

Brown-Spot Resistance in Longleaf Pine

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Abstract. Field tests of open- and control-pollinated progenies of selected parents of *Pinus palustris* Mill, have shown that resistance to infection by *Scirrhia acicola* (Dearn.) Siggers is heritable. *Forest Sci.* 76: 204-209.

Additional key words. *Scirrhia acicola*, controlled pollinations, *Pinus palustris*, disease resistance.

IN THE research reported here, controlled pollinations were made to determine if resistance to the brown-spot needle blight is heritable. This disease, caused by the fungus *Scirrhia acicola* (Dearn.) Siggers, is a severe obstacle to management of longleaf pine. Unless controlled by prescribed burning, it prolongs the trees' characteristic grass stage and causes considerable mortality by killing the foliage. It is a disease of seedlings almost exclusively; if trees survive to the sapling stage infection becomes light or disappears.

Though there is no record of any progeny tests, earlier researchers occasionally observed healthy individual seedlings among heavily infected neighbors (Verrall 1934). In 1937 Dr. Paul V. Siggers, then a pathologist for the U. S. Department of Agriculture, found one such tree in an abandoned nursery bed. He had it moved to the Palustris Experimental Forest, near Alexandria, Louisiana, where it remained free of the disease and developed normally.

Wind-pollinated progeny of this tree have consistently shown greater resistance than unselected controls (Derr 1963). In 1961, the tree was used as a male or female parent in controlled crosses with trees that had had low infection rates during their seedling stage and with others having no recorded history of apparent resistance. This paper summarizes data from field tests of the resulting progenies.

Methods and Materials

The controlled crosses, with the addition of wind pollinations of the several parents, provided 22 progenies in four groups:

1. Reciprocal crosses between the 1937 resistant selection (tree 1-1) and two 12-year-old plantation trees (1-2 and 1-3) having a field record of low infection.
2. One-way crosses between tree 1-1 (as male parent) and four trees (2-1, 2-2, 2-3, and 2-4) whose seedling history was unknown but whose dominant position in even-aged unburned stands hinted that they were resistant as seedlings. This group also contained wind-pollinated seedlings from the four female parents.
3. One-way crosses between tree 1-1 (as female parent) and three 36-year-old plantation trees (3-1, 3-2, and 3-3) that had been infected only lightly as seedlings.
4. Wind-pollinated controls from four trees (4-1, 4-2, 4-3, and 4-4) with unknown histories.

Within-group identities of the crosses may be found in Table 1.

Controlled pollinations were accomplished in March 1961; techniques for flower isolation and pollen handling were those recommended by Cumming and Righter (1948). Though yields varied considerably, enough seeds were harvested from each cross to produce at least the

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200 grade-1 seedlings (Wakeley 1954) required for the main progeny tests. Seedlings were grown in a small nursery at a bed density of approximately 15 per sq ft. They received normal nursery culture, including periodic spraying with bordeaux mixture for control of brown spot. They were lifted in December, potted in a 1:3 mixture of peat moss and sandy topsoil, and then stored on

elevated beds in the open until planted in March.

Field tests were established on three sites in central Louisiana. The main test, containing all progenies, was replicated on two sites that were considered moderate and severe in regard to brown-spot hazard. Differences between the two sites were chiefly in the number of infected wild seedlings within or adjacent

TABLE 1. Brown-spot infection (as percent of needle tissue infected) and height growth of 3-y ear-old progenies of longleaf pine planted on two test sites in central Louisiana,

