R. B. Smith
Department of the Environment
Canadian Forestry Service
Pacific Forest Research Centre
Victoria, British Columbia

Factors Affecting Dispersal of Dwarf Mistletoe Seeds from an Overstory Western Hemlock Tree

Introduction

Hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G. N. Jones) is a destructive parasite throughout most of the range of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) in coastal western North America (Buckland and Marples, 1952; Wellwood, 1956; Shea, 1966; Smith, 1969). It spreads primarily by explosive discharge of its sticky seeds from the mature, berry-like fruits. However, seed flight is influenced by strong winds (Roth, 1953; Weir, 1916), and long-distance transport is probably accomplished by birds and animals.

A study of dwarf mistletoe seed dispersal from a small, isolated, severely infected western hemlock tree showed that almost 70 percent of the seeds were trapped in the southern sector (Smith, 1966). The reason for this peculiar pattern of seed dispersal was investigated because it might bear on planning the harvesting of infected stands. The investigation centered around the measurement of wind, but the distribution of the parasite in the source tree and the effects of other weather elements on seed dispersal were also examined.

Methods

The source tree, 45 ft in height, was located 500 ft msl, on a flat valley bottom near Cowichan Lake, British Columbia. The individual 2-ft square traps used in the earlier study (Smith, 1966) were replaced by eight triangular-shaped traps, located 45° apart and radiating from the tree (Fig. 1). The traps, covering 7.64 percent of the sample area, were 50-ft long and 3-ft wide at their bases, and were raised 3 to 4 ft above the ground. They consisted of a wooden frame covered with light, unbleached, preshrunk cotton cloth on which 20 sections were marked off at 2.5-ft intervals.

In 1967 and 1968, the trapped seeds were counted and removed twice each day at approximately 0900 and 1600 hours. Temperature and humidity were recorded on two hygrothermographs housed in standard double-louvred screens. Rainfall was measured in the early morning and late afternoon in two standard copper gauges. Wind speed and direction were measured with a Taylor Windscope set 20 ft above the ground at the approximate average height of dwarf mistletoe infections on the infected tree. Wind data were recorded automatically with a pair of Rustrak DC recorders powered by a 6-volt, wet-cell battery. The recorders were calibrated after use each year and chart data summarized by 2.5-minute periods. The wind category for each 2.5-minute

Figure 1. Dwarf mistletoe-infected source tree surrounded by eight triangular-shaped seed traps. In the foreground is one of the instrument screens.

period was determined by the maximum velocity (gust) recorded to the nearest 5 mph during the period. The magnitude of the wind (hereafter referred to as the "wind factor") was expressed by summing for each hour the gust velocities for all periods with a velocity above 5 mph. Gusts of less than 5 mph would presumably have little effect on seed dispersal.

During the summer of 1969, branches on the infected tree were removed and examined, and a record was kept of the quadrant in which the branch was growing. All dwarf mistletoe infections were counted, and the length and the diameter of swellings were recorded. Mistletoe aerial shoots and fruit were tallied, and the longest shoot on each infection was measured. Branches on eight additional trees growing in open situations in the same general area were sampled and fruit counted to compare their distributional pattern of ripening fruit with the experimental tree.

Results

Distribution of Dwarf Mistletoe in the Source Tree

A total of 4318 live branch infections, 6 stem infections, and 2901 dead infections on otherwise living branches were tallied on the source tree. Live infections were found 6.0 to 31.7 ft from the ground. About twice as many live infections occurred in the southeast (SE) and southwest (SW) sectors of the tree as in the northeast (NE) and northwest (NW) (Fig. 2A). While the average length of swellings, number of aerial shoots, and maximum height of aerial shoots per infection were fairly similar among sectors, the number of fruit produced on fruit-bearing infections was over twice as much in the southwest portion of the tree's crown (Fig. 2B). Of the approximately 73 thousand fruit counted, 40 thousand were produced on branches in the SW sector (Fig. 2C).

An approximation of the capacity of branches to sustain infections was made by roughly calculating their volume, using branch length and the square of branch diameter. For the portion of the crown that bore dwarf mistletoe infections, the SW sector contained the highest branch volume and the NE the least (Fig. 2D).

