A Progeny Test of (Shortleaf x Loblolly) x Loblolly Hybrids to Produce Rapid-Growing Hybrids Resistant to Fusiform Rust

By T. La Farge and J. F. Kraus[1])

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Abstract

Shortleaf × loblolly pine hybrids were produced to combine the high resistance of shortleaf pine to fusiform rust with the rapid growth rate of loblolly pine and were compared in a 5-year-old progeny test. Progeny of selected F_2 hybrids backcrossed to loblolly pine were significantly more rust resistant than loblolly but equalled, and in many backcrosses exceeded, it in growth rate. Likewise, F_1 hybrids and progeny of open-pollinated F_2 hybrids were significantly faster growing than shortleaf pine but retained almost as high a level of resistance to fusiform rust.

Key words: Backcross, *Pinus echinata, P. taeda, Cronartium quercuum* f. sp. *fusiforme*, interspecific hybridization, rust resistance, rapid growth.

Zusammenfasung

Pinus echinata × *taeda* Hybriden wurden erzeugt, um die hohe Resistenz von *Pinus echinata* gegen Fusiform-Rost mit der schnellen Wachstumsrate von *Pinus taeda* zu kombinieren, und in einer jetzt 5 jährigen Nachkommenschaftsprüfung verglichen. Eine Nachkommenschaft selektierter, mit *Pinus taeda* zurückgekreuzter F_2-Hybriden war signifikant stärker rostresistent als *Pinus taeda*, aber vergleichbar und bei manchen Rückkreuzungen besser im Wachstum. Vergleichbar damit sind F_1-Hybriden und eine Nachkommenschaft frei abgeblühter F_2-Hybriden signifikant schnellwüchsiger als *Pinus echinata*. Sie behielten aber stets einen hohen Grad an Resistenz gegen Fusiform -Rost bei.

Introduction

Although early attempts at interspecific hybridization in the southern pines have provided information on crossabilities (Critchfield, 1963) and taxonomic relationships, they have produced little evidence of heterosis. Instead F_1 hybrids have usually proved to be intermediate for most economic traits. However, as Schmitt (1968) has demonstrated, hybridization and backcrossing in advanced generations can be used as a means of combining desirable traits from both parent species into a new strain which can then be used to advantage in a tree breeding program. Similar conclusions have been reached by Sluder (1970), La Farge and Kraus (1975, 1977), and Wells *et al.* (1978).

Our orginal study of 30 seed lots representing three hybrid types and both parent species was designed to test advanced - generation hybrids, principally in the form of *(Pinus echinata × taeda) × taeda* hybrids, to determine the feasibility of combining the resistance to fusiform rust *(Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme)* Burdsall and Snow, 1977) of shortleaf pine *(P. echinata* Mill.) with the rapid growth rate of loblolly pine *(P. taeda* L.) (La Farge and Kraus, 1977). Third-year results were reported in 1977, and this paper reports 5th-year results.

[1]) Plant Geneticist and Principal Plant Geneticist, respectively, USDA Forest Service, P. O. Box 5106, Macon, Georgia 31208. Land and facilities donated by the Georgia Forestry Commission and Georgia Kraft Company are gratefully acknowledged.

Procedure

Plant material grown for the study included:

- Group 1, open-pollinated shortleaf.
- Group 2, shortleaf × loblolly F_1 hybrids.
- Group 3, progeny of wind-pollinated shortleaf × loblolly F_2 hybrid selections (F_2 selections).
- Group 4, progeny of selected shortleaf × loblolly F_2 hybrids backcrossed to loblolly plus trees progeny-tested for superior growth rate (Select backcrosses).
- Group 5, open-pollinated loblolly.

Criteria for selection among the best of the shortleaf × loblolly F_2 hybrids used to produce the select backcrosses (Group 4) were discussed in La Farge and Kraus (1975). In summary, the F_2 hybrids were selected when a one-acre-block planting of 425 of these trees on the Hitchiti Experimental Forest in Jones County, Georgia, was thinned to 40 select trees. These trees were selected on the basis of superiority in height, diameter at breast height, and stem form.

All 425 hybrids were free of fusiform rust galls in spite of the fact that each of 10 loblolly pine vounteers found within the block was heavily galled. Further, the plantation was surrounded by stands of old-field loblolly pine which were also heavily infected.

Because of the location of the Hitchiti, the male parentage of the wind-pollinated F_2 hybrids is open to question. In addition to loblolly, there is a minor component of shortleaf pine in the surrounding stands. Flowering times of the hybrids are variable, but they range from late March to late April, a period which almost completely overlaps flowering times of shortleaf but only briefly overlaps the flowering period for loblolly. Hence, the male parentage seems more likely to be either shortleaf or the hybrids themselves.

