Effect of Inoculum Density and Fertilization on Greenhouse Screening of Loblolly Pine Seedlings for Resistance to Fusiform Rust

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ABSTRACT

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Loblolly pine (*Pinus taeda*) with resistance to fusiform rust caused by *Cronartium quercuum* f. sp. *fusiforme* is selected indirectly through controlled inoculation of greenhouse seedlings. Progeny of 29 half-sib families with known field resistance were inoculated using two inoculum densities under two fertilization regimes. Families were ranked on the basis of seven symptom types. Fertilization did not significantly alter family rankings for most symptom types. The exception, presence of galls, was more highly correlated with field resistance when seedlings received a high level of fertilization. Changes in inoculum density did not alter family rankings. Greenhouse screening appeared to be more reliable for selecting resistant families than for differentiating among moderately resistant and susceptible ones.

Additional key words: disease resistance, indirect selection.

The most destructive forest disease on loblolly pine (*Pinus taeda* L.) in the southeastern United States is fusiform rust, caused by *Cronartium quercuum* Berk. Miyabe Shirai f. sp. *fusiforme*. Controlled inoculation of progeny under greenhouse conditions is used as an indirect selection method to identify genetically resistant loblolly pine families. Such a service is offered by the USDA Forest Service's Resistance Screening Center in Asheville, NC, where seedlings from different pine families are inoculated with the fusiform rust fungus, and their response is evaluated after a period of growth in a greenhouse (2,9).

The utility of indirect selection depends, among other things (11), on there being a high correlation of responses in the greenhouse with those in operational field plantings. Genetic gains in rust resistance from indirect selection are directly proportional to the genetic correlation of greenhouse and field resistance of pine families. Thus, greenhouse screening should be performed under those conditions that yield the highest genetic correlation between greenhouse and field resistance of pine families.

Changes in environmental conditions may affect predictions of relative resistance of pine families if they cause families to respond in different ways. Only two environmental factors have been shown to cause family × greenhouse environment interactions for rankings of loblolly pine resistance to fusiform rust. Loblolly pine seedlings inoculated in the greenhouse and grown under different fertilization levels showed a family × fertilization rank interaction for percentage of seedlings with galls (10). In another greenhouse study, a family × inoculum density rank interaction was demonstrated for loblolly pine and for percentage of seedlings with galls (8).

The major objective of this study was to determine if the alteration of fertilization level or inoculum density in greenhouse screening tests would improve the correlation between greenhouse and field resistance rankings of loblolly pine families.

MATERIALS AND METHODS

Field assessments. Twenty-nine half-sib loblolly pine families were selected to represent the range of field resistance to *C. quercuum* f. sp. *fusiforme* (Table 1). These families along with other families were established during 1975–1977, in progeny trials on up to 26 sites across the range of loblolly pine, under the direction of the North Carolina University-Industry Tree Improvement Cooperative (1). The tests had nine replications of 10-tree row plots at each site. Cronartium score (c-score) was assessed by the North Carolina State Tree Improvement Cooperative on each tree 4–6 yr after planting as follows: 1 = no rust infection; 2 = branch infection only; 3 = stem infection above 4.5 ft; 4 = combination of 2 and 3; 5 = stem infection below 4.5 ft.

TABLE 1. Field resistance expressed as performance levels of 29 half-sib loblolly pine families inoculated with *Cronartium quercuum* f. sp. *fusiforme* in greenhouse screening tests

	Mean field performance level		
Family	c-score[a]	Galled (%)	Progeny test sites (no.)
19-24	25	7	2
12-12	14	9	1
19-17	9	13	3
8-102	13	16	3
6-9	15	16	6
1-523	32	23	3
3-34	33	27	2
2-40	27	29	6
8-509	38	32	2
19-16	35	37	2
6-20	36	37	8
17-4	34	38	4
8-61	41	39	7
8-59	41	42	7
3-36	46	43	6
4-18	44	46	9
8-1	50	47	7
4-6	50	50	5
8-76	55	52	8
7-56	60	61	8
3-17	68	61	2
9-17	60	64	6
8-120	73	64	1
11-16	71	70	6
11-9	73	73	3
7-34	71	73	7
15-42	76	75	7
10-5	80	77	6
18-102	76	82	4

[a] The cronartium score. 1 = no rust infection, 2 = branch infection only, 3 = stem infection above 4.5 ft, 4 = combination of 2 and 3, and 5 = stem infection below 4.5 ft.

