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Hypoxylon Canker of Aspen: Seasonal Development of Cankers and Ascospore Ejection in Winter

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ABSTRACT

Ascospores of *Hypoxylon pruinatum* were ejected from perithecia and the fungus continued to grow in the wood during winter in Minnesota. Melting snow and rain supplied moisture; the temperatures of the cankered bark were as much as 13 C above ambient air temperatures. Spore discharge occurred during weeks when the air temperature did not exceed —4 C. Maximum average monthly increase in length of cankers (7.5-8 cm) occurred between 24 May and 10 August; from 1 October through 4 February total increase in length was 2.4 cm, and 5 February through 25 March, 3.8 cm. Coremia were produced most abundantly in May and June, and new perithecia most abundantly in August and September.

Hypoxylon pruinatum (Klotzsch) Cke. causes a canker of quaking aspen (*Populus tremuloides* Michx.) and related species throughout most of the range of aspen in North America, and is most important in the Lake States region where 1-2% of the standing volume is killed annually on the 18 million acres of aspen (1).

Little is known about the rate of growth and sporulation of *H. pruinatum* in the host. It has been reported that the annual increase in length of cankers is 25 to 40 cm (2, 4), and monthly increases in length of two artificially induced cankers, from July through December of the same year, have been determined (2). No studies have been made on the development of natural cankers throughout the year, although it has been stated that *H. pruinatum* grows only during the same period as the tree (4).

Ejection of ascospores by *H. pruinatum* requires free moisture which is usually provided as rain. It has been reported that ascospores of *H. pruinatum* are not ejected during the early spring or late fall when the mean air temperature is below 45 F (5). In the fall of 1959, ascospores were ejected in Minnesota when the air temperature was below 45 F (6, 8).

The objectives of this study were: (i) to determine the rate of canker elongation at different times of the year, (ii) to determine the time of year at which the sexual and asexual spores are produced, and (iii) to determine under what conditions ascospores are discharged during the winter.

METHODS AND MATERIALS.—Thirty cankers were selected in April 1960. A nail, placed in the approximate center of each canker, was used as a reference point for subsequent measurements. The margins of each canker and the areas where coremia and perithecia were present were marked with paint. The cankers were measured at intervals and checked for new coremia or perithecia.

To determine if ascospores were ejected during the winter, microscope slides, coated on one side with a thin film of petroleum jelly, were mounted in paper clips on cankers at a distance of 1-3 cm in front of perithecial stromata. The first slides were set out in November 1959 and were changed every week until March 1960. A hygrothermograph was placed in the approximate center of the stand, and air temperature and relative humidity were recorded. Slides were similarly exposed from January to April 1961, but the slides were changed after each snow instead of weekly. To insure that the perithecia were mature and capable of discharging ascospores, if favorable conditions should prevail, perithecial stromata were removed from each canker near where slides were exposed, brought to the laboratory, and moistened; in every case ascospores were discharged.

To compare the temperatures of *Hypoxylon* cankers, the surrounding healthy bark, and the adjacent air at different times during the winter and early spring, four trees, three with cankers on their south sides and one without a canker, were selected in January 1961. Two trees with cankers were near the south edge of the stand and received full available sunshine from leaf fall in autumn to spring. The other two trees were in the center of the stand and received intermittent sunshine. Copper-constantan (24-gauge) thermocouples were inserted for a distance of about 5 cm vertically, approximately 2 mm below the surface of cankers and adjacent healthy bark (Fig. 1). Air temperature was measured with a shaded thermocouple exposed to the air approximately 10 cm from the south side of the trees. A portable potentiometer was used to measure the temperature at the various thermocouple locations. The temperature was measured at hourly and half-hourly intervals on selected days when the sky was clear and wind movement low.

