated as one-half the maternal breeding value plus one-half the paternal breeding value, i.e., $\frac{1}{2}\,BV_{female} + \frac{1}{2}\,BV_{male}$. For example, the expected gain from a seed orchard after roguing is the average breeding value of all the clones remaining in the orchard, assuming that all clones in the seed orchard contribute pollen and there is zero pollen contamination. Considering a seed orchard with 15% height gain, the gain from collecting seeds from a mother tree with 25% gain will be 20%, i.e., 1/2(25%)+1/2(15)%.

In an orchard where the number of ramets per parent is quite variable, the average breeding value for the orchard can be adjusted to reflect this imbalance in parental representation by weighting by the number of ramets. Likewise, the average breeding value for the orchard, or for a given half-sib family, can be adjusted by the estimated pollen contamination.

Identifying Selections for Third-Cycle Orchards

Selections for third-cycle seed orchards can come from the second-cycle breeding program, from second-generation selections evaluated in open-pollinated progeny tests of second-generation seed orchards, and from third-cycle selections identified in diallel progeny tests. When selecting parents evaluated in the open-pollinated progeny tests and the diallel tests, it is well to keep in mind the differences in breeding values estimated from the two populations. Those differences are enumerated in Table 10.

Since breeding values are a function of the population evaluated, the breeding values, for the reasons noted above, probably are not equivalent. It is recommended that the majority of the parental selections for third-cycle orchards be made from selections in the breeding program. When using a second-generation parent, whether from the second-generation orchard population or from a second-generation diallel in the breeding program, <u>it is important to verify the parents of the selection to identify possible relatedness problems.</u>

Table 10. Differences in breeding values from diallel tests and 2nd-generation orchard open-pollinated tests.

Diallel Values	Open-Pollinated Values
Are based on 5-crosses	Wind-pollinated from Orchards, thus many parents
True half-sibs	Mix of half-sibs, full-sibs, and selfs
No Contamination	Pollen Contamination
Sampling Error (6-parent diallel)	Sampling Error (Early Seed Collection
Higher Selection Intensity (Have 2nd-gen selections and plantation selections – lots of unrelated selections	Lower Selection Intensity (Only 2nd-gen selections – many of which are related)

It is strongly recommended that third-cycle seed orchards be parental orchards. However, if third-cycle selections are to be included in a third-cycle orchard, they should be restricted to "exceptional" selections. Third generation selections considered for inclusion would be from full-sib families where both parents are of high enough quality that they would have been included in a parental orchard. Offspring selections from such families would have almost no adverse impact on the selection intensity, yet would have the potential for some added gain from within family selection.

Identifying Fullsib Families for Deployment

Many organizations are considering using either mass control-pollinations or vegetative propagation to generate seedlings of fullsib families for deployment. Fullsib families for these programs can be identified by two methods:

By selecting the best parents from the breeding population or second-generation orchard population with the highest mid-parent breeding value. The two parents may or may not have actually been crossed.

By selecting the best fullsib families from the diallel breeding program with the highest breeding values.

In the first method above, the expected genetic gain for two parents that have not been mated before is the average of the two parent's breeding values, if specific combining ability is negligible. For example, the genetic gain from crossing parent A (with GCA of 18%) with parent B (with GCA of 26%) is approximately 22%, i.e., 1/2(18%) +1/2(26)%. Based on the analysis of diallel data, specific combining ability ranges from approximately +8% to -8%. In the second method, the fullsib family or families from the breeding program with the highest breeding values are utilized. With over 9500 crosses made in the breeding program, some extremely good fullsib families exist with known breeding values. It is recommended that selection for fullsib programs be made from these "tested" fullsib families.

Incorporating Genetic Gains Into Financial Analysis

Breeding value estimates in terms of % genetic gain over wild seed at assessment age (6 years) are very useful for ranking parents, roguing seed orchards and identifying families for operational deployments. The ranks of these breeding values will not change even when converted to rotation age volume. However, for financial analysis or for estimating wood production at the rotation age, a more meaningful estimate would be genetic gain at harvest age, say 25. There are a couple of alternatives that can be used to translate age-6 height or volume gains into harvest age volume gains but each has an important shortcoming.

One alternative is to use the height gain estimates provided as an estimate of the juvenile difference in height - age or site index at (age 10 to 12), and convert this juvenile height - age difference into a harvest age volume difference using your organization's growth and yield model. Such height over age driven estimates are useful but fail to take into account the genetic differences in diameter for trees

Third cycle seed orchard site of Temple Inland Forest near Centre, AL. Rootstock are planted and a good cover crop established. Grafting will be done in the Spring of 2000.

with similar heights. Recent analysis of the Cooperative's rotation age genetic tests point out the importance of these diameter differences when predicting harvest age volume. What is needed is a growth and yield model that can incorporate juvenile volume - age relationships in the prediction of harvest age volumes. We are not aware of the existence of such a model.