Percentage of infected trees per family and per site was calculated from the c-score. Trees at nine test sites had a mean percent infection of more than 30% as of March 1982, with a range of 32–63% infection. Field resistance rankings were based on measurements at these nine sites. Only a few of the 29 families had been progeny tested at all nine sites (Table 1).

To obtain relative rankings of the 29 families, performance level (5) was calculated for each family. Performance levels are defined as:

$$\mathrm{PL} = 100\,(F_y - M_y)/4 \times \sigma_y$$

where F_y = family mean at site Y, M_y = minimum family mean at site Y, and σ_y = standard deviation of family means at site Y. Performance levels were calculated for each of the 29 families at each site for two traits, mean c-score, and mean percent galled and averaged over sites (Table 1).

Fertilizer-inoculum density experiment. Seedlings from the 29 half-sib families were screened at the Resistance Screening Center under four sets of conditions (treatments). Four control lots used routinely for Resistance Screening Center tests were also included. Seedlings were grown under one of two fertilization regimes and inoculated with basidiospore suspensions at one of two inoculum densities, making a 2 × 2 factorial of fertilization levels and inoculum densities.

Seedlings were grown in 5-cm-diameter single tree tubes in a medium with an equal ratio of peat, perlite, and vermiculite. The seedlings were inoculated with rust basidiospores when they were 9 wk old (2). Half of the seedlings received no fertilizer until 4 wk after inoculation, whereas for the same period the remaining seedlings received weekly fertilization with 278.6 g per 3.785 L of a commercial fertilizer that contained 15% N, 30% P, 15% K, 0.05% Mn, 0.05% Zn, 0.10% Fe, and 0.05% Cu by weight. Fertilizer was applied to fertilized seedlings until it began to drain from the bottom of the tube. Seedlings were all subsequently fertilized on a monthly basis. These two fertilization regimes were similar to those used in the study, which indicated significant family × fertilizer rank interactions for percent galled in the greenhouse (10).

Inoculum density treatments involved inoculation with spore suspensions of 35,000 spores per milliliter and 50,000 spores per milliliter. These densities were chosen to achieve a range of percent galled among the treatments similar to that used in the inoculum density study, which indicated family × inoculum density interactions (8).

Standard operational procedures for the Resistance Screening Center (2) were followed for aeciospore collection and processing, oak inoculation, basidiospore collection, and pine inoculation. Oaks were inoculated with an equal volume composite of spores from 30 galls, 10 from forest stands in each of three locations near Perry, GA.

Treatments were replicated three times. In each replication, all four treatments were inoculated in the same week. Replications were 1 wk apart. Physical constraints of the size of the postinoculation incubation chamber dictated that only two treatments could be inoculated per day. Inoculation was, therefore, carried out in a randomized incomplete block design (4). Each replicate week consisted of two inoculation days (blocks) with two treatments inoculated on each day. For each replication, 40 seedlings from each family were subjected to each treatment, so that 80 seedlings from each family were inoculated each day. The total number of seedlings in the trial was 15,840.

Operational screening. The same set of 29 pine families was screened under standard operational procedures (2) approximately 2 yr before the fertilizer-inoculum density experiment. All procedures were the same as in the fertilizer-inoculum density experiment except that seedlings were grown in 20-tree plastic flats (33 × 13 × 11 cm) in a 5:3:1 mix of Appalachian mountain soil, sand, and peat. The flats received no fertilizer until 4 wk after inoculation of 6-wk-old seedlings. Seedlings were then fertilized monthly for the next 3 mo and bimonthly after that, with the same fertilizer as in the fertilizer-inoculum density test. Seedlings were inoculated with a basidiospore suspension of 50,000 spores per milliliter. This suspension was produced from a composite of 30 single-gall inocula collected from three forest stands in the Coastal Plain of South Carolina. One hundred and eighty seedlings of each family were inoculated. Three flats of each family (60 seedlings) were inoculated in each of three replications. Replications were inoculated on consecutive days. The results from this operational trial were compared with the results of the fertilization/inoculum density experiment.

Greenhouse assessments. In both the fertilizer-inoculum density experiment and the operational screening, seven symptom types were assessed 6 mo after inoculation. In the fertilizer-inoculum density experiment the same symptom types were assessed again 9 mo after inoculation.

