Fusiform Rust Disease in East Texas Loblolly Pine: An Evaluation of Resistance and a Test of Two Hypotheses†

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Abstract: A set of 21 loblolly pine families produced by crossing trees from east Texas were tested for resistance to fusiform rust disease. The parents of these families were surviving trees in stands that experienced extensive mortality in the 1960s due to southern pine beetle infestation. Seedlings were artificially inoculated in the greenhouse with *Cronartium quercuum* (Cq) from five different sources of inoculum, each consisting of basidiospores derived from single gall collections of aeciospores. Four of the collections originated from galls on loblolly pine (*C. q. fusiforme* or Cqf), whereas the remaining collection was obtained from a shortleaf pine gall (*C. q. echinatae* or Cqe). Two collections of Cqf and Cqe were taken from round-shaped galls, while the other two Cqf collections were taken from typical fusoid-shaped galls. The design allowed for the testing of two long standing hypotheses in fusiform rust biology, namely (1) that Texas loblolly pine and shortleaf pine share genes for resistance to Cqf and (2) that Cqe and Cqf collected from round galls share genes for gall shape. No apparent relationship was observed between percent gall by the Cqe inoculum and that for any of the Cqf inocula, suggesting that different resistance genes are effective for Cqf and Cqe in these families and that Texas loblolly pine and shortleaf pine apparently do not share resistance genes. All galls produced by the Cqe inoculum were about round shaped with gall form values ranging from 0.88 to 1.54 and averaging 1.04. However, for the Cqf inocula (average gall form ranged from 1.85 to 2.38) no relationship was found between shape of source galls and the shape of galls formed on diseased seedlings, suggesting that gall shape is not strongly controlled by Cq genes and that these genes are not apparently shared between Cqe and round galled collections of Cqf. In addition, the variance observed among families in percent gall suggests that genetic gains in resistance to fusiform rust disease are possible within this Texas seed source.

INTRODUCTION

In general, resistance to fusiform rust disease in natural stands of loblolly pine increases from east to west in the southern pine region. The gradient starts near the Mississippi-Alabama state line, continues west across Mississippi and Louisiana, and ends with the highest levels of resistance in east Texas and Arkansas (Wells and Wakeley 1966, Grigsby 1973, Wells et al. 1982).

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The studies that documented higher levels of fusiform rust resistance in the western populations of loblolly pine were all conducted with bulk seed lots, i.e., a mixture of seeds from several trees was used for each area sampled. As a consequence, variation in resistance among individual trees could not be evaluated. The results seemed to imply that all the trees had some form of general resistance and were often interpreted this way (Wells et al. 1982). Studies with full-sib families of loblolly pine from Livingston Parish, Louisiana have shown that fusiform rust resistance is highly variable among individual trees and that the seed source's higher level of resistance is due to a high frequency of resistant genotypes (Snow et al. 1982). In addition our current understanding of this pathosystem suggests that trees do indeed differ in the resistance genes that they carry and that these genes interact specifically with corresponding genes in the pathogen to determine gall formation (Kubisiak et al. 2005; Nelson et al. 2008).

The Livingston Parish stock and those from even more resistant western seed sources, e.g., western Louisiana, Texas, and Arkansas are potentially valuable to tree breeders attempting to breed for fusiform rust disease resistance in loblolly pine (Powers et al. 1981). The present experiment was designed to obtain information on the rust resistance levels in a sample of east Texas loblolly pines and to test two long standing hypothesis in fusiform rust biology, namely (1) that Texas loblolly pine and shortleaf pine share genes for resistance to Cqf and (2) that Cqe and Cqf collected from round-shaped galls share genes for gall shape.

MATERIALS AND METHODS

The studied parent trees were originally selected as survivors of a southern pine beetle epidemic that occurred in east Texas in the 1960s (referred to as 'Coyne' trees for Jack Coyne, the entomologist who made the selections). The selection criteria were that the trees be surrounded by beetle killed trees, free of fusiform rust, and in the dominant or co-dominant crown class. This resulted in a sample of trees with a potential for resistance to both southern pine beetle and fusiform rust disease. Three experiments are described here in which the progeny from 7 of these trees were evaluated for fusiform rust resistance.

