THE VERTICAL SPREAD RATE AND INTENSIFICATION OF DWARF MISTLETOE IN WESTERN HEMLOCK

by

KENNETH STANLEY RICHARDSON

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ABSTRACT

The vertical rate of spread of dwarf mistletoe was studied in two actively growing, young hemlock stands. This was done by determining the height and age of successive oldest and highest female infections. The rate of spread was calculated by dividing the sum of the heights of advances by the total number of years lapse between successive advances.

The mean vertical spread rate was 2.1 $\pm$ 0.1 ft./yr. in a relatively open stand and 1.0 $\pm$ 0.1 ft./yr. in a relatively dense stand.

The mean rate of tree growth during the maximum growth phase in the open stand was 2.5 ft./yr. and for the dense stand 1.5 ft./yr. However, over the past 25 years, the growth rate of the trees in the open stand was 1.9 ft./yr. and for the dense stand 1.1 ft./yr.

The number of new infections per year increased geometrically, doubling every four years in both the dense and open stands. However, the geometric increase levelled off six years ago in the open stand and five years ago in

the dense stand.

During the maximum growth phase of hemlock in an open and dense stand, the most photosynthetically active upper portion of the crown remains free of mistletoe infection. Until the senescent phase is reached, the trees can be expected to outgrow the mistletoe and intensification will be restricted to the lower portions of the crowns.

It is tentatively concluded that provided there is no overstory seed source and no disruption of the natural stand, such as thinning, dwarf mistletoe on hemlock will not become serious until the rate of height growth of the trees falls below the rate of vertical spread, i.e., not until after the presently accepted rotation age.

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Introduction

Hemlock mistletoe (Arceuthobium campylopodum Engelm. forma tsugensis (Rosend.) Gill), native throughout the coastal range of western hemlock (Tsuga heterophylla (Raf.) Sarg.), is responsible for severe growth losses and low wood quality in heavily infected overmature and mature stands (Buckland and Marples, 1952; Smith, 1969; and Wellwood, 1956).

Wellwood (1956) quantitatively assessed the differences between ten uninfected to heavily infected over-mature trees averaging 210 years old with a range of 146 to 256 years. He found that severely infected trees were seriously affected in terms of volume increment, vigour and lower wood density.

Smith (1969) recently studied the effects of dwarf mistletoe in a hemlock stand with an average age of 110 years. He found that the severely infected trees not only showed the greatest reduction in volume increment but also the greatest losses of height increment.

It is evident that if maturing hemlock stands lightly to moderately infected with dwarf mistletoe remain unharvested they will suffer increasing injury by the parasite.

Silvicultural procedures for the control of dwarf mistletoe in regenerating hemlock stands were discussed by Buckland and Marples (1952). They stated that since mistletoe occurred only in widely scattered areas in subsequent reproduction, the parasite may not constitute a major problem in future rotations if such stands are managed on an even-aged basis. This conclusion was not substantiated quantitatively in the publication.

Smith (1966), however, demonstrated the threat of a 35-ft. infected residual hemlock to regenerating hemlock stands. After trapping 1,962 seeds based on a 4% sampling intensity, he estimated that over 49,000 dwarf mistletoe seeds were dispersed. The dispersal area was 5,800 sq. ft. and the maximum distance of seed dispersal was 49.5 ft.

He concluded that it is essential to remove all infected residual trees during or immediately after logging in order to control mistletoe damage effectively since an infected 10 ft. tree at the time of logging can become a heavy seed producer within 25 years.

More quantitative data on the epidemiology of dwarf mistletoe in regenerating and maturing hemlock stands are needed to determine the necessity of control measures as cutting practices shift to earlier rotations. Damage may be of little consequence in infected stands managed on a shorter rotation since the parasite would be prevented from intensifying throughout the crown.

It was decided, therefore, to study an epidemiological aspect of hemlock dwarf mistletoe in immature hemlock, viz., the vertical rate of spread. If the rate of tree height growth during the phase of maximum growth rate significantly exceeds the rate of dwarf mistletoe vertical spread then there will be a significant proportion of the most photosynthetically active upper crown free of infections. In addition, the highest proportion of infections will be in the less photosynthetically active lower crown.

Literature Review

Much of the work on epidemiology has been done on mistletoe species which infect pines. Muir (1968) found a logarithmic decrease in the number of seed of _A. americanum_ Nutt. ex Engelm. with increasing distance from the seed source in lodgepole pine (_Pinus contorta_ var. _latifolia_ Engelm.). This distribution was in contrast to the near-normal distribution he observed on the number of infections from an infected single residual tree and infected stand edges. This was attributed to the small target area of trees within 10 ft. of the infected trees.

