Susceptibility of Southern Oaks to Cronartium fusiforme and Cronartium quercuum

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ABSTRACT

In a greenhouse study, 21 species of oaks were inoculated with aeciospores of *Cronartium fusiforme* and *C. quercuum*. Based on an evaluation of telia/cm², water and willow oaks were highly susceptible to *C. fusiforme*. Blackjack, cherrybark, bluejack, running, southern red, northern red, and turkey oaks were moderately to highly susceptible to *C. fusiforme*. Scarlet and black oaks were generally hypersensitive to *C. fusiforme*. Water oak was most susceptible to *C. quercuum*. Northern red and black oaks were also highly susceptible to *C. quercuum*, followed by bluejack, blackjack, southern red, and scarlet oaks. Northern red and black oaks were more susceptible to *C. quercuum* than to *C. fusiforme*. Water, willow, cherrybark, bluejack, running, turkey, and overcup oaks were more susceptible to *C. fusiforme* than to *C. quercuum*. The black oak group was much more susceptible to both pathogens than the white oak group. For several oak species, this is the first report of them as hosts of either *C. fusiforme* or *C. quercuum*.

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The important pine stem rusts in the southeastern United States are fusiform rust, caused by *Cronartium fusiforme* Hedgc. & Hunt ex Cumm., and eastern gall rust, caused by *Cronartium quercuum* (Berk.) Miy. ex Shirai. Although the oak hosts are seldom damaged by these obligate parasites, several commercially valuable pine species suffer considerable damage and mortality, particularly from *C. fusiforme*.

Most previous research on oak infection, recently reviewed by Czabator (1), has been concerned with overall susceptibility and host range. Because so little information is available about the relative susceptibility and telia-production potential of various southern oak species in relation to *C. fusiforme* and *C. quercuum*, this study was undertaken to define more precisely the role of southern oaks in the life cycles of both pathogens. This information should also be useful in determining which oaks can produce basidiospores for tests to evaluate pines for rust resistance.

MATERIALS AND METHODS.—Twenty-one oak species used in this greenhouse inoculation study were as follows: white (*Quercus alba* L.), scarlet (*Q. coccinea* Muenchh.), southern red (*Q. falcata* var. *falcata*), cherrybark (*Q. falcata* var. *pagodaefolia* Ell.), bluejack (*Q. incana* Bartr.), turkey (*Q. laevis* Walt.), laurel (*Q. laurifolia* Michx.), overcup (*Q. lyrata* Walt.), blackjack (*Q. marilandica* Muenchh.), swamp chestnut (*Q. michauxii* Nutt.), dwarf live [*Q. minima* (Sarg.) Small], water (*Q. nigra* L.), willow (*Q. phellos* L.), chestnut (*Q. prinus* L.), running (*Q. pumila* Walt.), northern red (*Q. rubra* L.), post (*Q. stellata* var. *stellata*), dwarf post [*Q. stellata* var. *margaretta* (Ashe) Sarg.], black (*Q. velutina* Lam.), live (*Q. virginiana* var. *virginiana*), and sand live [*Q. virginiana* var. *maritima* (Michx.) Sarg.] oaks. Acorns were collected from five to 10 open-pollinated trees of each species. Trees (within a species) were separated by a minimum of 8 km (5 miles), and were located in Georgia, Florida, South Carolina, or North Carolina, depending on the species. After stratification (14), the seedlings were grown in a 1:1:1 soil mix (sand:loam:pine bark) in 10.1-cm (4-in) diam plastic pots in the greenhouse. Growth was induced by a 16-h photoperiod.

Mass aeciospore collections of *C. fusiforme* from loblolly pine (*Pinus taeda* L.) and *C. quercuum* from Virginia pine (*P. virginiana* Mill.) were used as inoculum. Collections were preserved and stored according to the technique of Roncadori and Matthews (11). Before use, the aeciospores were rehydrated for 24 h at 20 C in an atmosphere saturated with water vapor. The percentage germination for both collections (86-92%) was determined by dusting aeciospores onto water oak decoction agar and placing them in an atmosphere saturated with water vapor for 24 h at 20 C.

When the second flush of leaves was 6 or 7 days old, seedlings were inoculated with a mixture of viable spores and talc (1:10), using a bell jar under a vacuum equal to 25-cm (10 in) of mercury (12). Approximately the same amount of spore-talc mixture was used to inoculate each seedling, and all seedlings remained in the bell jar for 1 min after the vacuum was released. This technique produced a uniform coverage of spores on the undersurface of the leaves. After inoculation, the oak seedlings were placed in an incubation chamber saturated with water vapor at 20 C for 24 h, then moved to a greenhouse. Inoculations were made over a 3-mo period, because the seedlings flushed at random.

