

## INTERPROVENANCE CROSSES IN LOBLOLLY PINE USING SELECTED PARENTS

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### ABSTRACT

Pollen from five North and South Carolina coastal plain orchard clones, and five central Florida orchard clones was applied to five Livingston Parish, Louisiana (LPL) loblolly pine (*Pinus taeda* L.) clones in an orchard in southeastern Louisiana. Also included in the test were open-pollinated progenies from each of the orchard clones, a woods-run collection from Livingston Parish, and a half-diallel among the five LPL clones. Test plantings were established in south Mississippi, central Georgia, and central Florida. In all three plantings, the LPL trees were least infected with fusiform rust (*Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*) and the Florida trees were the most susceptible. Infection in the interprovenance crosses was slightly less than expected based on the infection in the open-pollinated parent clones, indicating possible heterosis. There were large and significant location  $\times$  interprovenance cross interactions in growth characters, which were expected due to climatic differences between the seed sources and planting locations. Interprovenance crosses performed slightly better than expectations based on the means of the parent seed sources, also indicating possible heterosis. Crossing provenances also appeared to increase genetic variation relative to environmental variation.

**Key words:** hybrids, *Pinus taeda*, heritability, geographic variation

### INTRODUCTION

The extensive geographic variation in loblolly pine (*Pinus taeda* L.) has been an important factor in the selection of planting stock for afforestation in the southeastern United States. Provenance tests have shown that the local source does not always achieve the highest yield (Wells 1983). The results of the South-wide Southern Pine Seed Source Study (SSPSSS) (WELLS & WAKELEY 1966) and other provenance tests have resulted in large-scale planting of non-local sources across the South. Tremendous quantities of loblolly pine seed originating in Livingston Parish, Louisiana (LPL) have been moved to Georgia, north Florida and Alabama where this source is fast growing and less infected with fusiform rust caused by the fungus *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme* than local sources (WELLS 1985). In another large-scale transfer of genetic material, seeds originating on the coastal plain of North and South Carolina have been planted in Arkansas, where they outgrow the local sources (LAMBETH *et al* 1984).

Few loblolly pine provenance tests have included sources from the southern-most part of the distribution, in central Florida. A representative from this part of the natural range was not included in the SSPSSS, but it

was the fastest growing source in several provenance trials in southern Africa (MULLIN *et al* 1978). In plantings established on the lower Gulf coastal plain, growth of a source from Marion County exceeded the highly-touted Livingston Parish, Louisiana, source. PAIT *et al* (1985) found that the growth of a Marion County source exceeded the growth of all sources, including a Livingston Parish source, in a planting in central Florida.

DRAPER (1975) compared growth of sources from Marion County, and Nassua County, Florida to sources from Alabama and Georgia in four plantings in Florida, Georgia and Alabama. The Marion County source grew the fastest in all but one of the northernmost plantings in Alabama. In a similar test of seed sources from Marion County, Livingston Parish, East Texas, Maryland, and north Florida, planted in six locations in Florida and Georgia, PAIT and DRAPER (1983) found that the Marion County source was fastest growing in the southern-most planting in Marion County, but not in the more northern plantings.

The possibility of combining desirable traits, such as fast growth and disease resistance, from different provenances by crossing among them could provide an attractive means of increasing gain as well as increasing genetic diversity in breeding populations. In addition,

evidence of heterosis for some traits has been reported in crosses among widely separated populations of loblolly pine (WOESSNER 1972, OWINO & ZOBEL 1977), as well as in other forest tree species (MAGNUSSEN & YEATMAN 1988, NELSON & MOHN 1993).

The present study attempts to determine the feasibility of combining the desirable qualities of loblolly pine populations from Livingston Parish, LA, Marion County, FL, and the Carolina Coastal Plain, to produce a variety of wide adaptability for planting in the south-eastern United States.

## MATERIALS AND METHODS

Pollen from five North and South Carolina coastal plain orchard clones and from five central Florida orchard clones was applied to five Livingston Parish, Louisiana orchard clones in the Crown Zellerbach (now Cavenham Forest Industries) orchard near Bogalusa, LA (Figure 1) in a female tester design. Also included in the test were open pollinated seed from each of the 15 orchard clones, a bulk collection from natural stands in Livingston Parish, and a half-diallel among the Livingston Parish clones (Table 1).

Seed from the controlled crosses and other collections were sown in the nursery in south Mississippi in the spring of 1976. In January of 1977, bare-root stock from the nursery sowing were planted at three locations: South Mississippi (Harrison County), south-central Georgia (Dodge County), and central Florida (Marion County) (Figure 1). Each planted block contained 75 full- and half-sib families plus 15 plots of Livingston Parish bulk. Eight blocks of the 76 treatments were planted in 4-tree plots. Spacing in the plantings was 8 by 10 ft (2.6 by 3.3 m). At age 6 years, fusiform rust galls were counted and heights were measured at all plantings. The Georgia planting had a severe infestation of Nantucket pine shoot tip moth (*Rhyacionia frustrana* [Comstock]). All trees in the Georgia planting were scored for severity of damage using an approximate index: 0 = none, 1 = light (up to 10 % buds killed), 2 = medium (10 % to 40 % buds killed), and 3 = heavy infestation (above 40 % of buds killed). After 10 years of growth, height and diameter at 1.6 m (dbh) of the trees was measured.

The statistical model for the complete study was:

$$Y_{ijklm} = \mu + L_i + R_j(L_i) + P_k + LP_{ik} + F_l(P_k) + LF_{il}(P_k) + \epsilon_{ijklm} \quad [1]$$

where:  $Y_{ijklm}$  = the mean of the  $m$ -th plot of the  $l$ -th family from the  $k$ -th provenance (or interprovenance cross) in the  $j$ -th replication at the  $i$ -th location,  $\mu$  = the population mean,  $L_i$  = effect of the  $i$ -th location,  $i = 1$  to 3,  $R_j(L_i)$  = effect of the  $j$ -th replication in the  $i$ -th location,  $j = 1$  to 8,  $P_k$  = effect of the  $k$ -th provenance

(or interprovenance cross),  $k = 1$  to 7,  $LP_{ik}$  = effect of the interaction between the  $k$ -th provenance and the  $i$ -th location,  $F_l(P_k)$  = effect of the  $l$ -th family from within the  $k$ -th provenance,  $l = 1$  to 76 (60 full-sib families, 15 half-sib families and 1 bulk collection),  $LF_{il}(P_k)$  = effect of the interaction between the  $i$ -th location and the  $l$ -th family from within the  $k$ -th provenance, and  $\epsilon_{ijklm}$  = residual.

