Phenology of Comandra Blister Rust in Arkansas

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ABSTRACT

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The Comandra blister rust fungus, Cronartium comandrae is a macrocyclic, heteroecious rust fungus that is an obligate parasite of some hard pines (Pinus spp.) and the genus Comandra (Santalaceae). In Arkansas, rupture of aecial peridia of C. comandrae on pine was associated with the passage of a cold frontal system. Aecia cast spores for approximately 1 wk in mid-April. Uredia were first visible on comandra 8 days after the initial release of aeciospores. Early infections were restricted to lower portions of the comandra plants. As surrounding vegetation grew in height, new infections developed higher on the comandra. The passage of another cold frontal system in midMay favored the uredial

repeating stage and was followed by a notable increase of uredia in late May on upper portions of the plants. Telia first appeared on 11 May, with the increase inincidence paralleling that of uredia, but telia reached maximum development after a 7-day lag. Maximum germination of teliospores followed the passage of another cold front on 23–24 June. After 24 June telial production declined. July was hot and dry and the comandra population defoliated completely during this time. Pycnia were evident on the pine host by late August and actively continued to exude pycniospores through mid-November.

Cronartium comandrae Pk. is a macrocyclic, heteroecious rust fungus that is an obligate parasite of some hard pines and the genus Comandra (Santalaceae). Invasion produces typically fusiform swellings on pine branches or stems and eventually weakens or girdles them. Although now distributed over most of North America (7, 9), C. comandrae was probably introduced in the southeastern states on infected ponderosa pine (Pinus ponderosa) planting stock from the western United States in the late 1930s or 1940s (12). The rust has since spread to Tennessee, Alabama, Kentucky, Mississippi, Missouri, and Arkansas (2,8,12,14). In Arkansas, the rust is restricted to areas in the Ozark and Ouachita plateaus where the alternate host, comandra, or bastard-toadflax (C. umbellata [L.] Nutt. ssp. umbellata Piehl) grows in the immediate vicinity of infected pine trees.

The work reported here more fully characterizes the phenology of Comandra blister rust in Arkansas.

MATERIALS AND METHODS

Most of the phenological work reported here was done in 1975–1977 but is also based on general phenological observations made during the previous 4 yr by the second author. Three study areas consisting of widely separated shortleaf pine (*P. echinata*) plantations in the Ozark plateau in Arkansas were established in 1975. In a 4-m² plot in each plantation, 10 plants were chosen for observation. Comandra phenology, date of first appearance of each of the spore stages, and development of spore stages on host and alternate host were recorded. Weekly observations began in early April and terminated in early August.

In 1976 more detailed phenological observations were taken at the most heavily infected site, which was near Red Star, Arkansas. Twenty-five comandra plants were

randomly selected in a 2.02-ha plot. Date of plant emergence, stem height, probable dates of infection by the rust, and development of spore stages were recorded. A 7day recording hygrothermograph (Bendix Model 594) recorded temperature and relative humidity. Precipitation data were provided by the Buffalo Tower fire control station located 4.8 km east-southeast of the plot site. Aeciospore samples were obtained with a 24-hr Kramer-Collins spore sampler (6) modified with a rotary intake adaptor to improve spore trapping efficiency (4). Spores were trapped on petroleum jelly-coated microscope slides. Airflow was regulated at 22 liters/min with four samples taken each hour, each of 3-min duration. The spore sampler and hygrothermograph were enclosed in a standard instrument shelter at 0.9 m with the rotary intake adaptor situated on top of the shelter.

In 1977 data were collected to elucidate the spatial development of uredial and telial spore stages on eight randomly selected comandra plants in the same plot used in 1976. A 9.0-mm diameter cork borer was used to remove disks from leaves from the upper, middle, and lower portions of the comandra plants. The uredial and telial sori on the disks were counted with the aid of a binocular dissecting microscope. These data were used to compute linear regressions, power curves, and the line of best fit in each case.

RESULTS

The timing of the major phenological events was very similar during the past 7 yr with, at most, several days of variation from year to year. All quantitative data presented here are from the more detailed 1976 and 1977 studies.

Comandra was one of the first plants of the local forest flora to emerge in spring, during late March. At 1 mo after emergence, the plants had grown to 75% of their eventual total height. Height ranged from 24–29 cm with an average of 25 cm.

Rupturing of the outer bark tissue on branch swellings on pine caused by *C. comandrae* occurred in early April. The peridia remained intact for the first 2 wk following their first appearance and did not rupture until a cold frontal system arrived on 13 April (Fig. 1). A few peridia were still intact on 14 April, but all had ruptured by 17 April. Rupture of peridia seemed associated with either the abrupt change in temperature or with the high humidity associated with passage of the cold front. Daily maximum and minimum temperatures for that date were 14 C and 10 C, respectively, and relative humidity approached saturation (90% or greater) during 21 of the 24 hr. From the time that aecia initially appeared, the only days before 13 April with relative humidities of 90% were 4 and 5 April, with a duration of 1 and 2 hr, respectively.

