Spread, Intensification, and Upward Advance of Dwarf Mistletoe in Thinned, Young Stands of Western Hemlock in Southeast Alaska

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ABSTRACT

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Examinations of 206 young western hemlock trees growing beneath residual trees infected with hemlock dwarf mistletoe (*Arceuthobium tsugense*) in two thinned stands were made from 1981 to 1987 to evaluate disease spread and intensification. The percentage of trees infected increased over this period, as did the number of infections on 79% of the trees that were infected in 1981. However, few of the infected trees had three or more infections and only eight trees had 10 or more infections by 1987. The probability of a tree being infected was significantly greater if the tree was in the understory before logging rather than having become established in the understory after logging. There was no significant orientation by distance or direction of infected trees from the infected residual trees. Infections were significantly concentrated in interior portions of the lower crown. From 1981 to 1987, infected hemlock trees grew an average of two times greater in height than the dwarf mistletoe advanced upward in their crowns. The low number of infections on these trees, their concentration over time in interior portions of the lower crown, the sparsity of witches'-brooms, the rapid increases in tree height after thinning, and the common interspersion of resistant Sitka spruce trees all indicate that there is little likelihood of damaging disease levels developing in thinned stands on high quality sites within the planned 90- to 120-yr rotation.

Hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G. N. Jones) is widespread in old-growth stands of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) in southeast Alaska (14). The parasite occurs in old-growth western hemlock from Haines south to Portland Canal (11), but infection intensities vary from stand to stand. *A. tsugense* also infects, albeit rarely, mountain hemlock (*T. mertensiana* (Bong.) Carrière) (20) and Sitka spruce (*Picea sitchensis* (Bong.) Carrière) (13) in the region. These hosts are, however, considered to be resistant for management purposes.

In regrowth stands, infections occur on young hemlock trees that are growing near infected residual trees that were left after "clear-cut" logging. These residuals were left because of their nonmerchantability (9). They have different intensities of infection and occur at various densities across the more than 120,000 ha of old-growth western hemlock-Sitka spruce forest that have been harvested by clear-cutting on the mainland and islands of southeast Alaska.

After dissecting more than 3,400 young hemlocks in dense, young stands beneath infected residual trees in southeast Alaska, Shaw (19) concluded, in contrast to reports from Washington and Oregon (27), that infection levels on potential crop trees in these unmanaged stands were too low and their distributions too limited to allow for damaging disease levels to develop within the planned 90- to 120-yr rotation. These conclusions agreed with earlier, cursory examinations by Drummond and Hawksworth (8).

This conclusion was reached in spite of reports that the opening of stands by thinning might favor spread and intensification of the parasite (16,22). This study was initiated in recently thinned stands of young western hemlock growing beneath infected residual trees on high quality sites to clarify whether or not stand openings would increase disease

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levels beyond those predicted (19). In addition, these plots serve as a demonstration area to train foresters in the recognition, biology, and management of hemlock dwarf mistletoe (12).

MATERIALS AND METHODS

Plot establishment and data collection. Two stands of young-growth western hemlock-Sitka spruce near Thorne Bay on Prince of Wales Island (see Fig. 1 in reference 19) that developed after clear-cut logging of the old-growth forest in 1962 were selected for study. The stands contained several scattered residual trees that were infected with *A. tsugense*. The stands were thinned in 1980 to an approximate 3.7 × 3.7 m spacing and all residual trees were killed by girdling.

Five plots were established in each stand in 1981 by selecting five heavily infected residual trees (27–38 cm dbh). All live trees whose crown fell within 9.14 m of the stem of each residual tree constituted a plot. Another plot was established in 1982 for a total of 11 plots. This plot radius was selected for compatibility with previous studies (19) and because 95% of the seeds ejected from infections in such residual hemlocks land within 9.14 m of that residual (23).

All young trees were thoroughly examined, branch by branch, for infections in the year of plot establishment and at 2-yr intervals until 1987. This examination often necessitated climbing larger trees. Infections on live branches were tagged, measured for their aboveground height and distance out the branch from the bole, the presence or absence of shoots and/or basal cups, and the condition (dead/alive) of the branch distal to each infection. In addition, we recorded if infections had been chewed by rodents, primarily squirrels, and if infections could be classed as causing an incipient or developed witches'-broom (4). Trees were measured for dbh, age at 20 cm above ground, total height, height to live crown, and distance and azimuth from the infected residual tree at the plot center.