Branches on the additional trees also exhibited a skewed pattern of dwarf mistletoe seed production, but there was no consistent bias toward any one sector. On the average, branches in the NW sectors sustained the most seed production and those in the NE the least.

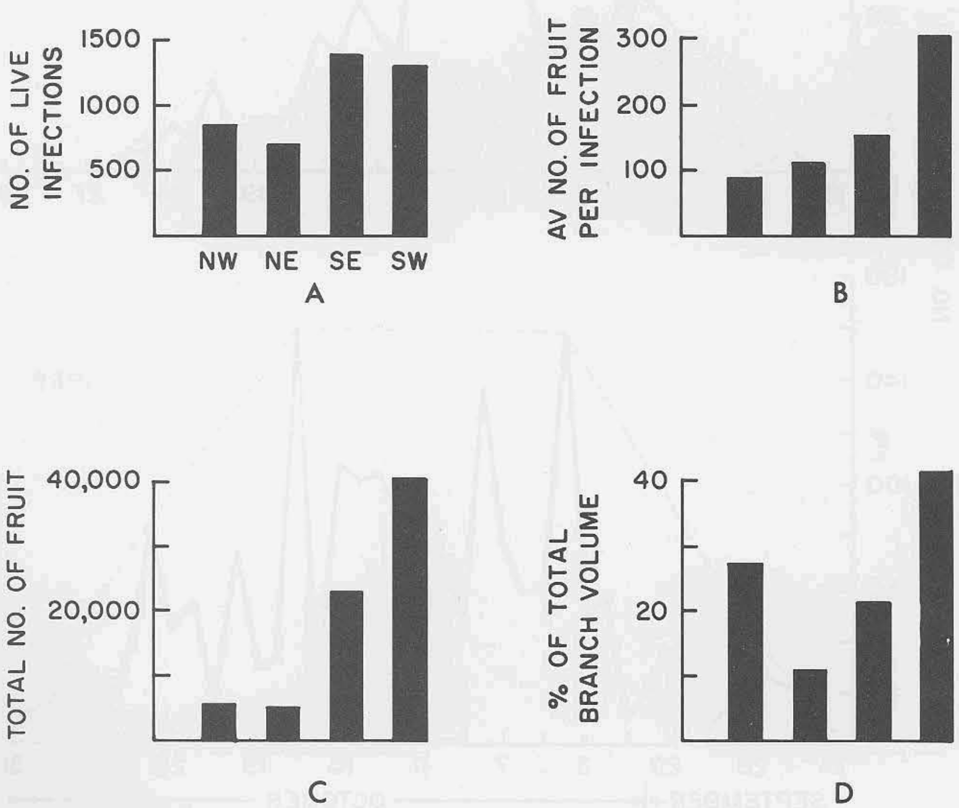

Figure 2. Characteristics of dwarf mistletoe infections for NW, NE, SE, and SW sectors on the source tree.

General Time and Pattern of Seed Dispersal

In both 1967 and 1968, seed dispersal began in the third week of September (Fig. 3). In 1967, there was a peak in dispersal rate on October 8, and dispersal was almost completed by October 26. In 1968, dispersal was more evenly spread out, with peaks occurring on October 4, 8, 12 to 15, and 17. Very limited dispersal occurred after October 31.

As in the previous three years, seeds were dispersed more abundantly to the south of the tree than to the north (Table 1).

Seeds were trapped in highest concentrations at the perimeter of the tree crown, about 7.5 ft from the bole of the source tree (Fig. 4). Fewer seeds were trapped under

