Sporulation by *Cronartium quercuum* f. sp. *fusiforme* on Loblolly and Slash Pine

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ABSTRACT

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Aecial sporulation by *Cronartium quercuum* f. sp. *fusiforme* occurred on an average of 76% of the galls in a slash pine plantation in South Carolina and on 65 and 44% in two loblolly pine plantations in North Carolina in four successive springs. Spermatial occurrence during three successive falls averaged 58% for the three plantations. Aecia appeared 10–13 days earlier on the South Carolina slash pine than on the North Carolina loblolly pine, whereas spermatial appearance was 12–14 days earlier on loblolly pine. Recurrent sporulation for five to seven of seven seasons was least frequent in the northernmost plantation. Most galls produced both aecia and spermatia, but some produced only one or the other during the 4-yr study. The average aecial appearance was 6–26 days before emergence of susceptible oak leaves. The major cause of gall death was natural pruning of shaded branches. Branch galls made up 73% of the dead gall population, but only 27% of the total gall population.

Additional key words: Pinus taeda, Pinus elliottii var. *elliottii,* fusiform rust, *Quercus* spp.

Fusiform rust of loblolly pine (*Pinus taeda* L.) and slash pine (*P. elliottii* Engelm. var. *elliottii*) is common throughout the range of these hosts in the southeastern USA (9,10,12). The causal organism, *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme* is a heteroecious macrocyclic fungus that is an obligate parasite of its pine and oak hosts (2,3).

Synchronization of aecial sporulation with oak leaf development is reported to be good in Mississippi and Florida (5,13). However, sporulation by fusiform rust varies considerably among individual plantations and is reported to be dependent on temperature (1,3). The proportion of galls on slash pine that developed aecia was reported to be a relatively uniform 66–73% over 5 yr in Mississippi (6) and as variable from 30–73% over 6 yr in Florida (1). Furthermore, most aeciospores are dispersed in the initial period following rupture of the peridial covering (8). Therefore, the timing of initiation of sporulation relative to the availability of susceptible oak leaves may be more critical than the duration of sporulation in completing the pathogen's life cycle.

This study determined the patterns of sporulation on individual rust galls in one slash and two loblolly pine plantations during four spring (aecial) and three fall (spermatial) seasons.

MATERIALS AND METHODS

Plantations for the study were selected near Tillery, Halifax County, NC, 161 km southwest near Apex, Wake County, NC, and 161 km farther southwest near Patrick, Chesterfield County, SC. In 1974 the loblolly pine plantations in North Carolina were 9 and 11 yr old, respectively, and the slash pine plantation in South Carolina was 10 yr old. Sample tree rows were systematically selected across the plantations. Within each selected row, each gall within 2.4 m of the ground was numbered and information was recorded on its size, condition, and position in the tree (ie, on stem or branch and height in the tree). Approximately 200 galls were tagged in each plantation.

Aeciospore production by live galls was observed at weekly intervals from early March to early June for four seasons, 1974–1977, except biweekly observations were made at Patrick in spring 1974. Observations on spermatial production by live galls were made at weekly intervals from early September to mid-November for three seasons (1974–1976). Duration of sporulation was based on the dates the spores were first and last seen. If spores were seen at only one time, the sporulation period was given as 1 day.

When branches or trees with galls died, the cause of death was determined. Shading was considered the cause of death for branch galls if rust-free branches in the whorl and in higher whorls were already dead. Rust was considered to be the cause of death of trees if a gall encircled the entire stem.

To determine the sequence of sporulation in specific gall areas, paint was used to outline areas with spermatia on 20 galls at Apex and areas with aecia on 15 galls at Tillery in 1975.

RESULTS

During the four spring seasons, aecial sporulation occurred on 44, 65, and 76% of the live galls at Tillery, Apex, and Patrick, respectively (Table 1). Aecia were initiated at an earlier date and over a longer period of time at Patrick than at the other locations. Initiation of sporulation by individual galls occurred over half of the entire sporulation season in each area.

The proportion of live galls with spermatia was more uniform among the three locations and within the locations for the 3-yr sample period (Table 1). Spermatia were initiated earlier and persisted longer in the North Carolina loblolly pine plantations than in the South Carolina slash pine plantation.

The data for duration of spermatia at Apex vary somewhat from the other two plantations because spermatia were observed on single galls as early as 28 July and as late as 17 February. Spermatia were initiated and occurred for a longer period at Tillery than at Patrick.

