

## CLONAL VARIATION IN FOUR-YEAR-OLD LOBLOLLY PINE IN COASTAL NORTH CAROLINA

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**Abstract.** -- Four clonal field trials of loblolly pine rooted cuttings were established in coastal North Carolina during 1990 and 1991. From measurements of these trials, age four variance components as well as full-sib family and clonal best linear unbiased predictions (BLUPs) for height, diameter at breast height (DBH), wood specific gravity and branching characteristics were calculated via restricted maximum likelihood (REML) techniques.

Age four full-sib family mean heritability estimates for height, DBH, wood specific gravity and branching traits were: 0.33, 0.53, 0.59 and 0.73-0.76, respectively. Clonal mean heritabilities for the same traits were considerably higher: 0.52, 0.67, 0.74 and 0.80-0.90, respectively. Genetic gains (BLUPs) for the best full-sib family for age four height, wood specific gravity and number of branches/height were 5.2, 5.2 and 8.5%, respectively, over the mean of the second generation full-sib families being tested. Similar genetic gains for the best 5% of the clones were 7.9, 8.9 and 13.0%, respectively.

Although based on young trees, these data corroborate expectations that, when operationally feasible, clonal production of loblolly pine will offer substantial benefits over full-sib family production.

**Keywords:** *Pinus taeda*, clonal forestry, vegetative propagation, rooted cuttings, genetic variation, heritability, genetic gain, BLUPs

### INTRODUCTION

Worldwide recognition of the benefits of clonal forestry has given rise to operationally successful clonal forestry programs in some species (Ahuja and Libby 1993). Although no operational clonal forestry programs currently exist for loblolly pine, industrial, governmental and academic research programs are underway to develop vegetative propagation technology for loblolly pine toward this end. The two most promising clonal propagation systems are 1) the use of rooted cutting technology for clonal testing and operational production coupled with a micropropagation system for maintenance of juvenile stock material and 2) somatic embryogenesis technology for clonal testing and operational production with cryostorage techniques to maintain juvenility stock material (Handley et al. 1995).

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Although some general knowledge about the field growth and development of loblolly pine vegetative propagules relative to seedlings exists (Frampton 1987, Frampton and Foster 1993), little information is available concerning the field performance of loblolly pine clones. In 1989, the within-clone specific gravity variation for a single tissue-cultured loblolly pine clone was described (Frampton and Jett 1989). Based on wood samples from three sites in coastal Georgia and Florida, at age five years, the within-site variation in wood specific gravity for a single clone was 29% that of the open-pollinated family from which it was derived. In 1993, five-year-old data was reported for five clonal field trials of loblolly pine rooted cuttings in coastal Alabama, Georgia and Florida (McRae et al. 1993). Height, DBH, stem volume and the presence or absence of fusiform rust galls were measured. Strong clonal effects were present for all traits measured and some G X E interaction was detected for the growth traits. Select clones performed substantially better than commercial checklots for both growth and rust resistance at three sites.