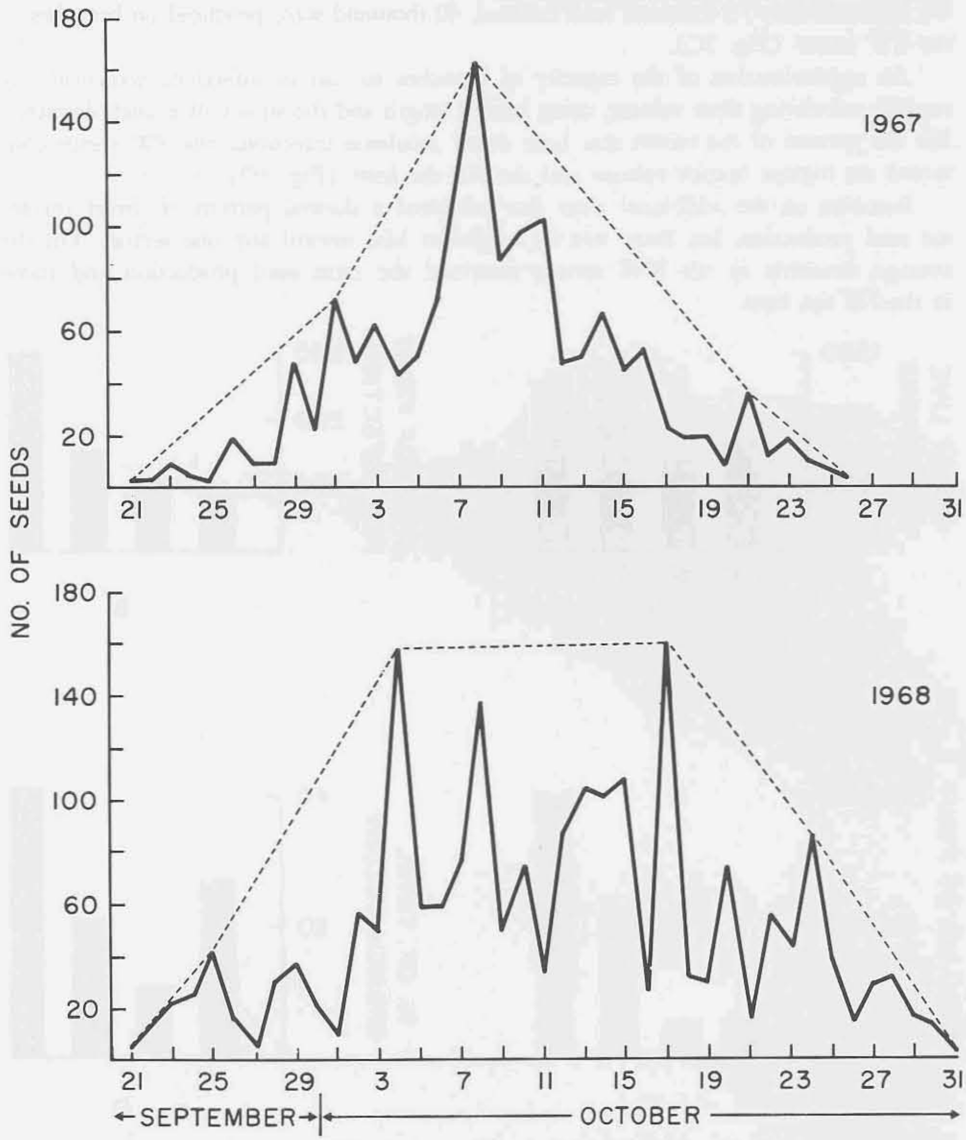

Figure 3. Number of seeds trapped in 1967 and 1968 (combined day and night counts). Dotted lines indicate the assumed maximum number of seeds available for dispersal.

TABLE 1. Dwarf mistletoe seeds trapped in each quadrant for 5 years.[1]

Year	Northeast		Southeast		Southwest		Northwest	
	No.	%	No.	%	No.	%	No.	%
1964	35	12	69	25	120	42	60	21
1965	248	15	484	29	622	37	320	19
1966	70	13	186	34	218	40	67	13
1967	276	18	466	30	503	32	317	20
1968	348	16	646	30	790	37	372	17

[1] Traps covered 4.0 percent of the sample area for 1964 to 1966, and 7.6 percent for 1967 and 1968.

the crown, and the concentration decreased rapidly beyond the crown edge by about 20 percent for each additional foot of distance. Proportionally, more seeds were trapped under the crown in the NE and SE quadrants than in the NW and SW.