Hawksworth (1961) found that _A. vaginatum_ (Willd.) Presl. forma _cryptopodum_ (Engelm.) Gill spread approximately 1.0 ft./yr. in even-aged ponderosa pine (_Pinus ponderosa_ Laws.) and that _A. americanum_ had a rate of spread in young lodgepole pine of 1.5 ft./yr. in open and 1.0 ft./yr. in closed stands.

Muir (1968) also found a logarithmic increase in the number of infections of _A. americanum_ in 30 yr. old stands of lodgepole pine from infection age 10 to 3 years.

The absence of infections less than three years old were attributed to the two year incubation period.

Hawksworth (1969) determined the upward spread of a dwarf mistletoe by inoculating five uninfected trees. He found that the mean upward rate of spread of *A. occidentale* Engelm. on *Pinus sabiniana* Dougl. was 2.3 ft./yr. while growth rate of the trees averaged 2.0 ft./yr.

The work of Hawksworth, Muir and many others has provided a quantitative insight into the behaviour of several mistletoe species, the majority of which infect pines. These epidemiological aspects apply generally to western dwarf mistletoe but not to the mistletoe-hemlock complex because of obvious differences in stand and crown characteristics, ecological conditions as well as differing mistletoe species.

Methods

It was mentioned earlier that Hawksworth (1969) studied the vertical spread of dwarf mistletoe by inoculating five uninfected trees. The difficulty with this method was that a period of 16 years was required. One of the main objectives of the present study was to develop a technique to determine the vertical rate of spread in naturally infected, actively growing stands. Details of the development will be discussed in the following sections.

Trees were selected under the following restrictions:

1. Trees currently in their maximum growth phase (linear growth phase).
2. Trees having no lateral light source from openings created by logging. Additional light from these sources can stimulate abnormally high development of mistletoe plants and fruits. (Baranyay, 1962).
3. Trees occupying a codominant or dominant position in the stand. Trees with an inferior position in the stand are subjected to seed bombardment from above which would result in an inaccurate estimate of upward spread.
4. Trees out of the range of infected overmature residuals. Trees within the range of infected residuals are subjected to seed fall from above which would result in an inaccurate estimate of upward spread.
5. Areas having a relatively level terrain.

Two distinct stand densities were recognized. Three trees in a dense stand and 12 trees in an open stand met the above described specifications. The dense stand consisted of two broadly distinct height and age classes. The selected trees, which had been growing vigorously for an average of 47 years following suppression for an average of 44 years, occupied the dominant position in the stand. The understory was composed of 80 per cent hemlock and 20 per cent cedar all of which were 6 inches or less in diameter. The open stand was relatively uniform and had been actively growing for an average of 42 years. Further information on the sample trees is presented in Table I.

Calculation of the Vertical Rate of Spread

After the selected trees were felled, the heights of the apparent oldest female infections on each branch were recorded. The infections were labelled and taken to the laboratory for age determination. The age of each infection was found according to the technique outlined by Scharpf and Parmeter (1966). The tabulation of heights and ages of infections for one of the sample trees is given in figure 1. The successive oldest and highest infections for each tree was determined (Figure 1). The difference between the heights and ages of these successive oldest highest infections provided individual heights of advance and the number of years lapse

Table I

Sample tree basic measurements

	Dense		Open	
no. trees	3		12	
avg. ht. (ft.)	61.3	(46.2-72.8)	85.2	(68.0-93.7)
avg. dbh (in.)	10.1	(8.8-12.2)	12.5	(9.3-15.4)
avg. age (yrs.)	91	(86-97)	56	(38-78)
avg. no. yrs. suppressed	44	(37-51)	14	(0-35)
avg. no. yrs. actively growing	47	(45-49)	42	(35-48)
avg. ht. when released from suppression (ft.)	9.8	(7.5-12.0)	3.6	(0-10.0)
avg. ht. growth from release (ft.)	51.8	(39.7-62.8)	81.1	(66.6-91.8)
Site index (Barnes, 1962)	80		160	

	infection no.	height of infection	age of infection (yrs)	height of advance (ft.)	no. of yrs. lapse
	1	9.7	24		
oldest highest infection	2	13.4	24		
	3	15.2	16	11.2	8
	4	21.1	12		
second oldest highest infection	5	24.6	16		
	6	27.8	8		
	7	30.2	9	8.2	2
	8	31.4	11		
third	9	32.8	14		
	10	38.2	8	11.6	5
fourth	11	49.4	9	2.0	3
fifth	12	46.4	6		

Figure 1. Example of determination of heights of advances and number of years lapse.

between each advance.