Each symptom type was scored as either present or absent on each seedling. The symptom types were: 1) galls of any shape (hypertrophy caused by *C. q.* f. sp. *fusiforme*); 2) symptoms without swelling (purple or red spots on the stem but no gall); 3) fewer than two acute angled adventitious shoots arising from the gall; 4) rough galls (dark, purple, or brown sunken areas on the surface of a gall, indicative of periderm formation); 5) short galls (galls less than 25 mm in length); 6) atypically shaped galls (hypertrophy absent from one side of the stem); 7) thin galls (diameter of gall less than twice the normal stem diameter); and 8) reaction zones (purple or brown zones in the pith or xylem).

Each of these symptom types has been correlated with field resistance (3,12). The presence of galls was negatively correlated with field resistance, whereas the other symptom types were positively correlated.

Statistical analysis. A group or flat of 20 seedlings represented the smallest unit in the experimental design. Data points were percentage of seedlings per 20-tree group with each symptom type. Rough galls, short galls, atypically shaped galls, and thin galls were each expressed as a percentage of galled seedlings; and trees with galls, symptoms without swelling, and adventitious shoots were each expressed as a percentage of all seedlings.

Seedlings in one replication of the high fertilizer treatments of the fertilizer-inoculum density experiment were not inoculated satisfactorily because of malfunctions of the mechanized inoculation system. These data were excluded from the analyses.

Because of the low percentage of infection achieved on the low fertilizer treatments, some groups of 20 seedlings could not be assessed for the proportions of galled seedlings with rough galls, atypically shaped galls, short galls, and thin galls. These groups were considered as missing observations in the analyses.

The analysis of variance (ANOVA) model used to evaluate the effects of fertilizer and inoculum density on relative family resistance in the fertilizer-inoculum density experiment included a block effect, a family effect, a treatment effect, and a family × treatment interaction effect. Fertilization, inoculum density, and fertilization × inoculum density contrasts were made for the treatment and for the family × treatment effects. All of the other interaction terms (i.e., interactions involving blocks) were pooled to form an experimental error. All effects were tested against this error, but the significance tests are only approximate because of the imbalance inherent in an incomplete block experiment with missing cells.

Family means were calculated for all symptom types for each treatment in the fertilizer-inoculum density experiment and the operational screening test. These five sets of family means were

TABLE 2. Means of seven symptom types expressed on loblolly pine seedlings[a] assessed 6 and 9 mo after inoculation with *Cronartium quercuum* f. sp. *fusiforme* using two inoculum densities under two fertilizer regimes

Treatment	Fertilizer	Inoculum density	Percent galled		Symptoms without swelling		Fewer than two adventitious shoots		Rough galls		Atypically shaped galls		Short galls		Thin galls	
			6	9	6	9	6	9	6	9	6	9	6	9	6	9
1	Low	Low	7	9	1	3	78	95	40	33	11	7	16	7	64	54
2	Low	High	25	25	3	2	72	84	43	34	12	1	19	7	68	61
3	High	Low	70	70	8	3	91	89	57	34	10	2	12	1	79	73
4	High	High	70	73	4	3	68	81	65	39	7	1	4	1	87	66

[a]Seedlings were from 29 half-sib families and four control seedlots.

TABLE 3. Significant *F* values[a] for analysis of variance of seven symptom types 6 mo after inoculation of loblolly pine seedlings[b] with *Cronartium quercuum* f. sp. *fusiforme* using two inoculum densities under two fertilizer regimes

Source of variation	df	Percent galled	Symptoms without swelling	Fewer than two adventitious shoots	df	Rough galls	Atypically shaped galls	Short galls	Thin galls
Blocks	5	64.81**[a]	4.33*	74.70**	5	7.87**	13.28**	NS	10.91**
Family	32	13.65**	2.95**	3.38**	32	1.54*	NS	NS	2.05**
Treatments									
Fertilizer	1	1,078.97**	20.71**	17.65**	1	10.82**	NS	9.68**	NS
Inoculum density	1	191.71**	NS	50.70**	1	8.14**	NS	NS	NS
Fertilizer × inoculum density	1	42.75**	12.68**	NS	1	NS	4.16*	4.12*	NS
Family × treatments									
Family × fertilizer	32	5.26**	NS	NS	32	NS	NS	NS	NS
Family × inoculum density	32	NS	NS	NS	32	NS	NS	NS	NS
Family × fertilizer × inoculum density	32	NS	NS	NS	32	NS	NS	NS	NS
Error									
Experimental	192	NS	1.53**	1.34*	174	1.43*	NS	1.54*	NS
Sampling	321				263				
Total	649				573				

[a]*F* values followed by two asterisks are significant at $P \leq 0.01$; those with one asterisk at $P \leq 0.05$.
[b]Seedlings were from 29 half-sib families and four control seedlots.

then linearly correlated with the two measures of field resistance, both as individual symptom types and in a multiple regression with symptom types used as independent variables. The correlation coefficients were interpreted as approximate estimates of genetic correlations.