When the location by provenance (or interprovenance cross) interaction was statistically significant (0.05 level of probability), The plantings were analyzed separately using the simplified model:

$$Y_{ijklm} = \mu + R_j + P_k + F_l(P_k) + \epsilon_{ijklm} \quad [2]$$

Notation as above.

Within each planting there are two factorials, LPL  $\times$  NC/SC and LPL  $\times$  Fla, as well as the LPL half-diallel. Each are analyzed separately for each planting. The model for the factorials was:

$$Y_{ijkl} = \mu + R_i + F_j + M_k + FM_{jk} + \epsilon_{ijkl} \quad [3]$$

where:  $Y_{ijkl}$  = the mean of the  $l$ -th plot of the  $k$ -th male and the  $j$ -th female in the  $i$ -th replication,  $\mu$  = the population mean,  $R_i$  = effect of the  $i$ -th replication,  $i = 1$  to 8,  $F_j$  = effect of the  $j$ -th female,  $j = 1$  to 5,  $M_k$  = effect of the  $k$ -th male,  $k = 1$  to 5,  $FM_{jk}$  = effect of the interaction between the  $k$ -th male and the  $j$ -th female,  $\epsilon_{ijkl}$  = residual.

The half-diallel of Livingston Parish families was analyzed for each location using the model:

$$Y_{ijkl} = \mu + R_i + G_j + G_k + S_{jk} + \epsilon_{ijkl} \quad [4]$$

where:  $Y_{ijkl}$  = the mean of the  $l$ -th plot of the  $j$ -th male and the  $k$ -th female in the  $i$ -th replication,  $\mu$  = the population mean,  $R_i$  = effect of the  $i$ -th replication,  $G_j$  = general combining ability effect of the  $j$ -th male,  $G_k$  = general combining ability effect of the  $k$ -th female,  $S_{jk}$  = specific combining ability effect of the  $j$ -th male and  $k$ -th female,  $\epsilon_{ijkl}$  = residual.

Heritabilities were calculated on a cross mean basis for the factorials and the diallel for each location (HALLAUER & MIRANDA 1981):

$$h^2 = 4\sigma_f^2 / (4\sigma_f^2 + 4\sigma_{fm}^2/M + \sigma_e^2/RM) \text{ (Factorials)} \quad [5]$$

$$h^2 = 4\sigma_{gca}^2 / (4\sigma_{gca}^2 + 4\sigma_{sca}^2 + \sigma_e^2/R) \text{ (Diallels)} \quad [6]$$

Where:  $h^2$  = narrow-sense heritability,  $\sigma_f^2$  = variance due to females,  $\sigma_m^2$  = variance due to males,  $\sigma_{fm}^2$  = variance due to the interaction of females and males,  $\sigma_e^2$  = variance due to error,  $\sigma_{gca}^2$  = Variance due to general combining ability,  $\sigma_{sca}^2$  = variance due to specific

Table 1 Sources of loblolly pine seed used in the experiment, and manuscript abbreviations

Provenance designation	Clone	Ortet origin
NC/SC	8-61 8-73 FM-7 FM-8 FM-12	Bertie Co., North Carolina Craven Co., North Carolina Berkeley Co., South Carolina Berkeley Co., South Carolina Berkeley Co., South Carolina
NC/SC × w	Open-pollinated seed of the above 5 clones	
Fla	601 602 603 604 605	Marion Co., Florida Marion Co., Florida Marion Co., Florida Marion Co., Florida Marion Co., Florida
Fla × w	Open-pollinated seed of the above 5 clones	
LPL	2-1 2-3 5-3 5-4 5-7	Livingston Pa., Louisiana Livingston Pa., Louisiana Livingston Pa., Louisiana Livingston Pa., Louisiana Livingston Pa., Louisiana
LPL × w	Open-pollinated seed of the above 5 clones	
LPL × LPL	Half-diallel of the above 5 clones	
LPL woods-run	Bulk collection from natural stands in Livingstone Parish	
LPL × Fla	The 5 LPL clones as females crossed in all combinations with the 5 Fla clones	
LPL × NC/SC	The 5 LPL clones as females crossed in all combinations with the 5 NC/SC clones	

combining ability,  $M$  = harmonic mean number of males, and  $R$  = harmonic mean number of replications.

Female components were used in the heritability calculations because the same females were used in both the diallel and factorials.

A heterosis statistic was also computed on a plot mean basis for each interprovenance cross in each replication:

$$H_{ijklm} = F_k(P_i)M_l(P_j) - \{ O_k(P_i) + O_l(P_j) \} / 2 \quad [7]$$

where:  $H_{ijklm}$  = the heterosis of the  $k$ -th female from the  $i$ -th provenance when crossed with the  $l$ -th male from the  $j$ -th provenance from the  $m$ -th replication,  $F_k(P_i)M_l(P_j)$  = the plot mean of the  $k$ -th female from the  $i$ -th provenance when crossed with the  $l$ -th male from the  $j$ -th provenance,  $O_k(P_i)$  = the plot mean of the  $k$ -th open-pollinated female family from the  $i$ -th provenance,  $O_l(P_j)$  = the plot mean of the  $l$ -th open-pollinated male family from the  $j$ -th provenance.

A simple "T" test was used to determine if the heterosis statistic differed from zero for each dependent variable in each of the three plantings.

Analyses were done using SAS (1985) GLM and VARCOMP procedures. The diallels were analyzed using SANDERS' (1987) adaptation of the GLM and REG procedures of SAS (1985). The fixed model is assumed except for the computation of variance components and heritability estimates.

## RESULTS AND DISCUSSION

### Provenance and Interprovenance Crosses

**Survival.** Survival at 10 years varied widely among the three plantings, ranging from 42% in Georgia to 76% in Mississippi (Figure 2). Survival at ages 6 and 10 years were the only variables for which the provenance by planting location interaction was not significant ( $p = 0.55$  at age 10) (Table 2).

