Hypoxylon Canker Incidence and Mortality in Naturally Occurring Aspen Clones

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ABSTRACT

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A survey of stem canker caused by *Hypoxylon mammatum* in 29 clones of *Populus tremuloides* in central New York showed that incidence increased with tree size, but mortality was highest in small trees. Cankers low on the bole were associated with mortality. Small stems had more cankers below the lowest living branch. The frequency of cankers above the lowest living branch increased with tree size, suggesting that the infection court occurs on branches. With increasing tree size, cankers on branches originate farther away from the bole and fewer cankers cause mortality. Considerable variation existed in disease incidence and mortality among the clones and four sample locations.

Additional keywords: canker location, population variation

Hypoxylon canker, caused by *Hypoxylon mammatum* (Wahl.) Miller, is one of the most damaging diseases of trembling aspen (*Populus tremuloides* Michx.) (11). Tree size influences the incidence of Hypoxylon canker, but previous work on this relationship is contradictory. Povah (15) observed that both incidence and mortality from Hypoxylon canker decreased with increasing tree size, and suggested that decreasing incidence may be explained by the increasing thickness of the periderm. Honey (9) and Gruenhagen (8) observed Hypoxylon incidence increased to a maximum in trees of 7.5–10.0 cm (3–4 in.) diameter at breast height (dbh), then decreased in larger trees. Reduced incidence in old stands also was observed by Bier (4) and Anderson (1). Several authors have noted that cankers on large trees were located high on the main stem (bole) (4,6,17). Bier (4) suggested that the age of bark rather than the age of the tree determined susceptibility because the green cortex present in young bark becomes replaced with resistant cork tissue on the lower boles of large trees.

In this study, a survey of Hypoxylon canker was conducted in a sample of 29 naturally occurring clones of *P. tremuloides* from central New York state. An examination of the distribution and location of cankers with respect to tree size made it possible to test the hypothesis that the infection court occurs on branches. The specific objectives were to determine 1) the relationship of disease incidence and mortality to tree size, 2) the distribution of bole cankers with respect to relative tree height, and 3) the location of lethal cankers. In addition, the variability in disease incidence among clones was determined.

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MATERIALS AND METHODS

Clone selection. Twenty-nine naturally occurring clones of *P. tremuloides* were sampled from central New York state at Heiberg Forest in Cortland County, Pompey in Onondaga County, Hammondsport in Steuben County, and the Happy Valley Wildlife Management Area in Oswego County. The clones were first-generation, old-field colonists. The ortet, or seedling tree, that originated the clone was identifiable in most clones by its size and presence of large branch stubs low on the bole. The following criteria were used for selection: clones should be distinct from each other so that their boundaries could be determined, they should be easily accessible, and they should contain at least 50 stems. Ramets were subjectively determined to be part of the same clone by using some of the characters outlined by Barnes (3). Bark color and texture, stem form, time of leaf flush, leaf color, and leaf shape were the most useful. Ramets were excluded if they did not fit the appearance of the other ramets in the clone. Some of the characteristics of the clones at the four sample locations are shown in Table 1.

Disease incidence. The incidence of canker caused by *H. mammatum* in each clone was determined during the winter of 1984 by examining every living or dead stem of *P. tremuloides* for the presence of cankers. A total of 3,976 stems were examined for Hypoxylon canker. During the winter, cankers can be seen through the crown with the aid of binoculars. The

yellow or orange color around the edges of active cankers and the mottled bark caused by light and dark stromatal patches and pieces of sloughed-off bark are characteristic. Perithecia and/or conidial pillars of *H. mammatum* were associated with these characteristics when cankers could be examined on the low branches and the bole. Each tree was visually divided into four equal height segments. The presence of cankers on the bole or branches was noted and recorded by the relative height at which they occurred, as estimated by these quarter bole segments. The living, dead, or broken condition of the bole and branches distal to cankers was recorded. Dead trees with Hypoxylon canker were assumed to have died from the infection.

Tree and clone measurements. The diameter at breast height of all aspen stems over 2 cm dbh (1.4 m aboveground) was measured and the relative height to the first living branch was measured in quarter bole segments. Clone age was obtained from increment cores taken at 1.4 m aboveground from the ortet or estimated oldest tree. The transverse surfaces of cores were shaven smooth, moistened, and yearly growth rings were counted under a dissecting microscope. Four years were added to the number of rings to compensate for the time taken to reach 1.4 m. The approximate area of each clone was calculated from the distance to the clone boundary in the eight compass directions around the ortet or estimated oldest tree. The number of ramets per hectare was obtained by counting all ramets in each clone and dividing by the clone area.

