INTENSIFICATION AND INFECTION MORTALITY OF DWARF MISTLETOE IN TWO STANDS OF WESTERN HEMLOCK

by

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ABSTRACT

The number, height and age of western hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones) infections were recorded in two western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) stands (44 and 130 years old) located on similar sites on the University of British Columbia Research Forest at Maple Ridge, B.C.. The rapid decrease in numbers of infections with infection age was shown to be largely due to infection mortality. The rate of intensification of the disease expressed as "doubling time" was estimated to be 40 or more years in both stands. Also estimated was a rate of vertical spread of .15 metres per year. The results differed markedly from those of other studies in similar stands, which generally predict "doubling times" of 2 to 4 years and vertical spread rates of up to .5 metres per year.

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INTRODUCTION

Western hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones) is a parasitic vascular plant found primarily on western hemlock (*Tsuga heterophylla* (Raf) Sarg.). The other known hosts are mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.), pacific silver fir (*Abies amabilis* (Dougl.) Forbes), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), grand fir (*Abies grandis* (Dougl.) Lindl.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), white pine (*Pinus monticola* Dougl.), and Engelman spruce (*Picea engelmannii* Parry). *A. tsugense*, in what is thought to be variant form, also parasitizes lodgepole pine (*Pinus contorta* var. *contorta* Dougl.) (Smith and Wass, 1976). *A. tsugense* is found throughout the coastal range of western hemlock (coastal North America) but not the interior where western hemlock grows (Baranyay and Smith, 1972).

Understanding the life cycle of dwarf mistletoe is the key to any discussion of the parasite. *A. tsugense* is dioecious with the male and female flowers on separate plants (infections). Flowering occurs in the spring with the pollination mediated by wind or insects as occurs with other *Arceuthobium* species (Hawksworth, 1978). Approximately fourteen months after pollination (late summer) the seeds are mature and ready for dispersal. A water powered explosive mechanism fires the seed from the fruit with an initial velocity of 100 kilometres per hour. In spite of the high discharge speed the very low seed mass makes seed flight dependent on stand density, plant height, wind direction, wind velocity and discharge angle. Flight continues until a target (a western hemlock needle is a very good target) is hit, then a sticky substance adheres the seed to the

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landing surface. Rain washes the seed to the target base where the seed germinates the following spring. Infection occurs when the seed radicle penetrates the bark at the needle base and a perennial endophytic system develops in the host cortex. One or two years after infection a fusiform swelling develops at the penetration site. One or two years after the swelling development, shoots appear followed a year later by flowers that produce more seed. These shoots are relatively short-lived. The shoots are not required for the infection to survive as the shoots are virtually unable to photosynthesize but do produce more seed. The life cycle therefore takes four to five years to complete (Hawksworth 1978).

Dwarf mistletoe as a parasite decreases the performance of the host and the greater the number of infections the greater the loss (Smith 1969). Effects of dwarf mistletoe on western hemlock are varied and significant. In order of importance the losses are; reductions in height and diameter growth, increased mortality of heavily infected trees, decreased seed production, reduction of wood quality and increased susceptibility to other damaging agents (Buckland and Marples 1952; Smith 1969; Hawksworth 1979).

The British Columbia Ministry of Forests reported western hemlock comprised 41% (12.0 million cubic metres) of the coastal harvest (Anonymous 1980) and dwarf mistletoe caused the loss of 1.7 million cubic metres (Van Sickle and Smith 1978).

This study was initiated to address the forest management problem of dwarf mistletoe infected advance regeneration and highly stocked infected immature stands of western hemlock. The forest manager is faced with this disease affecting approximately 15% of his (or her) western hemlock stands (Van Sickle and Smith 1978) and must have the information to make efficient

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decisions.

The recommended way to decrease the losses is the eradication of the infected advance regeneration followed by planting uninfected stock if required (Van Sickle and Smith 1978). The eradication procedure, in addition to the planting expense, could result in erosion and brush problems. Spacing infected immature stands has not been recommended because of the proliferation of infections of dwarf mistletoe. However, failing to space dense immature stands prevents maximizing volume on fewer stems over a shorter rotation.

