Genetics

Frequency of Single-Gall Isolates of *Cronartium quercuum* f. sp. *fusiforme* with Virulence Toward Three Resistant Loblolly Pine Families

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ABSTRACT

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Basidiospores from 11 of 19 aeciospore isolates of *Cronartium quercuum* f. sp. *fusiforme* derived from single galls were highly virulent on half-sib progeny of resistant loblolly pine selection 10-5 (family 10-5). Virulence was indicated by a high frequency of seedlings with galls (68–83%) 9 mo after inoculation compared to a normal frequency of 34–50% for the other isolates of this family. The high proportion of isolates with increased virulence toward progeny of 10-5 was unexpected because seedlings of this resistant selection have been widely planted with no evidence of breakdown in resistance, and the sources of the rust isolates were geographically distant from the original source of the 10-5 ortet. These isolates with virulence toward family 10-5 were common in North Carolina and Maryland, whereas the parent, 10-5, originated 400–775 km away in South Carolina. In contrast, only one of 77 isolates had virulence toward resistant family 11-20 in a second study. The one virulent isolate was from Colleton County, SC, which was the source of another isolate highly virulent toward family 11-20 in a previous test. In a third study, increased virulence toward resistant family 29R was confirmed in three of six isolates. One of these isolates came from a gall on a half-sib offspring of 29R. Isolates with virulence toward families 10-5 and 11-20 were collected in pine stands that had been established with progeny not selected for rust resistance.

Additional keywords: fusiform rust, *Pinus taeda*.

Selecting and breeding loblolly pines (*Pinus taeda* L.) for resistance is the most promising method for control of fusiform rust disease caused by *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*. Resistance to fusiform rust has been demonstrated in both loblolly and slash pines (*P. elliottii* Engelm var. *elliottii*) (1,14,15,21,26). Resistance can be increased by interbreeding resistant individuals (12). These pairings should be most effective if resistant individuals have different genes for resistance.

The identification of virulence genes in a pathogen population toward specific host sources of resistance can be important in the development of broadly based resistance in a host population. Quantifying the occurrence of virulence genes in the pathogen population is important for relating their prevalence to stability of resistance. Identification of similarities and differences between resistant host sources in response to different pathogen populations has been used effectively to manage gene resources in disease resistance breeding programs (9).

In studies of *C. q. fusiforme*, aeciospores produced on the pine host are collected, preserved, and used to inoculate oaks to produce basidiospores to inoculate pines and thus determine variations in host and pathogen (7,20). Such aeciospore collections

are termed "field isolates" because they are collected directly from nature and genetically unaltered by laboratory manipulation (25). Single-gall field isolates of *C. q. fusiforme* can vary in pathogenicity toward progenies (families) of resistant loblolly and slash pine selections (1,6,11,16,17,21–24). Powers et al (17) used 56 single-gall field isolates collected from seven southeastern states to inoculate three loblolly pine families rated as resistant, intermediate, and susceptible. One isolate, SC-10, was highly virulent on the resistant family 11-20 and produced rust galls on 86% of the seedlings compared to an average of 40% for the 56 isolates. This infection by SC-10 on family 11-20 was equal to its infection (84%) on susceptible family 11-23. However, in a composite inoculum derived from aeciospores from SC-10 and seven other galls from Colleton County, SC, the virulence genes were not expressed (6) probably because basidiospores with the virulence genes were infrequent in the composite inoculum. Isolate SC-10 was used in other studies of variation in host and pathogen (6,11,16), and inadvertently the collection was depleted. Fortunately, 43 single-gall aeciospore collections had been made in a pine stand less than 1 km from the original SC-10 collection. These 43 collections provided an opportunity to determine if virulence genes toward family 11-20 in this area were as infrequent as the earlier small sample suggested.