Individual rates of spread for each advance and the number of years lapse between successive advances were calculated. It would be incorrect simply to sum these rates and divide by the total number of observations since this would exclude the effect of the variation in the number of years lapse between each advance. A vertical spread rate value is possible for a range of years and heights of advance. For example a 11.2 ft. advance with a lapse of 8 years and a 7.0 ft. advance with a lapse of 5 years both have a vertical spread rate of 1.4 ft./yr. The rate of vertical spread and variance were calculated according to the following weighted formulae:

$$\bar{r} = \frac{\Sigma r_i y_i}{\Sigma y_i} = \frac{\Sigma h_i}{\Sigma y_i} \qquad S^2 = \frac{\Sigma y_i (r_i - \bar{r})^2}{\Sigma y_i - 1}$$

where: $\bar{r}$ = weighted average rate of vertical spread

$r_i = \frac{h_i}{y_i}$ unweighted rate of spread

h_i = height of an advance

y_i = number of years lapse between an advance

S^2 = weighted variance

Each r_i value has its own relative frequency which is determined by its y_i value. These data were grouped into a frequency distribution which closely approximated a negative binomial distribution. Logarithmic and square-root transformations were applied which enabled a t-test comparison between the means of the dense and open stands. The rates of vertical spread in the infected portions of the upper and lower crown were also calculated. The loss of branches with infections older and higher than the recorded oldest highest infections will result in a greater height of advance, a lower number of years lapse, and hence an upward bias in the estimated mean vertical rate of spread. These losses will occur more often in the lower crown due to branch suppression.

Calculation of the Intensification Rate

All of the infections of the trees in the dense stand and all of the infections of nine of the trees in the open stand were collected to determine the rate of intensification. The rate was estimated according to Muir's (1963) technique. He observed a logarithmic relationship between the number of infections and infection age. The slope of the straight line obtained by a transformation of the logarithmic relationship was regarded as a meaningful parameter of increase of the mistletoe population.

Calculation of Tree Growth Rate during the Linear Phase

Each tree was bucked into five-foot sections and ages were recorded at each section in order to find the age when the maximum growth phase was initiated. The average growth rate of a tree during the linear phase was determined by dividing the difference in height of the tree at the start and end of the linear growth phase by the duration of the linear phase in years. In addition, the average height growth rate for the last 25 years was calculated.

Results and Discussion

Heights of Advances and Number of Years Lapse (Table II)

The average height of an advance was 6.0 ft. with a range of 0.4 to 25.6 ft. The observed frequency distribution (Figure 2) was, statistically, uniformly distributed up to 11.9 ft. The average number of years lapse between advances was 3.7 years with a range of 1 to 11 years. The observed frequency distribution did not approximate any of the standard mathematically defined distributions (Figure 3).

The results were given the following interpretation. After the seeds have reached the host, they are subjected to the destructive effects of wind, snow, rain, fungi and insects (Gill and Hawksworth, 1961; Roth, 1959

Table II

Mean and range of heights of advance and number of years lapse between successive advances and their 95% confidence limits

	Average height	Range	Average number of years lapse	Range
Pop'n. estimate	6.0 ± 0.8	0.4-25.6	3.7 ± 0.6	1-11
Dense stand	4.1 ± 1.6	0.7-9.0	4.0 ± 1.5	1-11
Open stand	7.4 ± 1.2	0.4-25.6	3.5 ± 0.6	1- 9