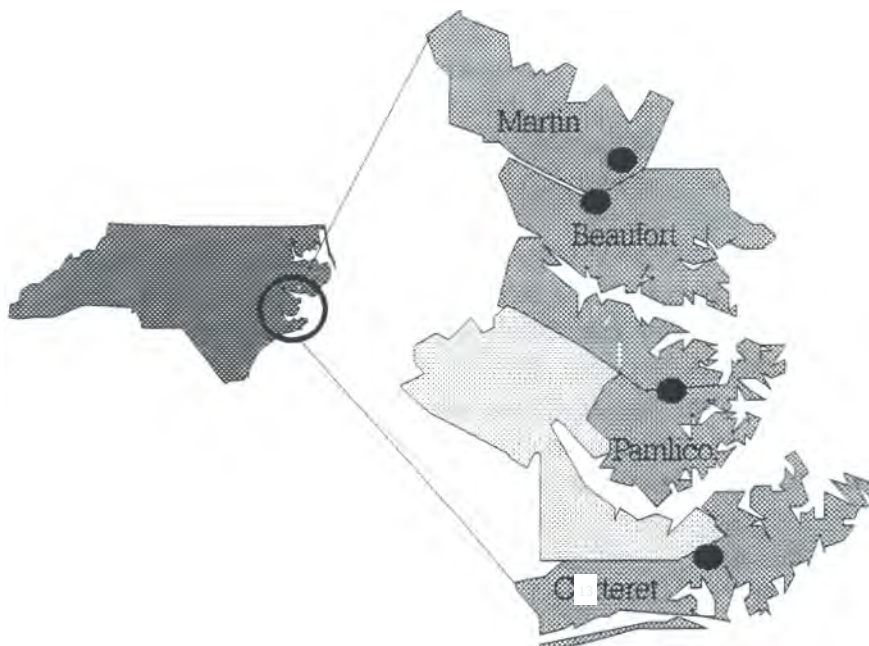
In 1990, Weyerhaeuser's Loblolly Pine Rooted Cuttings Project developed a scoping initiative to assess the field performance of clones of loblolly pine rooted cuttings. From 1990 to 1992, a series of eight clonal rooted cutting field trials were established. Trials were established in each of the three Southern Timberlands regions existing at the time: four in North Carolina, two in Mississippi/Alabama and two in Arkansas/Oklahoma. This report describes some of the early findings from the four trials established in coastal North Carolina.

## **MATERIALS AND METHODS**

### **Propagation**

During 1987 and 1988, a loblolly pine hedge orchard was established at the Weyerhaeuser seedling nursery near Magnolia, AR. The seedlings planted in 1988 were from 20 second-generation full-sib crosses and 1 unimproved checklot. The crosses included in the hedge orchard were those demonstrating the fastest field growth based on data available at the time and also having sufficient available seed. The hedge orchard seedlings were regularly sheared and subjected to an intensive management regime involving irrigation, fertilization and pest control to produce cuttings for a research propagation program.

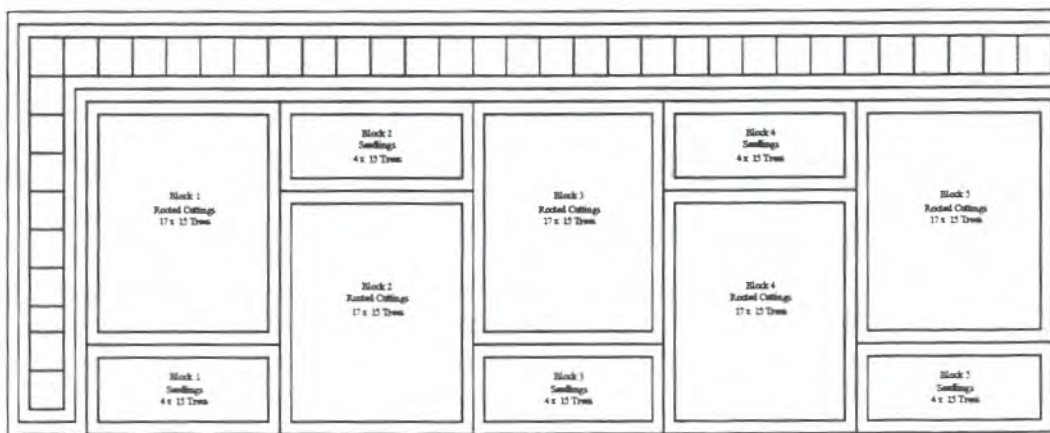
Cuttings collected from these hedges were rooted in a propagation greenhouse at Weyerhaeuser's Southern Forestry Research Center in Hot Springs, AR. Cuttings for the 1990 and 1991 plantings were collected and set in the winters of 1989 and 1990, respectively. The greenhouse was equipped with a gantry irrigation and injection system, a fog system, supplemental lighting, a wet-wall and fan cooling system and a forced air bottom-heat system. Cuttings were rooted in a peat:perlite medium in 10 cm<sup>3</sup> Ray Leach Supercells. Upon rooting, cuttings were hardened-off in an outdoor holding area prior to planting. Containerized seedlings were also cultured in the greenhouse for these field trials.



