Spread of *Arceuthobium pusillum* and Rates of Infection and Mortality in Black Spruce Stands

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ABSTRACT

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Based on 3–13 yr of observations of 25 permanent plots in infection centers of *Arceuthobium pusillum* in stands of black spruce (*Picea mariana*) in Minnesota, an average of 8% of the infected trees died each year, and each year 11.1 healthy trees became infected per 100 trees that had been infected. In one plot white spruce (*Picea glauca*) had an annual mortality rate of 2.7% of the infected trees, and newly infected trees appeared at the rate of 0.9 trees per year per 100 infected trees. The lateral rate of spread of *A. pusillum* was 0.74 m/yr.

Additional key words: *Picea glauca*, *Picea mariana*

Arceuthobium pusillum Peck is the most serious pest of black spruce (*Picea mariana* (Mill.) B.S.P.) in the Lake States (1), although an accurate measure of the magnitude of losses is not available. In 1949, using aerial photography, Anderson estimated that in the Big Falls Forest Management Block, Koochiching County, Minnesota, 3–11% of the black spruce type was infested with dwarf mistletoe (1). Today, dwarf mistletoe is prevalent in most areas in the Lake States where black spruce occurs (2,3,11,12). Little has been done, however, to demonstrate the need to control this parasite.

Dwarf mistletoe is frequently reported as the major cause of mortality in black spruce stands. In an ecological survey of bogs in Michigan, Gates reported that infection by dwarf mistletoe kills black spruce in a few years (6). Anderson, however, reported a 45-yr-old witches' broom with *A. pusillum* (1). Such reports on the longevity of infected trees often differ because they are based on one-time observations of stands. We report rates of infection, spread, and host mortality observed on permanent plots in dwarf mistletoe-infested black spruce stands in northern Minnesota.

METHODS

Twenty-five permanent plots were established throughout northern Minnesota in black spruce stands where dwarf mistletoe was present. Stands were 60–130 yr old and were even-aged, except for Cromwell plots 5-5, 5-6, 5-7, and 5-9. Basal area ranged from 40 to 230 ft^2 acre, and site index ranged from 21 to 42.

The plots were either 0.05 ha or 0.07 ha and originally included several infected trees at one end of the plot, so the rate of lateral spread could be observed (10). Each plot was established in the first year of the initial observation period shown in Table 1.

Trees were marked with paint and later with metal tags. Presence or absence of dwarf mistletoe on each tree was recorded and stand maps were prepared for plots established in 1966. At intervals of 4–5 yr, plots were examined, and both dead and newly infected trees were noted and recorded on maps of the plots.

On plots established in 1972, 1974, and 1975, only infected trees were tagged.

The relative annual infection rate was calculated by dividing the number of trees that became infected during the interval between observations by the number of trees infected at the beginning of the interval, and dividing the figure by the number of years between observations. The relative annual mortality rate of infected trees was computed similarly, except that the number of trees with dwarf mistletoe that died during the interval was substituted for the number of newly infected trees. Relative rates of mortality and infection were computed to minimize the effects of different initial levels of infection. No attempts were made to examine the effects of stand age, density, or site quality on relative rates of infection and mortality because of insufficient replication.

Rates of spread, only for the plots established in 1966, were determined by averaging the lateral map distance between a newly infected tree and the nearest two infected trees that were alive within the past 10 yr.

Observations of a plot containing both black and white spruce (*Picea glauca* [Moench] Voss) are included. This plot represents one of the few stands in Minnesota where significant numbers of white spruce are infected. Data are presented separately for each species.