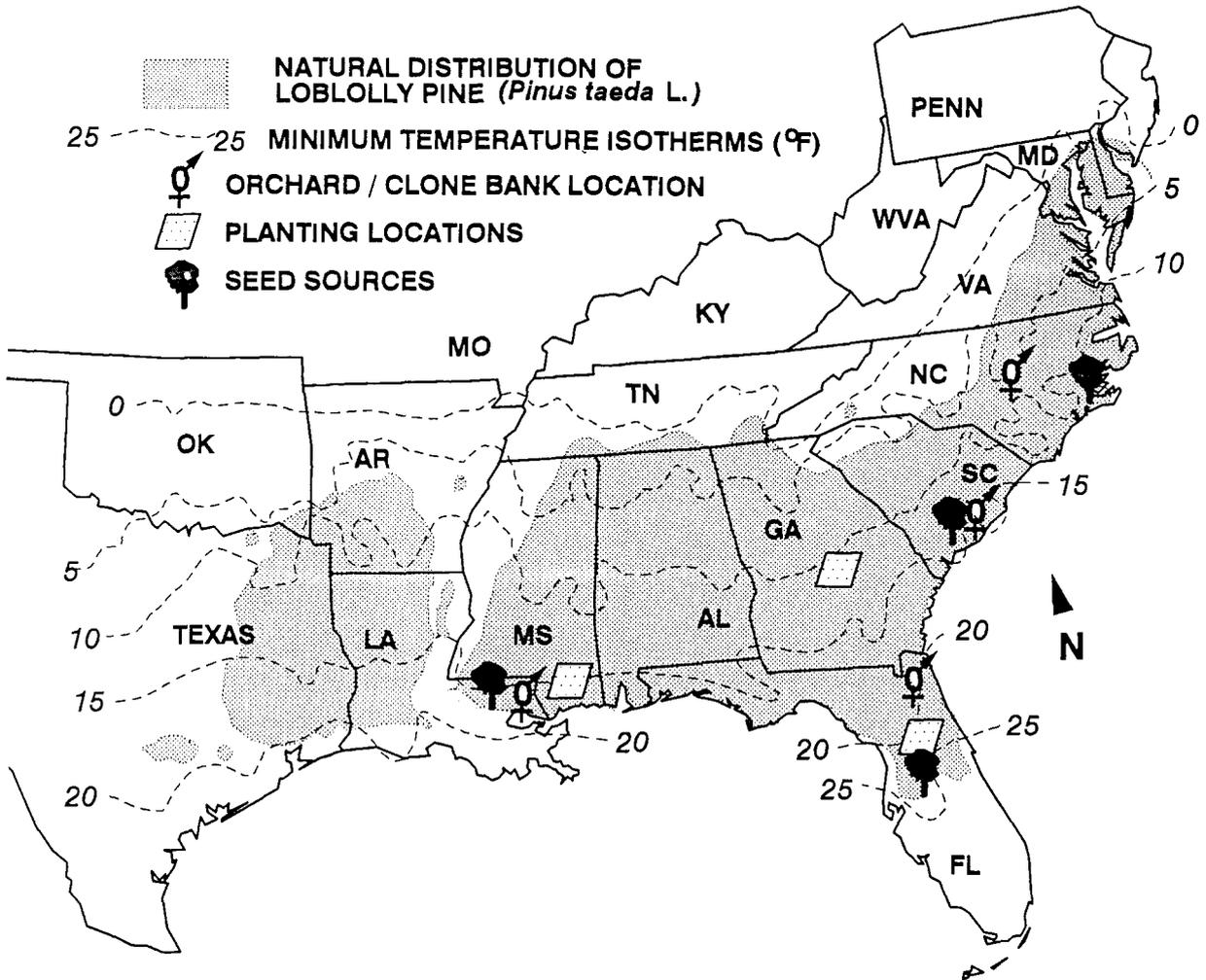


Figure 1 Map of the southeastern United States showing the natural distribution of loblolly pine (*Pinus taeda* L.), the location of the seed sources and planting sites, and the location of the seed orchards or clone banks where the wind-pollinated seed were collected. Also shown are minimum-temperature isotherms that are used in horticulture to determine plant hardiness zones (USDA 1990)

Survival at age 6 years averaged 63% over the three plantings. Most of the mortality up to age 6 occurred in the first year after planting. By age 10, survival averaged 59%. The pattern among provenances at age 10 was similar to that at age 6, except that there was a decline in survival of the southern-most source, Fla. × wind, relative to the other sources from the 6th to the 10th year (Figure 2). The best surviving source was one of the wide crosses, LPL × NC/SC, with 67% of trees alive at age 10 years.

In most provenance tests, seed sources from colder or drier climates survive the best no matter where they are planted, although they often grow slower than other sources (WELLS & WAKELEY 1966). In a loblolly pine provenance test with seed sources and plantings covering the entire north-south range in the center of the natural distribution, SLUDER (1980) found that northern sources definitely survived better than southern sources,

with no planting location by seed source interaction. The tenth-year survival in the current experiment generally follows the expectation that cold-climate sources survive better than warm-climate sources (Figure 2). The Fla × w source, which is the source from the warmest climate (in terms of minimum temperatures, Figure 1) survived the poorest, with just over 50% alive at age 10. The source from the coldest climate, NC\SC × w had the best survival at over 60%, and the LPL × w source was intermediate in both source climate and survival.

Survival in the interprovenance cross LPL × Fla was intermediate to that of LPL × w and Fla × w (Figure 2) and heterosis was not apparent (Table 3). Survival in the interprovenance cross LPL × NC\SC, on the other hand, was better than either LPL × w or NC\SC × w, and the heterosis statistic was positive and

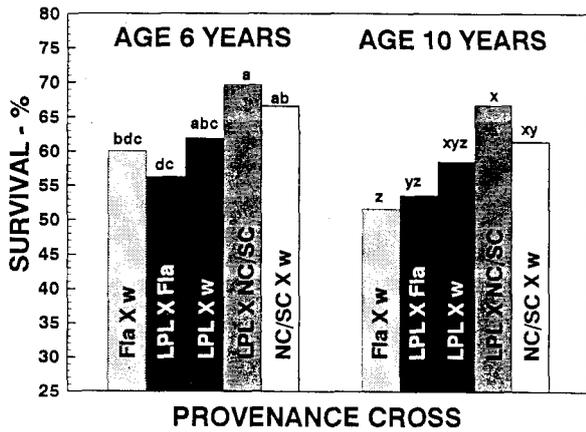


Figure 2 Field survival after 6 and 10 years of the interprovenance crosses planted at three locations. Bars topped by the same letter do not differ significantly according to Duncan's multiple range test at the 0.05 level of probability. Code for cross designation is in Table 1