**Figure 1.** *Approximate locations of four loblolly pine clonal field trials in coastal North Carolina.*

**Field**

Two trials were established in May of 1990 in Pamlico and Martin Counties and two trials were established in April of 1991 in Beaufort and Carteret Counties (Figure 1). These sites represented organic-based, mineral-based and transition coastal plain soils. These cut-over sites were operationally site-prepared, bedded and received phosphorus fertilization prior to planting. After establishment, herbicides were applied either aerially or via back-pack sprayers during the first and/or second growing season(s) to reduce weed competition.



**Figure 2.** *Generalized map of four loblolly pine clonal field trials in coastal North Carolina.*

**Table 1 . Design of 4 loblolly pine clonal field trials located in coastal North Carolina.**

Location	Pamlico and Beaufort Counties, NC	Martin and Carteret Counties, NC	Combined
Establishment Date	May 1990	April 1991	
# Full-Sib Families	16 in Blocks 1-5 29 in Block 6	16 in Blocks 1-5 28 in Block 6	18 Total 14 in Common
# Clones/Family	9-11 in Blocks 1-5 13 in Block 6	15 in Blocks 1-5 27 in Block 6	
# Clones/Block	1 in Blocks 1-5 9 in Block 6	1 in Blocks 1-5 9 in Block 6	347 Total 63 in Common
# Total Trees	1061	1452	2513

Studies established within the same year were identical except for the randomization pattern (Table 1, Figure 2). Studies planted across years contained some common genetic material. All studies involved a randomized complete block design. Blocks 1-5 included a single tree plot of each clone from each full-sib family represented in the study. Block 6 consisted of nine-tree square plots of a sub-sample of the clones in blocks 1-5. A split-plot of seedlings was established in each of blocks 1-5 and seedlings were also included in the nine-tree square plots of block 6. The seedlings were established to compare propagule types but, due to lack of seed, were not of the same families as the rooted cuttings and were not included in any of the analyses in this report.

Total tree height was measured on the trees prior to planting (age "0") and after each of the first four growing seasons in the field. After the fourth growing season, diameter at breast height (DBH), wood specific gravity of a bark-to-bark increment core collected between 30-60 cm above ground line, the number of branches/height, the number of whorls/height and a branch angle scale (0=0°, 1=15°, 2=30°, 3=45°, 4=60°, 5=75° and 6=90° from horizontal) were assessed.

### Data Analysis

For each trait analyzed, full-sib family and clonal best unbiased predictors (BLUPs) as well as variance components were estimated via restricted maximum likelihood (REML) techniques using the following model (and ignoring the plot layout of block 6):

$$y_{ijklmn} = \mu + l_i + b_j(l)_i + g_k + g_l + s_{kl} + c_m(s_{kl}) + lg_{ik} + lg_{il} + ls_{ikl} + l_i c_m(s_{kl}) + e_{ijklmn}$$

where,

$y_{ijklmn}$  =  $n^{\text{th}}$  observation of the  $m^{\text{th}}$  clone of the  $kl^{\text{th}}$  family in the  $j^{\text{th}}$  block of the  $i^{\text{th}}$  location,

$\mu$  = overall mean,

$l_i$  = random variable location  $\sim \text{NIID}(0, \sigma^2_{\text{location}})$ ,

$b_j(l)_i$  = random variable block within location  $\sim \text{NIID}(0, \sigma^2_{\text{block}(\text{location})})$ ,

$g_k$  and  $g_l$  = random variables female and male general combining ability (GCA),

respectively  $\sim \text{NIID}(0, \sigma^2_{\text{gca}})$ ,  
 $S_{kl}$  = random variable specific combining ability (SCA)  $\sim \text{NIID}(0, \sigma^2_{\text{sca}})$ ,  
 $c_m(S_{kl})$  = random variable clone within full-sib family  $\sim \text{NIID}(0, \sigma^2_{\text{clone(family)}})$ ,  
 $lg_{ik}$  and  $lg_{il}$  = random variables location interaction with female and male GCA,  
 respectively  $\sim \text{NIID}(0, \sigma^2_{\text{location*gca}})$ ,  
 $lS_{ikl}$  = random variable location interaction with SCA  
 $\sim \text{NIID}(0, \sigma^2_{\text{location*sca}})$ ,  
 $l_i c_m(S_{kl})$  = random variable location interaction with clone within full-sib  
 family  $\sim \text{NIID}(0, \sigma^2_{\text{clone(family)}})$ ,  
 $e_{ijklmn}$  = random error  $\sim \text{NIID}(0, \sigma^2_{\text{error}})$ .