Causes of gall death. During the 1974–1977 period, 203 galls died (Table 2). The major cause of death was shading, which killed 83 branch galls. Most (53 of 58) galls in the cause-unknown group also were branch galls. Although branch galls made up only 27% of the total gall population (166/615), branch galls were 73% of the dead gall population.

Relative recurrence of sporulation. There were opportunities to observe sporulation on each gall for up to seven seasons (four aecial and three spermatial). At Apex and Patrick galls usually sporulated for four-to-seven seasons, whereas at Tillery most galls sporulated for three-to-five seasons (Table 3). A chi-square test for goodness-of-fit indicated that the three populations were significantly different. At Tillery, more galls failed to sporulate but remained alive throughout the seven seasons than at the other two locations.

Most galls at all three locations had both aecial and spermatial sporulation at some time during the seven seasons of observations (Table 4). However, some galls produced only one spore form. At Tillery, 19% of the galls produced only spermatia.

Within the spermatial areas painted in 1975 at Apex, aecial sporulation occurred on only 4 of 20 galls in 1976 and 2 of 20 in 1977. Six of 20 galls had spermatia in the same areas in 1976. Subsequent sporulation in aecial areas painted in the spring 1975 at Tillery was similar. Spermatia occurred in six of 15 aecial areas in fall 1975. In spring 1976, aecia occurred in areas on four galls that had aecia in 1975.

Oak leaf development and infection. At Patrick, leaves on susceptible bluejack (*Quercus incana* Bartr.), turkey (*Q. laevis* Walt.), and blackjack oaks (*Q. marilandica* Muenchh.) first emerged 23, 26, and 14 days after the average starting date for aecial sporulation in 1974, 1975, and 1976, respectively. Uredia or telia or both were present 14 days after emergence of oak leaves in 1974 and 1975, but were never observed in 1976. At Tillery, leaves on susceptible water (*Q. nigra* L.), willow (*Q. phellos* L.), and blackjack oak were first seen 12, 13, and 6 days after the average aecial start in 1974, 1975, and 1976, respectively. Uredia and telia were present 14 days after emergence of oak leaves in 1974 and 1975 and 21 days later in 1976. Oak leaf infection was not observed in Apex.

DISCUSSION

The proportion of galls with aecia varied considerably among the three plantations (Table 1). This variation could have been due to the genetic variation of the hosts or pathogen or to environmental differences among locations. Because these observations were made in only one plantation at each location, no conclusions can be drawn about host or pathogen effects. The complexity of the environmental effect is exemplified by the 1977 data. The percentage of live galls with aecia was especially low in 1977 at Tillery (31%) and Apex (34%), whereas it was nearly average at Patrick (72%). The period from September–April, 1976–1977, was unusually cold with cumulative departures from monthly means of −16.5 C (−29.7 F) at Moncure (Apex) and −17.8 C (−32.1 F) at Cheraw (Patrick) according to climatological records (14,15). Normal temperature data were not available for the Tillery area. The effect of this departure from normal on production of aecia was not the same in the two areas, and other factors are probably involved in the reduced sporulation at Apex. Until these factors are evaluated under controlled conditions, their relative contribution to aecial sporulation will remain uncertain.

Chappelka and Schmidt (1) reported aeciospore initiation in Florida was significantly correlated with average, minimum, and maximum air and soil temperatures in January. Aeciospore initiation generally occurred in February and March in the Florida plantation. Climatological records for U.S. weather stations nearest the North Carolina and South Carolina plantations were compared to determine average temperature effects on rust sporulation in these plantations (14,15). The maximum percentage

TABLE 1. Relative sporulation, duration, and starting dates for aecia and spermatia of *Cronartium quercuum* f. sp. *fusiforme* in two loblolly pine plantations (Tillery and Apex, NC) and one slash pine plantation (Patrick, SC)

	Aecial (1974–1977)			Spermatial (1974–1976)		
Sporulation category	Tillery	Apex	Patrick	Tillery	Apex	Patrick
Proportion of live galls sporulating (%)						
Average	44	65	76	58	64	56
Range	31–59	34–86	64–86	57–60	56–70	50–68
Period of initiation (days)[a]						
Average	21	27	34	39	56	28
Range	14–29	20–35	22–42	35–48	42–78	21–34
Duration of sporulation (days)[b]						
Average	41	51	61	48	99	31
Range	16–55	27–80	30–84	42–52	50–156	22–44
Peak initiation date[c]						
Average yearly mean	4/8	4/5	3/26	10/2	9/30	10/14
Range of yearly means	4/3–4/12	3/31–4/12	3/22–3/31	9/21–10/11	9/21–10/6	10/8–10/19

[a] Time from initiation of first aecium or spermatium to the initiation of the last aecium or spermatium that season.
[b] Time from initiation of first aecium or spermatium to the cessation of sporulation that season.
[c] Mean date of initiation of sporulation.