Data analysis. The percentage of trees infected and those bearing three or more or 10 or more infections were calculated by plot for each sampling year. Increases in tree height were calculated as an annual increment based on the 1981 and 1987 measurements of tree height. The upward advance of dwarf mistletoe was calculated as the annual increase (or decrease) in height up the stem from the previous highest live infection (regardless of sex) to the current highest live infection. This calculation was made for each infected (1981) tree. This method differs from that of Scharpf and Parmeter (18), who measured from the lowest female infection to the highest new infection (male or female), and Richardson and Van Der Kamp (16), who measured the distance between female infections. Our method was selected because the scarcity of mature shoots on infections made reliable sex identification difficult. We also calculated the number of infections within each third of the crown and determined their relative distance out from the bole.

The annual height growth from 1981 through 1987 for trees infected in 1981 vs. uninfected ones was compared by an analysis of variance, with stand, plot, and tree infection status as factors. We tested the null hypothesis of no difference in tree height and increment between infected and uninfected trees. The use of 1981 heights as a covariate to adjust for initial differences between infected and uninfected classes was attempted, but the correlation between initial height and annual increment was not significant. We used a paired *t* test on trees infected in both 1981 and 1987 to compare tree height growth with the upward advance of dwarf mistletoe during these years. We then used confidence intervals on these differences to estimate the excess in height growth over upward advance of dwarf mistletoe.

To determine if infected trees were clustered by their distance from the infected residual tree, we used an analysis of variance with stand, plot, and tree infection status as factors to test the null hypothesis that there was no difference in probability of infection with distance from the residual. This procedure was considered appropriate because distance data were normally distributed and the variance was homogeneous between infected and uninfected tree classes. A Rayleigh test (5) was used to evaluate if infected trees are concentrated by direction (azimuth) from the residual.

Contingency tables were used to evaluate the location of infections within the crowns of infested trees. Infection locations were summarized by height (crown third) and as inner or outer based on their location along branches (Fig. 1). The probability of a tree being infected at any time during the study was evaluated by age class (advance regeneration present before logging vs. new regeneration after logging) with a contingency table. Results of statistical tests were judged to be significant at $P \leq 0.05$.

RESULTS

All plots but one contained one or more infected trees in 1981 (Table 1). A greater percentage of trees in all plots were infected by 1987 than in 1981, indicating disease spread, the appearance of latent infections, or both. In addition, the number of infections increased on 79% of the trees that were initially infested—indicative of some intensification. In all, 206 hemlocks were examined. However, by 1987, few trees had three or more infections each (Table 1) and only eight trees had 10 or more infections. Seven of these eight trees were advance regeneration, as were 88% of all trees that became infected by 1987. The probability of a tree being infected was significantly greater if it was advance regeneration rather than having become established after logging.

Infections on all plots were significantly concentrated in the inner portion of the lower crown of infected trees (Fig. 1). Only seven of the 103 infections recorded in 1981 were in the midcrown of infected trees and none were in an upper crown; by 1987, only two of the 334 infections were in an upper crown. On the eight trees with 10 or more infections in 1987, 35 infections on six trees were above the lower crown, only one of which was in an upper crown.

Regardless of sampling year or their location in the crown, most infections were characterized primarily as fusiform-shaped swellings that frequently bore dwarf mistletoe shoots or basal cups that indicated previous shoot production (Fig. 1). Few mistletoe shoots, however, bore flowers or fruits that would allow for accurate identification of sex.

Interestingly, only 2% of the infections present in 1981 showed evidence of rodent chewing, whereas 22% of the infections showed such activity by 1987, including 26 infections where the branch had died distal to where the infected portion was chewed. Nine branches with gnawed infections died from the bole out, but this morbidity could not be directly associated with the rodent activity. Only 12 of the infections present in 1981 had died by 1987, two of which had been gnawed by rodents. To our knowledge, this is the first report of rodent activity on infections of *A. tsugense* on western hemlock, although Wass (29) reported rodent chewing on infections of *A. tsugense* on shore pine (*Pinus contorta* Douglas ex Loud. var. *contorta*) in British Columbia and noted the absence of such activity on similarly infected western hemlock.

Nine of the 334 infections recorded in 1987 were considered to be causing witches'-brooms, an increase from four in 1981. Two of the four brooms noted in 1981 were infections low on the bole. Four additional infections had the appearance of incipient brooms in 1987. All 13 brooms or incipient brooms noted in 1987 were located in the lower crown of 11 trees, 10 of which were advance regeneration trees.