The parents of these 40 F_2 hybrid selections were F_1 hybrids from a controlled cross between a shortleaf pine form North Carolina and a loblolly pine from Virginia growing in the Eddy Arboretum, Placerville, California. These F_1 hybrids were grown in a test planting far out of their range at the Institute of Forest Genetics in Placerville, so that pollen for the F_2's came from the F_1 hybrids in that planting or from loblolly or shortleaf trees in the other experimental plantings established by the Institute.

The seeds were germinated in the laboratory in December 1973, and within 2 days after germination each seedling was transplanted to a peat pot in the greenhouse. The peat pots were placed in ceder flats to form a 4 × 5 = 20-seedling rectangular plot. Flats for this study occupied six greenhouse benches, each bench representing one replication.

The seedlings were outplanted during the last week of June 1974 on a typical old-field site on the Upper Coastal Plain in Houston County, Georgia. The use of peat pots made late planting possible. The test was arranged in a randomized complete block design with five replications. There were 30 seed lots and 16 trees in each square plot. Four of the six greenhouse replicates were outplanted intact with the four extra seedlings in each plot used for border rows. Because of shortages in some plots, the fifth and sixth replicates were merged into one when outplanted. After three growing seasons, survival was 94.7 percent; after five, 91.5

For 5th-year data, the plantation was measured in November 1978. Height, crown width:height ratio, and the numbers or stem and branch galls were recorded for each tree.

In addition to the above variables, the within-plot coefficients of variation for each trait were analyzed. For this analysis, the number of galls per tree was transformed to $\sqrt{X + 0.5}$, and the coefficients of variation were transformed to the arcsin $\sqrt{\text{percent}}$. Differences among groups and among within-group seed lots tested by analysis of variance were planned orthogonal comparisons.

Results and Discussion

The select backcrosses, Group 4, had far fewer galls per tree (1.57) than the loblolly check (8.97, Group 5), yet these groups did not differ significantly in average height (*Table 1*). Moreover, the high level of rust infection on the loblolly check is typical of that on other loblolly pines in test plantations at the Houston County location.

Table 1. — Summary of 5th-year measurements in a progeny test of shortleaf × loblolly pine hybrids in Houston County, Georgia.

Groups and seed lots in Groups	Height (m)	No. galls per tree	Crown width: height ratio (%)
Group 1 (Progeny of wind-pollinated shortleaf)			
TVA x Wind	2.7	0.01	48.5
Z15 x Wind	2.7	.00	48.6
Piedmont Commerical	2.4	.00	47.5
Mean	2.6	.00	48.2
Group 2 (F_1 hybrids)			
Z15 x 536 [1]	3.2	.05	50.3
Z15 x 541	3.2	.09	51.3
Z15 x 631	3.0	.36	55.7
Mean	3.1	.16	52.4
Group 3 (Progeny of wind-pollinated F_2 hybrids)			
HH 5 x Wind	3.0	.01	52.0
HH 6 x Wind	3.0	.93	56.4
HH 8 x Wind	3.2	.01	47.8
HH 15 x Wind	3.1	.97	54.7
HH 20 x Wind	3.0	.17	49.3
Mean	3.1	.42	52.0
Group 4 (Progeny of F_2 hybrids backcrossed to loblolly)			
HH 5 x 520	3.5	.82	59.1
HH 5 x 624	3.8	.20	50.5
HH 6 x 515	3.4	5.53	54.6
HH 6 x 617	3.5	1.76	54.9
HH 8 x 520	3.7	.98	54.3
HH 8 x 600	3.7	1.51	48.2
HH 11 x 515	3.4	.88	51.4
HH 11 x 607	3.0	1.29	55.6
HH 13 x 518	3.4	2.77	52.7
HH 13 x 603	3.5	3.36	51.5
HH 15 x 541	3.5	.87	50.7
HH 15 x 600	3.4	1.58	46.4
HH 17 x 518	3.7	.34	52.4
HH 17 x 541	3.3	.47	55.7
HH 19 x 607	3.5	.29	55.3
HH 19 x 624	3.5	.08	46.9
HH 30 x 603	3.5	3.93	54.2
Mean	3.5	1.57	52.6
Group 5 (Progeny of wind-pollinated loblolly)			
GCIA 2G-9-5-3	3.4	9.02	56.3
GCIA 2G-65-D1	3.5	8.92	58.9
Mean	3.4	8.97	57.6

1) Parent trees designated "HH" are F_2 hybrids; those represented by 3-digit numbers are loblolly.