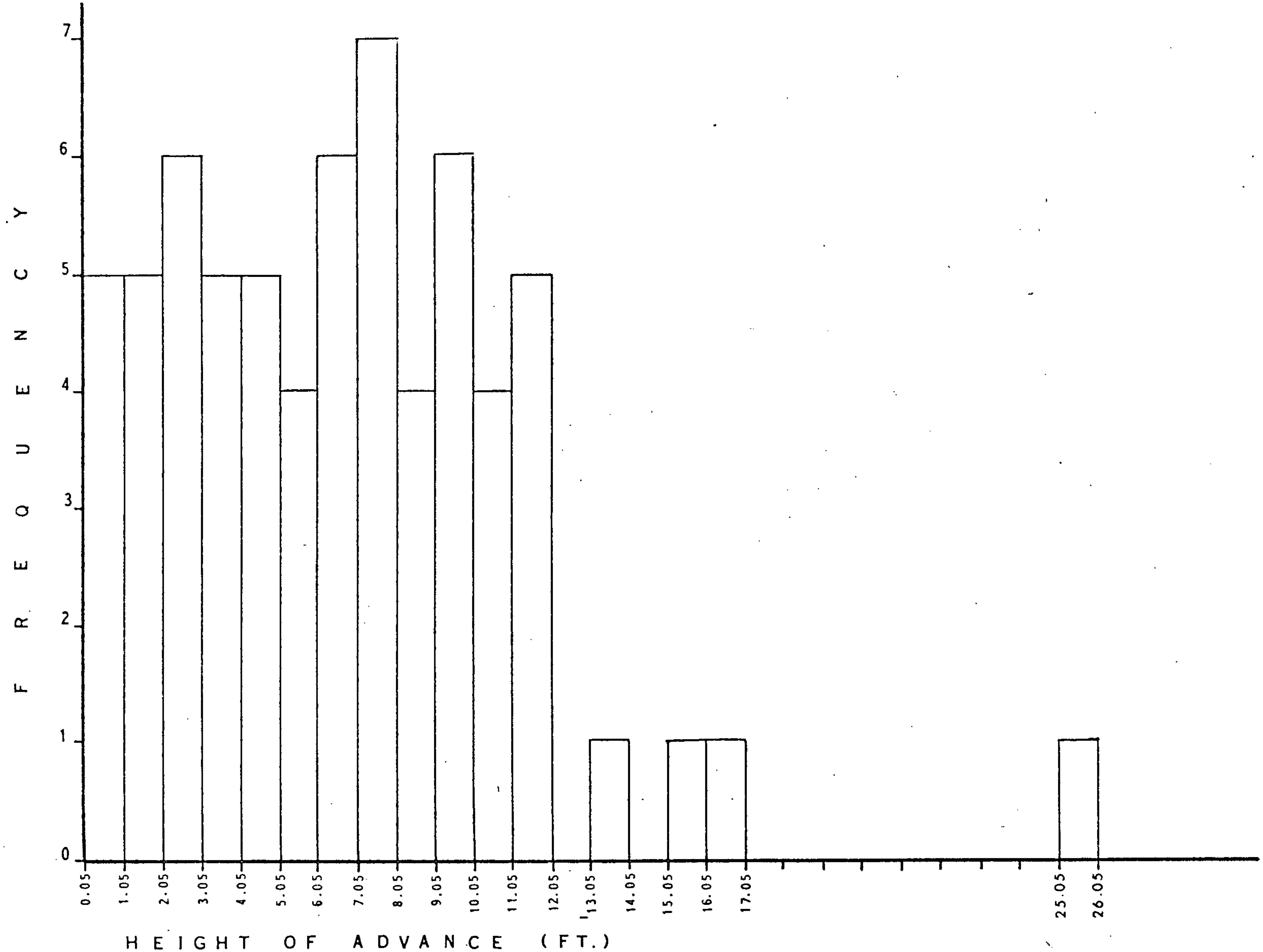

Figure 2. Observed frequency distribution for heights of advances.