Full-sib family and clonal mean heritability estimates were calculated as follows:

$$h^2_{\text{FS Family Mean}} = \frac{(2\sigma^2_{\text{GCA}} + \sigma^2_{\text{SCA}}) / (\sigma^2_{\text{location}} / l + \sigma^2_{\text{block(location)}} / lb + 2\sigma^2_{\text{GCA}} + \sigma^2_{\text{SCA}} + \sigma^2_{\text{clone(family)}} / c + 2\sigma^2_{\text{location*GCA}} / l + \sigma^2_{\text{location*SCA}} / l + \sigma^2_{\text{location*clone(family)}} / lc + \sigma^2_{\text{error}} / lbcn)}{}$$

$$h^2_{\text{Clonal Mean}} = \frac{(2\sigma^2_{\text{GCA}} + \sigma^2_{\text{SCA}} + \sigma^2_{\text{clone(family)}}) / (\sigma^2_{\text{location}} / l + \sigma^2_{\text{block(location)}} / lb + 2\sigma^2_{\text{GCA}} + \sigma^2_{\text{SCA}} + \sigma^2_{\text{clone(family)}} + 2\sigma^2_{\text{location*GCA}} / l + \sigma^2_{\text{location*SCA}} / l + \sigma^2_{\text{location*clone(family)}} / l + \sigma^2_{\text{error}} / lbn)}{}$$

where,

$l$  = number of locations (4)

$b$  = number of blocks/location (6)

$c$  = number of clones/family/block/location (harmonic mean = 8.66)

$n$  = number of ramets/clone/family/block/location (harmonic mean = 2.15).

Among full-sib family and clonal genetic correlations among traits were estimated by calculating correlations among the respective BLUPs. Genetic gain estimates for the best 5 and 1% of the clones was calculated for height, wood specific gravity and number of branches/ht at age four by averaging the best 17 and three clones (out of 347), respectively, for each trait. The full-sib family and clonal BLUPs for these three traits were also linearly combined into a selection index using arbitrary weights as follows:

$$\text{Index Value,} = 4 \text{ HT} + 2 \text{ SG,} - \text{BRHT}$$

where,

Index Value = index value for the  $i^{\text{th}}$  full-sib family or clone

HT = standardized age four height BLUP for the  $i^{\text{th}}$  full-sib family or clone

SG = standardized age four wood specific gravity BLUP for the  $i^{\text{th}}$  full-sib family or clone

BRHT = standardized age four branches/ht BLUP for the  $i^{\text{th}}$  full-sib family or clone.