In the greenhouse, the seedlings were examined daily for the appearance of symptoms and signs. When uredial development ceased (normally 9 to 10 days after inoculation), a thin aluminum template with a 1-cm² opening was placed on the right or left center of the leaf, and uredia were counted on two to four leaves per seedling. The same procedure was used 6 to 7 days later to determine the number of telia/cm².

To estimate the number of telia/leaf, two to four leaves from each seedling were removed and copied on a Xerox Model 2401, and the surface area of the resulting image was determined with a planimeter. The surface area for 100 leaves per species was also determined.

Approximately 50 leaves each were collected from mature trees of black, water, scarlet, and post oaks, and their leaf surface area was measured. There was a highly significant correlation between surface area of leaves from field and seedling oaks from the greenhouse (r = 0.80**). The number of telia/leaf was estimated by multiplying the telia/cm² by the leaf surface area.

The data (telia/cm² and telia/leaf) were analyzed by analysis of variance procedures. Kramer's (5) extension of Duncan's Multiple Range Test was used to group means with unequal numbers of replications. Statistical differences between *C. fusiforme* and *C. quercuum* on individual oak species (telia/cm² data) were determined by Student's *t* test.

RESULTS.—*Cronartium fusiforme.*—The number of telia/cm² was used as a measure of relative susceptibility. Water and willow oaks were the most susceptible species to *C. fusiforme* (Table 1). Cherrybark, bluejack, and running oaks were highly susceptible, but less so than water and willow oaks. Blackjack, southern red, northern red, and turkey oaks were moderately susceptible. The other species (laurel, swamp chestnut, scarlet, overcup, chestnut, black, dwarf live, sand live, post, dwarf post, white, and live oaks) were poor hosts.

Telial production of these southern oaks was measured by estimating the number of telia/leaf; cherrybark and northern red oaks exceeded or equaled water oak (Table 1). The ranking of swamp chestnut oak also increased because of its large leaf surface area, although the average number of telia/cm², 5.8, was relatively low. Willow oak, which has long, narrow leaves, equaled blackjack, southern red, and swamp chestnut oaks when telia/leaf was the criterion for evaluation.

Necrotic flecking, usually considered a resistant response, was fairly common on oak seedlings inoculated with *C. fusiforme;* 23.8% of the seedlings showed this response. The types of infection observed on the oaks were similar to four of the *Puccinia graminis* types originally described by Stakman & Levine (13). The infection types produced by *C. fusiforme* on black and scarlet oaks are as follows: no macroscopically recognizable symptoms (type 0); hypersensitive flecks (type 0;); necrotic tissue developing around either the uredia or telia (type 1); and uredia and telia developing normally (type 4). After inoculation with *C. fusiforme,* 76.6% black and 63.3% scarlet oak seedlings were hypersensitive (Table 2). This explains their low ranking in relative susceptibility to *C. fusiforme* (Table 1). This *C. fusiforme*:black oak interaction was discussed in an earlier paper (2). With the possible exception of laurel (50%) and chestnut (40%) oaks, necrotic flecking (type 0; and type 1) in the other oak species (X = 16%) was probably caused by the effect of temp or other environmental factors on the *C. fusiforme*:oak interaction.

This is the first report that cherrybark, running,

TABLE 1. Relative susceptibility and potential for telia production of southern oak seedlings inoculated with aeciospores of *Cronartium fusiforme* and *C. quercuum*