The predicted development of the parasite in advanced regeneration and spaced stands is based on computer models (Bloomberg et al 1980). Information on the present stand dwarf mistletoe status is used to determine the doubling time of the parasite. The doubling times predicted range between two and four years producing huge infection totals by rotation age (a four year doubling time is also supported by Richardson and van der Kamp 1972) but these totals have not been observed and reported. Over-estimating the rate would result in a prediction of high infection numbers, a correspondingly high timber loss, and support an eradication program.

What is the cause of the inconsistency between predicted and observed numbers of infections? The difference is caused by the failure of models to fully appreciate the effect of infection mortality on intensifcation. Therefore the purpose of this study is to examine the effect of infection mortality on the development of dwarf mistletoe in western hemlock. The two particular characteristics of the parasite studied are intensification and vertical spread.

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1.0 LITERATURE REVIEW

What is known about the population dynamics of the parasite? Two areas that have been studied are the rates of vertical spread and intensification.

The vertical spread rate of the parasite is too low to keep pace with the height growth of the host on sites allowing western hemlock to grow in excess of 45 centimetres per year. The tree's greater growth rate allows for development of a significant portion of infection free upper crown (Richardson and van der Kamp 1972). Scharpf and Parmeter (1976) observed the same phenomenom in red fir (Abies magnifica A. Murr.) and white fir (Abies concolor (Gord. and Glendl.) Lindl.). Therefore, advanced regeneration on the better sites may be left provided no overhead source of dwarf mistletoe is present and the resulting stand is dense enough to achieve early crown closure, and if it is not already so heavily infected that it will never produce merchantable boles.

The intensification of dwarf mistletoe in western hemlock advanced regeneration following the removal of overstory infection source was studied by Smith (1977). He observed that where advance regeneration was heavily infected, the intensification rate was high due to internal reinfection. The heavily infected trees showed a decrease in growth. The dwarf mistletoe population in the lightly infected trees did not intensify rapidly and were not likely to show a decrease in growth. The heavily infected trees were concentrated within three to five metres of the infected residual tree. Smith found an initial rapid increase in the infection totals per tree per year and that eight years after the overstory removal infection levels appeared to be levelling off.

Smith (1969) observed old heavily infected trees to have 84% less height growth and 41% less volume growth than lightly infected trees. However, actual losses in volume or value have yet to be correlated to numbers of infections.

Intensification and vertical spread rates of several dwarf mistletoe species on their respective hosts have been observed. Muir (1972) estimated doubling to occur after 1.25 years on lodgepole pine. Richardson and van der Kamp (1972) found four years to be the doubling time on western hemlock. Inoculations on red and white fir had doubling times which varied from 3 to over 15 years (Scharpf and Parmeter 1976). A determining factor in intensification rates is the degree of crown closure. A very young ($<$10 years) stand's degree of crown closure would be less than that of a mature stand. Very high rates of intensification have been observed in a very young stand by Smith (1977). As crown closure increased, the intensification rate decreased markedly. The stand examined by Muir (1972) was also immature. Hawksworth and Lusher (1956) developed a 6-class rating system for dwarf mistletoe infected lodgepole pine. Ratings were found to increase by 1 class every 10 years. Smith (1969) altered the system to rate western hemlock to a 6-class system based only on the infection status of the middle third of the crown.

Vertical spread rates in open and dense stands of western hemlock of 65 and 30 centimetres per year respectively, (Richardson and van der Kamp 1972) and 7.8 centimetres per year on red and white fir stand (Scharpf and Parmeter 1976) have been observed. The Richardson and van der Kamp (1972) rates are based on an advancing front of the parasite. The rates of the

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other authors are based on the average height of all infections each year.

The ratio of male:female infections for *Arceuthobium* species has been found to be 1:1 for species of western United States and Canada. Mexican dwarf mistletoe species favour the female plant (Hawksworth 1978).

Smith (1977) discussed infection mortality but did not incorporate it in intensification calculations.

2.0 METHODS

2.1 Stand Selection

Two stands were selected using the following four criteria. First, the site indices were to be similar. Second, the stands were western hemlock with complete crown closure. Third, the mature stand was to exhibit evidence of early dwarf mistletoe development. The fourth criterion was for the terrain to be level with sample trees occupying dominant and co-dominant positions in the canopy. The stands selected were on the fringes of two separate fires. The natural regeneration was infected from unburned neighbouring stands which were eventually harvested (younger stand) or burned (older stand). The older stand appeared to have been released by the fire of 1867. Evidence for the infection history relationship of the two stands came from two observations. The first observation was that large stem infections, which require decades for development, were present in the mature stand. The second was that branch stubs, previously recorded as dead (Anonymous 1977), were actually live dwarf mistletoe infections of up to 93 years of age. Some of the undatable trunk infections occurred below the 93 year branch infections and hence were considered to be older. It was apparent that an overlap in infection ages between the two stands existed. Figure 1 shows the location of the two stands and details the history of the area. Study plot details are given in Table 1.