Almost no aeciospores were trapped before 13 April, with most being trapped between 13–17 April during the daylight hours. Although aecia appeared to be depleted of spores by 18 April, a few aeciospores were trapped until 6 May.

A few uredia were first observed on 21 April, 8 days after the initial release of aeciospores. These pustules were on leaves a few centimeters above ground but below the height of surrounding vegatation. Early uredial development was confined to the leaf margin, the area immediately adjacent to the protruding midvein, or the base of the leaf. Moisture collected in these areas after rainfall. Several hours of high humidity or heavy dews undoubtedly enhanced spore germination and infection. Few early infections were observed in the area between the midvein and leaf margin. By mid-May and following apparent secondary infection, uredia developed here also.

Leaves that became infected first and that also displayed the highest incidence of uredial sori were those below the height of the surrounding vegetation (Fig. 2). The relative humidity was 7–10% higher there than at 0.9 m. During the second week of May there were an average of 50 uredia per 9.0-mm diameter leaf disk on leaves collected from the lower third of the plants. This number

decreased linearly through mid-June.

Infection was evident on more elevated leaves by early May, when a few uredia were observed on the middle third of the leaves (Fig. 2). The upward progression roughly paralleled the increasing height of surrounding vegetation. Uredia increased in a linear though insignificant manner until late May when the incidence decreased in a negatively exponential fashion (Fig. 2). Uredia on the upper third of leaves were first observed on 25 May and increased linearly until 8 June when they also decreased in a negatively exponential fashion.

A few telia were first observed on 11 May (Fig. 2), 20 days after the initial observation of a few uredia on these same plants. The incidence of telia on the lower third of leaves increased linearly. The time necessary for transformation of a given uredial pustule to a telium gradually decreased. In mid-May, this required 10–14 days, but by early June this was reduced to several days, and several days later secondary infections converted directly to telia, with no uredial phase evident. In early June lower leaves became necrotic and abscised.

Development of telia on middle and upper leaves began in late May and increased exponentially (Fig. 2). By late June, telial production was at a maximum on the upper leaves. On middle leaves this maximum was achieved in mid-June. The largest average number of infected leaves per plant was observed in mid-June (Fig. 3).

In 1976 the only conditions favorable for teliospore germination occurred on 23 and 24 June when a frontal system brought 7.3 cm of precipitation, high relative humidity, and cool temperatures (12–22 C) (Fig. 1). Germination of teliospores was observed by microscopic examination after passage of this front. The next major precipitation (7 cm) occurred 1–4 July, but by this time teliospores had lost most of their germinative capacity. The upper leaves of surviving plants were becoming necrotic. For the next 24 consecutive days, temperatures ranged from 25 to 30 C and there was no precipitation. All the comandra plants became completely defoliated in

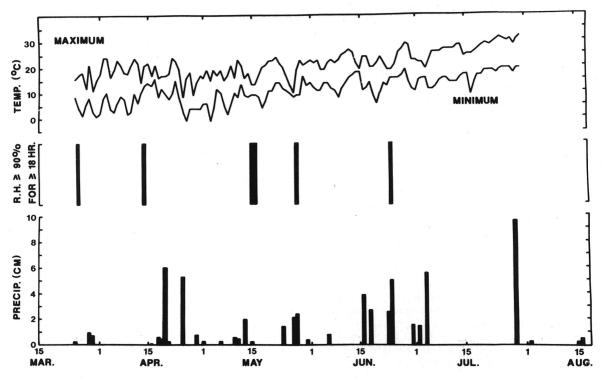


Fig. 1. Climatic conditions in the comandra blister rust study area during part of the 1976 growing season. The top portion indicates maximum and minimum daily temperatures, the middle portion shows the dates in which the relative humidity was $\geq 90\%$ for 18 hr or more, and the bottom portion indicates the daily precipitation.

July (Fig. 3).

New branch and stem swellings on shortleaf pines were evident during early August. These developed from infections of the previous year. Amber-colored pycnial droplets formed in late August and continued to be produced through mid-November. The margins of older swellings that produced aecia in April 1976 also produced pycnial droplets during this same period.

DISCUSSION

Based on information in the literature and on our previous experience (F. Tainter, *unpublished*), it was surmised that an incubation period of at least 18 hr with a 90 ≥ relative humidity was necessary for optimum germination of spores of this rust.