RESULTS

High fertilization produced significantly more galls, symptoms without swelling, and rough galls, but fewer short galls at both 6 and 9 mo after inoculation (Tables 2, 3, and 4). Seedlings inoculated with the high inoculum density had significantly more galls and more adventitious shoots.

Block effects in the fertilizer-inoculum density experiment were large for most symptom types (Tables 3 and 4). Replications are often significantly different in operational screening tests (6,7,13; Resistance Screening Center, *unpublished data*). Because this experiment was unbalanced with respect to blocks and treatments, the ANOVA results are biased. However, treatment means adjusted for blocks were in most cases in the same relative order as and similar to the raw means. F tests can, therefore, be considered as reasonable approximations.

The family × fertilizer interaction was highly significant for percent galled at both assessments. The significant interaction appeared to arise because family rankings differed with the two fertilization regimes. Family means (percent galled) from the high fertilizer treatments were generally more highly correlated with field resistance traits than family means from the low fertilizer treatments (Tables 5 and 6).

The family × inoculum density interaction was not significant for percent galled at either assessment. Within the same fertilization level and assessment time, correlations of family means with field resistance traits were, in three out of the four cases, very similar for the two inoculum densities (Tables 5 and 6). The poor correlation at 6 mo for the low fertilizer, low inoculum density treatment is probably related more to the low level of infection (only 7% galled) (Table 2) than to the treatment per se.

For the other symptom types, F values for the family × treatment interactions were either nonsignificant or small (Tables 3 and 4), and no clear patterns emerged from the correlations between the greenhouse symptom types and field infection (Tables 5 and 6).

When all symptom types were used as independent variables in a multiple regression on field resistance (Tables 5 and 6, last column), the multiple correlation coefficients for the 6-mo assessment were either almost as high or higher than for the 9-mo

TABLE 4. Significant F values[a] for analysis of variance of seven symptom types 9 mo after inoculation of loblolly pine seedlings[b] with *Cronartium quercuum* f. sp. *fusiforme* using two inoculum densities under two fertilizer regimes

Source of variation	df	Percent galled	Symptoms without swelling	Fewer than two adventitious shoots	df	Rough galls	Atypically shaped galls	Short galls	Thin galls
Blocks	5	57.91**[a]	3.05*	80.97**	5	36.75**	NS	3.00*	11.42**
Family	32	12.40**	3.31**	5.51**	32	NS	NS	NS	1.80**
Treatments									
Fertilizer	1	1,134.07**	8.45**	57.53**	1	6.09*	NS	7.88**	NS
Inoculum density	1	212.44**	NS	213.75**	1	NS	NS	NS	5.29*
Fertilizer × inoculum density	1	34.13**	NS	39.69**	1	NS	NS	NS	NS
Family × treatments									
Family × fertilizer	32	5.47**	1.86**	2.82**	32	NS	NS	NS	NS
Family × inoculum density	32	NS	1.88**	NS	32	NS	NS	NS	NS
Family × fertilizer × inoculum density	32	NS	1.74**	NS	32	NS	NS	NS	NS
Error									
Experimental	190	NS	NS	NS	176	NS	NS	NS	NS
Sampling	323				272				
Total	649				584				

[a] F values followed by two asterisks are significant at $P \leq 0.01$; those with one asterisk at $P \leq 0.05$.
[b] Seedlings were from 29 half-sib families and four control seedlots.