A second alternative is to use an indirect selection or correlated genetic response analysis to predict harvest age volume from juvenile volume measurements. The problem is the lack of reliable estimates of mature phenotypic variance for our tests. The estimates of mature phenotypic variance that we have are from different tests (the Cooperatives first generation rotation tests or the heritability study) and the structure of the variance estimates are so different that their use with these test data to predict harvest-age volume gains would be unreliable. Adjustments to these variance estimates would be a major assumption that would render the resulting estimates of gain little more valuable than an experienced guess.

As evidenced by the discussion above, breeding values are very useful in managing production populations and in optimizing deployment decisions. With this valuable tool now in hand, decisions in production programs should be much easier.

ASSOCIATED ACTIVITIES

Graduate Student Research and Education

The education of graduate students and the research they conduct as part of their degree programs continues to be an important activity of the Cooperative. During the past year 10 graduate programs have been developing in association with the Tree Improvement Cooperative. Five were directed toward a Masters degree and five were involved in Ph.D. programs. Of special note is the completion of the M.S. degree program by Paul Belonger during the past year and two other students, Angelia Kegley and John Mann have only to complete a final draft of their thesis and defend it successfully in order to be awarded their degree. The graduate students working in association with the Cooperative, the degree to which each aspires and the subject of their research project are listed in the highlighted box on the next page.

Visiting Scientists

In September, Dr. Tim Mullins, Genesis Forest Science Canada, Inc. spent a five week consultancy with the Cooperative working with Bailian and staff to develop simulation analysis capabilities for our use. With Dr. Mullins assistance, the breeding strategy simulation program, POPSIM, was modified for use in simulations of our Cooperative's future breeding alternatives.

Professor Dag Lindgren, research specialist in Forest Tree Breeding Theory, from the Swedish University of Agricultural Science, Faculty of Forest Genetics and Plant Physiology, along with two Ph.D. students, Torgney Persson and Thuy Olson visited for five weeks during the winter to work with Bailian Li on several issues relating to breeding theory. We anticipate that their work may provide information that will be useful in the formulation of our Cooperative Breeding Plans in the future. Ms. Thuy Olson remained in Raleigh through mid-April and worked on the Group Merit Selection Project. Portions of her work are summarized earlier in this report.

We are also pleased to announce that Dr. Xinsheng Hu arrived at N.C. State University in March of 1999 to begin a 2-year assignment working on the Search for Major Genes special project. Dr. Hu received his Ph.D. from the University of Edinburgh in Scotland and comes to us from The Chinese Academy of Forestry where he is a Research Associate Professor specializing in quantitative genetics.

Program Staff

The program staff and areas of responsibility are depicted in the Cooperative Tree Improvement Program Organizational Chart on the next page. There were no changes in program personnel during the 1998-1999 year. However, we were pleased to announce that effective November 1, 1998, Bailian Li was promoted to Associate Director of the Cooperative. This promotion was made in response to the recommendation of the Executive Committee and endorsed by the Advisory Committee. In just three years of work with The Cooperative Bailian has made an enormous contribution to the success of the Program, which is reflected in both our accomplishment and direction.

Student, Degree, Research Project

Paul Belonger, M.S. Completed 1998
Wood density assessment of diverse families of loblolly pine using x-ray densitometry.

James Grissom, Ph.D.
Regulation of biomass partitioning in loblolly pine seedlings: Influence of root versus shoot processes.

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

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

Angelia Kegley, M.S.
Screening coastal and Piedmont loblolly pine families and their hybrids for growth and cold hardiness.