2.2 Plot Establishment

The immature plot was .01 of a hectare in size and contained 6 trees. The mature stand plot had 5 trees in .025 of a hectare. The plot trees

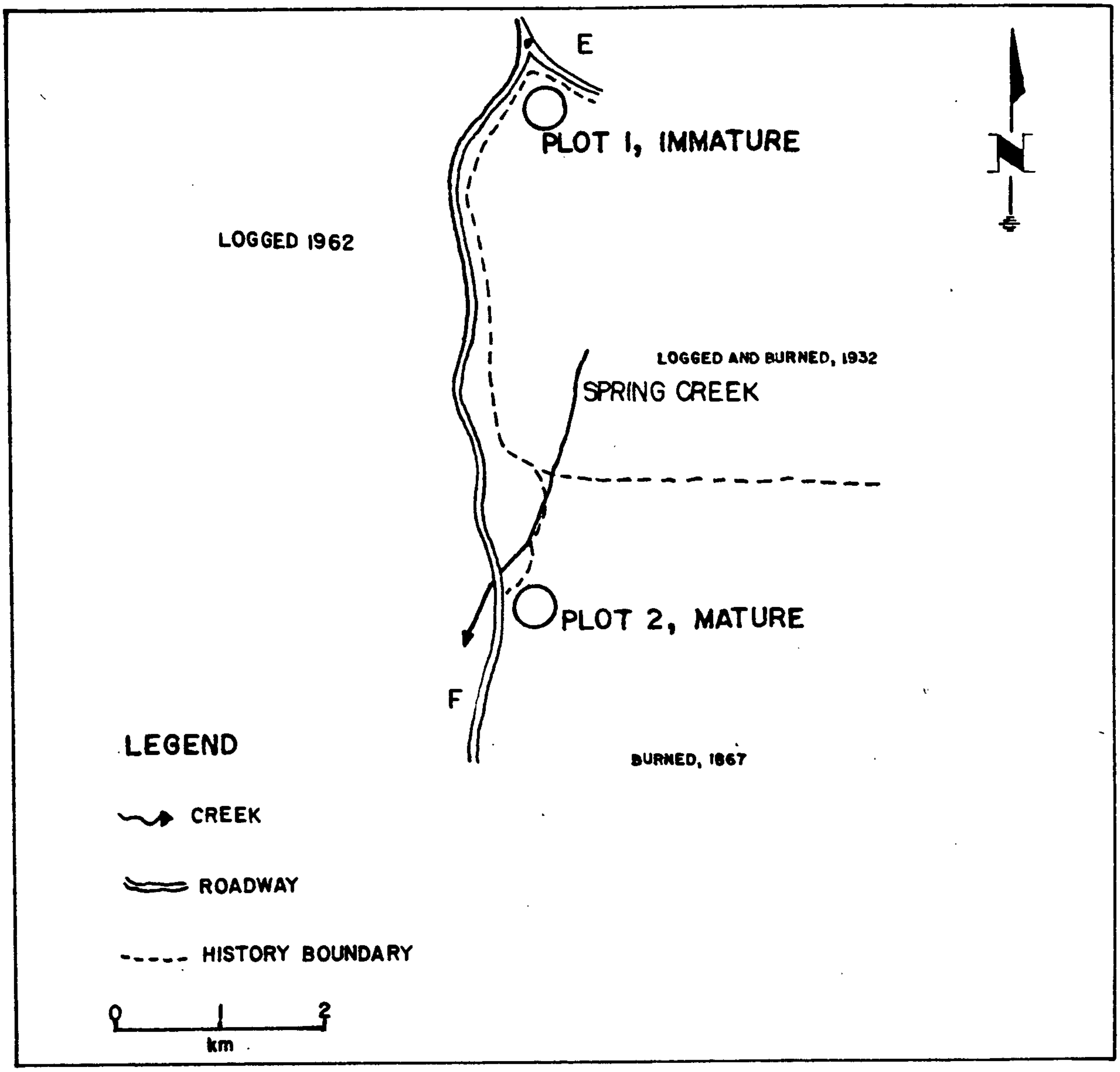

Figure 1. The location and history of the immature and mature dwarf mistletoe infected western hemlock stands in the University of British Columbia Research Forest, Maple Ridge, B.C., Canada, Latitude 49°15', Longitude 122°33'.