TABLE 5. Correlation coefficients[a] for fusiform rust resistance of 29 loblolly pine families measured in field progeny tests correlated with seven greenhouse symptom types assessed 6 mo after inoculation with *Cronartium quercuum* f. sp. *fusiforme* using two inoculum densities under two fertilizer regimes

Treatment	Fertilizer	Inoculum density	Field performance level	Percent galled	Symptoms without swelling	Fewer than two adventitious shoots	Rough galls	Atypically shaped galls	Short galls	Thin galls	All symptom types
1	Low	Low	c-score[b]	−0.28	0.00	0.14	0.24	0.14	0.20	0.10	0.52**
			% galled	−0.28	0.10	0.17	0.32	0.10	0.17	0.10	0.57**
2	Low	High	c-score	−0.45*	0.37*	0.30	0.20	0.24	0.36	0.56**	0.66*
			% galled	−0.44*	0.45*	0.33	0.20	0.20	0.33	0.54**	0.67**
3	High	Low	c-score	−0.65**	0.57**	0.32	0.37*	0.00	0.22	0.33	0.71**
			% galled	−0.65**	0.57**	0.37*	0.37*	0.00	0.22	0.33	0.70**
4	High	High	c-score	−0.62**	0.28	0.20	0.14	0.40*	0.00	0.14	0.74**
			% galled	−0.65**	0.32	0.20	0.10	0.42**	0.00	0.10	0.78**
Operational screening			c-score	−0.55**	0.53**	0.28	0.26	...	0.50**	0.60**	0.66**
			% galled	−0.57**	0.54**	0.28	0.30	...	0.49**	0.60**	0.67**

[a] Coefficients followed by two asterisks are significant at $P \leq 0.01$; those with one asterisk at $P \leq 0.05$.
[b] The cronartium score. 1 = no rust infection, 2 = branch infection only, 3 = stem infection above 4.5 ft, 4 = combination of 2 and 3, and 5 = stem infection below 4.5 ft.

assessment for all treatments. In the high fertilizer treatments, the correlation coefficient for percent galled was not much less than the multiple correlation coefficient for all symptom types. However, in the low fertilizer treatments information from the additional symptom types in most cases substantially increased the correlation between greenhouse and field results over that obtained for percent galled only.

For the operational screening test, correlation coefficients between family symptom type means and those for field resistance traits were about the same as in the fertilizer-inoculum density experiment (Table 6). In both the operational screening test and the fertilizer-inoculum density experiment, correlation coefficients for the two measures of field resistance with the same greenhouse symptom type means were virtually identical (Tables 5 and 6).

For the high fertilizer, high inoculum density treatment at 6 mo after inoculation, the eight families with the fewest galls in the greenhouse had a mean field performance level of 70, whereas the mean for all 29 families was 45 (Fig. 1). On the other hand, the eight families with the most galls in the greenhouse had a mean field performance level of 40, which is not much lower than the mean of all families. Further, the 13 families with intermediate values in the greenhouse performed worse in the field than the other groups, with a mean performance level of 32. Resistance rankings based on percent galled from the other treatments as well as rankings based on the other greenhouse symptom types showed a similar pattern of better discrimination of resistant families compared with susceptible families.

DISCUSSION

The two field measurements of fusiform rust symptoms appear to provide almost identical family rankings, suggesting that the additional information on gall position provided by the c-score does not assist in differentiating resistant families. Assessment of the presence or absence of a gall in field trials would require less time than assessment of c-score and yet be equally as effective for selecting loblolly pine families resistant to fusiform rust.

Increasing inoculum density increased infection as in previous experiments. However, in contrast to previous experiments (8), a significant change in family rankings did not occur. The significant change in family rankings reported previously was based on the performance of one family, family 11-20. The type of response exhibited by this family does not appear to be common, as it was not observed in any of the 29 field-tested families in the fertilizer-inoculum density experiment. The results of this experiment suggest that changes in inoculum density do not greatly influence the indirect selection of resistant loblolly pine families through controlled inoculation of greenhouse seedlings with the fusiform rust fungus.

Fertilization of greenhouse inoculated seedlings increased infection as reported previously (10). Fertilization enhanced symptom expression for both resistance responses (symptoms without swelling and rough galls) and susceptibility responses (presence of galls and absence of short galls).

Fertilization did significantly alter greenhouse family rankings based on percent galled, confirming results of previous experiments (10). Family rankings for percent galled obtained with high fertilization were more similar to those obtained in field progeny tests than family rankings obtained with low fertilization. Fertilization, however, did not significantly alter family rankings for any of the other symptom types.

Family rankings for percent galled alone obtained with high fertilization correlated about as well with field resistance as did correlations including all symptom types. With low fertilization the correlations were improved in most cases when all symptom types were used. The better correlations between field and greenhouse assessments obtained with the high fertilizer treatments suggest that using highly fertilized seedlings would yield the greatest gains from indirect selection of loblolly pine for fusiform rust resistance.