Statistical methods. Statistical analysis was performed using SAS (SAS Institute, release 82.3) procedures (16) through Syracuse University Academic Computing Services. The incidence of Hypoxylon canker was examined with respect to tree size and the locations of cankers by using the clonal means to calculate a population mean and its standard error (18).

RESULTS

The mean percent Hypoxylon canker incidence on all living and dead stems of *P. tremuloides*, and the incidence on living stems only, followed a similar pattern with respect to stem diameters (Fig. 1). Incidence increased with increasing tree size and stabilized or decreased slightly with trees greater than 21 cm dbh. The percent mortality from Hypoxylon canker (Fig. 2) was higher in the smaller stem diameter classes. Mortality decreased above 17 cm. An increase in mortality occurred in the 30- to 45-cm dbh class, but only 30 trees of this size occurred in eight clones and the large standard error of this size class suggests that this may not be representative. Mortality from other causes was highest in the 2- to 5-cm dbh class, lower in the 10- to 25-cm trees, and increased again in large trees (Fig. 2). A few trees showed fruiting of *Cryptosphaeria populina* (Pers.: Fr.) Sacc. (6.5% of trees killed by other causes) or *Cytospora chrysosperma* (Pers.: Fr.) Fr. (3.2% of trees killed by other causes), but their role in mortality was not examined.

The distribution of Hypoxylon cankers with respect to their relative height in quarter bole segments and occurrence on the bole or branches varied with disease condition (Table 2). In living and dead aspen with cankers, more bole cankers occurred low on the tree, whereas branch cankers occurred more in the upper quarters. In living trees (about half of all diseased trees) there was little difference in the location of bole cankers, but branch cankers occurred more in the upper quarters. In trees killed by Hypoxylon canker (about half of all diseased trees), most bole cankers occurred in the lower half of the tree, with most of these in the lowest quarter.

Most cankers caused death of tissue distal to the canker. An average of 78.7% of bole cankers and 89.8% of branch cankers had dead tissue distal to the canker. In dead trees, 49.4% were

Table 1. Characteristics of clones of *Populus tremuloides* at four locations in New York state

Location	Clone area[a] (ha)	Largest dbh[b] (cm)	Ramets per hectare[c]	Clone age[d] (yr)
Heiberg Forest				
Mean	0.020	19	6,332	27
Range	0.006–0.053	11–29	2,714–9,211	20–36
Pompey				
Mean	0.061	29	4,902	40
Range	0.017–0.133	14–44	1,072–8,773	18–62
Hammondsport				
Mean	0.042	26	3,109	39
Range	0.015–0.085	20–34	1,500–6,303	22–51
Happy Valley				
Mean	0.041	24	2,950	35
Range	0.017–0.087	12–30	1,846–7,240	26–44
All				
Mean	0.040	24	4,571	35
Range	0.006–0.133	11–44	1,072–9,211	18–62

[a] Estimated from length from ortet to clone boundary in each of eight compass directions.
[b] Diameter at breast height at 1.4 m aboveground of largest tree.
[c] Total number of aspen stems divided by clone area.
[d] Number of growth rings in an increment core (at 1.4 m) from the ortet or oldest tree with 4 yr added.