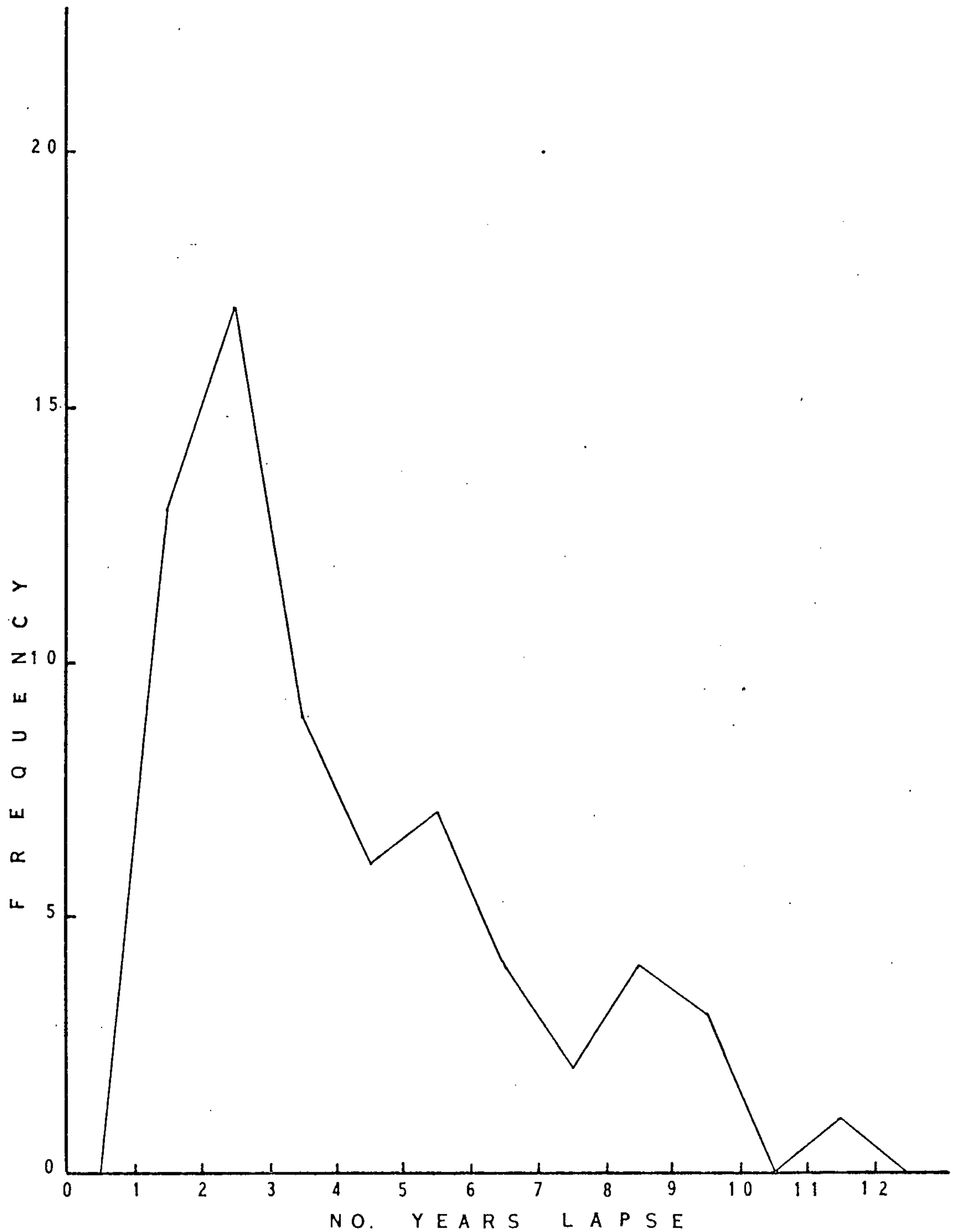

Figure 3. Frequency polygon of the observed distribution of the number of years lapse between the heights of advance.

and Wicker, 1967). These factors were responsible for removing or killing 90-96% of mistletoe seeds on several coniferous species (Wicker, 1967).

In the present investigation, the maximum number of fruits observed on the shoots of a single infection was approximately 300 while the average infection had 50-100 fruits. The crown of a tree, therefore, is exposed to cross-infection from a finite number of seeds. Furthermore, there is an uninfected portion of the crown above the highest existing female infection which is exposed to seed from one or more infections at one or more levels from one or more surrounding trees. The success of a seed in establishing an infection from 0.4 ft. to 25.6 ft. with a lapse of 1 to at least 11 years is dependent on destructive factors acting with variation in severity from year to year. It is possible, therefore, to have, a range of advances for lapses from 1 to at least 11 years. This was substantiated by plotting the observed heights of advances over the corresponding number of years lapse (Figure 4). There was no relationship between the variables which was indicated statistically using the Pearson product-moment coefficient of correlation formula for ungrouped data. The r value was -0.06.