Height growth differences between hemlocks infected in 1981 and uninfected ones were not significant. The mean, annual height growth (1981–1987) of trees that were infected in 1981 was significantly greater (by a factor of two) than the mean, annual upward advance of mistletoe in these trees (Table 2). Infected trees averaged 21.4 ± 9.2 cm more in annual height growth than the dwarf mistletoe moved upward in their crowns. In only nine trees did mistletoe advance up the crown at a rate faster than the tree increased in height. There was no

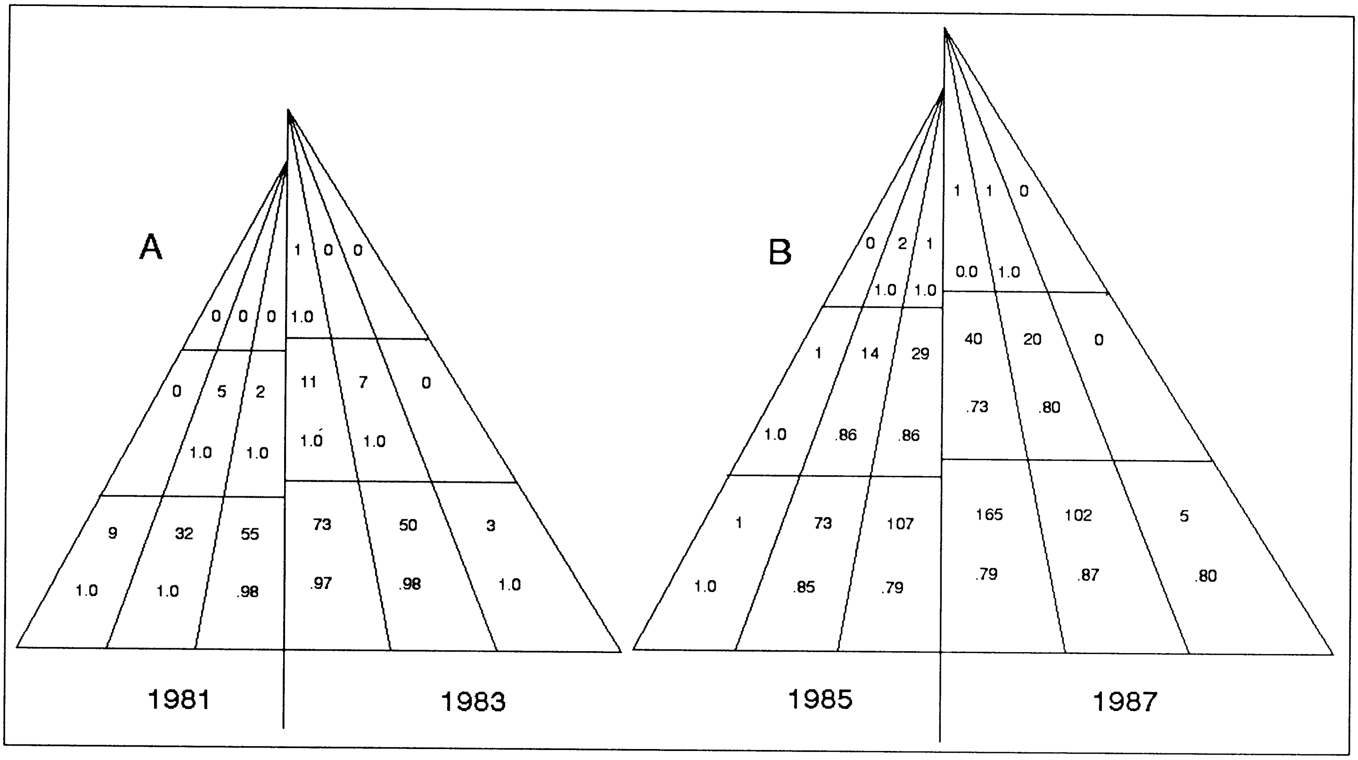

Fig. 1. Distribution of all dwarf mistletoe infections and the proportion (i.e., .85 = 85%; 1.0 = 100%) of these infections bearing shoots in **(A)** 1981 and 1983 and **(B)** 1985 and 1987 by crown location (upper, middle or lower third; inner, middle, or outer third). Differences among years and crown locations represent the cumulative effects of newly developing infections, appearance of latent infections, mortality of old infections, and tree growth.