Female	Male	Average brown-spot infection ¹		Survivors classed as resistant ²		Average height of all trees	
		Moderate site	Severe site	Moderate site	Severe site	Moderate site	Severe site
<i>Percent</i>							
Group 1						<i>Inches</i>	
1-1 X 1-2		24 ab	34 ab	60	21	29.0 a	11.4 ab
1-2 X 1-1		15 a	26 a	58	39	26.8 ab	15.2a
1-1 X 1-3		28 abc	33 ab	52	42	20.5 bede	12.9 ab
1-3 X 1-1		17 a	34 ab	72	38	28.9 a	9.9 be
1-1 X wind		42 cde	43 be	31	24	20.7 abede	12.1 ab
1-2 X wind		49 def	(66) ³	13	0	16.5 defg	(6.0) ³
1-3 X wind		53 defg	0)	19	—	12.8 efghi	C)
Group 2							
2-1 X 1-1		49 def	45 be	30	25	13.0 efghi	8.6 bed
2-1 X wind		72 g	70 de	3	0	3.8 j	3.2e
2-2 X 1-1		27 abc	(4)	53	—	18.9 bede	(*)
2-2 X wind		44 cde	66 de	28	4	13.6 efgh	4.8 de
2-3 X 1-1		39 bed	57 cd	36	10	22.6 abed	10.0 be
2-3 X wind		70 g	73 e	3	0	9.0 ghij	4.0e
2-4 X 1-1		30 abc	40 b	54	35	25.3 abc	11.3 ab
2-4 X wind		59 efg	61 de	5	4	8.4 hij	4.9 de
Group 3							
1-1 X 3-1		17a	(36) ⁴	65	(24) ⁴	22.4 abed	(10.3) ⁴
1-1 X 3-2		37 bed	42 be	39	20	16.7 defg	6.6 de
1-1 X 3-3		36 bed	42 be	37	20	17.7 cdef	8.8 bed
Group 4							
4-1 X wind		65 fg	68 de	1	3	6.5 hij	3.9 e
4-2 X wind		63 fg	74 e	7	0	10.0 fghij	3.9 e
4-3 X wind		65 fg	71 de	1	0	5.3 ij	4.1 e
4-4 X wind		67 fg	71 de	3	0	8.2 hij	3.9 e

¹ Means not followed by the same letter are different at the 1-percent level.

² Seedlings with less than 10-percent needle loss in each of the first 3 years.

³ Means of only two replications.

⁴ Not planted on the severe site.

to the plots, and in the severity of their infection. Three smaller test plantings compared selected progenies on a relatively low-hazard site from which all natural longleaf had been removed.

Seedlings were planted by removing the containers and inserting the roots, with potting soil intact, into holes made with a posthole auger in the center of shallow furrows. This technique was especially well suited to the tests: it maximized field survival and it accelerated initial buildup of the disease by exposing seedlings fully to spores disseminated by wind and rain splash.

The experimental design in each test was a randomized complete block with four replications. Plots contained 25 seedlings planted at 6-ft intervals. Thus, the evaluation of each progeny in an individual planting was based on performance of the survivors from 100 planted seedlings.

Survival was exceptionally high for longleaf pine. It averaged 96 percent for all tests combined after three growing seasons.

Relative brown-spot susceptibility was determined from ocular estimates of the proportion of the current year's needle tissue destroyed or infected. Estimates were made for all survivors during the dormant seasons following each of the first 3 years in the field. These data permitted evaluation of resistance in terms of either the mean infection rate or the proportion of a progeny having less than a specified level. For the latter, needle loss of 10 percent or less in each of the three seasons was arbitrarily selected as the indicator of inherent resistance for individual seedlings.

Total seedling heights were measured at age 3 years to the nearest inch.

Brown-Spot Resistance

There were large differences between progenies in average brown-spot infection at age 3. These were significant at the 1-percent level in all tests under each of the three site conditions. From site to site individual progenies varied somewhat



FIGURE 1. *The medium-hazard test area after 3 years. The row of resistant progeny (f-3 X 1-1) at right center is between two rows of nonresistant checks.*

in amount of infection or average height, but their rankings tended to be similar on all sites. This similarity is illustrated by the (progeny) means for the moderate and severe sites in Table 1. Results observed on the site classified as a moderate brown-spot hazard are emphasized in the following discussion, as this site most closely represented typical field conditions.

The four intraspecific hybrids that were produced by crossing resistant parents demonstrated the greatest resistance to infection (Table 1, Group 1). They averaged only 21 percent needle loss on the moderate site, and 60 percent were classified as resistant. Most were growing vigorously after 3 years in the field.

On the Group-4 controls, by contrast, nearly two-thirds of the 3rd-year foliage had been destroyed by brown spot, and only 3 percent of the trees were in the low-infection or resistant category. A stand with this level of infection is practically lost. However, these rates are much higher than normal for 3-year-old trees; they were the result of planting on scalped soil, and they indicate rigorous test conditions (Fig. 1).