RESULTS.—Cankers increased an average of 38.4 cm in length and 9 cm in width during the year. Average increase upward and downward was about the same, 20.7 cm up and 17.7 cm down. However, there was substantial variation among cankers (Table 1). The highest increase in length was about 58 cm. From 24 May through 9 August the average monthly increase in length was 7.5 to 8 cm; from 1 October through 4 February the total increase was 2.4 cm; and from 5 February through 25 March, 3.8 cm (Table 1). Nine of the 30 cankers accounted for the increase in length observed from 1 October through 4 February; all of

Fig. 1. Copper-constantan thermocouple embedded in the healthy bark of an aspen tree just below a *Hypoxylon* canker. The thermocouple junction is approximately 5 cm above the point at which the lead enters the bark.

these were on the south side of trees. Greatest increase in canker length observed during this period was 14.2 cm. This suggests the fungus continued to grow during the winter.

To determine whether this increase in canker size was a result of fungus growth or merely the development of bark symptoms, cankers were collected during the spring, summer, fall, and winter, and growth of the fungus beneath the bark beyond the external bark symptoms was measured. Approximately 20 cankers were collected in each of May, July, September, and December, 1960. The surface extremities of the cankers were marked and the bark was removed to expose the extent of the fungus. The data are summarized in Table 2. Growth in the wood extended beyond the external evidence of the canker, from 0-14 cm at the lower end and from 0-13 cm at the upper end of the cankers (Fig. 2). Apparently the growth of *H. pruinatum* beneath the bark beyond the external evidence of a canker varied as much in any one season as between seasons.

TABLE 2. Mycelial extent of *Hypoxylon pruinatum*, in the wood, beyond the external bark symptoms

Month	Extent beyond upper border of canker	Extent beyond lower border of canker	Total canker length
	cm	*cm*	*cm*
May	2.9[a]	2.3	38
July	3.6	2.5	36
September	3.0	3.3	57
December	2.0	2.3	49
Average	2.9	2.8	45

[a] Average of measurements of 15 to 25 cankers each month. Differences among months were not significant at the 0.05 level when tested with Duncan's Multiple Range Test.

Coremia were present on 16 of the cankers at the beginning of the study. Twenty-seven of the 30 cankers produced new coremia during the year. New coremia appeared by midMay and were produced abundantly until the end of June.

Perithecia were present on 13 of the cankers at the beginning of the study. Twenty-two of the 30 cankers produced new perithecia during the year. Perithecial initials appeared sporadically from May through August and abundantly during September. The perithecia produced during the summer months matured during the winter and ejected ascospores the following spring.

As a general rule, perithecia are not produced until the third year after infection (3). However, a canker was found in June 1960 at Cloquet, Minnesota, on a 2-year-old aspen sprout. The canker, which was about 50 cm above the ground, had mature perithecia which discharged ascospores when moistened.

The record of ascospore discharge in Table 3 shows that ascospores were ejected at five different times between November 1959 and March 1960. Two of these periods coincided with rain and the other three with

TABLE 1. Average increase in length of 30 cankers

Time of year	Upward increase: Mean	Upward increase: Standard deviation	Downward increase: Mean	Downward increase: Standard deviation	Total increase	Average monthly increase
	cm	*cm*	*cm*	*cm*	*cm*	*cm*
16 April-23 May	1.4	1.7	1.1	1.7	2.5	2.0[a]
24 May-29 June	5.4	2.4	4.2	2.7	9.6	8.0
30 June-9 Aug.	5.8	3.7	4.4	2.4	10.2	7.5
10 Aug.-30 Sept.	5.6	2.5	4.3	3.4	9.9	5.8
1 Oct.-4 Feb.	0.9	1.7	1.5	2.8	2.4	0.6
5 Feb.-25 March	1.6	1.2	2.2	2.5	3.8	2.3
Total	20.7		17.7		38.4	

[a] Values obtained by dividing total increase by number of days in period and multiplying by 30 (no. days/month).

