

**PROPORTION OF SPECIES' GENOMES AFFECTS SURVIVAL AND
GROWTH OF SHORTLEAF X LOBLOLLY PINE HYBRIDS**

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Abstract. To study the performance of shortleaf x loblolly pine hybrid progenies with differing proportions of the two genomes, families with 25, 50, or 75 $\frac{1}{2}$ of each genome and the corresponding 75, 50, or 25 $\frac{1}{2}$ of the other were produced and outplanted along with pure families of each species. In February 1986, 39 seed lots grouped into five genome proportions and eight progeny types were planted in four randomized blocks in each of two areas. At age five years, variation among seed lots without regard to genome proportion or progeny type was significant ($P < 0.01$) for survival, height, and within-plot coefficient of variation in height in both plantations. Progeny groups (either genome proportion or progeny type) differed in height in both plantations and in survival in one ($P < 0.01$). Generally, the greater the percentage of the loblolly genome, the better the survival and growth. Hybrids with 75 % of the loblolly genome performed almost the same as pure loblolly in height and survival; those with 75 % of the shortleaf genome, almost the same as pure shortleaf. Infection by fusiform rust was too low for evaluation of rust resistance.

Keywords: *Pinus taeda* L., *P. echinata* Mill., *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. fusiforme, selection, breeding

INTRODUCTION

Interspecific hybridization of forest trees may produce planting stock that will outperform either parent species under unfavorable conditions, such as poor site, severe climate, or high disease and insect incidence (Duffield and Snyder 1958). The southern fusiform-rust fungus (*Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. fusiforme) is a serious pest on loblolly pine (*Pinus taeda* L.) throughout most of its range. In contrast, shortleaf pine (*P. echinata* Mill.), a closely related species, is rarely affected by the fungus. Because the two species overlap in range and have relatively weak reproductive barriers, hybridization might be used to transfer genes for rust resistance from shortleaf to the faster-growing loblolly pine.

Shortleaf and loblolly pine apparently hybridize naturally (Mergen et al. 1965, Zobel 1953). The first control-pollinated hybrids of these two species were produced in 1933 in Placerville, CA (Duffield and Righter 1953). The hybrid has been botanically described (Little and Righter 1965), with distinguishing characteristics noted by Mergen et al. (1965). F₂ hybrid progenies produced in Placerville have grown well and demonstrated fusiform rust resistance in progeny tests in Louisiana (Henry and Bercauw 1956) and Georgia (Sluder 1970).

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Based on the promising results from these tests, the USDA Forest Service, Southern Research Station, has continued the research with hybrids of these two species in Macon, GA. Shortleaf and loblolly pine clones from Georgia Forestry Commission's seed orchards and the largest, best-formed trees from an F₂ hybrid progeny produced at Placerville and grown in Georgia were used as parents. Results indicate that resistance to fusiform rust is inherited from the shortleaf parent (LaFarge and Kraus 1975, 1977, 1980; Kraus 1985, 1986).

The most recent study assesses the relative performance of the two species and a series of their hybrids containing three different proportions of the genomes of each species. Fifth-year results from the two experimental plantations in this study are reported.

METHODS

Hybrid families with 25, 50, or 75 percent of the loblolly genome and, respectively, 75, 50, or 25 percent of the shortleaf genome were produced. The 50:50 loblolly:shortleaf group had three types of progenies and the 75:25 group had two types. Each of the other three genome proportion groups (0:100, 25:75, and 100:0 loblolly:shortleaf) had one type of progeny, bringing the total to eight types. Five families from each of the **six** hybrid types plus five pure loblolly and four pure shortleaf families or bulks comprise the 39 seed lots in the study (Table 1).

The 50:50 hybrids (types 3-5) were F and F₃ progenies. Backcrosses (types 6-8) were made with F₁ and F hybrids. with the exception of progeny types 5 and 6, the hybrid progenies² were produced by controlled pollinations. Progeny type 5 was assumed to be an F from wind pollinations among F parents in an older study plantation. Progeny³ type 6 was assumed to be a backcross to surrounding loblolly pines from wind pollinations on the F₁ female parents growing in a young hybrid seedling seed orchard (Table 1).