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Table 1. Mortality and infection of black and white spruce trees by *Arceuthobium pusillum* on permanent plots in Minnesota

Plot Observation period	No. of trees infected at beginning of period	 during period	Infection rate (trees/yr/ 100 infected trees)	Mortality Total during period	 Rate (trees/yr/ 100 infected trees)
McGrath 1					
1974-1978	18	8	11.1	8	11.1
McGrath 2					
1974-1978	56	28	12.5	16	7.1
Duxbury 1					
1974-1978	9	0	0.0	2	5.6
Duxbury 2					
1974-1978	10	40	100.0	20	50.0
Blackduck 1					
1974-1978	21	9	10.7	7	8.3
Blackduck 2					
1974-1978	4	1	6.2	2	12.5
Gemmel					
1974-1978	22	0	0.0	9	10.2
Togo					
1975-1978	13	1	2.6	0	0.0
Cromwell 2-1					
1966-1970	21	0	0.0	13	15.5
1970-1975	8	1	0.2	2	5.0
1975-1979	7	7	25.0	5	17.9

(*continued on next page*)

Table 1. (*continued from preceding page*)

Plot Observation period	No. of trees infected at beginning of period	 during period	Infection rate (trees/yr/ 100 infected trees)	Mortality Total during period	 Rate (trees/yr/ 100 infected trees)
Cromwell 2-2					
1966-1970	29	2	1.7	14	12.1
1970-1975	13	10	15.4	6	9.2
1975-1979	17	10	14.7	5	7.4
Cromwell 2-3					
1966-1970	41	7	4.3	20	12.2
1970-1975	24	7	5.8	14	11.7
1975-1979	17	7	10.3	9	13.2
Cromwell 2A					
1966-1970	9	0	0.0	2	5.6
1970-1975	7	2	5.7	4	11.4
1975-1979	5	3	15.0	2	10.0
Cromwell 3					
1966-1970	3	2	16.7	0	0.0
1970-1975	5	1	4.0	1	4.0
1975-1979	5	3	15.0	2	10.0
Cromwell 4					
1966-1970	6	1	4.2	0	0.0
Cromwell 5-5					
1966-1970	83	5	1.5	22	6.6
1970-1975	66	4	1.2	17	5.2
1975-1979	55	2	0.9	29	13.7
Cromwell 5-6					
1966-1970	26	10	9.6	4	3.8
Cromwell 5-7					
1966-1970	9	4	11.1	2	5.6
1970-1975	11	2	3.6	2	3.6
1975-1979	11	1	2.3	6	13.6
Cromwell 5-8					
1966-1970	7	2	7.1	3	10.7
1970-1975	6	2	6.7	1	3.3
1975-1979	7	0	0.0	2	7.1
Cromwell 5-9					
1966-1970	1	2	50.0	0	0.0
1970-1975	3	1	6.7	0	0.0
1975-1979	4	1	6.2	2	12.5
Cromwell 7-1					
1966-1970	2	1	12.5	0	0.0
1970-1979	3	5	18.5	2	7.4
Cromwell 7-2					
1966-1970	8	4	12.5	1	3.1
1970-1979	11	13	13.1	6	6.1
Cromwell 7-3					
1966-1970	3	3	25.0	0	0.0
1970-1979	6	14	25.9	7	13.0
Cromwell 7-4					
1966-1970	20	2	2.5	3	3.8
1970-1979	19	12	7.0	16	9.4
Kerrick 2					
1966-1970	4	5	31.2	1	6.2
1970-1979	8	12	16.7	1	1.4
Itasca (black spruce)[a]					
1965-1967	58	10	8.6	1	0.9
1967-1971	60	9	1.4	80	12.5
1971-1979	25	6	3.0	9	4.5
1962-1979	33	2	0.4	28	5.0
Mean			11.1		8.0
Standard deviation			15.9		7.6
Itasca (white spruce)[a]					
1965-1967	27	0	0.0	0	0.0
1967-1971	41	5	3.0	11	6.7
1971-1979	18	1	0.7	2	1.4
1962-1979	9	0	0.0	4	2.6
Mean			0.9		
Standard deviation			1.4		2.9

[a] The condition of each tree at each plot examination is not available, so results are presented for intervals where the condition of trees was known at the beginning and end of interval.

RESULTS AND DISCUSSION

The relative infection rate for black spruce ranged from 0 to 100 trees per year among 100 infected trees, with an average of 11.1 trees per year (Table 1). Values larger than 25 occurred on plots where the initial number of infected trees was small due to extensive mortality. Because of the open crown canopy, many black spruce seedlings appeared in the understory. Infection of these reproduction class trees contributed to large relative infection rates.

The relative infection rate for white spruce was 0.9 trees per year per 100 infected trees.