Table 1. Distribution of hemlock trees and dwarf mistletoe infections in 1981 and 1987

	Trees (no.)		Infections (total no.)		Trees infected (%)		Trees with three or more infections		Highest part of crown infected[a]	
Plot	**1981**	**1987**	**1981**	**1987**	**1981**	**1987**	**1981**	**1987**	**1981**	**1987**
I-1	18	18	34	85	44	67	22	39	L	M[8]
I-2	11	11	2	7	18	36	0	9	M[1]	L
I-4	20	20	27	121	45	70	20	40	M[3]	U[1]
I-5	20	20	4	10	16	20	0	15	L	M[2]
I-6	21	20	28	62	57	75	24	45	M[2]	M[7]
II-1	18	21	1	12	6	29	0	5	L	M[3]
II-2	14	15	0	6	0	33	0	0	. . .	L
II-3	23	22	1	6	4	14	0	5	L	U[1]
II-4	19	18	3	17	16	44	0	6	L	M[3]
II-5	19	19	1	4	5	16	0	0	M[1]	M[3]
II-6	22	22	2	4	5	9	0	5	L	M[1]

[a] L = Lower third, M = middle third, U = upper third. The number following a M or U is the total number of infections on the plot in that crown third.

Table 2. Height growth and upward advance of dwarf mistletoe on hemlock trees infected in both 1981 and 1987

Plot	Trees (no.)	Height growth (cm)[a]	Upward advance of mistletoe (cm)[b]
I-1	8	40.4	20.1
I-2	2	60.1	7.3
I-4	9	28.2	14.9
I-5	3	47.3	33.1
I-6	12	42.3	19.4
II-ALL	5	42.2	30.2
Mean[c]	6.3	40.0	20.4

[a] Calculated as an annual increment based on 1981 and 1987 measurements of tree height.

[b] Calculated as annual increase (or decrease) in height up the stem from the previous highest live infection (regardless of sex) to the current highest live infection.

[c] Differences are significant at $P < 0.001$ ($t = 4.4$).

significant orientation in regard to distance or direction of infected trees from the infected residual tree at each plot center.

DISCUSSION

Even though the number of infections and the proportion of trees that were infected increased substantially over the 7-yr period, there is little likelihood that *A. tsugense* will negatively impact stand growth and development within the planned 90- to 120-yr rotation. Because these plots were located in an area highly prone to infection (19), and because infected residual trees are not distributed uniformly across the stands, the relatively few infections present constitute even less of a threat on a stand basis. The interspersion of resistant Sitka spruce trees throughout these stands further reduces the probability of disease developing to damaging levels. The occurrence of nonhost species and the clumped distribution of infected residual trees are important factors that can lead to a lower index of stand infection by hemlock dwarf mistletoe (1,3).

The infected residual trees have died since girdling, although some took 3–4 yr to succumb, and will no longer serve as an overhead source of mistletoe seed. The young stands are estimated to close canopy around 1997 (W. Farr, *personal communication*); as such, the branches that are infected, which are concentrated in interior portions of the lower crown, should begin to die from shading (21). The overall stand conditions that will be present in 1997 and thereafter will probably be unsuitable for rapid tree-to-tree or vertical spread of dwarf mistletoe.

Certainly there are latent infections undetected by our observations; however, by the time these infections might possibly produce fruit (21), continued crown expansion should relegate most of these infections to interior portions of the lower crown (Fig. 1) where they too will have little opportunity to affect disease development. Their opportunity will be limited because of location, orientation of mistletoe seed capsules (28), and a relatively high rate of infection mortality on lower crown branches (21).

Assuming that the approximate 2:1 ratio of increase in height growth vs. upward advance of mistletoe holds for the next decade, substantial portions of the middle and upper crowns on most trees will be disease free. In contrast to the modeling projections for mistletoe-infested stands of western hemlock along the southern coast of British Columbia (2,7), we contend that in these thinned stands where infected residuals have been killed, the rates of increase in tree height are rapid enough to outgrow the disease—particularly because future stand conditions and tree crown development should further reduce upward advance of the parasite. In addition, the actual number of infections present, even on the most heavily infected trees, is far below the few to several infections on each major branch that are considered critical for loss of increment to occur (16,24). As summarized for *A. tsugense* on western hemlock, "if the dwarf mistletoe is hard to see, growth impact is light" (17).