Hua, Li, Ph. D.
New Student Research to be determined

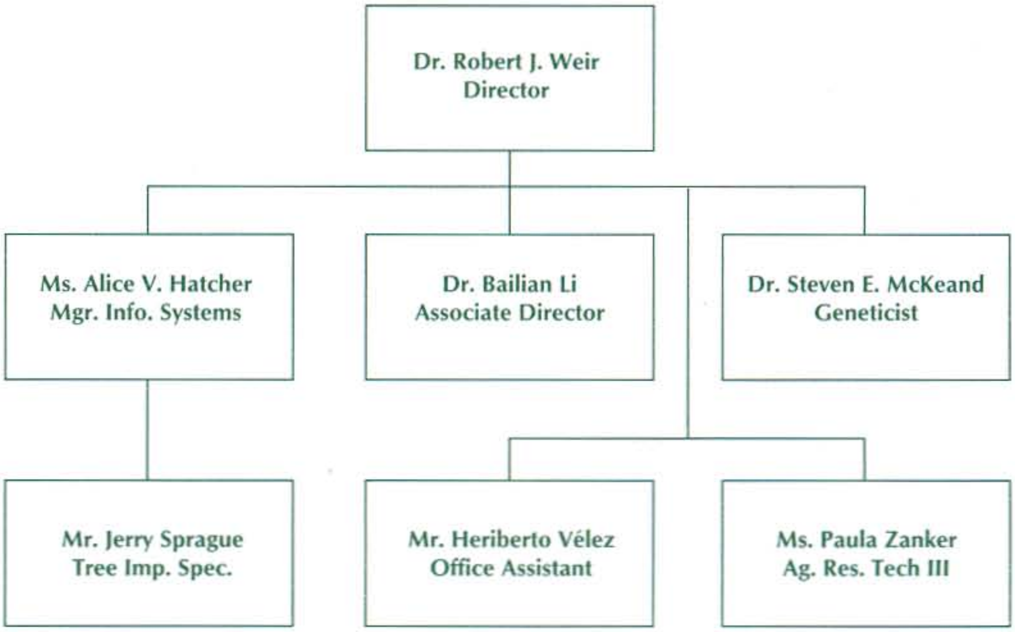
John Mann, M.S.
The effects of fertilization and irrigation on wood quality of loblolly pine.

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

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

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

Cooperative Tree Improvement Program Organizational Chart - May, 1999



MEMBERSHIP OF THE TREE IMPROVEMENT COOPERATIVE

Alabama Forestry Commission
Champion International Corp.
Fort James Corp.
Gulf States Paper Corp.
Kimberly Clark Corp.
Mead Coated Board
Packaging Corporation
S.C. Commission of Forestry
Tennessee Forestry Division
The Timber Company
U. S. Alliance Coosa Pines Corp.
Westvaco Corp.
Bowater, Inc.
Chesapeake Forest Products
Georgia Forestry Commission
International Paper Company
MacMillan Bloedel Packaging, Inc.
N.C. Division of Forest Resources
Rayonier, Inc.
Smurfit-Stone Container Corp.
Temple Inland Forest, Inc.
Union Camp Corp.
Virginia Department of Forestry

We are pleased to welcome a new member into the Cooperative. The Tennessee Department of Agriculture, Forestry Division joined the Cooperative on January 1, 1999. They will be participants in the Upper Gulf and Piedmont breeding regions. We look forward to a long and rewarding association with our newest member. Below is a short profile of the Forestry Division Program.

NEW MEMBER PROFILE

Tennessee Department of Agriculture, Forestry Division

The Tennessee Forestry Division celebrates its 85th year of existence this year. One of the older agencies in the state's oldest department is dedicated to the enhancement, protection, and promotion of the wise use of Tennesee's forestland.

The Tree Improvement section is 32 years old. Beginning with research at the University of Tennessee, genetic research and tree improvement in Tennessee has evolved to the Tennessee Forestry Division having its own Tree Improvement Section with several cooperative agreements with other entities. Managed by Mr. Russ Cox, the Tree Improvement Section is headquartered on the Agriculture Campus at the University of Tennessee in Knoxville. He has staff located at nurseries in Pinson and Delano. Anticipating membership and involvement in the Tree Improvement Cooperative, Dianne Graveline has been added to the tree improvement staff.

Approximately 75,000 private landowners constitute the bulk of the ownership of the Tennessee's 12.8 million forested acres. These landowners and their ownership objectives are many and varied. Add to this Tennessee's seven unique physiographic regions and it is easy to see the challenge our Tree Improvement Section faces in meeting such diverse needs. One shoe does not fit all. The Tennessee Forestry Division currently has orchards producing genetically improved Shortleaf Pine, Virginia Pine, Loblolly Pine, White Pine, Black Walnut and Yellow Poplar. Five other hardwood orchards will soon be on line with others still in the developmental stages. However, the number one species planted in Tennessee is Loblolly Pine. This fact plus the need to provide the state's landowners the best product available has made joining the Tree Improvement Cooperative very desirable.

The Tree Improvement Section of the Tennessee Forestry Division looks forward to being a fully participating member in the Cooperative and stands ready to begin active participation immediately.

As illustrated above by Temple-Inland, most new members to the Cooperative begin their participation in the Cooperative by grafting selections for a breeding orchard.