Table 1. Sample plot measurements for immature and mature dwarf mistletoe infected western hemlock stands at the University of British Columbia Research Forest, 1979.

Characteristic	Stand	
	Immature	Mature
Site index $_{100}$ (m)	40	40
Number of plot trees	6	5
Average height (m)	20.8	38.1
Range	19.3-22.9	33.8-46.0
Average live crown base (m)	3.7	9.2
Average tree age (years)	44	130
Range	nil	81-160
Plot area (ha)	.01	.025

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were felled and examined from ground level to terminal on a branch by branch basis in the field. The average age of trees in the plots was determined by aging a ground level cross-section of each tree and obtaining a plot average.

2.3 Vertical Rate of Spread Calculation

The four month (May to August, 1979) branch by branch search located the dwarf mistletoe infections which were collected and taken in for lab examination. The age of infections was determined using a technique developed by Scharpf and Parmeter (1966). The procedure consists of cross-sectioning the widest point of the infection and counting from the first irregular ring out to the cambium. The first irregular ring is the result of the parasite causing abnormalities in the pattern of annual ring formation at the time of infection.

2.4 Vertical Height Growth of Trees

The trees of both plots were sectioned (from ground level up) at 2-metre intervals and the age of each section was determined to find out when the maximum vertical rate of growth of the trees started. The height growth of the trees occurring in the linear phase was divided by the number of years in the linear phase and averaged to obtain a stand value of height growth. The rate of growth was compared to the vertical spread rate of the parasite.

2.5 Male:Female Infection Ratio Determination

In the laboratory the sex of the infections was determined using the characteristics of the mature plants with a dissecting microscope at 10 power. Male flowers contain pollen sacs and have 3 or 4 sepals. Female flowers have 2 sepals, no pollen sacs, and had mature or immature fruit. Infections with shoots that could not be identified to sex were not included in the sex ratio determination.

3.0 RESULTS AND DISCUSSION

The data (see Appendices I and II) were analyzed on a stand basis for several reasons. First, the canopies were dense with the individual crowns meshed together. The branch overlap would prevent the development of a self-contained dwarf mistletoe population in any one crown. Second, western hemlock is managed on an even-aged basis (clearcut harvesting). Therefore, any volume losses due to infections would appear on a stand basis.

The last 3 years of infection data were not used in calculations because infections less than 4 years old cannot be detected with certainty. Therefore calculations and figures with infection age are infection age minus 3. (The sample plot observations were presented in Table 2).

3.1 Rate of Intensification

The intensification rate is usually estimated from the number and age of infections present in a stand at the time of sample collection (Muir 1963; Richardson and van der Kamp 1972). The data were arranged to show the number of infections established each year over a period of time (usually more than a decade) and the rate of increase estimated (Figures 2 and 3). The method assumed that as the parasite infections were perennial all the infections established in the period under study were still present at sample collection. A second assumption was that the number of new infections established annually was proportional to the number of seeds produced when the crown volume (target area) in the stand remained constant. Some variation will be observed each year, largely due to weather, but the general proportional increase in numbers should be described by a logarithmic equation. The equation would relate number of infections (Y) to the

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Table 2. Sample plot results for immature and mature dwarf mistletoe infected western hemlock stands at the University of British Columbia Research Forest, 1979.