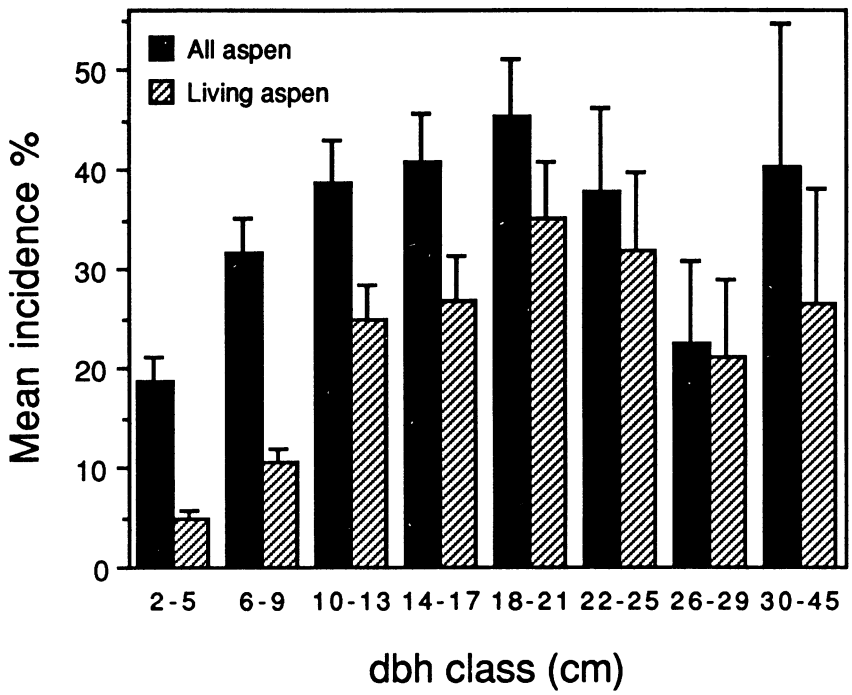

Fig. 1. Mean total Hypoxylon incidence in all living and dead aspen stems, and in living aspen stems. The incidence for each diameter at breast height (dbh) class is the unweighted mean of trees of that size from each of the clones. The number of clones represented at each size class are as follows: 29 at 2–5 cm dbh, 29 at 6–9 cm dbh, 29 at 10–13 cm dbh, 25 at 14–17 cm dbh, 22 at 18–21 cm dbh, 17 at 22–25 cm dbh, 12 at 26–29 cm dbh, and 8 at 30–45 cm dbh. Bars represent 1 standard error.

broken. Breakage at the site of a canker occurred in 65.9% of trees; 34% were broken in the lowest quarter, and 23% in the second quarter of the bole.

In living diseased trees it was possible to classify cankers as top or bottom depending on their relationship to the lowermost living branch. Top cankers occurred on the bole or branches above the lowermost living branch, whereas bottom cankers occurred on the bole below the lowermost living branch. Table 3 shows the mean percentage of top and bottom cankers in living diseased trees with respect to stem diameter. Bottom cankers were relatively more frequent in smaller stems (2- to 5- and 6- to 9-cm dbh class), with their proportion decreasing with increasing stem diameter at breast height. Conversely, the largest stems contained mainly top cankers.

The total incidence of Hypoxylon canker, the incidence on living trees, Hypoxylon-caused mortality, and mortality from other causes were extremely variable across the sample of clones and at each sample location (Table 4). Standard errors indicate differences that occurred among some sample locations for each of the variables examined.

DISCUSSION

The incidence of Hypoxylon canker was found to vary with tree size. The incidence on all living and dead stems, and on living stems only, increased with increasing tree size and then remained high in large trees. This is in contrast to the studies by Honey (9) and Gruenhagen (8), where incidence increased up to 7.5–10 cm dbh but was followed by a decrease. The high incidence in large trees in the present study may be due to the inclusion of more branch cankers. Hypoxylon-caused mortality was found to be highest in the 6- to 9-cm dbh class. Smaller trees may have had lower mortality because some cankers were less developed and had not yet caused mortality. Lower mortality occurred in trees larger than 9 cm dbh, even though incidence was found to increase. This lower mortality associated with higher incidence is due to differences in the location of cankers.

Observations on the location of cankers on all living and dead stems showed that branch cankers tend to be more frequent higher on the tree, whereas bole cankers were more frequent low on the bole. This suggests that low branches with cankers are probably lost as part of the natural branch shedding as the lower branches become shaded out. Branch death has been suggested as a resistance mechanism causing premature branch abscission (19). Bole cankers appear to accumulate in the lower portions of the bole because there is no mechanism for shedding them unless the tree is killed. In fact, when only living trees were examined bole cankers were found to be more evenly distributed. Trees that died from Hypoxylon canker always died from a bole canker; most of these were low on the bole.

Cankers mostly resulted in death of tissue distal to the canker. When this resulted in the death of a tree it occurred either by girdling the bole or by a breakage at a canker before girdling occurred. About half of the Hypoxylon-killed trees in this study were still standing. The other half had broken, many of these at the site of a canker. Breakages at the sites of cankers mostly occurred low on the bole, emphasizing the importance of low bole cankers to Hypoxylon-caused mortality.