In the first experiment (Experiment 1), pine seedlings from each of 19 seed lots were artificially inoculated using five different inocula of *Cronartium quercuum* (Berk.) Miyabe ex Shirai (Cq) (Table 1). Seventeen of the seed lots were from controlled crosses produced in a half-diallel mating design (Table 2). Two check lots were also included in the test—bulk loblolly pine and bulk shortleaf pine each from south Mississippi. The Cq inocula consisted of one single gall aeciospore collection from shortleaf pine and four single gall collections from loblolly pine (Table 1). Two of the loblolly inocula were collected in Louisiana while the other two loblolly inocula and the shortleaf inoculum were collected in east Texas. One loblolly inoculum from each state was from a short, round-shaped gall and the other was from a long, fusoid-shaped gall.

Because of their origin on the two pine species, the inocula from loblolly pine were considered to be *C. quercuum*. f.sp. *fusiforme* (Cqf) and that from shortleaf pine *C. quercuum* f.sp. *echinatae* (Cqe) (Burdsall and Snow 1977). The two special forms of the pathogen were used to test a long standing hypothesis: Texas loblolly pine and shortleaf pine have common genes for fusiform rust resistance (Wells and Wakeley 1966, Wells et al. 1982). Approximately the same response of

the Texas loblolly pine and shortleaf pine progenies to Cqf and Cqe would support the hypothesis. Inocula from round- and fusoid-shaped galls on loblolly pine were used to test a second long standing hypothesis: Cqe and Cqf have common genes for determining gall shape. Similar reactions of inoculated pines to Cqe and to round gall Cqf collections would support this hypothesis and indicate relatedness in the fungal pathogen to match that which has been postulated for the pine host.

Table 1. *Cronartium quercuum* collections used to evaluate Texas loblolly pine for fusiform rust resistance.

Number	Source of spores	Gall Shape	Collection code
1	Shortleaf pine – Rusk County, TX	Round	MET-3
2	Loblolly pine – Trinity County, TX	Round	LT-3
3	Loblolly pine – Trinity County, TX	Fusoid	LT-1
4	Loblolly pine – Livingston Parish, LA	Round	LP-3
5	Loblolly pine – Livingston Parish, LA	Fusoid	WLP-6

Table 2. Diallel mating design and progeny code numbers for control-pollinated progeny of Texas loblolly pine.

Parent Trees	B11L	B123L	B134L	B142L	B144L	B145L
B7L	1	- -	3	4	5	6
B11L		7	8	9	10	11
B123L			12	- -	14	15
B134L				16	17	- -
B142L					19	20
B144L						21

The pine seedlings were grown in 4-inch plastic tubes with a 1:1 ratio of vermiculite and peat moss. When the plants were 6 to 8 weeks old, 10 seedlings from each seed lot were inoculated with each of the five inocula. This process was repeated to give three complete replications. The order in which pine families were inoculated and the order in which the inocula were used, were determined independently and randomly among and within replications. A forced air system (Snow and Kais 1972) with basidiospore counts maintained at 12-18 mm^2 was used for all pine inoculations. Afterwards, the pine seedlings were planted in nursery beds where they remained for 9 months until final evaluations were made.

A second experiment (Experiment 2) was established to compare the greenhouse inoculations with natural exposure. The seedlings were grown in the nursery in 1985 and were planted at a high rust hazard site on the Palustris Experimental Forest near Alexandria, Louisiana, in February 1986. The field experiment was designed as a randomized complete block with five replications. Each pine full-sib family and bulk seed source was represented by a 10-tree row-plot in each replication. A third experiment (Experiment 3) was established to conserve and

evaluate the genotypes of the pines that had remained gall-free after artificial exposure to the Cqf inocula. Twenty-five rust-free seedlings from each full-sib family were planted adjacent to Experiment 2 in February 1986 in five randomized complete blocks of 5-tree row-plots. In addition, a local Louisiana bulk source of loblolly pine was included as a third check lot.

Survival, height, DBH, and presence of fusiform rust galls were recorded for each tree at ages 4 and 20 years in both Experiments 2 and 3. In addition, resin yield (g / 24 hours, Roberds et al. 2003) was recorded on each of the surviving trees in the spring of year 20 (data not presented). The GLM procedure of SAS (SAS Institute, Cary, NC) was used to evaluate the significance ($p<0.05$) of the differences among full-sib families. Duncan's new multiple range test was used for comparing means.