Loblolly pine family 10-5 has been reported as highly resistant in a number of field tests (8,14,15,26). Furthermore, progeny of 10-5 were resistant (36–41% seedlings with galls) to four single-gall field isolates, whereas progeny of 13 other selections varied from 22 to 99% of seedlings with galls in response to these isolates (11). However, Kuhlman and Matthews (3), using an inoculum density of 75,000 basidiospores/ml (1.5 times normal concentration) reported a higher rate of infection (83–93%) on family 10-5 with composite inocula from eight galls each from North Carolina, Maryland, and Florida than the resistant rate of infection (34–48%) with composite inocula from Georgia, Mississippi, and Texas. The increased rate of infection with the composite inocula from North Carolina, Maryland, and Florida could have been due to increased virulence, the high inoculum density, or the composite inocula.

The purpose of this study was to determine the presence and relative occurrence of virulence in single- and composite-gall field isolates of *C. q. fusiforme* toward half-sib progeny of three resistant loblolly pine selections.

MATERIALS AND METHODS

Pine sources. Loblolly pine seedlings from resistant half-sib families 10-5, 11-20, and 29R were used in these studies. The standard response of these families averaged 37, 39, and 41%, respectively, of the seedlings with galls in previous greenhouse studies with 4–18 single-gall isolates (11,13,16–18). Susceptible families in these studies averaged 80% with galls. The relative resistance of these families also has been demonstrated in field progeny tests (14,15,26).

Rust sources. Aeciospores usually were collected from individual galls (single-gall isolates) located more than 30 m apart (20). For inoculation of family 10-5, single-gall isolates were collected in Somerset County, MD, in 1977, Wake and Halifax Counties, NC, in 1973, Clarke County, GA, in 1973, and Nacogdoches County, TX, in 1977. The single-gall isolates selected included some used by Kuhlman and Matthews (3). Aeciospores were collected from several galls (composite isolate) on infected half-sib progeny of 10-5 growing in Greene County, GA, in 1980 and 1983 (10-5-80 and 10-5-83, respectively) and from infected wildling loblolly pines in Clarke County, GA, in 1973 (1-73). In all, 19 isolates were tested on family 10-5.

Seventy-seven isolates were tested on family 11-20. Single-gall isolates were collected in Colleton, Sumter, and Georgetown Counties, SC, in 1975 (43, 17, and 15 isolates, respectively). In addition, composite isolates were collected from infected half-sib progeny of 11-20 in Greene County, GA, in 1980 (11-20-80) and from infected wildling loblolly pines in Clarke County, GA, in 1974 (2-74).

Virulence of single-gall isolates 0-5 and V-21, previously shown to be virulent on 29R progeny (13,18) were compared with composite isolates 29R-80 and 29R-83 (from 29R progeny in Greene County, GA) and composite isolate 29R × 10-5 (from 29R × 10-5 progeny in Greene County, GA) on progeny of 29R. Composite isolates 1-73 and 2-74 are our standards in testing for resistance (4).

Inoculation. Rehydrated aeciospore inoculum was sprayed on the ventral surfaces of immature leaves of seedlings of northern red oak (*Quercus rubra* L.). Basidiospores were harvested from telia 3–4 wk after aeciospore inoculations (7).

Pine seeds were germinated and seedlings were transplanted into flats containing 20 seedlings each (7). At 6 wk of age, the seedlings were inoculated with 50×10^3 basidiospores/ml dispensed in 8-ml portions per flat as seedlings moved on a conveyor under spray nozzles. Each of five or six flats (reps) of seedlings was inoculated with an inoculum source. The sprayer was cleaned with 95% ethyl alcohol and water before spores from the next inoculum source were applied. Immediately after inoculation, the seedlings were placed in a moist chamber and held at 21 C for 24 hr (7). They then were grown in a greenhouse for 6–9 mo.

Seedlings of family 10-5 were inoculated with 19 isolates in one day. Eight separate experiments were undertaken to compare the virulence of 77 isolates on seedlings of family 11-20. In the first six experiments, 12, 23, 21, 9, 6, and 11 isolates were compared with mass isolate 2-74 (the standard source) by analysis of variance (ANOVA) and Duncan's multiple range test (DMRT) to identify isolates highly virulent on seedlings of family 11-20. Five isolates tentatively identified as highly virulent were retested along with nine isolates of standard virulence in the final two experiments. In a separate experiment, seedlings of family 29R were inoculated with six isolates. Data from each experiment were subjected to an ANOVA. If significant differences among isolate treatments occurred, multiple comparisons were made with DMRT.