## RESULTS AND DISCUSSION

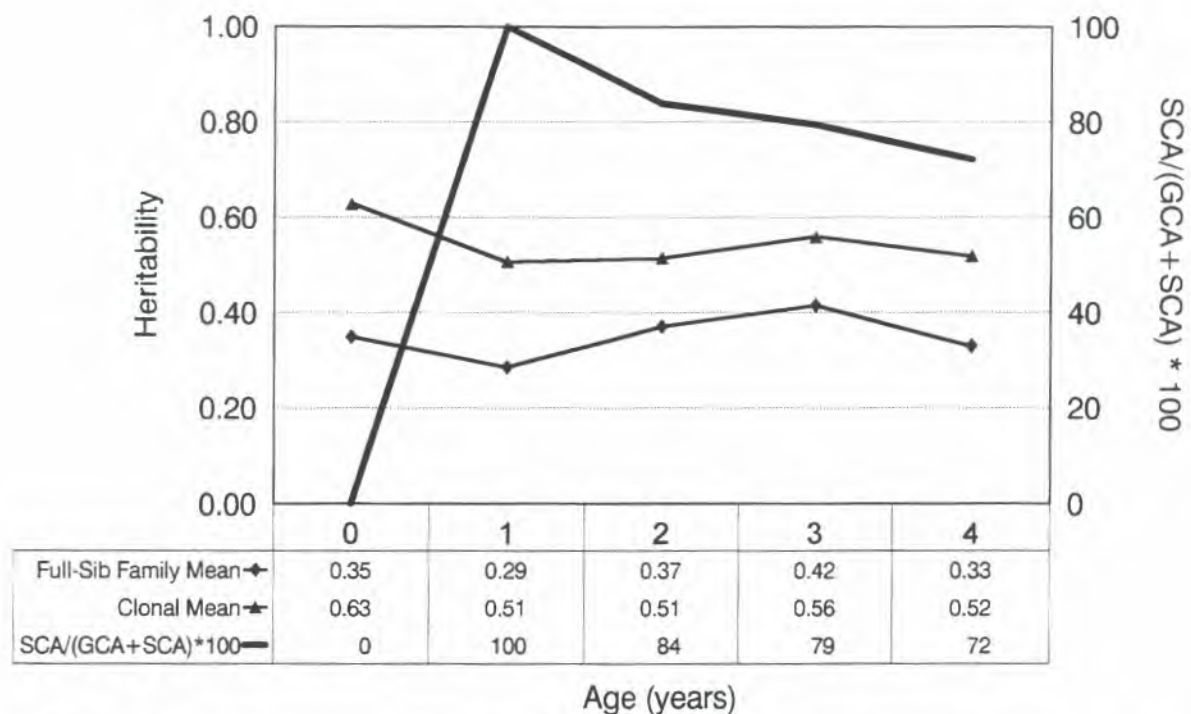
### Genetic Variation and Heritabilities

Due to the lack of a mating design among the parents of the full-sib crosses in this study, the power in partitioning the genetic variation between GCA and SCA was low. Further, since these estimates were based entirely on measurements of rooted cuttings, if the variation among full-sib families or clones was increased as a result of the rooted cutting process, these propagation or C-effects may have biased some variance component and heritability estimates in the following discussion.

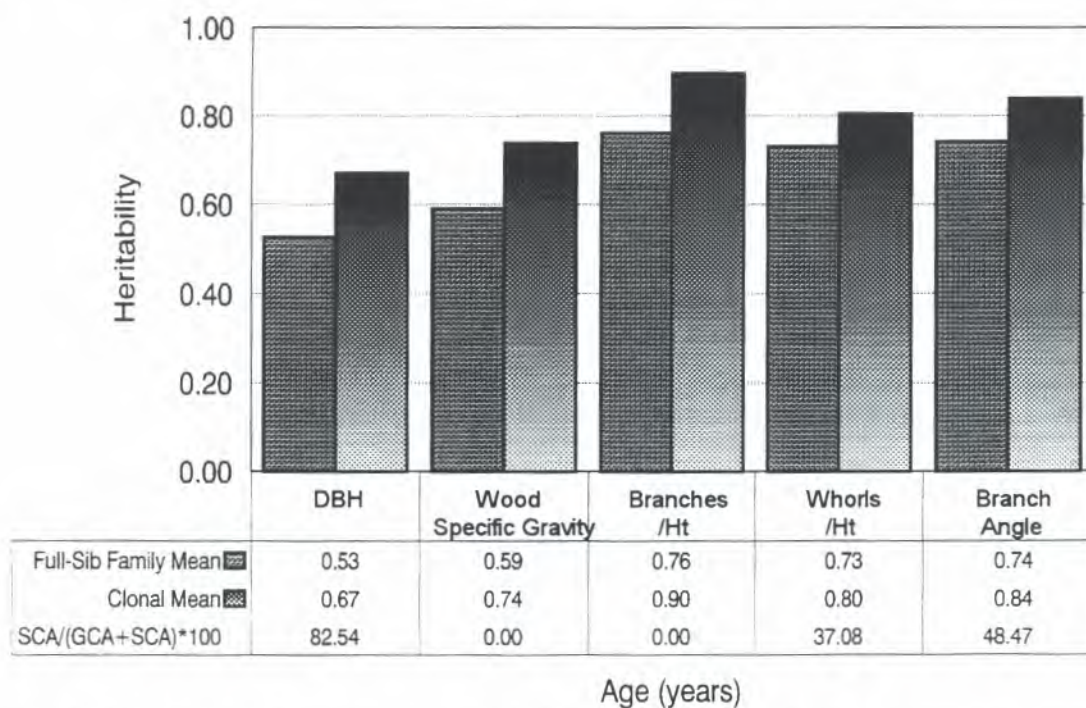
The allocation of genetic variance between general and specific combining ability for height dramatically changed from the greenhouse to age four in the field (Table 2, Figure 3). All the genetic variation detected for greenhouse rooted cutting height was GCA. After one growing season in the field, this allocation was reversed so that all detectable genetic variation was SCA. From years 1 through 4, the SCA proportion of the genetic variation for height steadily decreased. After four growing seasons, DBH, branch angle and the number of whorls/height displayed a moderate to high proportion of SCA relative to the total genetic variation (Figure 4). No SCA variance was detected after four growing