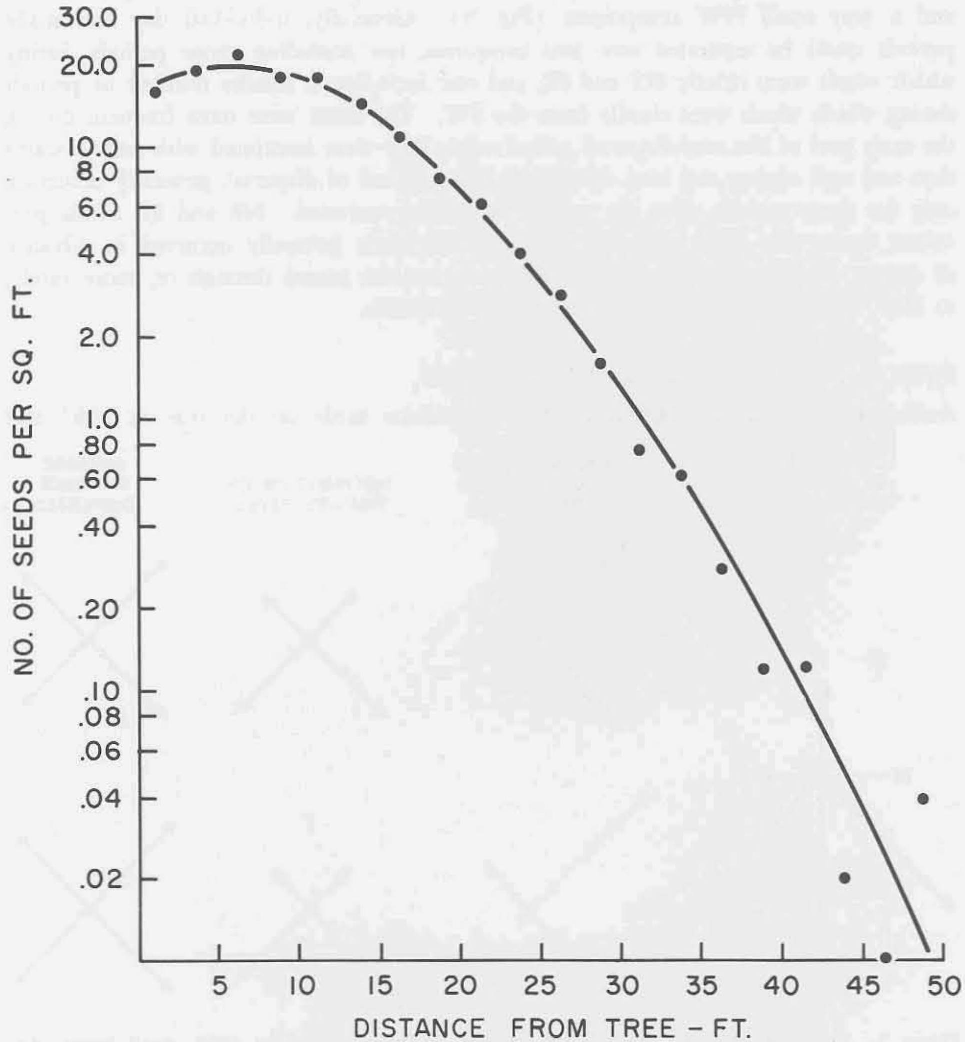

Figure 4. Concentration of dispersed seeds trapped from 0 to 50 ft from the bole of the source tree (average of 1967 and 1968).

Characteristics of the Wind During Seed Dispersal

There were few periods of wind over 15 mph and none over 20 mph during the 1967 and 1968 seed-dispersal periods. Over 90 percent of the 2.5-minute periods with gusts over 5 mph fell into the 5-10 mph category. The highest wind factor was 193, recorded for the daytime period of October 26, 1968. This was equivalent to an average gust speed of 8 mph.

In both years, the average wind factor was over twice as high during the day as at night. This greater windiness in the daytime period was most pronounced during weather featuring sunny days and cool, clear nights. For example, the first 12 days of the 1968 seed-dispersal period, characterized by clear skies, had an average wind factor during the day over five times as great as at night. This ratio narrowed considerably during later stormy weather.

For both 1967 and 1968, SE winds were most common, followed by NE, SW, and a very small NW component (Fig. 5). Generally, individual day and night periods could be separated into two categories, one including those periods during which winds were chiefly NE and SE, and one including a smaller number of periods during which winds were chiefly from the SW. The latter were most frequent during the early part of the seed-dispersal period when they were associated with sunny, warm days and cool nights, and least during the main period of dispersal, generally occurring only for short periods after the passage of storms eastward. NE and SE winds prevailed during the main dispersal period. NE winds generally occurred in advance of storms, the direction changing to SE as the storms passed through or, more rarely, to NW, depending on the actual course of the storm.