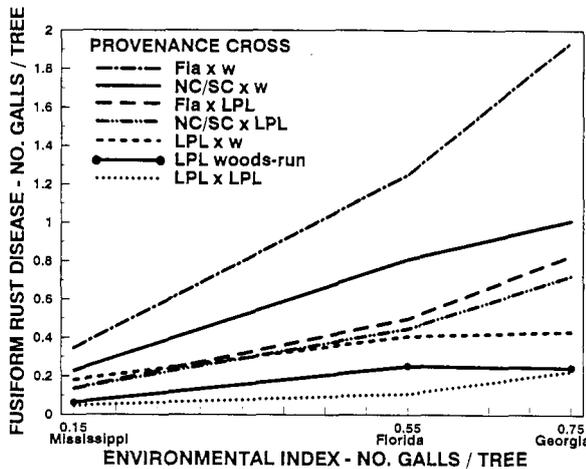


Figure 3 Plot of fusiform rust disease in interprovenance crosses of loblolly pine versus mean infection rates for three planting sites. See Table 1 for identification of crosses

significant in all three plantings.

**Fusiform rust.** The provenances and interprovenance crosses generally performed as expected with regard to fusiform rust disease (Figure 3). Although the planting location by interprovenance cross interaction was statistically significant ( $P = 0.04$ ), the rank of provenances for infection changed little across locations (Figure 3).

The most heavily galled provenance in all locations was the Fla x w source, averaging around 0.4 galls per tree in Mississippi, 1.2 galls per tree in Florida, and nearly 2 galls per tree in Georgia (Figure 3). The NC/SC x w cross had the second highest infection rate, averaging a little more than half as many galls per tree as the Fla x w source. Sources from coastal Carolina are not generally regarded as having much resistance to the

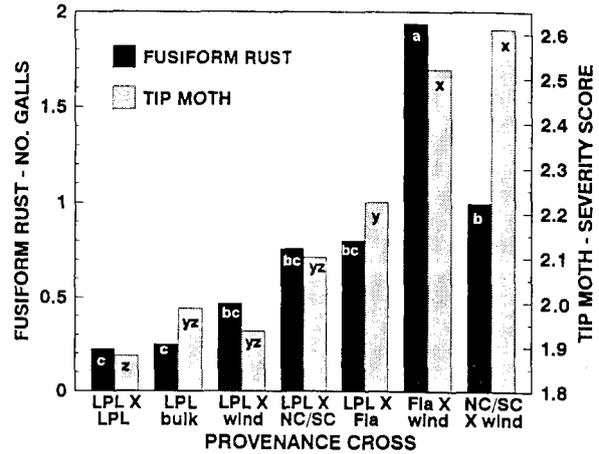


Figure 4 Tip moth infestation and fusiform rust disease in interprovenance crosses of loblolly pine planted in Georgia. Bars topped by the same letter do not differ from each other according to Duncan's multiple range test ( $P = 0.05$ ). See Table 1 for identification of crosses

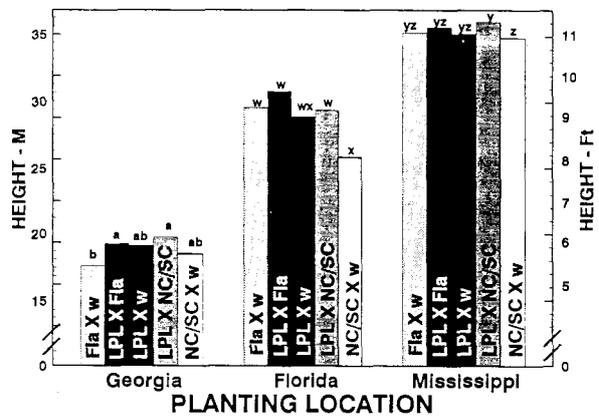


Figure 5 Tenth-year height of loblolly interprovenance crosses planted at three locations. Bars topped by the same letter do not differ from each other according to Duncan's multiple range test ( $P = 0.05$ ). See Table 1 for identification of the crosses

fusiform rust pathogen, but these sources are geographically close (Figure 1) to the resistant northeastern sources (WELLS & WAKELEY 1966), and therefore would be expected to be less susceptible than a source from Florida (SCHMIDTLING 1993). The LPL x LPL source was the least infected, as expected, averaging less than 0.2 galls per tree at all locations.

Infection rate in the interprovenance crosses LPL x NC/SC and LPL x Fla was generally intermediate to infection in the wind-pollinated provenances from which they were derived (Figure 3), but a little less than expected based on the mid-parent average. Heterosis values for rust infection were significant for four out of six planting location by interprovenance cross comparisons (Table 3). The LPL x Fla averaged from 0.06 to 0.38 fewer galls per tree than would be expected based on the average infection of the Fla x w and the LPL x

**Table 2** Least-squares analysis of variance for survival, height growth and plot volume at age 10, and fusiform rust infection at age 6, all plantings combined (Model [1]). SAS (1985) GLM procedure.

Effect	DF	Age 10 Survival		Age 10 Height		Age 10 Plot Volume		Age 6 Rust Infection	
		MS	P>F	MS	P>F	MS	P>F	MS	P>F
Location	2	9.574	0.0001	1945.89	0.0001	485198	0.0001	31.286	0.0001
Block (Location)	21	0.450	0.0001	3.46	0.0004	3396	0.0001	0.537	0.6305
Provenance Cross	6	1.047	0.0001	9.20	0.0001	9639	0.0001	15.123	0.0001
Provenance × Location	12	0.057	0.5461	4.92	0.0001	2878	0.0001	2.508	0.0001
Family in Provenance	69	0.451	0.0001	3.59	0.0001	4675	0.0001	2.314	0.0001
Family (Proven.) × Location	138	0.112	0.0001	2.92	0.0001	2281	0.0001	0.954	0.0001
Error	1575	0.063		1.44		882		0.617	

**Table 3** Apparent heterosis for interprovenance crosses for several measured traits. Heterosis is expressed as a percent deviation of the interprovenance cross from the mean of the two wind-pollinated parents on a plot mean basis for each replication (model [7])