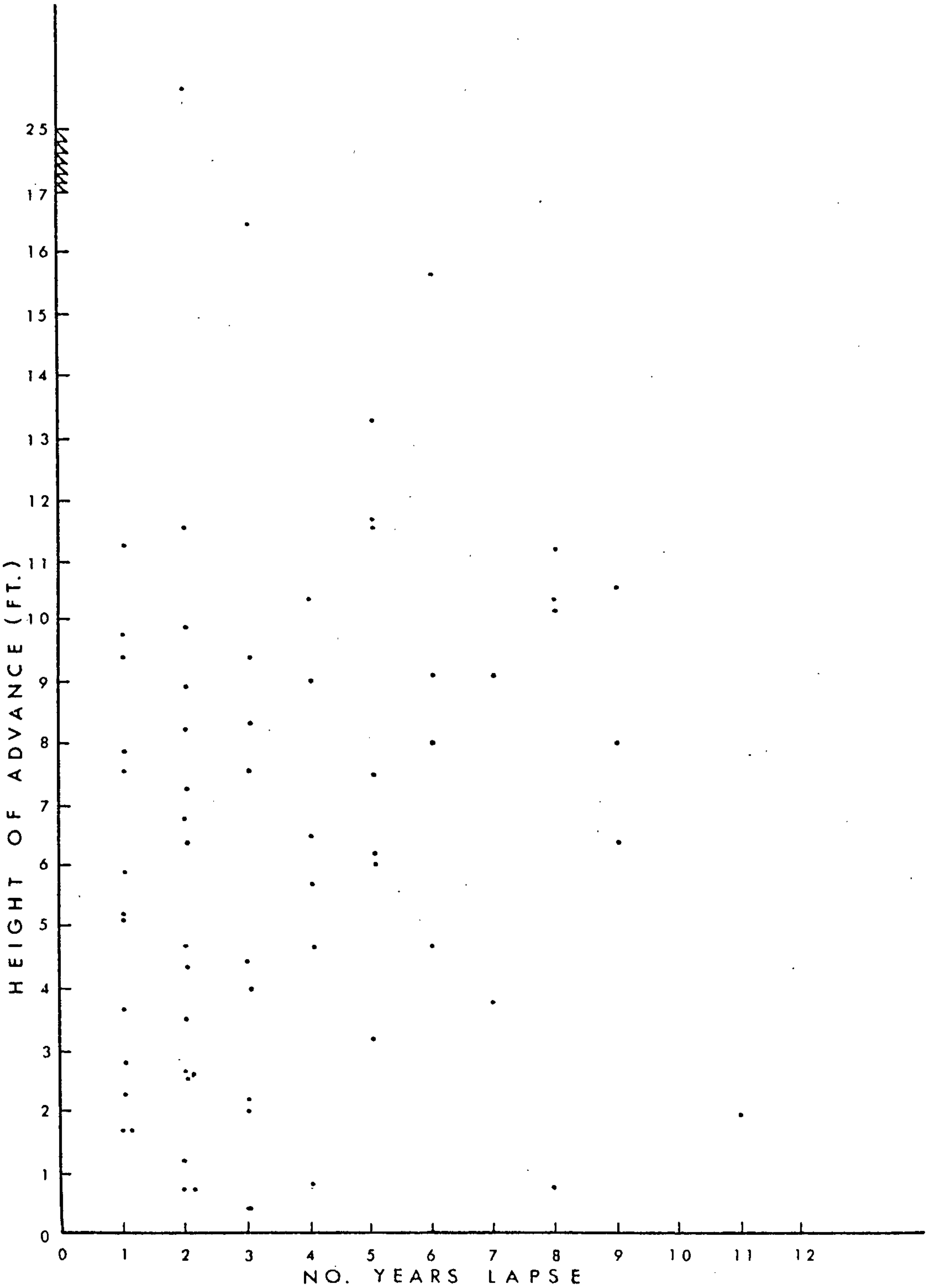

Figure 4. Plot of heights of advance over corresponding number of years lapse.

The observed equal frequency distribution for the heights of advances indicated that positions up to 25.0 ft. on the uninfected portion above the highest existing female infection have a chance of being infected. Positions up to 12.0 ft., however, have the greatest and an equal chance of being infected. The range of heights of advances observed approach the range of values obtained by Hawksworth (1961) in his study on seed flight of A. vaginatum forma cryptopodum. He found that the average vertical distance attained by naturally discharged seeds was 15.0 ft. from an average angle of 45 degrees. The maximum angle of discharge was 67 degrees and vertical distance 25 ft.

Rates of Vertical Spread, Tree Growth and Intensification

Table III summarizes the investigation of the vertical rate of spread of dwarf mistletoe and the growth rate of the sample trees.

It was mentioned in an earlier section that loss of infections from branch suppression in the lower crown may cause an upward bias in the estimated vertical rate of spread. The mean rate in the lower crown was not significantly different at the 5% level from the rate observed in the upper crown. It was observed that many mistletoe infected branches persisted at levels well beneath the canopy. The average height to the lowest living branch for the dense stand was 17.8 ft. and for the open stand 11.3 ft. This persistence of infected branches could account for the lack of a significant difference between the rates of vertical spread in the upper and lower portions of the infected crowns.

The average rates of vertical spread in the open and dense stands were 2.1 and 1.0 ft./yr. and the mean rates of tree height growth during the maximum growth phase for the open and dense stands were 2.5 and 1.5 ft./yr. respectively. However, over the past 25 years the rate of tree growth decreased to an average of 1.9 ft./yr. in the open stand and 1.1 ft./yr. in the dense stand. The differences between rates of vertical spread and between tree height growth in the open and dense stands were significantly different at the .05 probability level. The combined vertical rate of spread in both stands was 1.6 ft./yr. while that of tree growth rate was 2.1 ft./yr. The combined average tree growth rate for the past 25 years was 1.6 ft./yr.

The higher rate of spread in the open stand can be attributed to the open stand characteristic which provides more light stimulus for shoot and fruit production, seed germination and less obstruction for ejected seeds.

Table III

Weighted mean vertical rate of spread of dwarf mistletoe and mean growth rate of sample trees during the maximum growth phase and for the past 25 years

The 95% confidence limits are included.