Table 2. — Results of analyses of differences among 5-year-old shortleaf × loblolly pine hybrids and their parent species.

Source of variation	Degrees of freedom	Mean squares for: Height	Galls per tree	Crown width: height ratio
Block	4	58.26**1)	0.35**	86.69**
Progeny	29	54.90**	1.65**	62.87**
Within Group 1 2)	2	14.81	.00	1.95
Within Group 2	2	4.39	.01	40.82
Within Group 3	4	3.41	.09	65.02**
Within Group 4	16	17.14*	.74**	57.34**
Within Group 5	1	2.04	.00	17.27
Group 1 vs. Groups 2 + 3	1	276.20**	.10	173.50
Group 2 vs. Group 3	1	6.66	.04	1.61
Groups 1 + 2 + 3 vs. Groups 4 + 5	1	977.23**	11.27**	147.15**
Group 4 vs. Group 5	1	3.71	24.23**	22.06**
Block x Progeny (Error)	116	7.87	.06	15.19

1) * Significant at 0.05 level.
** Significant at 0.01 level.

2) Group 1 = progeny of wind-pollinated shortleaf.
Group 2 = F_1 hybrids.
Group 3 = progeny of wind-pollinated F_2 hybrids.
Group 4 = progeny of F_2 hybrids backcrossed to loblolly.
Group 5 = progeny of wind-pollinated loblolly.

Within Group 4, differences among families were significant for both traits. Four of these families exeeded the loblolly controls in height, and three of these fast growers had fewer galls per tree than the Group 4 mean. Only two of these families, HH11 × 607 and HH17 × 541, were outgrown by the loblolly controls, and no Group 4 family had as many galls per tree as did the loblolly controls.

The gains in the select backcross hybrids (Group 4) are the most meaningful because it is these progeny of F_2 hybrids backcrossed to loblolly that have the greatest potential for combining the desired growth rate and resistance to fusiform rust in a new strain of loblolly pine. However, gains in growth and resistance to rust were not limited to them. The F_1 hybrids (Group 2) and the progeny of the wind-pollinated F_2 hybrids (Group 3) were significantly taller than the shortleaf check (Group 1). Conversely, Groups 1, 2 and 3 collectively had a significantly lower number of galls per tree than did Groups 4 and 5. Hence, Groups 2 and 3 have a significant growth rate advantage over the shortleaf controls, and we may deduce that they probably have a rust resistance advantage over the loblolly controls, though this comparison was not tested statistically.

Some of the differences between and within groups for the crown width: height ratio were also highly significant (*Table 2*). This variation paralleled that of height, the shortleaf having narrow crowns, the loblolly checks wide crowns, and the hybrid groups consistently intermediate, except for some variation within groups. Although this trait has no bearing on the recombination of growth rate and resistance to fusiform rust, it serves to help distinguish the groups, and it may be useful for purposes of identifying the parental origins of individuals or groups in subsequent generations.

A major theoretical problem with hybrid breeding is that of segregation in the F_2 and subsequent generations. In a polygenic system we expect the variability of the F_2

and F_3 generations to be greater than either the F_1 or parental generations. At least, this is the expection if the parents are inbred and relatively homozygous, which probably is not the case with outcrossing species such as shortleaf and loblolly pines. In any case, in our example the F_2 selections (Group 3) and select backcrosses (Group 4) are two different kinds of F_3 hybrids. F_2 hybrids were not tested in this study. According to genetic theory, the variation within each F_3 family is less than the variation of the F_2 but greater than the variation of the F_1 or parental generations (MATHER and JINKS, 1971).

This variation is additive genetic variation, which means that it is heritable. Hence, the F_3 provides an opportunity to select the best families and trees within the best families to reduce the variability of the desired traits. However, this study was not designed to answer the question of whether the progeny of F_3 selections will be true breeding. The answer is probably a negative one, but by intensive selection it should be possible to accelerate the recombination of rapid growth rate with rust resistance in the same trees. To investigate the relative trends of variation due to segregation in this study, within-plot coefficients of variation for each seed lot for each trait were analyzed. Results are summarized in *Table 3*, and orthogonal comparisons are given in *Table 4*.

According to Mendelian principles, we should expect smaller coeffecients in the F_1 hybrids (Group 2) than in progeny of wind-pollinated F_2 hybrids (Group 3), which represent a putative F_3 generation. Only for numbers of galls per tree were coefficients of variability significantly greater in the F_3 than in the F_1 and this was true of both kinds of F_3 hybrids: The F_2 selections and select backcrosses. The high coefficients in the loblolly check may be due to natural variation within that species. For height and crown width: height ratio, there were no significant differences between the coefficients of F_1 hybrids and the F_2 selectinos (Groups 2 and 3). It must be said, however, that the flowering times of the F_2 selections (Group 3) overlap much more with shortleaf than they do with loblolly. Hence, these trees may be mostly natural backcrosses to the shortleaf parent, which would tend to reduce variability below that of a true F_3.