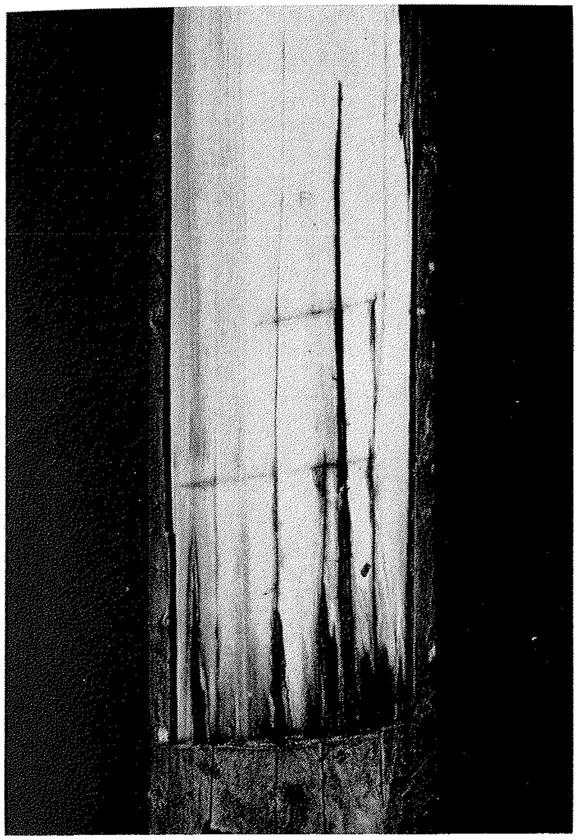

Fig. 2. Growth of *Hypoxylon pruinatum* beneath the bark, beyond external bark symptoms of a canker collected in September 1960 at Cloquet, Minnesota. Horizontal cut in the bark represents the extent of external bark symptoms. The fungus had grown approximately 13 cm beyond this point.

snow. Hygrothermograph records for the weeks of 9-12 January and 20-27 February 1960 showed that the air temperature remained below 0 C. Snow fell during each of these weeks and ascospores were discharged. Ascospores were ejected following a rain during the week of 19-26 March 1960. The highest air temperature recorded during this week was 2 C.

Ascospores were ejected three times from 2 February-22 April 1961. Two ejection periods coincided with rain and one with snow. Ascospores were not ejected after every snowfall.

Temperature measurements taken from one tree on 7 and 25 February and on 22 April 1961 are representative of the information obtained. In general, the temperature of cankers on the south side of trees was greater than that of the surrounding air. Differences as great as 10-13 C between canker and air temperature were recorded, and differences of this magnitude were recorded when the ambient air temperatures were from 2-4 C (Table 4) and from —4-0 C (Table 5). Smaller differences of 4-7 C were commonly recorded between the temperature of the healthy bark and that of the sur-

TABLE 4. Comparison of the temperatures of a *Hypoxylon* canker, the adjacent healthy bark, and the surrounding air on 7 February 1961

	Time of day						
Location[a]	11 AM	12 N	1 PM	2 PM	3 PM	4 PM	5 PM
	Temperature C						
N-Canker	3	5	6	4	3	3	3
S-Canker	12	18	13	14	10	6	6
E-Canker	4	6	6	5	4	3	3
W-Canker	7	9	11	12	9	6	6
S-Healthy	6	10	10	11	7	6	6
Air	2	5	4	3	2	2	2

[a] N = north; S = south; E = east; W = west.