	Weighted mean vertical spread rate (ft./yr.)	Mean height growth during the maximum growth phase (ft./yr.)	Mean height growth for the past 25 yrs. (ft./yr.)
Pop'n estimate	1.6 ± 0.2	2.1 ± 0.1 (1.4-3.2)	1.6 ± 0.3 (0.7-2.4)
upper crown	1.5 ± 0.2		
lower crown	1.9 ± 0.3		
dense stand	1.0 ± 0.1	1.5 ± 0.2 (1.4-1.5)	1.1 ± 0.7 (0.7-1.5)
upper crown	0.9 ± 0.5		
lower crown	1.1 ± 0.4		
open stand	2.1 ± 0.1	2.5 ± 0.2 (2.1-3.2)	1.9 ± 0.2 (1.5-2.4)
upper crown	1.9 ± 0.3		
lower crown	2.4 ± 0.6		

The differences between the tree growth rate during the linear phase and vertical rate of spread of dwarf mistletoe could not be tested statistically since their means are from different populations. However, the end result of these differences when accumulated over tens of years, should mean that a significant proportion of the crown will be either free of mistletoe infections or will have a very low number of infections. The average length of female mistletoe-free crown above the highest recorded female infection for the dense stand was 25.7 ft. (range 20-31 ft.) or 51% of the average crown length of 50.0 ft. The open stand had an average of 27.6 ft. (range 20-40 ft.) or 41% of the average crown length of 66.5 ft.

The length of mistletoe-free crown increased very little over the last 15 years (Table IV).

Table IV

Average length of mistletoe-free crown

	1955	1969
open	26.2	27.6
dense	24.5	25.7

It was noted in the sample trees that there was dense foliage up to at least 5 ft. from the top of the crown. The lack of increase of dwarf mistletoe-free crown length indicated in Table IV was not due to lack of target area but rather to the equalization of vertical spread rate and tree growth rate (Table IV). With the exception of a few male plants (less than 4 on any one tree) and latent infections, an average of 67 and 60 infections per tree occurred in the dense and open stands, respectively. These trees would be classed as lightly infected and will have lost an insignificant proportion of volume to the parasite (Smith, 1969).

The regression analysis of the number of dwarf mistletoe infections on age for infection age twenty to six in the open stand and from twenty to five in the dense stand is summarized in Table V. The linear relationship between the logarithm of the number of infections and the infection ages for both the open and dense stands were significant at the 1% level. The high coefficient of determination values further substantiated this significance in that for both stands close to 90% of the variation in logarithm of the number of infections was associated with the infection ages. There was no significant difference at the 5% level (F-test) between the slopes of the regression lines for the two stands indicating no difference between the rates of intensification. This agrees with Muir's results in his studies of A. *americanum* on lodgepole pine (1963 and 1968).

Table V

The regression analysis of the intensification rate of dwarf mistletoe infections

	open	dense
regression coefficient	-0.0847145	-0.0715295
intercept	2.15826	1.87958
F-test of difference in slopes	1.662 N.S.	
F-test of levels of regressions	5.708 *	

N.S. Not significant

* Significant at the .05 probability level

The difference between the levels of the regressions was significant at the .05 probability level. This indicated that separate equations are needed to represent the intensification rates in both stands.

The plotted data revealed that the number of infections in both stands doubled every four years (Figure 5).