		Cronartium fusiforme			*Cronartium quercuum*			
Oak host[w]	Leaf surface area,[x] (cm²)	No. plants inocu-lated	Avg telia/cm²	Avg telia/leaf	No. plants inocu-lated	Avg telia/cm²	Avg telia/leaf	Stat. diff.[z]
Water	9.5	63	44.8 a[y]	426	64	32.7 a[y]	310	**
Willow	6.1	44	40.0 a	244	24	1.5 e	9	**
Cherrybark	21.6	47	26.1 b	564	31	4.3 de	93	**
Bluejack	6.7	64	22.0 b	147	40	11.2 cd	75	**
Running	6.5	61	20.1 bc	131	55	2.8 e	18	**
Blackjack	16.5	62	16.6 cd	274	62	12.1 c	200	NS
Southern red	10.9	25	14.5 cde	158	16	10.5 cd	115	NS
Northern red	41.8	69	12.0 de	501	69	23.6 b	986	**
Turkey	11.5	50	11.8 de	136	35	2.8 e	32	**
Laurel	4.6	50	7.2 ef	33	20	2.6 e	12	NS
Swamp chestnut	48.0	50	5.8 f	278	50	2.0 e	97	NS
Scarlet	28.5	60	4.5 f	128	46	10.0 cd	285	**
Overcup	21.7	50	3.4 f	74	50	0.8 e	17	**
Chestnut	44.6	30	1.7 f	76	38	2.0 e	89	NS
Black	28.1	60	1.5 f	43	57	24.3 b	696	**
Dwarf live	4.3	20	1.0 f	4	20	0.0 e	0	NS
Sand live	5.4	46	0.8 f	4	49	0.0 e	0	NS
Post	12.2	58	0.4 f	5	58	0.4 e	6	NS
Dwarf post	9.0	20	0.2 f	2	20	0.1 e	16	NS
White	14.2	40	<0.1 f	1	35	1.1 e	16	NS
Live	6.2	25	0.0 f	0	25	0.0 e	0	NS
Mean	17.1	47	11.2	154	41	6.9	146	NS

[w]Ranked in order of decreasing relative susceptibility (telia/cm²) to *C. fusiforme*.

[x]Based on mean of 100 leaves of each *Quercus* spp. observed.

[y]Figures not followed by the same letter are significantly different, $P = 0.05$ [Kramer's (5) extension of Duncan's Multiple Range Test].

[z]** = statistical difference between *C. fusiforme* and *C. quercuum* (telia/cm²), $P = 0.01$; NS = no statistical difference.

TABLE 2. Distribution of infection types produced by *Cronartium fusiforme* and *C. quercuum* on scarlet (*Quercus coccinea*) and black (*Quercus velutina*) oaks

Pathogen	Oak	No. of plants	% Infection by types[a]			
			0	0;	1	4
C. fusiforme	Black	60	5.0	43.3	33.3	18.3
	Scarlet	60	5.0	50.0	13.3	31.7
C. quercuum	Black	57	7.0	0.0	0.0	93.0
	Scarlet	46	15.2	0.0	0.0	84.8

[a]Infection types: 0 = no macroscopically recognizable symptoms; 0; = hypersensitive flecks; 1 = necrotic tissue developing around either the uredia or telia; and 4 = uredia and telia develop normally.

TABLE 3. Relative susceptibility of the black and white oak groups to *Cronartium fusiforme* and *C. quercuum*

Pathogen	Oak group	No. species tested	Avg telia/cm²
C. fusiforme	Black	12	18.4[a]
	White	9	1.5
C. quercuum	Black	12	11.5[a]
	White	9	0.7

[a]Statistically different, $P = 0.01$ (black vs. white oaks).

overcup, and dwarf live oaks are hosts of *C. fusiforme*.

Cronartium quercuum.—In relative susceptibility, water oak was the best host of *C. quercuum* (Table 1). Northern red and black oaks were also highly susceptible to *C. quercuum*. Bluejack, blackjack, southern red, and scarlet oaks were moderately susceptible. Willow, cherrybark, running, turkey, laurel, swamp chestnut, overcup, chestnut, post, dwarf post, and white oaks were poor hosts. No uredia or telia were recorded on dwarf live, sand live, or live oaks.

In telial production (telia/leaf), northern red and black oaks were the most important species, followed by water, scarlet, blackjack, and southern red oaks. Leaf surface area had little effect on the rank of the other species because of their apparent resistance to *C. quercuum*.

Necrotic flecking on oaks inoculated with *C. quercuum* was not as common as on those inoculated with *C. fusiforme*. Chestnut oak showed the highest—23.7% of the seedlings developed a hypersensitive reaction. Other species that showed some necrotic flecking were cherrybark (6.4%), northern red (2.9%), turkey (2.8%), swamp chestnut (16%), overcup (8.0%), dwarf live (5%), sand live (10.2%), white (5.7%), and live (4.0%) oaks. The overall average for all species tested was only 4%.

This is the first report that cherrybark, running, turkey, laurel, and overcup oaks are hosts of *C. quercuum*.