RESULTS

Eleven of 19 isolates tested on seedlings of family 10-5 were highly virulent. That is, they produced a higher frequency of seedlings with galls (68–83%) at 9 mo than the standard frequency of 34–50% produced by the other isolates (Table 1). Highly virulent isolates were all from single galls. Isolates from Somerset County,

TABLE 1. Seedlings of half-sib loblolly pine family 10-5 with galls of *Cronartium quercuum* f. sp. *fusiforme* 9 mo after inoculation with basidiospores derived from 19 aeciospore isolates

Isolate[y]	Source (county and state)	Seedlings with galls (%)
LHNC-2	Halifax, NC	83 a[z]
LHNC-5	Halifax, NC	82 a
77M-13	Somerset, MD	81 a
77M-11	Somerset, MD	80 a
77M-4	Somerset, MD	77 a
77M-8	Somerset, MD	76 ab
LWNC-9	Wake, NC	73 ab
LCG-7	Clarke, GA	73 ab
LHNC-3	Halifax, NC	72 ab
LWNC-2	Wake, NC	71 ab
LHNC-6	Halifax, NC	68 ab
LHNC-1	Halifax, NC	61 bc
LWNC-6	Wake, NC	50 cd
10-5-83 (C)	Greene, GA	46 de
LWNC-3	Wake, NC	44 de
LWNC-8	Wake, NC	42 de
1-73 (C)	Clarke, GA	42 de
10-5-80 (C)	Greene, GA	41 de
77-T-4	Nacogdoches, TX	34 e

[y] Aeciospore isolates were collected from a single gall, except composite (C) isolates, which were collected from several galls.

[z] Means followed by the same letter do not differ significantly at $P = 0.01$ as determined by Duncan's multiple range test.

MD, and Halifax County, NC, usually were highly virulent toward seedlings of family 10-5. The three composite-gall isolates, including two that were collected from galls on progeny of family 10-5, produced a standard level of virulence. Single-gall isolates from Wake County, NC, had both standard and high virulence. The high virulence of isolate LCG-7 from Clarke County, GA, was unexpected because the composite inoculum, which included this isolate, was of standard virulence in a previous study (3).

Isolate 35 from Colleton County, SC, was the only isolate of 76 tested that was significantly more virulent on family 11-20 than the standard isolate 2-74 in more than one of the experimental test groups (Tables 2 and 3). Isolate 35 caused infection levels 35 and 39 percentage points greater than the standard composite isolate 2-74 in experiments II and VIII. Therefore, virulence genes toward resistant family 11-20 were confirmed in only one of 43 (2%) single-gall isolates from Colleton County, SC. In four of the six preliminary screening experiments, ANOVA indicated significant differences in virulence among isolates (Table 2), and DMRT at $P = 0.05$ suggested that five isolates were more virulent than the standard isolate. However, when the five isolates were retested in one of the two final experiments, only isolate 35 was significantly more virulent than 2-74.

Single-gall isolates 0-5 and V-21 and composite isolate 29R-83 were rated as highly virulent toward seedlings of family 29R (Table 4). The composite isolate 29R × 10-5 was rated as intermediate in virulence on progeny of family 29R because the infection level was not significantly different either from those of two virulent sources or from those of the two normal sources.

TABLE 2. Virulence of 77 isolates of *Cronartium quercuum* f. sp. *fusiforme* toward loblolly pine family 11-20 as indicated by the percentage of seedlings with galls 9 mo after inoculation

Experiment	No. isolates tested[y]	Galls (%)		ANOVA[z]
		Range	Standard 2-74	
I	12	20–41	39	NS
II	23	33–80	45	$P < 0.01$
III	21	21–55	33	$P < 0.01$
IV	9	41–70	53	$P < 0.05$
V	6	44–61	44	NS
VI	11	14–46	40	$P < 0.01$

[y] One composite and 75 single-gall isolates were compared with composite isolate 2-74 in six experiments. Single-gall isolates were from Colleton, Georgetown, and Sumter counties, SC; composite-gall isolates were from Greene and Clarke counties, GA.