RESULTS AND DISCUSSION

The full-sib families showed significant differences in resistance to all Cqf inocula (Inocula 2-5, Table 3) as measured by percent gall. Differences in resistance were also indicated among the pine families in response to Cqe inoculum (Inoculum 1, Table 3), but interactions across the replications apparently nullified their statistical significance. Consequently, a significant relationship could not be established between the Cqe inoculum and any one of the Cqf inocula. These results, therefore, cannot be used in support of the hypothesis that loblolly pine and shortleaf pine share common genes for resistance to Cqf. It is interesting to note, however, that the loblolly pine families were at least equally resistant (i.e., not significantly different) to Cqe as were the bulk shortleaf pine seedlings (Table 3) and that the bulk shortleaf were uniformly resistant to Cqf (0% gall for all Cqf inocula). Perhaps the two species or these specific trees have common genes for resistance to Cqe, but they are certainly different with respect to Cqf. This result is consistent with earlier data reported by Kraus et al. 1982. The uniform resistance of shortleaf pine to Cqf has been reported (Snow and Kais 1970; Powers 1972) as have exceptions (Kais and Snow 1972; Kraus et al. 1982).

All of the galls caused by Cqe were round shaped as are indicated by their low gall form values (Inoculum 1, Table 4). For Cqf (Inocula 2-5, Table 4), there was no relationship between the shape of galls from which the inocula were collected and the shape of galls that formed on inoculated seedlings. For example, Inoculum 3 consistently caused galls with lower gall form ratios than Inoculum 2, while the "parent" gall of Inoculum 3 was fusoid-shaped, and that for Inoculum 2 was round-shaped. Further, Inocula 4 and 5 were collected from round and fusoid galls, respectively, but the gall form values for galls caused by these inocula were not consistently high or low and varied by pine family. These results clearly fail to support the hypotheses that Cqe and Cqf have common genes that govern gall shape.

The data in Table 3 suggest the presence of interacting gene pairs between the full-sib families and the single gall rust collections (see Nelson et al. 2008 for further discussion on methodology). For example, both B7L and B11L do not appear to carry R genes (alleles) specific for the avirulence (Avr or A) genes (alleles) present in the four Cqf collections, since percent gall data for B7L x B11L exceed 75% for each inoculum. In addition, B123L may be alike in this regard as it responds similarly to the four Cqf inocula when crossed to B11L (note that B123L was not crossed with B7L for this experiment). On the other hand, parents B134L,

B142L, B144L, and B145L all appear to have R gene(s) that interact with one or more of the Cqf inocula. These interactions can be most easily seen by looking at the crosses of these trees with either B7L or B11L where several cells are in the 50%-60% range or lower. Also of interest is the suggestion by these data that the response of these trees differs among the Cqf inocula when crossed to B7L and B11L even though the latter two trees appear not to carry any R genes. This may be due to different background genetic effects (i.e., gene modifiers, enhancers, etc.) along with sampling effects given that only 30 trees were evaluated in each full-sib family-by-single gall inoculum combination.

Table 3. Percent of loblolly pine with fusiform rust galls 9 months after inoculation with five sources of *Cronartium quercuum*.

		Inocula[1]				
Family	Cross[2]	1 Cqe, R	2 Cqf, R	3 Cqf, F	4 Cqf, R	5 Cqf, F
1	7 x 11	0	83.3a[3]	91.7a	75.0abc	91.7a
3	7 x 134	6.7a	46.7abc	55.2abc	36.7c-g	70.0a-d
4	7 x 142	6.7a	60.0abc	70.0abc	43.3b-f	80.0abc
5	144 x 7	0	43.3abc	50.0bc	33.3d-g	40.0cd
6	7 x 145	5.6a	83.3a	72.2abc	38.9c-g	88.6ab
7	11 x 123	33.3a	66.7ab	91.7a	80.6ab	66.7a-d
8	134 x 11	0	58.3abc	78.3ab	51.6a-f	86.7ab
9	11 x 142	23.3a	60.0abc	56.7abc	90.0a	80.0abc
10	144 x 11	3.7a	46.7abc	60.0abc	33.3d-g	40.0cd
11	11 x 145	10.8a	49.2abc	67.8abc	79.6ab	70.0a-d
14	123 x 144	18.3a	22.2cd	40.4bc	32.9d-g	48.5cd
15	123 x 145	25.0a	38.9bc	50.0bc	91.7a	69.4a-d
16	134 x 142	17.4a	43.3abc	56.7abc	70.0a-d	90.0a
17	134 x 144	6.7a	45.0abc	36.7c	31.7d-g	30.5de
19	144 x 142	25.0a	66.7ab	72.2abc	27.8efg	30.5de
20	145 x 142	26.7a	66.7ab	56.7abc	85.6a	100.0a
21	145 x 144	10.7a	70.0ab	73.3abc	21.5fg	29.2de
22	MS Bulk Shortleaf	10.7a	0	0	0	0
23	MS Bulk Loblolly	7.0a	63.3ab	59.9abc	51.9a-f	62.7a-d
Means		12.5	53.4	59.9	51.9	62.8