TABLE 2. Cause of death of fusiform rust galls in three pine plantations in 1974–1977

Location	Host	No. of gall deaths by cause				
		Shading	Rust[a]	Broken-off	Unknown	Total
Tillery, NC	Loblolly	13	29	2	16	60
Apex, NC	Loblolly	37	20	0	14	71
Patrick, SC	Slash	33	8	3	28	72
Total		83	57	5	58	203

[a]Tree killed by rust.

of galls sporulating at Apex occurred in 1975 with a mean starting date of 8 April. The average temperature in February and March 1975 at the nearest station, Moncure, was exceeded in January and February at Cheraw (Patrick, SC) in 3 of 4 yr; however, sporulation at Patrick started only 6–17 days earlier than at Apex in these years. Therefore, average temperature appears to be only one of the factors influencing initiation of sporulation. Geographic specificity of the rust may be another factor.

To ensure survival of the rust, aeciospore production must be synchronized with flushing of oaks. Each year of this study, mean aeciospore initiation preceded initial oak flushing by 6–26 days; however, aeciospore dispersion was always still occurring when the oak leaves emerged. Kuhlman (8) indicated that 87% of the aeciospores produced on galls are dispersed within 7 days after initiation of sporulation. Therefore, most aeciospores are dispersed before oak flushing. In spite of being slightly out of phase, the pathogen is very successful.

Biotic factors such as mycoparasites and insects have been implicated in fluctuations in sporulation. Studies of these aspects will be reported separately (7).

The proportion of galls with spermatia varied less both within and among the three plantations than did aecial sporulation. Most spermatia appeared in the early fall (21 September–19 October) and were no longer present in early November. Generally spermatial appearance corresponded to the onset of cooler daily mean temperatures; however, earlier or later appearances did not seem related to similar changes in daily mean temperatures. Czabator (2) indicated that spermatia are present for approximately 2 mo beginning in mid-October in Mississippi. Hedgcock and Siggers (4) suggested that regular alternate sporulation by spermatia and aecia occurred; however, at Apex, the painted spermatial areas of 20 galls had a low frequency of aecial sporulation in both of the following 2 yr. Furthermore, some galls in all three plantations had only spermatia or only aecia, which indicates that the stages can occur independently of one another at least on older galls. Most galls had both aecia and spermatia (Table 4).

Shading was listed as the cause of death for galls on branches that died after other uninfected branches in their whorl had died (Table 2). In fact, these branches survived longer than their uninfected counterparts that had succumbed to shading. Rust galls had cytokinin levels 10 times higher than uninfected stems (11). This increased level probably offsets the normal sequence of reduced hormones that results in self-pruning.

Most galls that died sporulated up to the last season before death. For some, sporulation was occurring when they died, although most died during the summer or winter.

TABLE 3. Relative recurrence of sporulation by *Cronartium quercuum* f. sp. *fusiforme* on galls that remained alive for four aecial and three spermatial seasons in each of three plantations, 1974–1977

Host and plantation	No. of galls sporulating in season[a]								
	0	1	2	3	4	5	6	7	Total
Loblolly pine									
Tillery, NC	12	14	19	24	28	25	10	13	145
Apex, NC	3	8	8	11	23	35	35	16	139
Slash pine									
Patrick, SC	2	5	1	13	22	35	29	21	128

[a]Two seasons of sporulation per year (aecia in spring, spermatia in fall).

TABLE 4. Percentage of live fusiform rust galls with combinations of spermatial and aecial sporulation during seven seasons[a] in each of three pine plantations

Sporulation type	Loblolly pine Tillery, NC (%)	Loblolly pine Apex, NC (%)	Slash pine Patrick, SC (%)
Spermatia alone	19	6	3
Aecia alone	7	8	10
Both aecia and spermatia	64	84	86
No sporulation	9	2	2

[a]Two seasons of sporulation per year (aecia in spring, spermatia in fall) from 1974–1977.

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