The seedlings were planted in two plantations in Georgia during February 1986. The field design for each plantation consists of four randomized blocks, 16-tree square plots, and 2.5 m x 2.5 m spacing. In the plantation located in the Hitchiti Experimental Forest in Jones County, all four blocks are contiguous (plantation 150). In the second plantation, seed lots 3573, 3577, 3601, and 3604 are excluded. This plantation is located on two noncontiguous sites in Meriwether and Putnam Counties, with two blocks in each county (plantation 152). All sites were cut-over. The Jones County site was prepared by discing; the Meriwether and Putnam County sites by windrowing. All are in the Piedmont physiographic province, and site quality in each varied from medium to low.

Data recorded at age five years were survival, height, and infection by southern fusiform rust. Within-plot coefficients of variation (CV) in height were calculated. Survival, height, and CV in height data were subjected to analysis of variance (Table 2). Rust incidence was too low, even on pure loblolly, for meaningful analysis of rust data. Comparisons among group means (percentage loblolly, progeny type) were made with Bonferroni's method (Miller 1981), and eight contrasts between progeny types were tested with the F-statistic.

Table 1. Description of seedlots in the study.

Seed lot	Progeny type	Percentage		Parent ¹	
		Loblolly	Shortleaf	Female	Male
3566	1. Loblolly	100	0	520	W
3567				512	W
3568				541	W
3569				Bulk, seed orchard	
3570				Bulk, Piedmont	
3571	2. Shortleaf	0	100	2006	W
3572				2017	W
3573				2019	W
3574				Bulk, seed orchard	
3575	3. F ₁ hybrid	50	50	2006	512
3576				2017	541
3577				2019	541
3578				2004	617
3579				2008	625
3580	4. F ₃ hybrid	50	50	HH-5	HH-39
3581				HH-11	HH-26
3582				HH-19	CH-4
3583				HH-5	HH-3
3584				HH-10	HH-26
3585	5. F ₃ hybrid ²	50	50	HH-5	W
3586				HH-6	W
3587				HH-11	W
3588				HH-20	W
3589				HH-15	W
3590	6. Backcross, F ₁ to loblolly ³	75	25	2006 x 515	W
3591				2006 x 512	W
3592				2017 x 541	W
3593				2019 x 541	W
3594				Bulk lot	
3595	7. Backcross, F ₂ to loblolly	75	25	515	HH-6
3596				624	HH-6
3597				541	HH-11
3598				617	HH-39
3599				624	HH-26
3600	8. Backcross, F ₂ to shortleaf	25	75	2003	HH-6
3601				2019	HH-6
3602				2011	HH-29
3603				2004	HH-39
3604				2008	HH-11

¹ Three- and four-digit numbers (520, 2006) are loblolly and shortleaf clones, respectively, in Georgia Forestry Commission seed orchards. HH-5, etc., are F₁ hybrid trees in the Hitchiti Experimental Forest. CH-4 is a F₁ at Callaway Gardens. W is wind-pollinated.

² Female F₂ trees in a plantation in the Hitchiti Experimental Forest, assumed crossed with other F₂ trees in the plantation.

³ Female trees in a young seeding seed orchard in Baldwin County, assumed backcrossed to loblolly.

Table 2. Expected mean squares for the analysis of variance.

Source	Degrees of freedom		Expected mean square ¹
	Plant. 150	Plant. 152	
Block	3	3	$v_e + v_b$
Seed lot	38	34	$v_e + bv_1^b$
Progeny group ²	4 (7)	4 (7)	$v_e + bv_1^g + Q_g$
Lot in group	34 (31)	30 (27)	$v_e + bv_1^g$
Error	<u>114</u>	<u>102</u>	v_e
Total	155	139	

¹ v_e , error variance; v_b , block variance; v_1^g , lot in group variance; Q_g , quadratic function of progeny group; v_1^b , seed lot variance; v_1^g , progeny group variance.

² Genome proportion or progeny type (d.f. for progeny type in parentheses).

RESULTS

Seed Lots

Variation among seed lots without regard to genome proportion (Table 3) or progeny type (Table 5) was significant ($P < 0.01$) for all three variables in both plantations. Also, variation among seed lots within genome proportion and progeny type groups was significant ($P < 0.01$ or 0.05) for all traits except height in progeny type in plantation 150.