[1]Inocula code is as sown in Table 1: Cqe is *C. quercuun* f.sp. *echinatae*; Cqf is *C. quercuum* f.sp. *fusifome*; R is round-shaped source gall; and F is fusoid-shaped source gall.

[2]Cross code is female parent x male parent. Parent codes used here omit the B prefix and L suffix shown in Table 2.

[3]For each column, means not followed by the same letter are significantly different at the 5% level.

Table 4. Form (gall length / gall diameter) of fusiform rust galls on loblolly pine 9 months after inoculation with five sources of *Cronartium quercuum.*

Family	Cross[2]	Inocula[1] 1 Cqe, R	2 Cqf, R	3 Cqf, F	4 Cqf, R	5 Cqf, F
1	7 x 11	- -	2.12ab[3]	1.95ab	1.88c-h	2.45a-e
3	7 x 134	0.89bc	2.33ab	2.02ab	2.41a-d	1.98cde
4	7 x 142	0.86bc	3.14a	1.87abc	2.2b-f	2.60a-d
5	144 x 7	- -	2.03ab	1.91ab	2.58ab	2.23a-e
6	7 x 145	1.41ab	2.35ab	1.96ab	2.53abc	3.05ab
7	11 x 123	0.88bc	2.73ab	1.62bc	1.30h	1.98cde
8	134 x 11	- -	2.19ab	1.68abc	1.77d-h	2.09cde
9	11 x 142	0.87bc	2.38ab	1.78abc	1.82d-h	2.22a-e
10	144 x 11	0.84bc	2.00b	1.63bc	1.64e-h	1.80cde
11	11 x 145	1.05abc	2.73ab	1.77abc	2.25b-e	1.78de
14	123 x 144	1.18abc	1.75b	2.11a	1.55fgh	2.11b-e
15	123 x 145	0.73c	2.69ab	2.01ab	2.96a	1.52e
16	134 x 142	1.02abc	2.74ab	1.85abc	2.22b-f	2.43a-e
17	134 x 144	0.80c	2.30ab	1.44c	1.84d-h	1.62e
19	144 x 142	0.95bc	2.60ab	1.87abc	1.50gh	3.11a
20	145 x 142	154a	2.44ab	2.02ab	2.99a	3.09a
21	145 x 144	1.27abc	2.16ab	1.85abc	1.97b-h	2.23a-e
22	MS Bulk Shortleaf	0.88bc	- -	- -	- -	- -
23	MS Bulk Loblolly	1.11abc	2.23ab	1.90ab	2.02b-g	2.75abc
Means		1.04	2.38	1.85	2.09	2.28

[1]Inocula code is as sown in Table 1: Cqe is *C. quercuun* f.sp. *echinatae*; Cqf is *C. quercuum* f.sp. *fusifome*; R is round-shaped source gall; and F is fusoid-shaped source gall.

[2]Cross code is female parent x male parent. Parent codes used here omit the B prefix and L suffix shown in Table 2.

[3]For each column, means not followed by the same letter are significantly different at the 5% level.

The variance in fusiform rust resistance observed among the Texas full-families demonstrates that gains in rust resistance are possible within this seed source (Table 3). Selection of individual resistant trees should be part of tree improvement practice, as has been recommended for other western sources of loblolly pine (Sluder 1973), but knowledge of specific R and A genes also needs to be considered. Candidate parent trees should be evaluated against a panel of Cqf collections (preferably single-spore isolates, Kubisiak et al. 2005) to determine their likely R gene composition. This information can then be used to determine useful crossing schemes to combine R genes originating in Texas with those from other areas of the south, if in fact they are found to differ. In any event, the long-term performance of such materials at many field sites should be determined before they are used on a large scale.