Table 2. *Estimated generalized least squares mean, and restricted maximum likelihood variance components for 10 traits. Data are from four loblolly pine clonal field trials in coastal North Carolina.*

Trait	Age (Years)	Mean	Estimated Variance Component								
			Location	Block(Location)	GCA	SCA	Clone(Family)	Location*GCA	Location*SCA	Location*Clone	Error
Height (m)	0	0.174	0.000990	0.000034	0.000087	0.000000	0.000370	0.000053	0.000000	0.000124	0.000910
Height (m)	1	0.480	0.009550	0.000421	0.000000	0.001158	0.002160	0.000303	0.000000	0.001376	0.016810
Height (m)	2	1.511	0.039980	0.000387	0.000978	0.005049	0.007540	0.000932	0.000000	0.004660	0.098798
Height (m)	3	2.710	0.052650	0.008597	0.002046	0.007870	0.014820	0.001439	0.000000	0.011007	0.209718
Height (m)	4	4.058	0.126740	0.013012	0.004364	0.011326	0.032520	0.000604	0.000000	0.026619	0.355218
DBH (cm)	4	5.996	0.248740	0.077539	0.016554	0.079806	0.160640	0.018706	0.000000	0.074711	2.110472
Specific Gravity	4	0.381	0.000500	0.000005	0.000105	0.000000	0.000170	0.000001	0.000000	0.000007	0.000370
# Branches/Whorl	4	8.592	0.148500	0.076771	0.082053	0.000000	0.321820	0.000000	0.009005	0.027827	2.051350
# Whorls/Height ( m)	4	2.660	0.010440	0.002915	0.005998	0.003535	0.019340	0.000276	0.000000	0.010561	0.152330
Branch Angle (0-6 scale)	4	1.411	0.028980	0.006109	0.018405	0.017314	0.055710	0.002317	0.010662	0.000000	0.504060



**Figure 3.** SCA variance proportion, full-sib family and clonal mean heritability estimates for height in four loblolly pine clonal field trials in coastal North Carolina.



**Figure 4.** SCA variance proportion, full-sib family and clonal mean heritability estimates for several traits at age four in four loblolly pine clonal field trials in coastal North Carolina.

seasons for wood specific gravity and number of branches/height.

The full-sib family and clonal mean heritabilities for height decreased from 0.35 and 0.63, respectively, coming out of the greenhouse to 0.29 and 0.51, respectively, after the first growing season in the field (Figure 3). Both types of heritabilities increased after the second and third growing seasons in the field but then dropped after the fourth growing season. Four-year-old DBH and wood specific gravity displayed moderately high full-sib family mean heritabilities (0.53 and 0.59, respectively) and higher clonal mean heritabilities (0.67 and 0.74, respectively). Full-sib family mean heritabilities for four-year-old branching characteristics were high (0.73-0.76) with clonal mean heritabilities higher yet (0.80-0.90).

Unlike many heritability estimates, those reported here were estimated across four locations and therefore, not biased by genotype x environmental interactions. It should also be noted that the full-sib family and clonal mean heritability estimates reported apply to coastal North Carolina sites and further, such heritabilities vary as a function of the testing design (i.e., number of sites, block/sites, etc.).