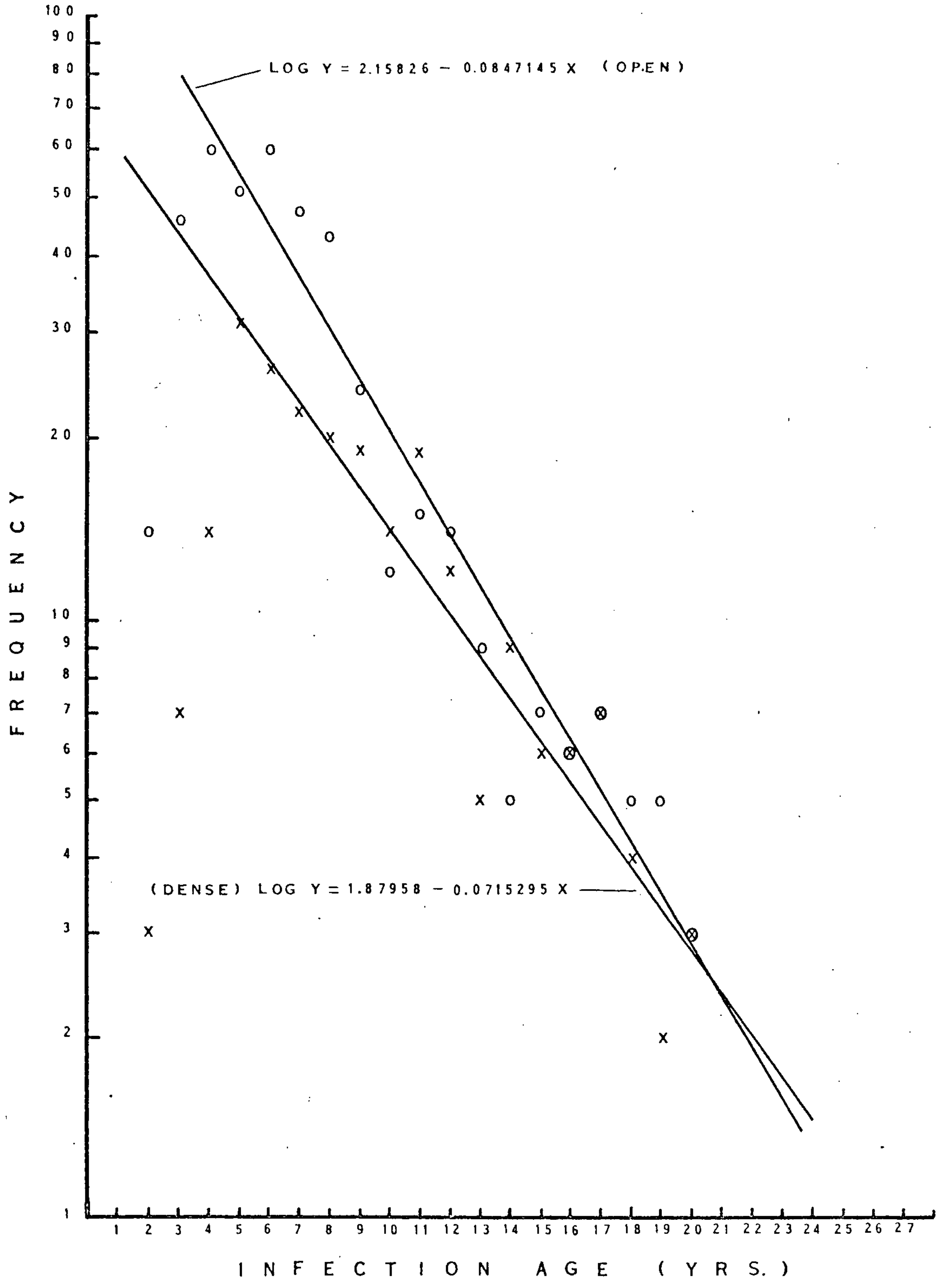

Figure 5. Intensification of dwarf mistletoe in the open (o) and dense (x) stands.

This increase appears to have levelled off six years ago in the open stand and five years ago in the dense stand. This may indicate that the parasite has passed its potential to increase logarithmically and that the number of new infections each year hence may remain more or less at a constant level. The loss of potential can be attributed to a closing canopy which results in lower light intensity in the lower portion of the infected crown. Low intensity of light restricts new infections and fruit production. If the stand were subsequently thinned or partially cut, a renewal of the geometric increase could be expected.

The results of the investigation indicate that during the maximum growth phase of hemlock in an open and dense stand, the most photosynthetically active upper portion of the crowns is free of mistletoe infections. Until the senescent phase is reached, the trees can be expected to outgrow the mistletoe, and intensification will be restricted to the lower portions of the crowns. It was also shown that in the stands examined the mistletoe has lost its potential to increase logarithmically, and that the number of new infections may be expected to remain more or less constant. A study of the further intensification of the parasite and a comparison of volumes of uninfected and infected maturing stands from 50 to 80 years is needed to determine the significance of dwarf mistletoe losses.

Conclusions

The vertical rate of spread of dwarf mistletoe was studied in two actively growing, young hemlock stands. This was done by determining the height and age of successive oldest and highest female infections. The rate of spread was calculated by dividing the sum of the heights of advances by the total number of years lapse between successive advances.

The mean vertical spread rate in a relatively open stand was 2.1 $\pm$ 0.1 ft./yr. and in a relatively dense stand was 1.0 $\pm$ 0.1 ft./yr.

The mean rate of tree growth during the maximum growth phase in the open stand was 2.5 ft./yr. and for the dense stand 1.5 ft./yr. However, over the past 25 years, the growth rate of the trees in the open stand was 1.9 ft./yr. and for the dense stand 1.1 ft./yr.

The number of new infections per year increased geometrically, doubling every four years in both the dense and open stands. However, the geometric increase levelled off six years ago in the open stand and five years ago in the dense stand.

It is tentatively concluded that provided there is no overstory seed source and no disruption of the natural stand, such as thinning, dwarf mistletoe on hemlock will not become serious until the rate of height growth of the trees falls below the rate of vertical spread, i.e., not until after the presently accepted rotation age.

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