Effect of Wind on the Pattern of Seed Dispersal

Assuming that the distribution of dwarf mistletoe seeds on the tree in 1967 and

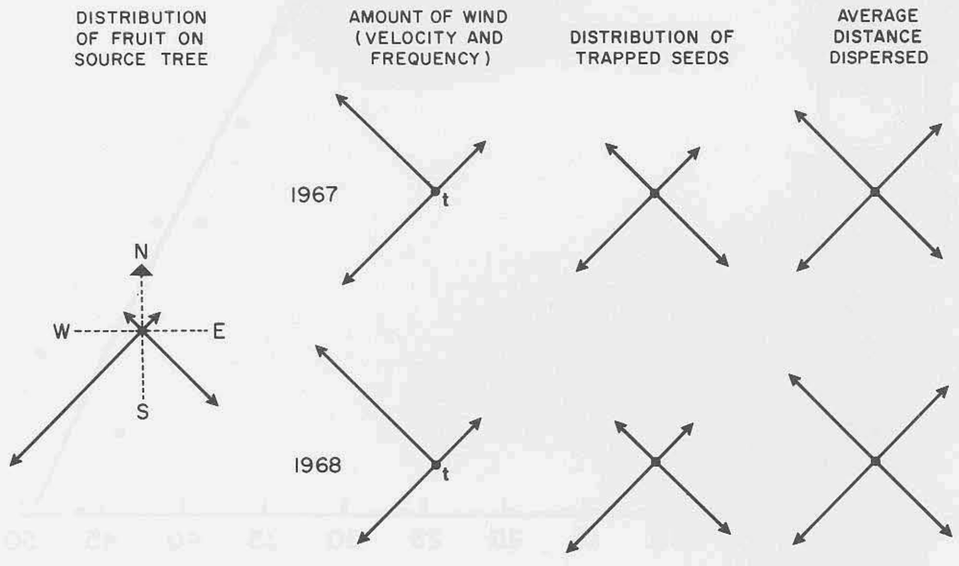

Figure 5. Diagrams showing the relative amount of fruit counted in 1969, wind factor, distribution of trapped seeds, and distance of seed dispersal by quadrants. t = trace of wind from NW.

1968 was proportional to that found in 1969 (Fig. 5), the NE and NW quadrants received more than twice the expected number of seeds, the SE quadrant about the same, and the SW quadrant 60 percent of the expected number. Wind direction and frequency partially explained these discrepancies, particularly the larger-than-expected catch in the NW which received benefit from a strong SE-wind component, but was not clearly responsible for the other departures from the expected pattern. Possibly the 1969 distribution of fruit was not a true representation of the 1967 and 1968 situations, or a greater number of seeds than expected were dispersed to adjacent or even opposite quadrants. To define further the relationship of wind to dispersal pattern, the 10 windiest days and nights were compared with the 10 calmest days and nights, with the assumption that seed distribution during calm periods could be used as a control. The number of seeds trapped was higher in the NE and NW quadrants and lower in the SE and SW quadrants during windy periods than during calm periods (Table 2). For example, on calm nights the SE quadrant received 28.4 percent and the NW 18.7 percent of the total catch, a difference of 9.7 percent. On windy nights, the difference was only 3.6 percent. The overall result of wind was a tendency to even out the pattern governed originally by the irregular distribution of dwarf mistletoe seeds in the tree.

Effect of Wind on Distance of Seed Dispersal

The distance of seed dispersal into the SW and NW quadrants, toward which most of the wind blew, was greater than into the NE and SE quadrants (Table 3). Confirmation of this wind effect was gained by comparing the calmest and windiest days and nights (Table 3). Dispersal distances for the NW and SW quadrants exceeded those for the SE and NE by the greatest margin during the windiest days

TABLE 2. Percentage of seeds trapped by quadrant for calm and windy nights and days (1967 and 1968 combined).

Quadrant	Calm days	Windy days	Calm nights	Windy nights
	%			
NE	16.8	17.9	16.4	18.1
SE	30.4	28.5	28.4	26.8
SW	35.2	33.0	36.5	31.9
NW	17.6	20.6	18.7	23.2

TABLE 3. Distance of seed dispersal by quadrant for calm, windy, and all nights and days (1967 and 1968 combined).