Greenhouse assessments made 6 mo after inoculation were at least as well correlated with field resistance as assessments made at 9 mo after inoculation. This result suggests that the most cost-effective method of indirect selection of this type would be with one assessment of percent galled only at 6 mo after inoculation. This would decrease the man-hours required for assessments as well as reducing the requirement for greenhouse space.

The best use of results of indirect screening for resistance would be for identification of highly resistant loblolly pine families, rather

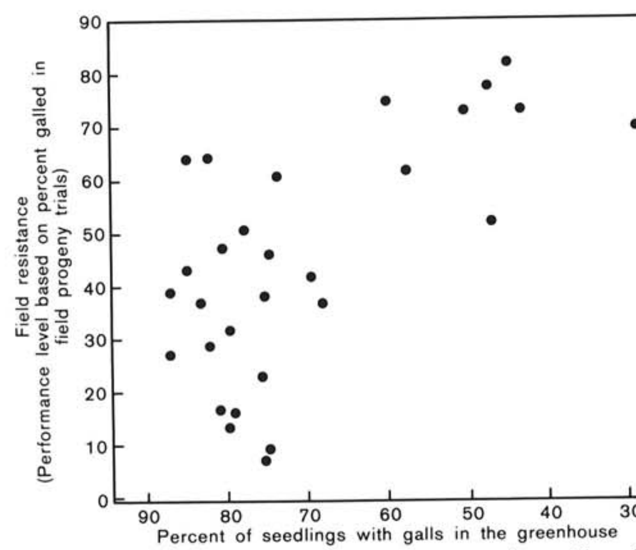

Fig. 1. Relationship of rankings from greenhouse screening and from field tests for resistance of 29 half-sib loblolly pine families to *Cronartium quercuum* f. sp. *fusiforme*.

TABLE 6. Correlation coefficients[a] for fusiform rust resistance of 29 loblolly pine families measured in field progeny tests correlated with seven greenhouse symptom types assessed 9 mo after inoculation with *Cronartium quercuum* f. sp. *fusiforme* using two inoculum densities under two fertilizer regimes

Treatment	Fertilizer	Inoculum density	Field performance level	Percent galled	Symptoms without swelling	Fewer than two adventitious shoots	Rough galls	Atypically shaped galls	Short galls	Thin galls	All symptom types
1	Low	Low	c-score[b]	−0.35	0.07	0.24	0.07	0.17	0.07	0.32	0.57**
			% galled	−0.37	0.07	0.25	0.11	0.18	0.07	0.37	0.66**
2	Low	High	c-score	−0.38*	0.35	0.47*	0.30	0.12	0.34	0.55**	0.47*
			% galled	−0.38*	0.38*	0.43*	0.31	0.05	0.26	0.54**	0.42*
3	High	Low	c-score	−0.59**	0.59**	0.44*	0.31	0.16	0.07	0.20	0.50*
			% galled	−0.59**	0.58**	0.47*	0.25	0.18	0.08	0.17	0.50*
4	High	High	c-score	−0.65**	0.49**	0.29	0.22	−0.08	0.14	0.03	0.66**
			% galled	−0.66**	0.50**	0.29	0.30	−0.11	0.08	−0.09	0.69**

[a] Coefficients followed by two asterisks are significant at $P \leqslant 0.01$; those with one asterisk at $P \leqslant 0.05$.

[b] The cronartium score. 1 = no rust infection, 2 = branch infection only, 3 = stem infection above 4.5 ft, 4 = combination of 2 and 3, and 5 = stem infection below 4.5 ft.

than highly susceptible families because, in this study, relative field resistance of the least resistant two-thirds of the families could not be predicted with the same accuracy as identification of the most resistant families. Results of greenhouse screening of loblolly pine for fusiform rust resistance would be best used to select parents for special resistant orchards. Using results to rogue highly susceptible parents from general purpose orchards would be less effective.

These data also illustrate that resistance screening was highly repeatable, because essentially the same relationships between greenhouse and field symptoms were obtained from greenhouse trials 2 yr apart with seedlings grown in different media and inoculated with spores from different regions. This suggests that the lack of infection in greenhouse seedlings is an expression of genetic resistance, and that families with little infection in the greenhouse can be used to reduce the incidence of fusiform rust in loblolly pine forests.

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