Cross	Mississippi planting			Georgia planting			Florida planting			
	Planting	N	Mean heterosis <sup>a</sup>	Std. error	N	Mean heterosis	Std. error	N	Mean heterosis	Std. error
<b>LPL × Fla</b>										
Height – m	171	0.15*	0.068	86	0.19	0.12	146	0.56*	0.18	
Survival – %	200	1.0	2.17	200	-0.01	0.023	200	-4.6	2.6	
Volume – m <sup>3</sup> .ha <sup>-1</sup>	200	5.9	3.84	200	2.35	1.38	200	-1.87	3.47	
Rust-galls <sup>b</sup>	175	-0.11*	0.034	100	-0.30*	0.149	166	-0.38*	0.088	
<b>LPL × NC/SC</b>										
Height – m	188	0.32*	0.049	116	0.34	0.088	157	0.69	0.18	
Survival – %	200	8.1*2	1.98	200	4.8	2.4	200	7.5	2.3	
Volume – m <sup>3</sup> .ha <sup>-1</sup>	200	1.5*	3.17	200	4.69	1.46	200	15.3	3.12	
Rust-galls <sup>b</sup>	188	-0.06	0.03	123	-0.03	0.12	181	-0.18	0.07	

<sup>a</sup> Asterisk indicates that the probability is less than 0.05 that the mean heterosis is zero in a "T" test.

<sup>b</sup> The negative values for fusiform rust disease indicate less infection than the expected, *i.e.*, positive heterosis.

w at the three locations.

The heterosis values for fusiform rust infection may be misleading because of the nature of the control populations. The LPL × w source averaged higher in infection than the LPL × LPL or LPL bulk at all three locations (Figure 3). This is probably due to the location of the orchard compared to the origin of the orchard clones (Figure 1) and to pollen contamination. In a provenance trial where populations were intensively sampled across the state of Mississippi and adjoining states, there was a very strong gradient of fusiform rust disease in the seed sources across southeastern Louisiana and southern Mississippi (WELLS *et al* 1991). Fusiform rust disease infection of Livingston Parish, LA sources averaged 4% infection, similar to sources from west of the Mississippi River. Sources from 90 km east of Livingston Parish, in Washington Parish, the orchard

location, averaged 22% infection. Infection increased for sources from eastward of Washington Parish to nearly 50% near the Mississippi – Alabama border, about 200 km east of Livingston Parish.

Pollen contamination in mature seed orchards is substantial even where great care is exercised in establishing isolation zones (FRIEDMAN & ADAMS 1985). In Washington Parish, contaminating pollen would result in seedlings with substantially less resistance to fusiform rust disease than the mother trees from Livingston Parish. In comparing the LPL sources the effects of contamination are evident (Figure 4). Although the infection levels of the LPL sources was generally very low, the LPL × w source had more than 2 times as many galls per tree as the LPL × LPL controlled crosses. Over all plantings the source by planting location

interaction was not significant for this sub-set of the data.

Since infection of the LPL  $\times$  w crosses are higher than expected because of pollen contamination, the heterosis values for fusiform rust in Table 3 may be biased upwards (more heterosis).

**Tip moth.** The severity of tip moth attack in the Georgia planting significantly affected height at age 6. Those trees in the light (0 or 1) infestation classification averaged 9.9 ft tall, whereas those in the medium (2) classification averaged 8.7 feet tall. Those in the heavy infestation category (3) averaged only 7.5 feet in height. The univariate analysis of variance showed significant interprovenance cross and family within interprovenance cross variation for both fusiform rust infection and tip moth infestation (Table 4), indicating strong genetic control.

The pattern of variation in tip moth infestation is remarkably similar to the pattern for fusiform rust infection on a provenance basis (Figure 4). The LPL sources appear to be more resistant to tip moth attack just as they are more resistant to fusiform rust. The only serious departure from the positive relationship between tip moth infestation and fusiform rust infection is in the NC/SC  $\times$  wind source, which was very susceptible to tip moth, but relatively less susceptible to fusiform rust. Nevertheless, the partial correlation between tip moth attack and fusiform rust infection is substantial on a interprovenance cross basis ( $r = 0.867$ , Table 3).

This strong partial correlation coefficient as well as the data shown in Figure 4 support the contention that there is a cause and effect relationship between tip moth damage and fusiform rust disease, as has been proposed previously (HEDDEN *et al* 1991, POWERS & STONE 1988). This suggests a strong environmental basis rather than the genetic basis shown in the present study. However, the two environmentally based partial correlation coefficients, for replication and residual, are weak or negative (Table 3). The negative correlation

coefficient for replication ( $r = -0.149$ ) indicates a slight tendency for fusiform rust infection to be lower in those replications where tip moth attack is higher. The partial correlation coefficient for residual ( $r = 0.118$ ) indicates that there is only a weak positive relationship between tip moth attack and fusiform rust infection after provenance, family and replication effects are removed.

Rejecting a cause and effect hypothesis on the basis of partial correlation coefficients hardly seems justified, but other hypotheses may be tenable in explaining the nature of the relationship between these two damaging pests.

**Height and Volume.** SCHMIDTLING (1994) used yearly average minimum temperature at the seed source to predict relative growth resulting from seed movement. In general, those analyses showed that moving seed sources northward from areas with minimum temperatures of 5 °F (2.8 °C) warmer than the planting site result in the maximum gain over local sources. Moving seed sources northward more than 10 °F (5.5 °C) resulted in growth that was less than that of the local source. Moving seed sources from colder to warmer climates also resulted in growth less than expected from a local source. The growth of the wind-pollinated provenances in the present study generally followed these expectations, considering climate differences between the sources and the planting sites (Figures 1 and 5). At the Florida planting, the most tropical site, the Fla  $\times$  w source grew the tallest, averaging 9.2 m. The LPL  $\times$  w source, from a climate approximately 5° colder in minimum temperature than the planting site (Figure 1) averaged 9.0 m in height (Figure 5). The NC/SC source, from a climate at least 10 °F colder than the planting site, averaged only 8.1 m tall.