The growth (height and DBH) heritability estimates were moderate while wood specific gravity was slightly higher and the branching characteristics showed the highest degree of genetic control. Observations in a clonal demonstration area adjacent to the Pamlico County trial corroborate these quantitative results. While some uniformity for growth is evident within clonal blocks in this demonstration area, the transition between clonal blocks is easily distinguishable by obvious changes in branching habit.

### **Genetic Correlations**

The height age-age genetic correlations were mostly high for both full-sib families and clones (Table 3). The height age-age correlation between consecutive years increased over time and was very high between ages three and four (0.96 and 0.94, respectively). This suggests that both family and clonal height rankings were stabilizing. As expected, full-sib family and clonal genetic correlations between DBH and height were also high (0.76 and 0.80, respectively, at age four). A negative genetic correlation between height and wood specific gravity was detected for both full-sib families and clones (-0.39 and -0.20, respectively, at age four) suggesting that faster growing trees produce less dense wood. On the other hand, a beneficial correlation was detected between wood specific gravity and number of branches/height (-0.31 and -0.16, respectively, for full-sib families and clones).

### **Genetic Gains**

The lack of a mating design among the parents of the full-sib crosses did not adversely effect full-sib family and clonal BLUP precision since the parental GCA estimates were recombined with the cross SCA for these estimates. Propagation or C-effects may have influenced these gain estimates. However, if these effects exist and if they



Table 3. Full-sib family (above diagonal, n=18) and clonal (below diagonal, n=347) genetic correlations among 10 traits in loblolly pine. Data are from four loblolly pine clonal field trials in coastal North Carolina. Probabilities below correlations assume BLUPs are known without error.

Trait		Height	Height	Height	Height	Height	DBH	Specific Gravity	Branches/Height	Whorls/Height	Branch Angle
	Age	0	1	2	3	4	4	4	4	4	4
Height	0		0.63 0.0050	0.58 0.0117	0.66 0.0028	0.63 0.0051	0.68 0.0017	-0.54 0.0218	0.48 0.0418	0.13 NS	0.018 NS
Height	1	0.60 0.0001		0.96 0.0001	0.93 0.0001	0.86 0.0001	0.77 0.0002	-0.19 NS	0.20 NS	0.047 NS	0.14 NS
Height	2	0.47 0.0001	0.86 0.0001		0.95 0.0001	0.86 0.0001	0.72 0.0007	-0.65 NS	0.15 NS	0.028 NS	0.17 NS
Height	3	0.47 0.0001	0.79 0.0001	0.92 0.0001		0.96 0.0001	0.75 0.0003	-0.28 NS	0.15 NS	-0.036 NS	0.27 NS
Height	4	0.42 0.0001	0.71 0.0001	0.84 0.0001	0.94 0.0001		0.76 0.0002	-0.39 0.1066	0.027 NS	-0.22 NS	0.29 NS
DBH	4	0.46 0.0001	0.67 0.0001	0.75 0.0001	0.79 0.0001	0.80 0.0001		-0.39 0.1115	0.23 NS	-0.0098 NS	-0.18 NS
Specific Gravity	4	-0.23 0.0001	-0.049 NS	-0.0089 NS	-0.15 0.0035	-0.20 0.0002	-0.24 0.0001		-0.31 NS	-0.088 NS	-0.18 NS
Branches/Height	4	0.13 0.0140	0.022 NS	-0.024 NS	-0.019 NS	-0.14 0.0111	0.033 NS	-0.16 0.0032		0.86 0.0001	-0.11 NS
Whorls/Height	4	0.0022 NS	-0.065 NS	-0.12 0.0217	-0.17 0.0014	-0.31 0.0001	-0.14 0.0074	-0.049 NS	0.79 0.0001		-0.062 NS
Branch Angle	4	0.045 NS	0.074 NS	0.036 NS	0.091 0.0894	0.063 NS	-0.20 0.0001	-0.16 0.0028	-0.068 NS	-0.025 NS	

Table 4. Genetic gain (best linear unbiased predictions) based on selection for three traits independently and in a selection index. Gains are for four-year-old loblolly pine in coastal North Carolina. Highlighted boxes include gains for trait under selection.