PUBLICATIONS OF SPECIAL INTEREST TO MEMBERS OF THE COOPERATIVE

Belonger, P.J. and S.E. McKeand 1998. Genetic and environmental effects on volume production and wood density in four southern provenances of loblolly pine. IEG-40 Workshop on Wood and Wood Fibers: Properties and Genetic Improvement. Abstract (invited talk).

Belonger, P.J., S.E. McKeand, and J.B. Jett. 1997. Wood density assessment of diverse families of loblolly pine using x-ray densitometry. P. 133-142. In: Proc. 24th South. For. Tree Impr. Conf.

Bridgwater, F.E. and S.E. McKeand. 1997. Early family evaluation for growth of loblolly pine. Forest Genetics 4:51-57.

Hodge, G.R., C.J. Masters, R.S. Cameron, W.J. Lowe, and R.J. Weir. 1997. Seed orchard pest management: The case for Forest Service R&D. Journal of Forestry, Vol 95, No1: pp29-32.

Jayawickrama, K.J.S., S.E. McKeand, and J.B. Jett. 1997. Rootstock effects on scion growth and reproduction in 8-year-old grafted loblolly pine. Can. J. For. Res. 27:1781-1787.

Jayawickrama, K.J.S., S.E. McKeand, and J.B. Jett. 1998. Phenological variation in height and diameter growth in provenances and families of loblolly pine. New Forests 16:11-25.

Jayawickrama, K.J.S., S.E. McKeand, J.B. Jett, and E.A. Wheeler. 1997. Date of earlywood-latewood transition in provenances and families of loblolly pine, and its relationship to growth phenology and juvenile wood specific gravity. Can. J. For. Res. 27:1245-1253.

Jett, J.B., M. Williford, S.E. McKeand, M. Powell. 1997. Timing of nitrogen applications in a loblolly pine seed orchard. P. 187-191. In: Proc. 24th South. For. Tree Impr. Conf.

Li, B., G. Howe, and R. Wu. 1998. Developmental factors responsible for heterosis in aspen hybrid (Populus tremuloides P. tremula). Tree Physiology 18:29-36.

Li, B., S. McKeand, A. Hatcher and R. Weir. 1997. Genetic gains of second generation selections from the NCSU-Industry Cooperative Tree Improvement Program. Proc. 24th Southern Forest Tree Improvement. Conference, p. 134-238. Orlando, Florida. June 9-12, 1997.

Li, B., S.E. McKeand and R.J. Weir. 1997. Genetically improved seedlings can benefit small forest landowners. Forest Landowner 56(5):20-23.

Li, B., S.E. McKeand and R.J. Weir. 1998. Tree improvement and sustainable forestry - impact of two cycles of loblolly pine breeding in the U.S. Invited paper presented at: IUFRO Division 2 Conference on Forest Genetics and Tree Improvement. Contribution of Genetics to the Sustained Management of Global Forest Resources. August 1998, Beijing, China. (in press).

Li, B., S.E. McKeand and R.J. Weir. 1999. Impact of forest genetics on sustainable forestry - results from two cycles of loblolly pine breeding in the U.S. Journal of Sustainable Forestry (in press).

Li, B. and R. Wu. 1997. Heterosis and genotype _ environment interaction in juvenile aspen: The implications for tree breeding. Canadian Journal of Forest Research 27: 1525-1537.

McKeand, S.E. 1997. Improving forest resources in the 21st century through tree breeding. In: Proc. of the 40th Commemorative Symposium on Forest Tree Breeding in Japan. Invited Paper. Sponsored by the Japanese Forest Tree Breeding Association. July 14, 1997. Tokyo.McKeand, S.E. and F.E. Bridgwater. 1998. A strategy for the third breeding cycle of loblolly pine in the Southeastern U.S. Silvae Genetica 47:223-234.

McKeand, S.E., R.P. Crook, and H.L. Allen. 1997. Genotypic stability effects on predicted family responses to silvicultural treatments in loblolly pine. South. J. Appl. For. 21:84-89.

McKeand, S.E., G. Eriksson, and J.H. Roberds. 1997. Genotype by environment interaction for index traits that combine growth and wood density in loblolly pine. Theor. Appl. Gen. 94:1015-1022.

McKeand, S.E., J.E. Grissom, J.A. Handest, D.M. O'Malley, and H.L. Allen. 1999. Responsiveness of diverse provenances of loblolly pine to fertilization - age 4 results. Journal of Sustainable Forestry (in press).

McKeand, S.E., J.E. Grissom, D.M. O'Malley, and H.Lee Allen. 1997. Early growth response of diverse families of l oblolly pine to nutrient amendments on a poor site. P. 2 67-274. In: Proc. 24th South. For. Tree Impr. Conf.