Genome Proportion

Variation due to genome proportion (percentage loblolly) was significant ($P < 0.01$) for survival in plantation 150 and for height in both plantations (Table 3). Percentages of the two genomes showed no significant effect on within-plot CV in height in the analyses of variance (Table 3), but Bonferroni's method of comparisons among treatment means ($P < 0.05$) showed pure shortleaf to be more variable in height within plot than 75 percent loblolly in plantation 150 and than pure loblolly in plantation 152 (Table 4). Generally, the greater the percentage of loblolly, the greater the survival and height and the less the within-plot CV in height (Table 4).

Progeny Type

The eight progeny types varied in survival in plantation 150 and in height in both plantations ($P < 0.01$) (Table 5). Tables 6 and 7 show progeny type means and multiple comparisons among them (Bonferroni's method). Table 8 shows F-statistic tests of eight of the more meaningful contrasts between progeny type means. While none of these contrasts were significant for plantation 152, seven were significant for plantation 150.

Table 3. Analyses of variance of fifth-year data grouped by percentage loblolly pine (genome proportion).

Source	Plantation 150			Plantation 152		
	Survival	Height	CV height	Survival	Height	CV height
	-----Mean square-----					
Block	753.56**	1.82**	0.0107	59.98	3.32**	0.0170**
Seed lot	512.35**	0.86**	0.0157**	386.20**	0.59**	0.0056**
Percent lob	2908.75**	5.15**	0.0278	253.22	2.55**	0.0119
Lot in pct.	230.42**	0.37*	0.0142**	403.93**	0.33**	0.0048**
Error	99.66	0.22	0.0080	112.26	0.12	0.0026

* P < 0.05

** P < 0.01

Table 4. Means data by percentage loblolly pine, age 5 years.¹

Percent loblolly	Plantation 150			Plantation 152		
	Survival (%)	Height (m)	CV height (%)	Survival (%)	Height (m)	CV height (%)
0	30.1b	1.95c	34.7a	72.1a	2.40b	21.5a
25	38.7b	1.96bc	32.0ab	72.1a	2.44b	18.1ab
50	61.4a	2.34b	29.1ab	72.4a	2.41b	20.3a
75	69.7a	2.88a	25.7b	77.9a	2.86a	17.9ab
100	68.6a	2.88a	29.0ab	83.4a	3.09a	15.4b

¹ Within a column, means followed by a common letter do not differ at the 0.05 level, Bonferroni's method (Miller 1981).

Table 5. Analyses of variance of fifth-year data grouped by progeny type.

Source	Plantation 150			Plantation 152		
	Survival	Height	CV height	Survival	Height	CV height
	-----Mean square-----					
Block	753.56**	1.82**	0.0107	59.98	3.32**	0.0170**
Seed lot	512.35**	0.86**	0.0156**	386.20**	0.59**	0.0056**
Progeny type	1257.50**	3.18**	0.0270	177.36	1.64**	0.0069
Lot in type	231.19**	0.34	0.0131*	440.35**	0.32**	0.0053**
Error	99.66	0.23	0.0083	112.26	0.12	0.0026

* P < 0.05

** P < 0.01

Table 6. Means data by progeny type, age 5 years, plantation 150.¹

Progeny type	Percent		Trait		
	Loblolly	Shortleaf	Survival (%)	Height (m)	CV height (%)
1. Loblolly	100	0	68.59a	2.88a	29.00ab
2. Shortleaf	0	100	30.08c	1.95c	34.07a
3. F ₁ , c.p.	50	50	64.06a	2.57abc	28.45ab
4. F ₃ , c.p.	50	50	64.73a	2.22bc	30.05ab
5. F ₃ , wind	50	50	55.31ab	2.24bc	28.72ab
6. B.C. to lob., wind	75	25	68.91a	2.84ab	30.07ab
7. B.C. to lob., c.p.	75	25	70.51a	2.93a	21.42b
8. B.C. to shtl., c.p.	25	75	38.75bc	1.96c	31.96ab

¹ Within a trait column, means followed by a common letter do not differ at the 0.05 level, Bonferroni's method (Miller 1981).