Survival and growth of trees on the Palustris Experimental Forest has been good through 20 years (Experiment 2, Table 5 and Experiment 3, Table 6). A few of the loblolly pine families grew as well, and in some cases, better than the south Mississippi or local Louisiana loblolly pine sources. This is encouraging, because the slow growth noted with some Texas seed sources (Wells and Wakeley 1966) is not clearly evident here. Rust incidence (percent gall) has been considerably lower than expected thus correlations between field and greenhouse data were not considered. Future plans for these plantings are to: (1) maintain the trees for genetic conservation; (2) maintain the galls for future experiments; and (3) monitor the trees for resistance to southern pine beetle attack should an outbreak occur.

Table 5. Survival, growth, and fusiform rust incidence for un-inoculated full-sib families (Experiment 2) of Texas loblolly trees planted on the Palustris Experimental Forest.

Family Code	Cross[1]	# Survivors 4 yrs	Height 4 yrs (m)	#Galled 4 yrs	Height 20 yrs (m)	DBH 20 yrs (cm)
3	7 x 34	41	2.86ab[2]	1	17.3abcd	20.9abc
4	7 x 142	45	2.72abc	1	18.4a	21.2ab
5	144 x 7	37	2.72cd	1	16.1de	18.0d
6	7 x 145	29	2.89ab	0	16.9bdc	22.6a
10	144 x 11	42	2.55bcd	2	15.7e	19.5bcd
11	11 x 145	45	2.76abc	2	17.5abc	21.9ab
12	134 x 123	23	2.99a	0	16.3cde	22.4ab
16	134 x 142	45	2.93ab	1	17.7ab	22.7a
17	134 x 144	39	2.76abc	1	16.3cde	18.7cd
21	145 x 144	28	2.29d	4	18.1ab	21.0abc
22	MS bulk Shortleaf	47	1.98e	0	14.31f	16.7d
23	MS bulk Loblolly	47	3.05a	1	18.0ab	22.3ab

[1]Cross code is female parent x male parent. Parent codes used here omit the B prefix and L suffix shown in Table 2.

[2]For each column, means not followed by the same letter are significantly different at the 5% level.

Table 6. Survival, growth, and fusiform rust incidence of rust-free survivors (Experiment 3) of Texas Loblolly pines inoculated in Gulfport, MS and planted on the Palustris Experimental Forest.

Family Code	Cross[1]	#Survivors 4 yrs	Height 4 yrs (m)	#Galled 4 yrs	#Survivors 20 yrs	Height 20 yrs (m)	DbH 20 yrs (cm)
1	7 x 11	16	2.59a-d[2]	0	15	17.2abcd	23.4bc
3	7 x 134	18	3.08abc	1	17	18.1abc	23.2bc
4	7 x 142	5	2.21cd	0	5	16.2bcd	22.1bc
5	144 x 7	3	2.21d	0	2	15.4d	25.7ab
6	7 x 145	19	3.14ab	0	16	18.9a	25.0abc
7	11 x 123	10	3.26a	0	9	17.4abcd	22.1bc
8	134x 11	17	3.01a-d	0	14	16.7abcd	21.1bc
9	11 x 142	16	2.81a-d	0	15	16.0cd	24.3abc
10	144 x 11	13	3.01a-d	0	9	17.4abcd	20.9bc
11	11 x 145	20	2.94a-d	0	20	18.7abc	23.1bc
14	123 x 144	7	2.79a-d	0	5	17.2abcd	22.1bc
15	123 x 145	15	3.12ab	1	15	17.9abcd	24.4abc
16	134 x 142	15	3.23a	0	14	17.6abcd	24.8abc
17	134 x 144	11	2.32bcd	0	11	17.0abcd	21.2bc
19	144 x 142	7	2.45a-d	1	7	17.1abcd	20.2c
20	145 x 142	23	3.11ab	0	23	18.5abc	24.4abc
21	145 x 144	14	2.87a-d	0	9	17.3abcd	25.0abc
22	MS bulk Shortleaf	9	2.33bcd	0	9	12.9e	16.1d
23	MS bulk Loblolly	14	2.91a-d	0	11	18.3abc	28.2a
24	LA bulk Loblolly	44	2.33bcd	0	37	17.1abcd	22.4bc

[1]Cross code is female parent x male parent. Parent codes used here omit the B prefix and L suffix shown in Table 2.

[2]For each column, means not followed by the same letter are significantly different at the 5% level.

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