The low variability in Groups 1 and 2 for the number of galls per tree is due the absence of infection in the shortleaf population and the very low rate of infection in the F_1 hybrids. It should be noted that this low infection rate in the F_2's suggests nearly complete dominance for the genes conveying resistance. However, the relatively high degree of within-plot variability in the backcrosses of Group 4 provides ample opportunity for selection for resistance to rust within the backcross families.

As stated above, the F_2 hybrids used as the donor parents in the backcrossing scheme, and from which the wind-pollinated "F_2" progenies of Group 3 were derived, were not variable with respect to rust resistance: they had no rust at all. Many people doubt the efficacy of hybridization between loblolly and shortleaf on the grounds that advanced generations will segregate and only parental types will survive. The results of this study do not support such concerns, but we have no conclusive explanation for the apparent lack of segregation for rust resistance in the F_2 generation. Possibly this result is an artifact of the very narrow genetic base of the F_2 population.

Table 3. — Summary of the within-plot coefficients of variation of the three principal measurements in a progeny test of shortleaf × loblolly pine hybrids at age 5 in Houston County, Georgia.

Groups and seed lots in groups	Coefficient of variation for: Height (%)	Galls per tree (%)	Crown width: height ratio (%)
Group 1 (Progeny of wind-pollinated shortleaf)			
TVA x Wind	22.0	3.5	22.3
Z15 x Wind	19.2	.0	21.1
Piedmont Commercial	21.6	.0	20.3
Mean	20.9	1.2	21.2
Group 2 (F_1 Hybrids)			
Z15 x 536 [1])	20.6	11.6	19.2
Z15 x 541	13.9	8.7	14.6
Z15 x 631	18.1	18.0	17.2
Mean	17.5	12.8	17.0
Group 3 (Progeny of wind-pollinated F_2 hybrids)			
HH 5 x Wind	18.4	3.7	18.5
HH 6 x Wind	13.8	55.4	23.3
HH 8 x Wind	18.6	3.5	16.9
HH 15 x Wind	20.8	56.4	17.4
HH 20 x Wind	14.5	15.5	13.8
Mean	17.2	26.9	18.0
Group 4 (Progeny of F2 hybrids backcrossed to loblolly)			
HH 5 x 520	12.8	41.3	18.4
HH 5 x 624	12.4	31.0	15.7
HH 6 x 515	17.7	52.7	17.0
HH 6 x 617	14.4	58.6	17.8
HH 8 x 520	13.9	52.3	15.5
HH 8 x 600	14.0	64.0	14.4
HH 11 x 515	24.6	42.2	16.8
HH 11 x 607	22.5	51.1	14.6
HH 13 x 518	14.0	51.8	13.0
HH 13 x 603	15.0	72.7	14.0
HH 15 x 541	11.2	48.4	17.1
HH 15 x 600	12.1	41.5	12.9
HH 17 x 518	14.8	38.2	15.6
HH 17 x 541	18.9	36.7	12.7
HH 19 x 607	9.6	35.7	17.0
HH 19 x 624	14.6	16.0	15.2
HH 30 x 603	14.0	53.5	13.4
Mean	15.1	46.3	15.4
Group 5 (Progeny of wind-pollinated loblolly)			
GCIA 2G-9-5-3	16.6	48.1	17.8
GCIA 2G-65-D1	14.4	42.7	16.8
Mean	15.5	45.4	17.3

[1]) Parent trees disignated "HH" are F_2 hybrids; those represented by 3-digit numbers are loblolly.

The general level of infection of fusiform rust increased greatly in Groups 4 and 5 between 3rd-year and 5th-year measurements. In Group 4, the average number of galls per tree increased by 0.32 galls (37.2 percent), and in Group 5 it increased by 1.62 galls (135 percent). The increases in Groups 1, 2, and 3 were 0.0, 0.4, and 0.11 galls (0, 5, and 15 percent) respectively. Hence, the data obtained at age 5 represent a much better test for resistance than do those taken at age 3.

Some other changes also occurred within groups, but these are best represented by correlations shown in *Table 5*. The correlations for Groups 1 and 2 are omitted because they have only 1 degree of freedom. However, the correlations based on groups, seed lots, and seed lots within Group 3 and 4 indicate a very strong agreement between ages 3 and 5 for both height and number of galls per tree.