[z] Analysis of variance. Test of frequency of galls among isolates. NS = not significant.

TABLE 3. Virulence of 15 single-gall aeciospore isolates toward loblolly pine family 11-20 in preliminary and final experiments (VII and VIII)

County and state	Isolate No.	Preliminary experiments		Final experiments	
		No.	Seedlings with galls (%)	Seedlings with galls (%)[y]	
				VII	VIII
Colleton, SC	35	II	80[z]	···	73 a
Georgetown SC	77	IV	71[z]	···	50 bc
Colleton, SC	28	II	70[z]	55 ab	···
Colleton, SC	20	II	65[z]	62 a	55 b
Georgetown, SC	78	IV	63	···	47 bc
Colleton, SC	43	V	61	40 bcd	···
Sumter, SC	69	V	59	56 abc	···
Georgetown, SC	84	V	56	23 e	···
Colleton, SC	49	III	55[z]	42 bcd	···
Colleton, SC	33	II	54	55 ab	···
Sumter, SC	57	V	51	39 bcd	···
Clarke, GA	2-74	I–VI	39–53	48 abc	34 bc
Colleton, SC	41	III	36	51 ab	52 b
Sumter, SC	56	VI	36	34 de	···
Colleton, SC	9	I	34	30 de	···

[y] Within columns numbers with the same letter do not differ significantly according to Duncan's multiple range test ($P = 0.05$).

[z] Significantly different from isolate 2-74 according to Duncan's multiple range test ($P = 0.05$).

DISCUSSION

Virulence toward three resistant loblolly pine families was detected among specific rust isolates in this series of experiments. Because virulence has been demonstrated to be under genetic control in other rust organisms (9), it is assumed that we are dealing with specific genes in these cases. Virulence toward family 10-5 was present in 11 of the 19 isolates used in one experiment (Table 1). Admittedly, the isolates were selected on the basis of a previous study (3) to increase the likelihood of finding single-gall field isolates with virulence toward family 10-5. Notwithstanding this biased sample, the frequency of isolates with virulence toward family 10-5 was unexpected. Tree (ortet) 10-5 was selected in a natural stand in Jasper County, SC, by Union Camp Corporation. Wake and Halifax Counties, NC, and Somerset County, MD, are 400–775 km from Jasper County. Somerset County, MD, is at the northern edge of the natural range of loblolly pine, whereas Jasper County, SC, is in the center of the range (5). Although progeny of family 10-5 have been widely planted in progeny tests (15,26), these plantings apparently have not been extensive enough to exert selection pressure on the pathogen. Furthermore, those counties in North Carolina and Maryland are in or north of areas of low rust incidence (<10%) (2). Therefore, virulence genes toward family 10-5 occurred commonly in a small sample and independently of selection pressure by this specific host genome, because the pine population was unselected for rust resistance.

A more intensive survey was conducted in South Carolina for single-gall field isolates with virulence toward family 11-20. In a previous study, only one, SC-10, of eight isolates from Colleton County, SC, expressed virulence toward family 11-20 (17). In the present study, only one of 43 single-gall isolates from a stand within 1 km of the SC-10 source had virulence genes, whereas none of the 32 isolates from Georgetown and Sumter counties, SC, expressed virulence toward family 11-20.

The pine stands from which the rust was collected in South Carolina also were not rust-resistant pine populations. The rust isolates, therefore, were unbiased samples of the pathogen population occurring on pines that had not been selected for rust resistance. However, virulence genes toward family 11-20 appear to be much less frequent than those toward family 10-5. Powers et al (17) reported that only one other isolate, besides SC-10, of the 56 isolates from seven southern states tested increased the infection rate by 25% over the host mean for family 11-20.