Cankers that resulted in the death of trees were, specifically, bottom cankers, those that occurred below the lowest living branch capable of becoming a new

Table 2. Percentage of trees with Hypoxylon canker in the indicated bole segment and with cankers located on the bole or branches within the categories of all living and dead aspen with Hypoxylon canker, living aspen with Hypoxylon canker, and aspen killed by Hypoxylon canker

Position on tree[a]	All aspen with cankers		Living aspen with cankers		Hyoxylon-killed aspen[b]
	Bole	Branch	Bole	Branch	Bole
4	11.4 ± 2.7[c]	12.6 ± 2.4	16.8 ± 2.9	22.9 ± 3.8	6.7 ± 3.6
3	15.5 ± 1.7	8.4 ± 1.7	16.7 ± 2.1	15.5 ± 2.7	14.6 ± 3.0
2	20.3 ± 2.2	4.0 ± 1.0	13.0 ± 2.8	6.9 ± 1.6	29.8 ± 3.0
1	36.3 ± 4.3	2.2 ± 0.8	19.6 ± 3.6	4.2 ± 1.4	52.7 ± 4.8
Total[d]	83.5 ± 3.7	27.2 ± 3.9	66.1 ± 4.9	49.5 ± 5.5	103.8 ± 0.9

[a] Numbers are quarter bole segments, with 1 = lowest and 4 = highest.
[b] Branch cankers accounted for only 0.75% and are not shown.
[c] Mean of 29 clones (28 for Hypoxylon-killed aspen) ± standard error percent.
[d] The sums of bole + branch cankers within each of the categories are greater than 100% due to multiple cankers.

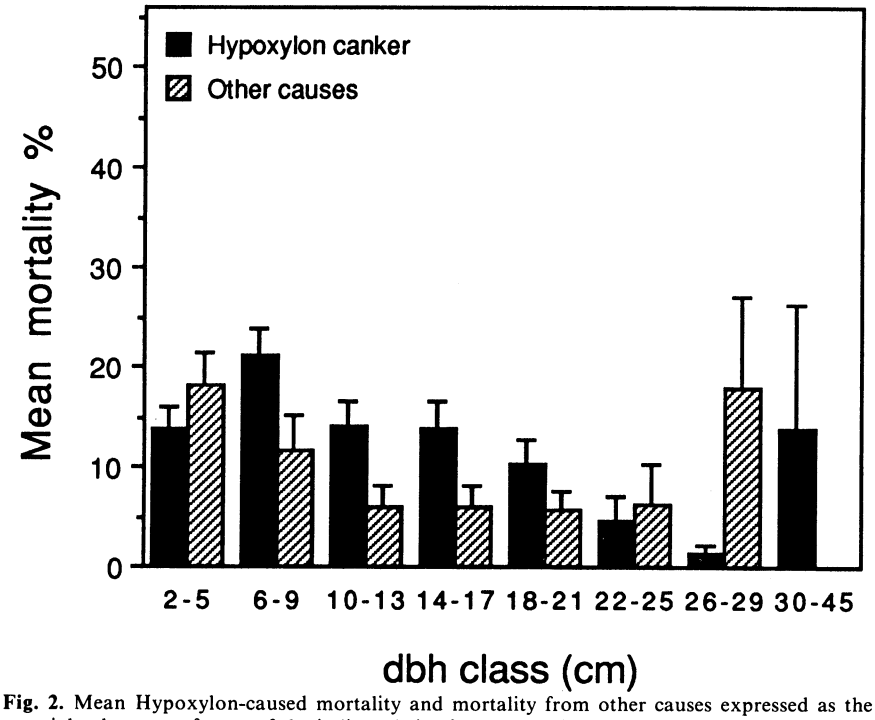

Fig. 2. Mean Hypoxylon-caused mortality and mortality from other causes expressed as the unweighted means of trees of the indicated size from each of the aspen clones. The number of clones represented at each size class are as follows: 29 at 2–5 cm diameter at breast height (dbh), 29 at 6–9 cm dbh, 29 at 10–13 cm dbh, 25 at 14–17 cm dbh, 22 at 18–21 cm dbh, 17 at 22–25 cm dbh, 12 at 26–29 cm dbh, and 8 at 30–45 cm dbh. Bars represent 1 standard error.