TABLE 3. Record of ascospore discharge during winter of 1959-60, starting 14 November 1959

	Stroma number							Weather conditions	
Date	1	2	3	4	5	6	7	Moisture	Maximum air temperature for exposure period
21 Nov. 1959	—	—	—	—	—	—	—		
5 Dec. 1959	—	—	—	—	—	—	—		
30 Dec. 1959	+++[a]	+	++	++	+++	+++	++	Rain	
9 Jan. 1960	+	++	+	+	+	++	++	Ice, snow	
12 Jan. 1960	+	+	+	—	+	+	+	Light snow	—3
16 Jan. 1960	—	—	—	—	+	—	—		3
23 Jan. 1960	—	—	—	—	—	—	—		4
30 Jan. 1960	—	—	—	+	—	—	—		2
6 Feb. 1960	—	—	—	—	—	—	—		1
13 Feb. 1960	—	—	—	—	—	—	—		3
20 Feb. 1960	—	—	—	—	—	—	—		3
27 Feb. 1960	+	+	+	+	+	+	+	Snow	—4
5 March 1960	—	—	—	—	—	—	—		5
12 March 1960	—	—	—	—	—	—	—	Snow	2
19 March 1960	—	—	—	—	—	—	—		1
26 March 1960	+++	+++	+++	+++	+++	+++	+++	Rain	2

[a] Scale: — = no ascospores discharged; + = few scattered spores; ++ = heavier deposits, not visible to the naked eye; +++ = heavy deposits, visible to naked eye.

TABLE 5. Comparison of the temperatures of a *Hypoxylon* canker, the adjacent healthy bark, and the surrounding air on 25 February 1961

Location[a]	Time of day									
	10:00 AM	10:30 AM	11:00 AM	11:30 AM	12:00 N	12:30 PM	1:00 PM	1:30 PM	2:00 PM	2:30 PM
	Temperature C									
N-Canker	—1	—1	—1	—1	0	0	2	2	1	1
S-Canker	7	4	8	8	9	7	6	4	2	0
E-Canker	2	1	2	3	2	2	3	2	1	0
W-Canker	—2	—1	—1	0	1	2	5	4	2	0
S-Healthy	0	0	2	2	3	4	4	3	2	0
Air	—5	—3	—1	—1	—1	0	0	—1	0	—1

[a] N = north; S = south; E = east; W = west.

TABLE 6. Comparison of temperatures of a *Hypoxylon* canker, the adjacent healthy bark, and the surrounding air on 22 April 1961

Location[a]	Time of day						
	9:30 AM	10:30 AM	11:30 AM	12:30 PM	1:30 PM	2:30 PM	3:30 PM
	Temperature C						
N-Canker	17	18	17	18	21	20	19
S-Canker	23	24	21	28	22	23	22
E-Canker	23	22	20	20	21	20	19
W-Canker	17	18	18	21	21	21	21
S-Healthy	20	23	22	27	25	23	22
Air	17	18	16	19	21	20	19

[a] N = north; S = south; E = east; W = west.

rounding air on the south side of the tree (Tables 4 and 5).

Temperatures recorded on 22 April 1961, when the ambient temperature was 17-21 C, showed a different trend (Table 6). Maximum differences between canker temperature and air temperature, on the south side of the tree, were only 5-9 C.

DISCUSSION.—Cankers increased in length more from 24 May through 9 August than during any other time of year, but apparently the fungus continued growth during the winter with average monthly increases up to 2.3 cm. This can be explained by the fact that the fungus can grow at the temperatures that prevail in the bark on the south side of a tree during the winter in Minnesota. The average total canker elongation for 1960 was 38.4 cm compared to 25 cm in 1959 (7).

Coremia were produced most abundantly in May and June and new perithecia most abundantly in August and September. Evidently the fungus is capable of producing perithecia within 2 years. The fact that ascospores were discharged during the winter means that ascospore inoculum would be available all year instead of just during the warmer seasons. Even when the air temperature was as low as —5 C, the bark and canker temperatures, on the south side of trees, were as high as 15 C; and this, coupled with melting snow and rain, enabled the fungus to discharge ascospores 7 out of 14 weeks from December through March.

The time of year that *H. pruinatum* becomes established in the tree is not known. According to Bier and Rowat (3), infection by ascospores can occur when bark turgidity is low, and the lowest relative turgidities occur during the dormant season. These facts suggest that infection may occur during the winter season.

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