Virulence toward family 29R has been reported in three of nine single-gall isolates collected from infected progeny of 29R and in one of nine single-gall field isolates from unselected susceptible progeny (18). Powers and Dwinell (13) reported no

TABLE 4. Seedlings of half-sib loblolly pine family 29R with galls of *Cronartium quercuum* f. sp. *fusiforme* 6 mo after inoculation with basidiospores from six aeciospore isolates from two counties in Georgia

Aeciospore isolate[y]	Source (county and state)	Seedlings with galls (%)
0-5	Greene, GA	87 a[z]
V-21	Greene, GA	78 ab
29R-83 (C)	Greene, GA	63 abc
29R × 10-5 (C)	Greene, GA	52 bc
1-73 (C)	Clarke, GA	39 c
29R-80 (C)	Greene, GA	38 c

[y] Aeciospore isolates were collected from a single gall, except composite (C) isolates, which were collected from several galls.

[z] Means within columns followed by the same lowercase letter do not differ significantly at $P = 0.01$ as determined by Duncan's multiple range test.

TABLE 5. Comparisons of virulence of composite- and single-gall isolate inoculum of *Cronartium quercuum* f. sp. *fusiforme* from several states toward progeny of family 10-5

Rust source	Composite (% galls)[x]	Single-gall isolates in present study: Virulent[y]/total from composite[z]	Single-gall isolates in present study: Virulent[y]/total tested
North Carolina	93	3/5	6/10
Maryland	87	2/2	4/4
Georgia	42	1/1	1/1
Texas	34	0/1	0/1

[x]Composite-gall inoculum (eight galls) reported by Kuhlman and Matthews (3) using an inoculum density of 75,000 basidiospores/ml.

[y]Isolates in most virulent group (Table 1) according to Duncan's multiple range test ($P = 0.01$).

[z]Single-gall isolates that were used in composite and tested singly in this study.

significant differences in virulence in spite of a range of 30% seedlings with galls among 12 single-gall isolates collected from 25- to 30-year-old galls using four reps per isolate. However, one of those 12 isolates (0-5) was highly virulent in my study.

In single-gall isolates, many genes may contribute to virulence toward specific resistant families. Although a gall may be the product of a single haploid basidiospore, the yearly production of spermatia presents opportunities for adding heterogeniety. Sexual recombinations in the basidia (promycelia) are expressed by the haploid basidiospores. Because the fusiform rust population on pine is the result of infection by basidiospores, distinct virulence phenotypes should be common. Roelfs and Groth (19) reported 100 distinct virulence phenotypes in a sexually reproducing population of stem rust of wheat but only 17 phenotypes in a larger asexual population. The frequency of virulence genes in the fusiform rust population varies considerably with location (Tables 1, 3, and 4). Because the presence of virulence genes in different single-gall isolates can vary considerably, it is helpful to identify single-gall isolates with specific virulence genes present before undertaking the lengthy process of establishing single-aeciospore isolates. Powers (10) established 10 single-aeciospore isolates from a randomly selected single-gall isolate and detected no isolate × pine family interaction on three pine families. With the identification of single-gall sources of virulence toward three loblolly pine families, efforts are now under way to establish single-aeciospore isolates.

Virulence and avirulence genes can be masked or diluted when inoculum derived from composite-gall isolates is used. Basidiospore inoculum prepared from composite-gall isolates usually has produced an infection level similar to the mean of the single-gall isolates in the composite (6,23,24). When one or two single-gall isolates with virulence genes present were part of an eight-gall composite inoculum, virulence was not expressed (6,17). In this study, virulence genes toward family 10-5 were present in 60 and 100% of the isolates tested from North Carolina and Maryland, respectively. This virulence also was expressed in composite inocula from these states (Table 5). Single-gall isolates from Georgia and Texas were included in this study with the expectation (3) that they would have normal levels of virulence, but the Georgia isolate had virulence genes that were expressed.

Identifying virulent isolates and determining the relative frequency of their occurrence are important steps in identifying and deploying pines with resistance to fusiform rust.

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