Table 4. — Results of analyses of differences among the within-plot coefficients of variation of 5-year-old shortleaf × loblolly pine hybrids and their parent species.

Source of variation	Degree of freedom	Mean squares of coefficients of variation for: Height	Galls per tree	Crown width: height ratio
Block	4	52.94* [1]	619.87**	9.38
Progeny	29	40.97**	1,194.24**	19.06**
Within Group 1 [2]	2	4.54	28.09	1.34
Within Group 2	2	35.97	57.55	14.86
Within Group 3	4	24.48	1,809.71**	31.21*
Within Group 4	16	42.42**	376.77**	10.15
Within Group 5	1	8.72	28.63	1.68
Group 1 vs. Groups 2 + 3	1	72.51*	2,430.12**	70.55**
Group 2 vs. Group 3	1	.47	854.95*	5.05
Groups 1 + 2 + 3 vs. Groups 4 + 5	1	243.84**	17,880.08**	141.21**
Group 4 vs. Group 5	1	3.90	.70	14.57
Block x Progeny (Error)	116	17.56	164.59	9.03

[1]) * Significant at 0.05 level.
** Significant at 0.01 level.

[2]) Group 1 = progeny of wind-pollinated shortleaf.
Group 2 = F_1 hybrids.
Group 3 = progeny of wind-pollinated F_2 hybrids.
Group 4 = progeny of F_2 hybrids backcrossed to loblolly.
Group 5 = progeny of wind-pollinatet loblolly.

Conclusions

These results lend support to the idea that desirable traits can be combined by means of backcrossing shortleaf × loblolly pine hybrids with fast-growing loblolly genotypes. In the present study, F_2 hybrids were backcrossed to loblolly pine plus trees, and most of the offspring were rust-resistant fast-growing hybrids. Actually, these progeny of select backcrosses to loblolly were not morphologically distinguishable from loblolly and effectively represent a rust-resistant strain of loblolly. In a breeding program, there is no particular reason why the hybrids used in the backcrossing scheme need to be F_2's. In the present study, F_2 hybrids were the only ones available, but essentially the same result probably would have been achieved by backcrossing F_1 hybrids to loblolly. In any case, as ALLARD (1960) has stated, backcross breeding, even in outcrossing species, can be a precise method for improving a particular trait.

Table 5. — Correlations between measurements made at age 5 with those made at age 3 for height and the number of galls per tree based on group means and seed lots within-group means.

Level	Correlation coefficients [1]) Height	Galls per tree
Groups	0.985**	0.995**
All seed lots	.953**	.900**
Seed lots within Group: [2])		
3	.979**	.966**
4	.885**	.859**

[1]) ** Significant at 0.01 level.

[2]) Group 3 = progeny of wind-pollinated F_2 hybrids.
Grooup 4 = progeny of F_2 hybrids backcrossed to loblolly.

Literature Cited

ALLARD, R. W.: Principles of plant breeding. John Wiley & Sons, Inc., New York, (1960). — BURDSALL, H. H., JR., and G. A. SNOW: Taxonomy of *Cronartium quercuum* and *C. fusiforme*. Mycologia 69: 503—508 (1977). — CRITCHFIELD, W. B.: Hybridization of the southern pines in California. South. For. Tree Improv. Comm. and Soc. Am. For. Tree Improv. Comm., For. Genet. Workshop Proc. 1962: 40—48 (1963). — LA FARGE, T. and J. F. KRAUS: Resistance of shortleaf × loblolly pine hybrids to inoculation with fusiform rust 13th South. For. Tree Improv. Conf. Proc.: 113—118 (1975). — LA FARGE, T., and J. F. KRAUS: Third-year results of a shortleaf × loblolly hybrid progeny test in Georgia. 14th South. For. Tree Improv. Conf. Proc: 63—69 (1977). — MATHER, K., and J. L. JINKS: Biometrical genetics. Cornell Univ. Press, Ithaca, N. Y. (1971). — SCHMITT, D.: Performance of southern pine hybrids in south Mississippi. USDA For. Serv. Res. Pap. SO-36 (1968). — SLUDER, E. R.: Shortleaf × loblolly pine hybrids do well in central Georgia. Ga. For. Res. Counc. Res. Pap. 64 (1970). — WELLS, O. O., P. E. BARNETT, H. J. DERR, D. T. FUNK, T. LA FARGE, E. R. LAWSON and S. LITTLE: Shortleaf × slash pine hybrids outperform parents in parts of the southeast. South. J. Appl. For. 2: 28—32 (1978).