McKeand, S.E. and S. Kurinobu. 1998. Japanese tree improvement and forest genetics. J. For. 96(4):12-17.

McKeand, S. And B. Li. 1997. Stability of fusiform resistance in loblolly pine. Proc. 24th Southern Forest Tree Improvement. Conference, p. 261-266. Orlando, Florida. June 9-12, 1997.

McKeand, S.E. and B. Li. 1997. Two generations of genetic gains with loblolly pine in the southeastern United States. Invited Paper. P. 16-20. In: Beaulieu, J. and J.D. Simpson (eds.), Proc. 26th Meeting of the Canadian Tree Impr. Assoc., Part 2 Symposium, Sainte-Foy, Québec.

McKeand, S.E. and J.C. Svensson. 1997. Loblolly pine, sustainable management of genetic resources. J. For. 95: 4-9.

McKeand, S.E., B. Weir, A. Hatcher, B. Li, J. Sprague, P. Zanker. 1997. Establishment of 2.5-generation seed orchards. Tech. Rep. 97-1. North Carolina State University - Industry Cooperative Tree Improvement Program. 11p.

Robison, D.J., B. Goldfarb and B. Li. 1998. Advancing hardwood production forestry. PaperAge, May 22-24.

Wu, R. and B. Li. 1999. A multiplicative epistatic model for analyzing interspecific differences in outcrossing species. Biometrics 55:24-32.

Wu, R., B. Li and Z-B Zeng. 1999. Molecular dissection of quantitative traits: new perspectives from Populus. In: S.M. Jain and S.C. Minocha (ed.), Molecular Biology of Woody Plants. Kluwer Academic Puplishers, The Netherlands. (In press).

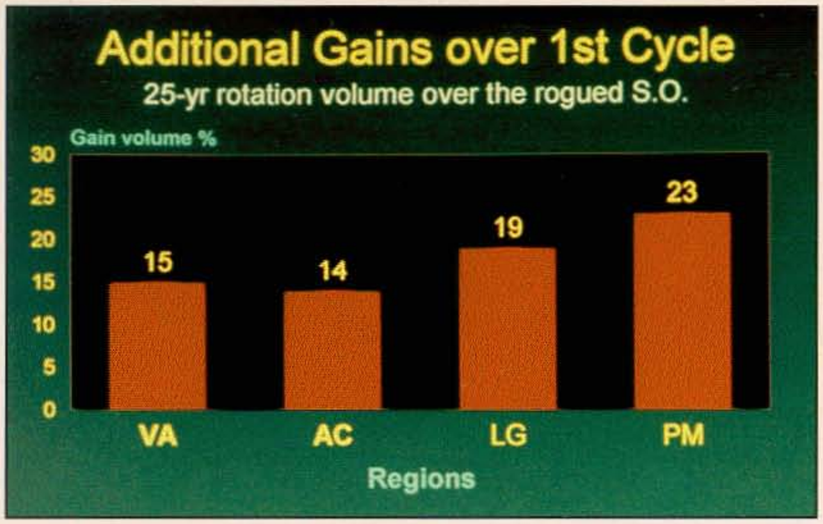
Wu R., J.E. Grissom, D.M. O'Malley, and S.E. McKeand. 1999. Root architectural plasticity to nutrient stress in loblolly pine. Journal of Sustainable Forestry (in press)

Wu, R.L, D.M. O'Malley, and S.E. McKeand. 1999. Understanding the genetic architecture of a quantitative trait in gymnosperms by genotyping haploid megagametophytes. Theor. Appl. Gen. (in press)

Wu R., D.M. O'Malley D.L, Remington, J.J. Mackay, and S.E. McKeand. 1999. Average effect of a mutation in lignin biosynthesis in loblolly pine. Theor. Appl. Gen. (in press)

van Buijtenen, J.P. and Zobel, B.J. 1998. Genetics and breeding of wood. Chapter in: Forest Genetics and Tree Breeding. Mandel and Gibson (eds). CBC Publishers & Distributors, New Delhi, India.

Zobel, B.J. and Sprague, J. R. 1998. Juvenile Wood of Forest Trees. Springer-Verlag 300pp.



Upper Left - Second Generation Seed Orchards throughout the Cooperative are producing seed with excellent gains in volume productivity compared to first-generation.

Middle Left - Dale Bates and Steve Raper inspect the condition of new grafts of 3rd-cycle selections, destined for Temple's Breeding Orchard.

Bottom - MacMillan Bloedel clearcut 20+ acres of 1.5 generation seed orchard and have begun establishment of a 3rd-cycle seed orchard. Cooperative members will be establishing most of their 3rd-cycle seed orchards between now and the year 2005.