The differential between height growth and upward advance of dwarf mistletoe on infected trees that we recorded is greater than Richardson and Van Der Kamp (16) reported for western hemlock along the southern coast of British Columbia. They concluded that the trees would outgrow the mistletoe—an assertion with which we are in full agreement for thrifty, managed stands on high quality sites in southeast Alaska. Because we were unable to determine the sex of most infections, particulary those high in the crown, our calculations of upward advance are actually more liberal than those of Richardson and Van Der Kamp (16). If 50% of the uppermost infections we recorded were male, the usual sex ratio for species of *Arceuthobium* (11) including *A. tsugense* (24,25), then the methodology of Richardson and Van Der Kamp (16) would yield an even slower rate of upward advance than we report.

How disease will develop in infected trees on poor quality sites where trees have a slower rate of height growth than those reported here is unknown and should be evaluated (16). The actual rates of height growth at which hemlocks infected with mistletoe will outgrow the disease is a critical factor on which data is needed (15) to effectively use the available model (2,6,7) to predict effects of *A. tsugense* on the growth and development of young, infected stands of western hemlock.

Results from our study also support the previous suggestion that discrimination against advance regeneration during precommercial thinning would reduce even further the levels of dwarf mistletoe infection in these stands (12,19). Implementation of this suggestion by management might, however, be impractical because it is difficult to determine tree ages by casual observation and advance regeneration is abundant on clear-cut areas in southeast Alaska (10,19). Even though the predominately infected trees in these plots were advance regeneration, they were not generally infected before harvest. They were the first trees of any size present after harvest (19) and presented a reasonable target area to intercept seeds of dwarf mistletoe dispersed from infected residual trees (30).

There is little information available on the ecological conditions and time needed for hemlock dwarf mistletoe infections to develop into witches'-brooms. Our data suggest that the opening up of thrifty stands by thinning may stimulate broom formation; certainly some developed over the 6 yr of our study. These broomed infections were concentrated in the inner portion of the lower crown; how they will develop as the stand canopy closes remains to be seen. Observations by Shea (22) suggest that these brooms could die or cease to increase in size after canopy closure.

Information on the development of witches'-brooms is important to predicting effects of *A. tsugense* on tree growth because the presence of numerous brooms appears to be the most detrimental effect of this parasite on the growth of western hemlock (24). In addition, the presence of large infections low on the bole where two of these brooms were located may lead to extensive stem damage and decay (8). Because of their potential impact, the limited number of brooms we found on infected trees further supports our conclusion that there is little likelihood of the disease developing to damaging levels within the planned rotation.

In contrast to the results of Smith (26), we found no significant association between the location of infected trees and their distance or direction from the infected residual tree. However, we agree with Smith's (26) conclusion that because of hemlock foliage and branch characteristics, "trees originally lightly infected [before death or removal of the overstory source of infection] may well escape significant growth impact."

Fewer trees in southeast Alaska are infected with dwarf mistletoe when growing beneath infected residual trees where high infection levels are expected than occurs in similar stands farther south along the western coast of North America. Reasons for this difference are not clearly understood (21), but they are under study (P. E. Hennon, *unpublished data*). Because of this situation, it appears that even more infected residual trees per hectare would be necessary for damaging disease levels to develop in southeast Alaska than in similar stands farther south. However, the opposite appears to be the case.

For example, Smith (26) suggests that 86 infected residuals per hectare are needed for *A. tsugense* to develop to damaging disease levels in stands of young-growth western hemlock along the southern coast of British Columbia. Embry (9) recorded 24 residual trees per hectare on tractor-logged ground in southeast Alaska and suggested that even fewer occur on sites, like the ones we studied, that were logged by a high-lead system. Even if all of these residual trees had been infected by *A. tsugense*, their numbers would still be much lower than that necessary for damage to occur, even in areas where the disease develops rapidly.

In summary, the following factors lead us to conclude that on high quality sites in southeast Alaska there is little likelihood of hemlock dwarf mistletoe developing to damaging disease levels within the planned 90- to 120-yr rotation: 1) the limited number and clumped distribution of infected residual trees in thrifty, young stands; 2) the removal of infected residual trees during precommercial thinning; 3) the limited number of infections on the selected crop trees; 4) the concentration of these infections over time in interior portions of the lower crown; 5) the sparsity of witches'-brooms; 6) the rapid increase in height of crop trees after thinning; and 7) the interspersion of resistant Sitka spruce trees.

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