During the 1976 growing season, conditions most favorable for spore dispersal and germination from aecia, uredia, or telia occurred only three times. The passage of a cold front on 13 April and 5-6 cm of precipitation during the following several days triggered dispersal and germination of acciospores (Fig. 1), with 1 day of ≥ 18 hr ≥ 90% relative humidity. The first wave of uredia developed 8 days later, but little secondary infection occurred until 14 and 20-28 May when two more frontal systems brought precipitation and 3 days with ≥ 18 hr ≥ 90% relative humidity. The rapid increase of uredia and telia (Fig. 2) after these dates was a result of the passage of these frontal systems, because no other favorable weather occurred until 14-23 June and 3 July, but only 23 June had nearly 18 hr of $\geq 90\%$ relative humidity. This would have been the only time when teliospore germination and

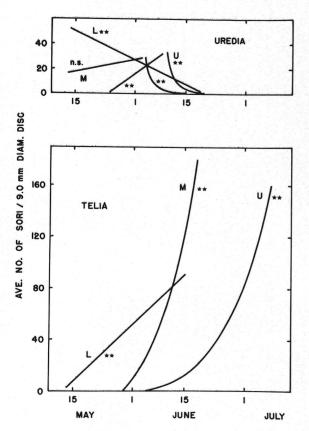


Fig. 2. Changes in incidence of uredia and telia of *Cronartium comandrae* on leaves of lower (L), middle (M), and upper (U) portions of comandra plants. All curves were statistically highly significant from zero (** = 1% L.O.C.) except for the increase in uredia on the middle portions of comandra (n.s. = nonsignificant).

major basidiospore production and germination could have occurred, because the comandra plants defoliated soon afterward.

Because climatic conditions are less favorable in July and August in Arkansas, the development of the comandra plant and the aecial, uredial, and telial spore stages of the fungus began and terminated earlier there than in areas of its more normal range, with the production of pycnia limited to the latter portion of the growing season.

Our observations agree with the report (11) that more aeciospores disseminate during the daylight hours and that aeciospore dissemination occurs during and shortly after rains associated with frontal systems (7).

Although 18-hr periods with ≥ 90% relative humidity were relatively rare, the frequent showers in Arkansas in May and June of 1975 and 1976 undoubtedly aided germination and subsequent infection by urediospores. In addition, high relative humidity resulting from transpiration by surrounding vegetation probably also favored germination and reinfection. Kimmey and Wagener (5) observed that dew causes the intensification of the uredial stage of white pine blister rust (*C. ribicola* J. C. Fisch.) in California.

In Arkansas, high rather than low temperatures were the apparent limiting factor. Temperatures above 25 C reduce the viability of telia (7), and in Arkansas, daily temperatures exceeded 25 C, often extending into the mid-30s, in late June and throughout July and August. Whether teliospore germination and basidiospore production will adjust to the selection pressures of these generally higher prevailing temperatures, as may have occurred with aeciospore germination, is not yet known (3). It would appear, however, that most basidiospore production would be limited to May and June, when both moisture and temperature conditions would be most favorable for successful germination and infection.

Premature leaf abscission of comandra also would have a limiting effect. Because of heavy rust infection, severe chlorosis and eventual necrosis caused premature abscission of the leaves. Kimmey and Wagener (5) found that if Sierra gooseberry is infected in the spring with spores of C. ribicola, many or all of its infected leaves were lost before the onset of autumn rains, shortly before the telial stage develops on the leaf. Premature abscission of comandra leaves that were heavily infected with the rust occurred in Minnesota by mid-August (1). Leaf abscission of healthy comandra plants generally begins in August and continues through September (10). Since leaves bearing telia in heavily infected comandra populations were nearly eliminated in Arkansas by early August, the first hard freeze in late October or early November had little effect. It is unlikely that the rust can overwinter in Arkansas on the comandra plant.

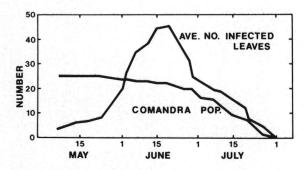


Fig. 3. Phenology of comandra through the 1976 growing season, showing the average number of infected leaves per plant and the number of surviving plants with no abscised leaves.

Pycnial production on shortleaf pine in Arkansas followed 4 mo after aeciospore dissemination. There was no overlapping or short interim phase such as in Minnesota and in the Rocky Mountain states (1, 7).

Comandra blister rust appears to be well established in the Ozark National Forest in Arkansas and can be devastating in young stands (13, 14). Because development of the rust appears to be limited by severe mid-season climatic conditions, a slight shift toward more favorable climatic conditions would likely result in a concurrent increase in its incidence.

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