The relative annual mortality rate for infected black spruce trees ranged from 0 to 50 trees per year per 100 infected trees, with an average of 8.0. The relative annual mortality rate for infected white spruce was 2.7 trees per year per 100 infected trees. This agrees with our observation that infected white spruce tend to live longer than infected black spruce. Mortality of mistletoe-free black spruce on the same plot was less than 1% per year and was usually associated with suppression.

During these observations, 11 infected trees became disease free, apparently because the infected branches died.

No significant correlations were found between mortality or infection rate and the number of trees initially infected.

The rates of spread were 0.6 ± 0.8 m/yr between 1970 and 1975 and 0.8 ± 0.5 m/yr between 1975 and 1979. Averaging these values with the 0.8 ± 0.4 m/yr observed by Hudler between 1966 and 1970 (10) yields an overall rate of spread of 0.7 ± 0.6 m/yr. The tree that became infected farthest from previously infected trees was 20.7 m and 21.3 m from the two closest sources of infection. This occurred between 1970 and 1975.

The small difference between the infection rate and the mortality rate is evidence that dwarf mistletoe spreads slowly through the stand. The number of infected trees increases slowly, as the infected trees are dying and being replaced by newly infected trees.

Of far more importance to the forest manager is the 8% average annual mortality rate of infected black spruce trees. With this figure in a model for simple interest disease increase, all infected trees would be dead in 12.5 yr (Table 2). Trees that have been infected longer than 12.5 yr are commonly observed, which suggests that a compound interest disease model may be more consistent with observed mortality. The predicted lengths of time for selected levels of mortality to occur are shown in Table 2. Although 75% of the infected trees would be dead in 16.6 yr, 1% of the infected trees could remain alive after 55 yr. Thus, the compound interest disease model can accommodate both the rapid rate of mortality reported here as well as

Table 2. Time (years) to reach given levels of mortality by simple and compound interest models

	% Mortality				
Interest rate	**10**	**25**	**50**	**75**	**99.99**
Simple interest	1.25	3.12	6.23	9.35	12.47
Compound interest	1.26	3.44	8.29	6.58	55.09

Anderson's observation of a 45-yr-old witches' broom. With a 120-yr rotation for black spruce pulpwood, dwarf mistletoe will cause significant losses.

A. pusillum causes more rapid mortality on black spruce than does *A. americanum* Nutt. ex Engelm. on *Pinus contorta* Dougl., *A. campylopodum* Engelm. on *Pinus ponderosa* Laws., or *A. vaginatum* f. *cryptopodum* (Engelm.) Gill on *P. ponderosa* (4,7,8). These western dwarf mistletoes are important pathogens primarily because they reduce volume growth, in addition to causing mortality. Based on limited data, black spruce trees are killed before their diameter growth differs significantly from that of trees without dwarf mistletoe. The average diameter breast heights of trees infected at the previous plot examination and of trees that became infected since the last plot examination did not differ significantly from that of uninfected trees. Growth loss, however, will be important only on trees that are infected and alive at rotation age and probably will be insignificant compared with mortality and losses to deformity caused by witches' brooms.

A. pusillum also causes more rapid mortality on black spruce than on white spruce (5) or on red spruce (F. G. Hawksworth, *personal communication*). Dwarf mistletoes that cause minimal damage to their host are generally thought to be better adapted than those that kill their hosts. Hawksworth and Wiens consider *A. pusillum* to be one of the most advanced New World species of *Arceuthobium* on the basis of morphology and host associations (9). They reconcile this apparent anomaly with the suggestion that *A. pusillum* is a relatively newly evolved species. Based on the results reported here, we suggest that *A. pusillum* may have evolved primarily with white spruce, and perhaps with red spruce, and then more recently spread to black spruce. With the elimination of pure stands of white spruce, the occurrence of dwarf mistletoe on this host is restricted to stands near black spruce, where spread of the parasite is not hampered by nonhost species growing in a mixed stand. In mixed stands trees that become infected may die before the parasite can spread to another host. In this way, man's activities may have restricted *A. pusillum* to the relatively pure stands of black spruce.

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