Comparison of C. fusiforme and C. quercuum.—When telia/cm² was used as the criterion of susceptibility, water, willow, cherrybark, bluejack, running, turkey, and overcup oaks were more susceptible to *C. fusiforme* than to *C. quercuum*. Northern red, scarlet, and black oaks were more susceptible to *C. quercuum* than to *C. fusiforme*. Blackjack, southern red, laurel, swamp chestnut, chestnut, sand live, dwarf live, post, dwarf post, white, and live oaks did not differ significantly in susceptibility to *C. fusiforme* and *C. quercuum*.

C. fusiforme interacted differentially with black (2) and scarlet oaks (Table 2). In contrast, *C. quercuum* produced only normal uredia and telia on black or scarlet oaks. These oak species, therefore, can be used to differentiate between aeciospore or urediospore collections of *C. fusiforme* or *C. quercuum* (2). Black oak, however, is easier to handle under greenhouse conditions and the symptoms (type 0; or type 1) are more clear-cut.

Black- vs. white-oak groups.—A statistical comparison of the black oak group (water, willow, cherrybark, bluejack, running, blackjack, southern red, northern red, turkey, laurel, scarlet, and black) with the white oak group (swamp chestnut, overcup, chestnut, sand live, dwarf live, post, dwarf post, white, and live) demonstrated that the black oaks were much more susceptible to both *C. fusiforme* and *C. quercuum* than were the white oaks (Table 3), also indicated earlier (1).

DISCUSSION.—Data on the relative susceptibility and telia-production potential of southern oaks should be considered in proper perspective; i.e., distribution, habitat, phenology, and habit of the individual species. Water oak, an excellent host of both *C. fusiforme* and *C. quercuum*, is common in the southern United States and occurs in open woods, mixed forests, fence rows, roadsides, bottomlands, and on city lots. Cherrybark oak, a lowland tree, is found only in certain habitats of the Coastal Plain. Willow oak develops best in the southern and southeastern bottomlands of the Coastal Plain. Black and northern red oaks, both excellent hosts of *C. quercuum*, are widely distributed in the eastern United States. Black oak, but not northern red, extends into the Coastal Plain (3, 6, 7). The ubiquitous water oak plays a primary role in the epiphytology of fusiform rust of southern pines. Other susceptible oaks, which may be limited by range or habitat, would be important in the areas in which they occur.

Maximum production of sporidia is necessary to develop artificial inoculation techniques for evaluating the resistance of pines to fusiform rust. Thus, the telia-production potential of various oak seedlings is important. Cherrybark, northern red, water, and blackjack oaks would therefore be primary candidates for the production of sporidia of *C. fusiforme*. Northern red and black oaks have the highest telia-production potential for *C. quercuum*. Other factors, such as availability of acorns, cultural requirements, and ease of handling under greenhouse conditions, would aid in deciding which oak species to use.

Because there has been little research on the biomass and leaf surface area of southern oak forests, it is difficult to interpret the telia-production potential of seedling oaks with that of oak trees in nature. Based on the limited data available, however, the significant influence of oaks in the epiphytology of fusiform rust can be realistically illustrated. A theoretical water oak, with a 17 cm dbh, 50 m^2 leaf surface area (8) (C. D. Monk, *unpublished*), bearing eight telia/cm^2 of leaf area (L. D. Dwinell, *unpublished*, 1968) would be capable of producing 3,800 sporidia/telial column (10). These columns could produce over 15 billion sporidia capable of infecting pines. The sporidia-production potential of a larger, mature water oak would be much greater. Other oak species, small or shrublike trees with their smaller biomass (e.g., bluejack, running, or turkey), should not be as important as the larger, highly susceptible trees (e.g., water, cherrybark, northern red, etc.).

The telial data presented are quantitative. No attempt was made to measure the qualitative aspects of the telial columns on the 21 species of oaks included in this study. Telia on white, chestnut, and post oaks, for example, were not as well developed as those on the more susceptible species (e.g., water, cherrybark, and northern red). Present studies now underway suggest that qualitative differences do occur. Furthermore, for logistic reasons only one aeciospore collection each of *C. fusiforme* and *C. quercuum* was used. Further research may show genetic variability in these rust pathogens on oaks, such as that already demonstrated on pine (4, 9). This may be why the willow, running, and cherrybark oaks differed so markedly in susceptibility to these two rusts.

Frequent reports show that susceptibility of the black oak group is greater than that of the white oak group (1). Data presented here confirm these earlier field observations and illustrate the magnitude of differences. The black oak group appears to play a much more important role in the epiphytology of both the fusiform and eastern gall rusts than the white oak group.

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