Quadrant	Avg distance						
	All days and nights	All days	Windiest days	Calm days	All nights	Windiest nights	Calm nights
	ft						
NE	14.4	15.4	14.3	16.4	12.9	12.1	13.6
SE	14.7	16.1	15.2	16.9	12.3	10.3	12.8
SW	16.6	17.3	18.8	17.0	15.6	15.8	14.9
NW	17.0	18.0	18.7	17.2	15.8	17.2	15.4
Average	15.8	16.7	16.9	16.9	14.2	14.0	14.2

and nights. During calm days and nights, the differences between quadrants were much reduced though distances were still slightly higher for the NW and SW quadrants.

The average distance of dispersal during the day was 2.5 ft greater than at night. The logical explanation of this might be that days were windier than nights. However, while there was an increase in the distance of seed flight in the direction of the wind, there was an equivalent reduction in the distance against the wind, for the average seed-dispersal distance did not differ between windy and calm days or nights (Table 3).

Nights and particularly days with high dispersal rates often had a low wind factor. However, a few days and nights occurred in which a high wind factor coincided with a high dispersal rate. In general, examination of these instances revealed no greater wind effects than were evident from comparison of the combined windiest and calmest periods. The most notable exception to this occurred on the night of October 16, 1968, when relatively strong winds were blowing primarily from the SE and for shorter periods from the NE. The average dispersal distance was 20.9 ft into the NW quadrant and only 7.2 ft into the SE quadrant.

Effect of Weather on Time of Seed Dispersal

The number of seeds dispersed during any one period depended upon factors other than the maturity of the fruit. The first indication of this was the greater rate of daytime than nighttime dispersal, i.e., 2.87 times greater in 1967 and 5.44 times greater in 1968. In addition, the ratio of day-to-night dispersal was highest during sunny days and clear nights in which there was a relatively large difference between minimum and maximum temperatures. With this type of weather prevailing for the first 12 days of 1968, day dispersal was 10.3 times that at night. For both 1967 and 1968, high average maximum temperatures and large differences between the maximum and minimum temperatures were associated with the highest day:night dispersal ratios, but relationships were statistically significant at $P<.05$ only for 1967 (Table 4).

Temperatures were compared for days and nights with high and low dispersal rates within the same period of time. For example, the five highest daytime rates in 1967 occurred on October 3, 7, 9, 11, and 14. Temperature data for these days were compared with data for October 4, 5, 6, 8, 10, 12, and 13, all of which had lower daytime dispersal rates. The average maximum temperature was higher for days with high dispersal rates than for days with low rates (Table 5). For nights with high dispersal rates, the average minimum temperature was higher than for nights with low rates (Table 5). These trends were consistent for both years but statistically significant only for nightly minimum temperatures in 1968.

TABLE 4. A comparison of average temperature for high and low daytime:nighttime ratios of seed dispersal.

Measure	1967—ratio day:night dispersal			1968—ratio day:night dispersal		
	>2.87	<2.87	P	>5.44	<5.44	P
Maximum T—°F	61.5	55.1	0.04	58.1	54.0	0.24
Minimum T—°F	41.5	45.1	0.17	38.8	40.8	0.43
Difference—°F	20.0	10.0	0.02	19.3	13.2	0.08

TABLE 5. A comparison of average temperature, wind, and rainfall for high and low rates of seed dispersal.

Measure	1967			1968		
	High rate	Low rate	P	High rate	Low rate	P
DAY						
Avg no. of seeds/hr	8.0	4.9		13.0	5.4	
Maximum T—°F	56.7	53.9	0.08	53.0	49.7	0.24
Wind factor	21.2	49.6	0.21	9.3	45.4	0.09
Rainfall—in	0.38	0.56	NS	0.06	0.16	0.32
NIGHT						
Avg no. of seeds/hr	3.9	1.4		3.1	1.0	
Minimum T—°F	52.0	48.2	0.08	44.1	39.3	0.02
Wind factor	24.7	5.3	0.17	36.3	18.8	0.38
Rainfall—in	1.23	0.86	0.36	1.02	0.44	0.01

The possible existence of a direct relationship between temperature and rate of seed dispersal was examined by expressing seed dispersal as a percentage of a theoretical maximum number available for distribution (Fig. 3). The effect of a varying number of seeds ready for dispersal would presumably be minimized (Green, 1962). Temperature was expressed as cumulative degrees over 40° F and summarized each year for early, middle, and late dispersal by daytime, nighttime, and whole-day periods. Significant positive correlations were obtained between cumulative temperature and percentage of maximum seed dispersal for 5 out of 18 combinations. Of the 13 remaining combinations, 12 showed the same trend, but the correlations obtained were not statistically significant.