Table 3. Percentage of top cankers (those occurring on the bole or branches above the lowermost living branch) and bottom cankers (those on the bole below the lowermost living branch) in living diseased trees with respect to stem diameter

Class of dbh (cm)	Clones (no.)	Canker type	
		Bottom	Top
2–5	21	45.0 ± 8.3[a]	57.5 ± 8.5
6–9	24	41.6 ± 6.7	62.8 ± 6.7
10–13	26	32.0 ± 7.0	74.4 ± 6.4
14–17	21	19.0 ± 6.4	85.2 ± 6.4
18–21	18	27.8 ± 8.4	80.3 ± 8.1
22–25	12	8.3 ± 6.0	94.4 ± 5.6
26–29	6	5.0 ± 5.0	98.3 ± 1.7
30–45	4	11.9 ± 7.9	91.7 ± 8.3

[a] Mean of indicated number of clones ± standard error percent.

leader. In this study, bottom cankers became proportionately less frequent with increasing tree size. Top cankers, those occurring above the lowest living branch capable of becoming a new leader, became proportionately more frequent with increasing tree size. This explains the finding of low mortality in large trees where disease incidence was still high. These cankers were mainly top cankers that do not pose a threat to tree survival.

These findings are consistent with the hypothesis that the infection court is on branches. Cankers often spread down branches causing lethal cankers on the bole (4). Ostry and Anderson (13) have demonstrated the importance of branch cankers leading to bole cankers because pruning of lower branches resulted in fewer bole cankers. Dead branches also may be important infection sites because they are often found in the centers of cankers (2). Manion (10) examined infections on 2- to 3-yr-old branches and stems and found that cankers were most often associated with dead and dying 1- to 2-yr-old branches. Infection of small stems and branches also may be associated with insect activity (12,14), although insect-associated infections occurred less commonly than infections through small branches in New York state (10). Because small trees have small branches the cankers can easily expand down branches and become bole cankers. In very small trees the bole itself may become infected directly. In large trees, however, the infection courts occur at the tips of branches and the very top of the tree. Increasing the distance a canker must expand to reach the bole decreases the frequency of bole cankers in large trees.

The clones used in this study showed considerable range in disease incidence and mortality, a finding that was consistent with previous studies. Copony and Barnes (5) found incidence ranged from 9 to 90% in their study of 80 clones of *P. tremuloides*. French and Hart (7) found a range from 0 to 58% in total disease incidence in 100 clones. The wide range in values across the whole sample and at each sample location demonstrates the extreme clonal variation in the population of *P. tremuloides*. However, differences were found among sample locations in disease incidence and mortality. Minor geographical differences among sample locations might be involved because they would interact with genetic differences and influence the disease condition.

Table 4. Total incidence of Hypoxylon canker on living and dead trees, Hypoxylon on living trees only, Hypoxylon-caused mortality, and mortality from other causes in clones of *Populus tremuloides* at four locations in New York state

Location	Clones (no.)	Hypoxylon canker incidence[a] (%)	Hypoxylon on living trees (%)	Hypoxylon-caused mortality (%)	Other mortality (%)
Heiberg Forest	9				
Mean ± SE		23.5 ± 4.2	12.1 ± 1.8	11.4 ± 2.9	4.1 ± 0.7
Range		10.4–46.6	6.6–23.6	2.0–22.9	1.7–8.6
Pompey	8				
Mean ± SE		42.6 ± 4.6	19.5 ± 2.9	23.2 ± 2.0	8.5 ± 1.7
Range		23.3–62.9	6.6–32.6	16.7–32.9	3.1–17.5
Hammondsport	6				
Mean ± SE		26.1 ± 5.6	10.7 ± 3.2	15.5 ± 5.9	15.5 ± 2.6
Range		9.6–40.3	2.1–24.6	0.0–35.1	4.5–23.7
Happy Valley	6				
Mean ± SE		24.2 ± 7.1	10.9 ± 2.9	13.3 ± 4.8	20.7 ± 5.4
Range		9.3–54.4	4.6–23.5	2.3–30.9	2.9–41.9
All	29				
Mean ± SE		29.4 ± 2.9	13.6 ± 1.4	15.9 ± 2.0	11.2 ± 1.7
Range		9.3–62.9	2.1–32.6	0.0–35.1	1.7–41.9

[a] Percentages are related: Hypoxylon canker incidence = incidence on living + mortality.

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