	Height (m)		Wood Specific Gravity		Branches/Height (#/m)		Index Value	
	Gain	% Gain	Gain	% Gain	Gain	% Gain	Gain	% Gain
Selection for Height Mean = 4.06 m								
Best Full-Sib Family	0.21	5.2	-0.025	-6.6	0.44	-5.1	0.34	--
Best 5% of Clones	0.32	7.9	-0.002	-0.5	-0.24	2.8	1.53	--
Best 1% of Clones	0.41	10.1	-0.030	-7.9	0.18	-2.1	1.39	--
Best Clone	0.44	10.8	-0.032	-8.4	0.12	-1.4	1.56	--
Selection for Wood Specific Gravity Mean = 0.381								
Best Full-Sib Family	0.07	1.7	0.020	5.2	-0.12	1.4	0.46	--
Best 5% of Clones	-0.02	-0.5	0.034	8.9	-0.13	1.5	0.11	--
Best 1% of Clones	0.05	1.2	0.042	11.0	-0.11	1.3	0.40	--
Best Clone	0.08	2.0	0.044	11.5	0.32	-3.7	0.07	--
Selection for Number of Branches/Height Mean = 8.59 branches/m								
Best Full-Sib Family	0.07	1.7	0.010	2.6	-0.73	8.5	1.02	--
Best 5% of Clones	0.13	3.2	0.001	0.3	-1.12	13.0	1.67	--
Best 1% of Clones	0.23	5.7	0.016	4.2	-1.54	17.9	2.50	--
Best Clone	0.06	1.5	0.010	2.6	-2.03	23.6	2.29	--
Selection for Index Value Mean = 0.00								
Best Full-Sib Family	0.07	1.7	0.010	2.6	-0.73	8.5	1.02	--
Best 5% of Clones	-0.24	-5.9	0.008	2.1	-0.93	10.6	1.92	--
Best 1% of Clones	0.32	7.9	0.022	5.7	-1.20	14.0	2.54	--
Best Clone	0.35	8.6	0.021	5.5	-1.31	15.3	2.75	--

are transmitted through the commercial clonal production process in a manner similar to the clonal production for these field trials, then these predicted gains properly reflect achievable results. The genetic gains in the following discussion are expressed as a percent of the mean of the second generation families which were tested.

The predicted genetic gains (BLUPs) for age four height and wood specific gravity were both 5.2% when selecting the best full-sib family (Table 4). When selecting the best 5% of the clones, the gains for these traits were 7.9 and 8.9%, respectively. Despite different heritabilities, these predicted gains for height and wood specific gravity were fairly similar due to a greater degree of variation present among the full-sib families and clones for height than for wood specific gravity. Predicted genetic gains for the number of branches/height were 8.5% and 13.0% when selecting the best full-sib family and best 5% of the clones, respectively. When selecting for individual traits, a genetic loss was generally incurred in other trait(s) due to the negative correlations among some traits. Using the selection index, the best 5% of the clones produced considerably greater height gain than did the best full-sib family while maintaining a similar genetic gain in wood specific gravity and reducing the number of branches/height (Table 4).

The best 5% of the clones represented 17 clones. No relatedness restrictions were placed on these selections. Clones from nine full-sib families were selected among the best 5% of the clones for height growth. Clones from six full-sib families were selected for wood specific gravity and number of branches/height. Using the index, eight full-sib families were represented in the best 17 clones.

These results demonstrate that clonal selection can yield considerably greater gains than full-sib family selection. Further, this increased genetic gain may be achieved at selection intensities that allow for more genetic diversity than would be achieved via full-sib family deployment. When multiple traits are combined in a selection index, "correlation breaker" clones or a group of complimentary clones can be selected to achieve gains not available through full-sib family selection. Additional advantages of cloning including better matching genotypes to sites and improving raw material uniformity were not addressed in this paper but will certainly further enhance the benefits derived from future loblolly pine clonal forestry programs.

## CONCLUSIONS

Much effort is currently underway to develop commercially feasible methods to clonally propagate loblolly pine. While based on juvenile assessments, the results of this study suggest that the genetic gains resulting from practicing clonal forestry with loblolly pine will more than compensate for these efforts.

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