Daytime periods with high dispersal rates were associated with a lower wind factor and less rain than those with low rates (Table 5). In contrast, nights with high dispersal rates were associated with a higher wind factor and more rain than nights with low rates. These trends in averages were consistent for both years but statistically significant only for 1968 nightly rainfall. Both types of weather favoring seed dispersal were associated with higher-than-average temperatures, i.e., calm, sunny days and windy, rainy nights.

High dispersal rates during the day occurred mostly when winds were from the SW. This condition was associated with fine weather with higher-than-average daytime temperatures. High nighttime dispersal occurred mainly when winds were from the SE and NE.

Discussion and Conclusions

The decrease in concentration of dispersed seeds with increasing distance from the source was logarithmic, as found for other dwarf mistletoe species, but the rate of decrease was greater (Hawksworth, 1961; Scharpf and Parmeter, 1971). The decrease in concentration of seeds from the perimeter of the tree's crown to the bole was most likely due to the screening action of the dense hemlock foliage. This screening action was not measured in the aforementioned studies, as Hawksworth used individual infections for seed sources and Scharpf and Parmeter did not record seed dispersal under the tree crowns.

Because of the generally low magnitude of the wind and the extremely biased distribution of dwarf mistletoe fruit in the source tree, the overall effects of wind were small. However, considering the windiest days and nights separately, there was a tendency toward equalization of dispersal in the four quadrants and a greater average distance of dispersal on the leeward side (SW and NW) of the tree. A more significant overall effect was reported by Scharpf and Parmeter (1971) in California, due perhaps to the stronger winds (up to an average of 32 mph) experienced in their study area, and the greater height of their source trees. Based on this two-year study, the wind would only exert a significant effect on the overall dispersal of hemlock dwarf mistletoe seed where infected trees are exposed to a much greater amount of wind than at the study area, e.g., on ridges and in some coastal situations.

The time of seed dispersal was affected by fruit maturity and by weather factors. Eighty percent of the seed was dispersed in about three weeks. Within the bounds of this primary restraint, dispersal rates were highest during warm, windy, and rainy nights, and warm, sunny days. Similar results were obtained during a study in the southwestern United States in which the greatest dwarf mistletoe seed dispersal occurred during either rainy or sunny days and the least on dry, cloudy days (Hawksworth, 1961). It is debatable whether the impact of raindrops or movement of branches by wind act to set off seed discharge, or whether the relationship with rain and wind at night is an indirect one involving higher temperatures during stormy rather than during clear, calm nights. During the day, at least, there is no need for either wind or rain to effect a high dispersal rate.

The large day:night dispersal ratio in 1968, particularly that experienced in the first two weeks, was associated with an early outbreak of cold air over much of western Canada (American Meteorological Society, 1968). Night temperatures recorded during the main period of seed dispersal (October 1-21) averaged 39° F, and the difference between maximum and minimum temperatures averaged 13° F. The cool nights and relatively wide differences between night and day temperatures would favor a large day:night seed-dispersal ratio. In contrast, the average night temperature for the same period in 1967 was 46° F, and the average difference between maximum and minimum temperatures was 9° F with a resulting lower day:night ratio.

The consistently greater distance of dispersal during the day than at night remains unexplained. As wind measured in the conventional manner was shown to have no effect on average dispersal distance, the explanation might be found in an assumed greater frequency of vertical air currents during the day than at night.

The study revealed the importance of knowing the actual distribution of the parasite on experimental trees before interpreting seed-dispersal patterns or rate of spread of the disease. In hemlock, the distribution often appears to be skewed toward a particular sector. The reasons for such bias may be historical, relating to an early, unequal exposure to infection, or to microclimatic factors. Because of the dense foliage on western hemlock, initial differences in distribution of the parasite would be more likely maintained or accentuated than for most other dwarf mistletoe host species.

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