At the planting site with the lowest minimum temperature, central Georgia, differences among wind-pollinated provenances were small (Figure 5). The tallest trees were from the LPL  $\times$  w source at 5.9 m (Figure 5). The LPL source is from a climate that is

Table 4 Analysis of variance (SAS type III sums of squares) results for fusiform rust disease infection and tip moth infestation for the Georgia planting (model [2])

Source of variation	DF	Fusiform Rust Infection			Tip Moth Infestation			Rust/Moth
		M.S.	F	P>F	M.S.	F	P>F	Correlation
Replication	7	0.787	0.62	0.740	4.944	17.45	0.001	-0.149
Interprovenance Cross	6	12.288	9.66	0.001	2.807	9.91	0.001	0.837
Family (Provenance)	69	2.333	1.83	0.001	0.522	1.84	0.001	0.069
Residual	412	1.272			0.283			0.118

<sup>a</sup> The partial correlation coefficients are based on the type III sums of squares and cross products matrices from the multivariate analysis of variance.

about 5 °F warmer in minimum temperature (Figure 1). The NC/SC × w source, from a climate very similar in minimum temperature to the planting site, averaged 5.7 m tall. Moving the Fla × w source to the Georgia planting constitutes a climatic move of more than 10° northward, which appears to be more than the optimum, as this source was the shortest at 5.4 m.

At the climatically intermediate site, south Mississippi, the differences among the wind-pollinated sources were small and not significant statistically, but the mean heights followed expectations. The Fla × w source, from a climate about 5° warmer in minimum temperature than the planting site (Figure 1), was the tallest at 11.1 m (Figure 5). The LPL × w source, from a climate identical the planting site, was intermediate in height at 11.0 m, and the NC/SC × w sources, which are from climates averaging slightly colder in minimum temperature than the planting site, was shortest at 10.9 m.

Variation in survival heavily influenced the plot volume data, but in general plot volumes followed the same pattern as the height except at the Mississippi planting (Figure 6). The Fla × w source was among the best in height growth at the Mississippi location (Figure 5), but because of relatively poor survival this source ranked last in plot volume. Also, the Fla × w source had the highest volume at the Florida planting (Figure 6), even though it was not the tallest in this planting (Figure 5).

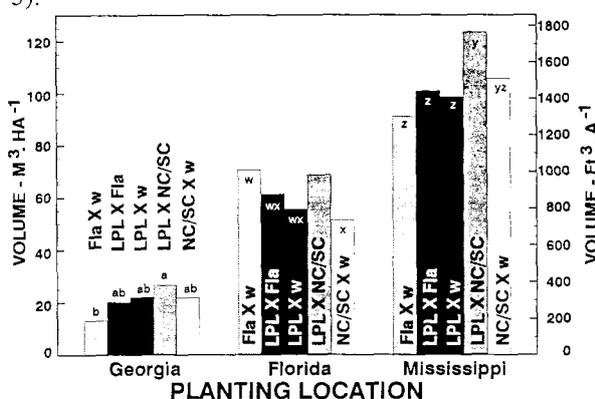


Figure 6 Tenth-year plot volumes of loblolly pine interprovenance crosses planted at three locations. Bars topped by the same letter do not differ from each other according to Duncan's multiple range test ( $P = 0.05$ ). See Table 1 for identification of the crosses

The interprovenance crosses in all cases exceeded the tallest of their wind-pollinated sources in height (Figure 5) although the differences were not statistically significant. The same was true for volume except for the LPL × Fla crosses planted in Georgia and Florida (Figure 6). The heterosis values computed from the mid-parent values for height were all positive, ranging from 0.15 m to 0.69 m, and were statistically significant

in five out of six comparisons (Table 3). The heterosis values were positive and significant for plot volume for the LPL × NC/SC crosses at all three locations.

Pollen contamination of the wind-pollinated sources would also bias heterosis values upward for 10-year height and volume, as it has for fusiform rust resistance. The differences in height among the various LPL × sources are small, but they can be used to provide an estimate of pollen contamination. The LPL × LPL crosses average 9.05 m tall over the three planting sites. The LPL woods-run sources average 8.59 m, which provides an estimate of genetic gain of 5.3%. The LPL × w source averages 8.85 m tall, which represents a gain of only 3.0%. This reduction in gain  $\{(5.3-3.0)/5.3\} = 43\%$  is consistent with a contamination rate of 86%. These calculations assume that the contaminating pollen in Washington Parish would have the same growth potential as Livingston Parish pollen (WELLS *et al* 1991).

It is possible to estimate what heterosis values would be if controlled-pollinated sources were used to calculate the mid-parent comparison. If we use the mean of the LPL × LPL crosses from the diallel rather than LPL × w, and add 2.3% to the means of Fla × w and NC/SC × w, the heterosis values from Table 3 are reduced, but remain positive for all six comparisons. For instance, the 0.69 m value obtained for heterosis in the LPL × NC/SC cross in the Florida planting becomes 0.41 m, still differing from zero by more than two standard deviations. If the mechanism for heterosis depends upon combining genotypes that are genetically quite different, then we might expect that the cross involving the two populations separated by the greatest geographic distance would show the greatest heterosis. This is exactly what we observed for growth, survival, and volume (Table 3). The LPL and NC/SC population are separated by about 1,200 km distance whereas the LPL and Fla populations are separated by only about 800 km. For all traits except fusiform rust disease, the LPL × NC/SC crosses had higher heterosis values than the LPL × Fla crosses at all locations. The situation for fusiform rust disease is undoubtedly complicated by geographic variation in the population structure of the pathogen.