Wind-pollinated offspring of the three parent trees in Group 1 also showed evidence of resistance. Their average infection rate was about midway between that of the highly resistant crosses and the controls. They were likewise intermediate in the proportion of resistant survivors. The three parents differed somewhat in relative degree of resistance, with tree 1-1 excelling. This tree was one parent in both pairs of reciprocal crosses involving the three resistant trees. In this limited sample, direction of the cross did not affect resistance of the progeny. They were the most resistant progenies on each of the three test sites, and differences among them were not significant.

Crosses between tree 1-1, as male parent, and four trees with unknown brown-spot histories produced seedlings that were considerably more resistant to infection than their respective wind-pollinated half sibs in Group 2. In each case but one, there was a tenfold increase in the proportion of resistant seedlings. The exception was tree 2-2, which proved to be resistant; its wind-pollinated progeny were comparable to wind seedlings from tree 1-1. Resistance among other crosses in this group was intermediate, or roughly equivalent to wind-pollinated progeny of a resistant tree.

Progenies in Group 3 represent additional crosses between tree 1-1 and three male parents that had scored high in brown-spot resistance during their first 5 years in the field. One cross (with tree 3-1) produced highly resistant progeny, while the other two

crosses were similar to wind-pollinated seedlings from the female parent, tree 1-1. Of the three phenotypes, only one appears to have a heritable trait for resistance.

The severe test site provided additional confirmation of brown-spot resistance. The initial disease buildup was faster on this site, and the general level of infection for all families at age 3 was higher than on the moderate site, but the relative degree of resistance among the progenies was about the same (Table 1). For example, average 3rd-year infection rates for the four highly resistant crosses in Group 1 increased from 21 to 32 percent, while rates for the controls increased from 65 to 71 percent. Levels of infection for progenies having one resistant parent were between these two extremes on both sites. The proportion of resistant X resistant seedlings having less than 10 percent infection at age 3 dropped from 60 to 37 percent between the two sites, an indication that resistance is not absolute and that even the most resistant families incur considerable infection under severe test conditions.

Inherent resistance was also clearly apparent on the low-hazard site. The three tests on this site included 19 of the 22 progenies listed in Table 1. Results at age 3 years are summarized by type of cross in Table 2; the classification of resistant or nonresistant is based on performance in the main test on the moderate site. Average needle infection of the five highly resistant crosses was 16 percent, while the nonresistant X wind progenies were 70-percent infected.

TABLE 2. Summary of 3d-year brown-spot infection data, by type of cross, from three supplemental field tests on a light-hazard site.

Type of cross	Progenies represented	Seedlings planted	Average brown-spot infection	Seedlings with < 10 percent infection
	Number	Number	Percent	Percent
Resistant X resistant	5	900	16	70
Resistant X wind	4	600	43	29
Resistant X nonresistant or reciprocal	5	500	29	54
Nonresistant X wind	5	600	70	6

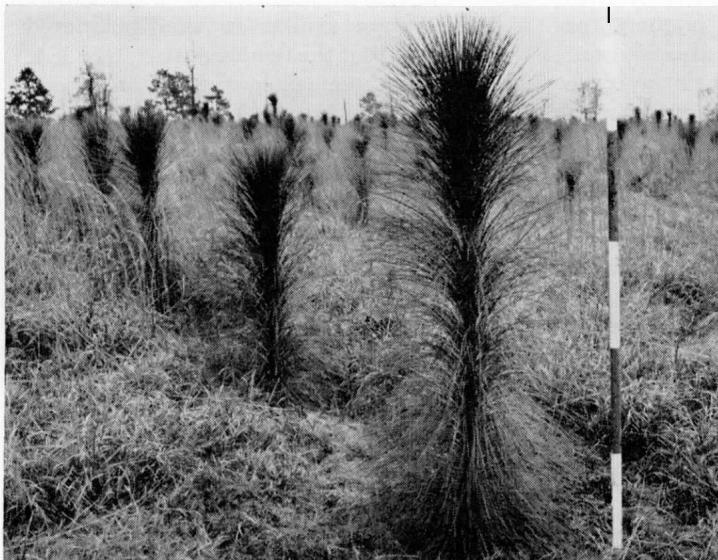


FIGURE 2. One of many exceptionally resistant intra-specific hybrids. At the end of the 3rd growing season 2nd-year foliage was clear of brown-spot infection to the groundline. Parentage: 1-2 X Z-7.