Table 7. Means data by progeny type, age 5 years, plantation 152.¹

Progeny type	Percent		Trait		
	Loblolly	Shortleaf	Survival (%)	Height (m)	CV height (%)
1. Loblolly	100	0	83.44a	3.09a	15.42a
2. Shortleaf	0	100	72.12a	2.40bc	21.53a
3. F ₁ , c.p.	50	50	76.17a	2.61abc	19.91a
4. F ₃ , c.p.	50	50	71.67a	2.24c	20.01a
5. F ₃ , wind	50	50	70.00a	2.41bc	20.78a
6. B.C. to lob., wind	75	25	78.44a	2.85abc	17.77a
7. B.C. to lob., c.p.	75	25	77.46a	2.86ab	18.01a
8. B.C. to shtl., c.p.	25	75	72.12a	2.44bc	18.07a

¹ Within a trait column, means followed by a common letter do not differ at the 0.05 level, Bonferroni's method (Miller 1981).

Table 8. Eight contrasts between progeny type trait means at age 5 years.

Contrast	Plantation 150			Plantation 152		
	Survival	Height	CV height	Survival	Height	CV height
-Type-	-----F-value-----					
1 vs 7	0.17	0.08	4.38*	0.74	1.65	1.28
2 vs 8	1.50	0.00	0.51	0.00	0.03	1.37
3 vs 7	0.85	3.92	3.77	0.04	1.72	0.61
3 vs 8	11.02**	10.77**	0.93	0.33	0.68	0.44
7 vs 8	18.01**	27.68**	8.46**	0.17	4.29	0.00
6 vs 7	0.14	0.26	5.71*	0.01	0.00	0.01
4 vs 5	2.45	0.01	0.13	0.02	0.91	0.11
3 vs 4	0.09	3.59	0.19	0.30	3.96	0.00

* P < 0.05.
 ** P < 0.01.

Correlations

Correlation between the two plantations was good for data means for height, reasonably good for survival, and poor for CV in height. For seed lots, progeny types, and genome percentages, respectively, correlation coefficients were: 0.76 ($P < 0.001$), 0.88 ($P < 0.01$), and 0.90 ($P < 0.05$) for height; 0.41 ($P < 0.05$), 0.61 (ns.), and 0.72 (ns.) for survival; and 0.27 (ns.), 0.32 (ns.), and 0.56 (ns.) for CV in height.

DISCUSSION

If the assumptions about pollen source for the wind-pollinated progenies are not totally correct, type 5 (F_1) may be more than 50 percent and type 6 (backcross) less than 75 percent loblolly. Each of these two wind-pollinated progeny types can be compared with its corresponding F_2 (type 4) or backcross to loblolly (type 7) produced by controlled pollinations. Contrasts shown in Table 8 indicate no differences between the two types of F_1 progenies (type 4 vs. type 5), but do indicate a difference between the two types of backcross to loblolly progenies (type 6 vs. type 7) in plantation 150 for within-plot CV in height ($P < 0.05$). The wind-pollinated type 6 progenies were more variable in height than the type 7 progenies, even though they differed little in mean height or survival (Table 6). This difference may be caused, in part, by greater variation within half sib than within full sib progenies.

Based on fifth-year results, hybrids with 75 percent of the loblolly genome performed almost the same as pure loblolly in survival and growth. Conversely, hybrids with 75 percent of the shortleaf genome performed almost the same as pure shortleaf. The 50-50 hybrids' performance was between the two.

The trait for which hybridization is deemed most beneficial, resistance to fusiform rust, could not be evaluated at age five years because almost no infection had occurred. Cool, moist weather early in the growing season is necessary for infection. This type of weather did not occur during the first five years of this study. Perhaps by age 10 years weather conditions will promote more normal exposure to inoculum, and resistance to fusiform rust can be evaluated.

These and earlier study results indicate that the favorable traits of loblolly and shortleaf pines can be combined into a genetic stock with the fast growth rate of loblolly and the high fusiform rust resistance and straight stems of shortleaf. Only one or two generations of backcrossing from 50:50 hybrids to loblolly will be required to regain the fast growth rate of loblolly. Still uncertain is how many generations of selection and breeding after backcrossing to loblolly will be required for high, stable rust resistance. Confidence and progress would be greatly enhanced if the number, location, and mode of action of all available resistance genes in each species and their interaction with genetic variation in the fungus were known. Breeding research with these two species should continue until broadly-based genetic stocks of resistant loblolly pines are developed for high fusiform rust hazard areas of the Southeast.

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