#### Families Within Provenance

The plantings were analyzed separately because of interactions (Table 2). Certainly, genotype × environment variances are important in estimating heritabilities, but in this case the interactions contain a strong effect of differences of climate among the seed sources and planting sites in addition to interactions due to physical site effects. At least one of the seed transfers, planting

**Table 5** Analysis of variance for height at age 10 for the diallel crosses and factorials for three plantings

Cross Source of variance	DF	Planting Site					
		Mississippi		Florida		Georgia	
		M. S.	F	M. S.	F	M. S.	F
<b>LPL × LPL</b>							
Replication	7	0.44		5.29		0.76	
GCA	4	1.41	3.60	12.01	0.89	1.78	5.27
SCA	5	0.39	1.19	13.47	4.76	0.34	0.41
Error	63	0.33		2.83	(57 DF)	0.82	(47 DF)
<b>LPL × NC/SC</b>							
Replication	7	1.73		6.18		1.91	
Female	4	1.76	2.55	12.89	4.86	2.95	3.44
Male	4	1.63	2.35	9.15	3.45	0.61	0.71
Female × male	16	0.69	1.93	2.65	0.84	0.86	0.90
Error	160	0.36		3.15	(137 DF)	0.96	(116 DF)
<b>LPL × Fla</b>							
Replication	7	0.90		3.54		0.82	
Female	4	1.86	3.32	17.81	5.99	1.56	3.10
Male	4	2.85	5.09	11.07	3.73	1.76	3.51
Female × male	16	0.56	1.80	2.97	0.96	0.50	0.77
Error	160	0.31		3.09	(152 DF)	0.65	(137 DF)

**Table 6** Narrow-sense heritability estimates and standard errors computed using plot means from the LPL X LPL diallels and interprovenance cross factorials at three planting locations

Trait	Planting Location	Cross					
		LPL × LPL		LPL × NC/SC		LPL × Fla	
		h <sup>2</sup> (standard error)					
Height (6 Years)	Georgia	0.30	(0.37)	0.90	(0.36)	0.84	(0.29)
	Florida	0	(0.13)	0.90	(0.22)	0.85	(0.21)
	Mississippi	0	(0.12)	0.61	(0.23)	0.75	(0.15)
Height (10 year)	Georgia	0.70	(0.23)	0.90	(0.35)	0.87	(0.17)
	Florida	0	(0.13)	0.93	(0.20)	0.95	(0.20)
	Mississippi	0.70	(0.26)	0.72	(0.22)	0.80	(0.13)
Plot Volume	Georgia	0.11	(0.11)	0.65	(0.44)	0.90	(0.24)
	Florida	0	(0.15)	0.94	(0.28)	0.89	(0.30)
	Mississippi	0	(0.12)	0.88	(0.14)	0.74	(0.15)
Fusiform Rust	Georgia	0	(0.14)	0.96	(0.19)	0.69	(0.43)
	Florida	0.30	(0.21)	0.84	(0.28)	0.91	(0.31)
Tip Moth	Georgia	0.89	(0.26)	0	(0.76)	0.71	(0.42)

a Florida source in Georgia (Figure 1), would exceed prudent seed transfer guidelines (SCHMIDLING 1994).

Family means varied considerably for all characters measured (means for height at age 10 and rust infection are shown in Appendices 1 to 3). F statistics from the

analyses of variance for family effects also varied considerably by cross type and location (Table 5). The different sites and climates represented in the plantings obviously had differing effects on the expression of heritable traits.

Heritabilities computed in this study provided a means of comparing genetic variation among inter- and intraprovenance crosses, rather than giving valid estimates of the heritabilities themselves. The required assumption of randomness is open to question.

Narrow-sense heritability estimates varied substantially by interprovenance cross type (Table 6). In all but two out of 24 comparisons, the wide-cross factorials yielded higher heritability estimates than the LPL diallels. The exceptions were for tip moth infestation, where the heritability estimate from the LPL diallel was 0.89 compared to 0 for the LPL  $\times$  NC/SC factorials and 0.71 in the LPL  $\times$  Fla factorial.

These findings seem to contradict conventional wisdom that F<sub>1</sub> hybrids are usually very uniform. This is probably true **within** a cross but would not be true when comparisons are made among F<sub>1</sub> crosses.

## CONCLUSIONS

Interprovenance crossing appears to be a feasible method for incorporating desirable traits such as resistance to disease and insects into fast-growing or hardy provenances in loblolly pine. Evidence presented here indicates also that positive heterosis may be a reality in such crosses, and that interprovenance crossing may be a reasonable method for increasing genetic diversity in breeding programs. Many breeding programs are using, or considering using, supplemental mass pollination (SMP) for operational seed production in orchards. This is used primarily to increase gain by decreasing pollen contamination from outside the orchard. With the choice of the appropriate pollen, SMP could also be used to produce interprovenance crosses for operational planting.

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Appendix 1 Height after 10 years and numbers of fusiform rust galls after 6 years for controlled cross and wind-pollinated progeny of select trees from 3 different provenances: Plantation in Dodge County, Georgia

Male	Female / Livingston Parish Clones						Wind-Pollinated	Heterosis
	2-1	2-3	5-3	5-4	5-7	Mean		
	Height - m							
FM-7	6.55	6.62	5.18	5.92	6.21	6.10	5.94	0.24
FM-8	6.75	6.59	5.61	6.15	6.59	6.34	6.01	0.53
FM-12	6.59	6.29	5.26	6.04	5.99	6.03	5.43	0.36
8-61	6.40	6.36	6.48	7.01	6.86	6.62	5.52	0.60
8-73	6.59	5.64	5.83	5.49	5.92	5.89	5.53	0.01
601	5.83	6.25	5.97	5.70	5.85	5.92	5.36	0.28
602	5.72	7.42	4.42	5.97	6.10	5.93	5.31	0.15
603	6.36	6.36	6.10	6.10	6.20	6.22	5.99	0.22
604	6.29	6.40	5.14	5.33	5.72	5.78	5.33	0.06
605	5.98	5.97	6.53	5.03	5.18	5.74	5.08	0.24
2-3	6.66	-	-	-	-	Livingston Parish Woods-run = 6.06		
5-3	7.05	6.25	-	-	-			
5-4	6.89	5.87	6.65	-	-			
5-7	6.63	5.92	6.25	5.92	-			
Wind	6.67	5.70	5.70	5.79	6.14			

Male	Female						Wind-Pollinated	Heterosis
	2-1	2-3	5-3	5-4	5-7	Mean		
	Galls / tree							
FM-7	0.66	0.14	1.38	0.14	0.53	0.57	0.83	-0.17
FM-8	0.04	0.75	0.68	0.17	0.58	0.44	0.38	0.11
FM-12	1.71	1.00	2.44	0.07	1.57	1.36	1.67	0.44
8-61	0.08	0.12	1.43	0.05	1.17	0.57	1.44	-0.52
8-73	0.47	0.08	1.68	0.57	0.60	0.68	0.71	0.08
601	0.74	0.00	1.00	0.57	0.00	0.46	1.00	-0.02
602	0.35	0.00	3.00	0.29	0.00	0.73	2.29	-0.78
603	1.17	0.48	1.75	0.75	0.39	0.91	2.17	-0.38
604	0.95	0.93	1.26	0.38	1.61	1.03	2.13	0.00
605	0.97	0.21	1.25	0.00	2.67	1.02	2.14	-0.30
2-3	0.17	-	-	-	-	Livingston Parish Woods-run = 0.25		
5-3	0.43	0.04	-	-	-			
5-4	0.00	0.09	1.31	-	-			
5-7	0.07	0.14	0.00	0.00	-			
Wind	0.91	0.30	0.50	0.00	0.45			