Progenies with a single resistant parent are separated into two groups—wind-pollinated progenies from all four resistant trees, and controlled crosses having tree 1-1 as one parent. The former averaged 43 percent needle infection, the latter 29 percent. As these two groups represent the same type of cross, the difference can be attributed to the effect of tree 1-1.

The proportion of survivors classified as resistant (less than 10 percent needle loss) on the low-hazard site also showed clearly the differences in resistance between the groups. These values ranged from a low of 6 percent for the wind-pollinated controls to 70 percent for the highly resistant crosses.

Pattern of Infection

Infection built up gradually over the 3-year period. Annual disease readings indicated that the performance of any progeny could have been predicted from 1st-year data. Highly significant correlations were found between 1st- and 3rd-year infection rates ($r = 0.77$), and between the 2nd- and 3rd-year readings ($r = 0.94$) on the moderate site. When the general level of infection is relatively light in the 1st year, however, the possibility of "escapes" must be considered in evaluating resistance.

Among the full- and half-sib progenies of resistant trees were individual seedlings that displayed very high resistance. Their proportion of the total population varied among the progenies, as indicated in Table 1 by the percent of survivors with less than 10 percent needle loss at age 3. These individuals maintained a low infection rate—often 1 or 2 percent—even when growing between heavily infected check rows. They were in active height growth at age 3, displaying full green foliage to the groundline (Fig. 2).

The mechanism of resistance is not fully understood. From field observation, it appears to be not an immunity but rather a restriction of the pathogen within the host. Some lesions could be found on any seedling that had been exposed in the field. The resistant individuals were characterized by bar lesions, which are external infections that encircle a needle in narrow bands but apparently do not impair its function. The resistant seedlings observed by Verrail (1934) usually also had restricted bar lesions rather than the generalized interior infections that kill entire needles.

Seedling Growth

There were significant differences between progenies in average total height

at age 3 (Table 1). Much of the difference was associated with variations in brown-spot infection. On the moderate site, individual seedlings exceeding 50 inches in height at age 3 were common among the highly resistant progenies; average total heights ranged from 20 to 29 inches and practically all survivors were in active height growth. While some of this exceptional growth can be attributed to the use of potted seedlings and to planting on furrowed sites, its equivalent has seldom, if ever, been attained in other studies where intensive cultural treatments, including spraying for brown-spot control, were applied to conventional planting stock. Brown-spot resistance, then, resulted in unusually fast juvenile growth and not merely in disease-free seedlings.

Discussion

The performance of the intraspecific hybrids and the open-pollinated progenies demonstrated the inheritance of brown-spot resistance in longleaf pine. There were substantial gains with one resistant parent, male or female; and the level of field infection dropped sharply when two resistant parents were crossed. The practical importance of low inherent infection is in the rate of early height growth; the resistant seedlings made substantially better growth than those with average infection.

These findings were, by necessity, developed from limited sources of plant material. Only one proven genotype (tree 1-1) was available when the study started. Five additional trees were considered resistant phenotypes because their

early plantation record showed exceptionally low infection. The balance of the parent trees had no individual-tree records of resistance. Though the sources of test material were limited, the expression of resistance was consistent from test to test among progenies having similar parentage. It suggests gains from seed orchards containing resistant genotypes.

The frequency of resistant genotypes within a natural population is unknown. It very likely varies from stand to stand with factors—such as fire or competition—that influence natural selection during the seedling stage. Phenotypes that appear resistant include some individuals that simply escape serious infection in the field; this was illustrated by the failure of two out of three apparently resistant trees to increase progeny resistance when mated with a tree of proven resistance. Thus, progeny testing is needed to confirm the apparent resistance of individual selections or to identify this trait among trees selected for other desirable characteristics.

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