Appendix 2 Height after 10 years and numbers of fusiform rust galls after 6 years for controlled cross and wind-pollinated progeny of select trees from 3 different provenances: Plantation in Harrison County, Mississippi

Male	Female / Livingston Parish Clones						Wind-Pollinated	Heterosis
	2-1	2-3	5-3	5-4	5-7	Mean		
	Height - m							
FM-7	11.2	11.2	10.8	11.2	11.8	11.2	10.8	0.13
FM-8	12.1	11.8	12.1	11.3	12.4	11.9	10.9	0.46
FM-12	11.5	11.1	10.5	11.4	11.2	11.1	11.5	0.17
8-61	12.1	11.4	12.2	11.5	11.8	11.8	11.2	0.39
8-73	11.4	11.4	11.8	11.2	11.8	11.5	10.6	0.45
601	11.4	10.8	11.2	11.4	11.8	11.3	10.2	0.53
602	11.0	10.7	11.1	8.9	11.4	10.6	11.2	-0.09
603	11.7	11.7	11.4	11.2	11.2	11.4	9.6	0.40
604	11.0	10.9	11.7	11.3	12.2	11.4	11.1	0.18
605	10.7	11.3	10.3	10.5	11.6	10.9	11.5	-0.40
2-3	11.2	-	-	-	-	Livingston Parish Woods-run = 10.8		
5-3	11.8	11.1	-	-	-			
5-4	11.4	11.0	11.4	-	-			
5-7	12.0	12.2	11.6	12.2	-			
Wind	11.4	10.7	11.1	10.6	11.5			

Male	Female						Wind-Pollinated	Heterosis
	2-1	2-3	5-3	5-4	5-7	Mean		
	Galls / tree							
FM-7	0.13	0.03	0.39	0.08	0.17	0.16	0.03	0.07
FM-8	0.23	0.13	0.04	0.03	0.00	0.09	0.25	-0.11
FM-12	0.16	0.15	0.82	0.13	0.09	0.27	0.29	0.05
8-61	0.13	0.00	0.19	0.00	0.11	0.09	0.31	-0.16
8-73	0.10	0.06	0.03	0.09	0.13	0.08	0.25	-0.14
601	0.16	0.04	0.17	0.00	0.00	0.07	0.43	-0.22
602	0.15	0.03	0.17	0.00	0.27	0.12	0.61	-0.25
603	0.00	0.06	0.27	0.31	0.20	0.17	0.18	0.01
604	0.17	0.03	0.13	0.00	0.04	0.73	0.16	-0.08
605	0.13	0.21	0.81	0.00	0.00	0.23	0.36	-0.02
2-3	0.15	-	-	-	-	Livingston Parish Woods-run = 0.06		
5-3	0.00	0.06	-	-	-			
5-4	0.00	0.00	0.00	-	-			
5-7	0.00	0.00	0.25	0.00	-			
Wind	0.46	0.00	0.31	0.00	0.03			

Appendix 3 Height after 10 years and numbers of fusiform rust galls after 6 years for controlled cross and wind-pollinated progeny of select trees from 3 different provenances: Plantation in Marion County, Florida.

Male	Female / Livingston Parish Clones						Wind-Pollinated	Heterosis
	2-1	2-3	5-3	5-4	5-7	Mean		
	Height - m							
FM-7	10.06	8.72	8.84	7.73	7.43	8.56	7.66	0.26
FM-8	10.02	9.56	9.68	8.08	7.67	9.00	9.18	0.15
FM-12	10.67	9.75	9.58	10.32	8.89	9.84	7.97	1.37
8-61	9.60	9.98	9.53	8.84	9.88	9.57	8.84	0.61
8-73	9.53	10.10	8.57	7.52	7.70	8.68	6.40	1.25
601	10.13	9.94	9.45	10.33	10.21	10.01	9.06	0.90
602	10.43	11.06	9.60	9.70	10.01	10.16	10.62	0.24
603	9.71	10.25	10.80	7.71	8.61	9.42	9.53	0.42
604	9.14	10.06	9.26	7.71	7.96	8.83	8.58	0.14
605	10.40	10.49	10.28	8.60	8.88	9.73	8.14	1.20
2-3	9.68	-	-	-	-			
5-3	9.56	9.07	-	-	-			
5-4	9.58	9.93	10.58	-	-			
5-7	8.65	9.75	9.09	5.75	-			
Wind	10.44	9.41	7.32	8.14	9.49			
							Livingston Parish Woods-run = 8.71	

Male	Female						Wind-Pollinated	Heterosis
	2-1	2-3	5-3	5-4	5-7	Mean		
	Galls / tree							
FM-7	0.15	0.31	0.84	0.44	0.24	0.40	0.65	-0.27
FM-8	0.06	0.53	0.33	0.00	0.00	0.18	0.46	-0.22
FM-12	0.30	1.11	1.41	0.00	0.24	0.62	0.94	-0.07
8-61	0.08	0.13	1.55	0.32	1.50	0.72	1.50	-0.25
8-73	0.03	0.08	0.94	0.00	0.57	0.32	0.49	-0.11
601	0.74	0.25	0.67	0.08	0.11	0.37	0.22	0.12
602	0.34	0.95	0.50	0.11	0.29	0.44	1.45	-0.52
603	0.29	0.67	1.81	0.04	0.97	0.76	2.01	-0.50
604	0.29	0.58	0.57	0.04	0.33	0.36	1.55	-0.64
605	0.13	0.63	1.38	0.00	0.14	0.46	1.02	-0.28
2-3	0.03	-	-	-	-			
5-3	0.00	0.40	-	-	-			
5-4	0.00	0.00	0.13	-	-			
5-7	0.06	0.41	0.05	0.00	-			
Wind	0.08	1.23	0.36	0.00	0.36			
							Livingston Parish Woods-run = 0.25	