Characteristic	Stand	
	Immature	Mature
Number of live infections	278	418
Number of dead infections	405	93
Total number of infections	683	511
Number of live infections per unit of plot area (m^2)	2.78	1.64
Average number of infections per tree	46.3	83.6
Range	3.78	10-244
Average top infection height (m)	12.4	25.4
Range	10.4-14.0	22.3-28.7
Average % live crown free of infection	58.7	54.5
Male to female infection ratio	18:14	88:107
Frequency	1:0.78	1:1.2
Average rate of current host height growth (m/year)	.54	.41
Range	nil	.35-.47
Rate of parasite advance (m/year) without mortality	.49	.42
Range	0.0-1.6	0.0-1.2
Rate of parasite advance (m/year) with mortality	.28	.19

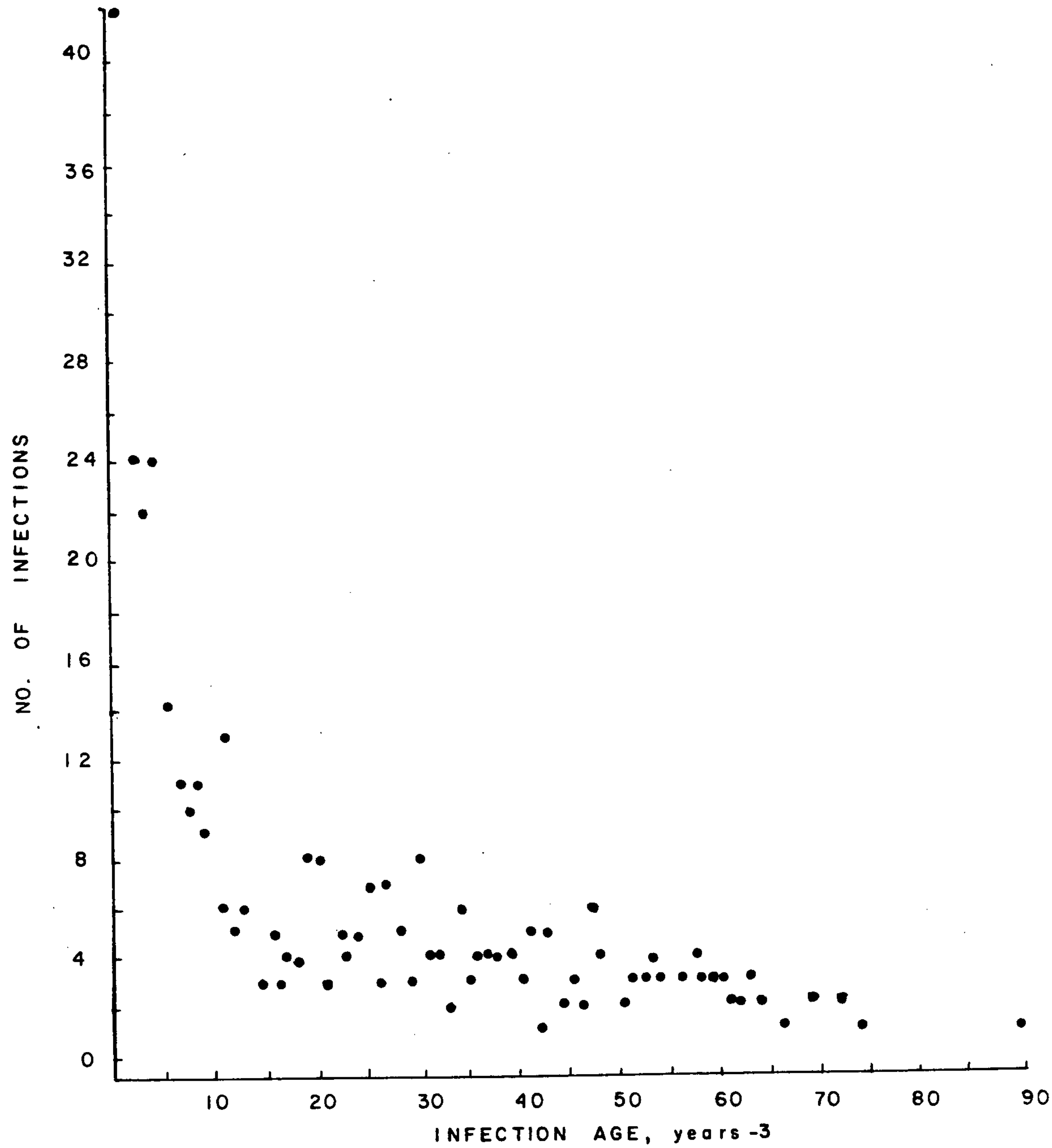

Figure 2. The number of live dwarf mistletoe infections per plot <u>versus</u> infection age for the mature western hemlock stand.

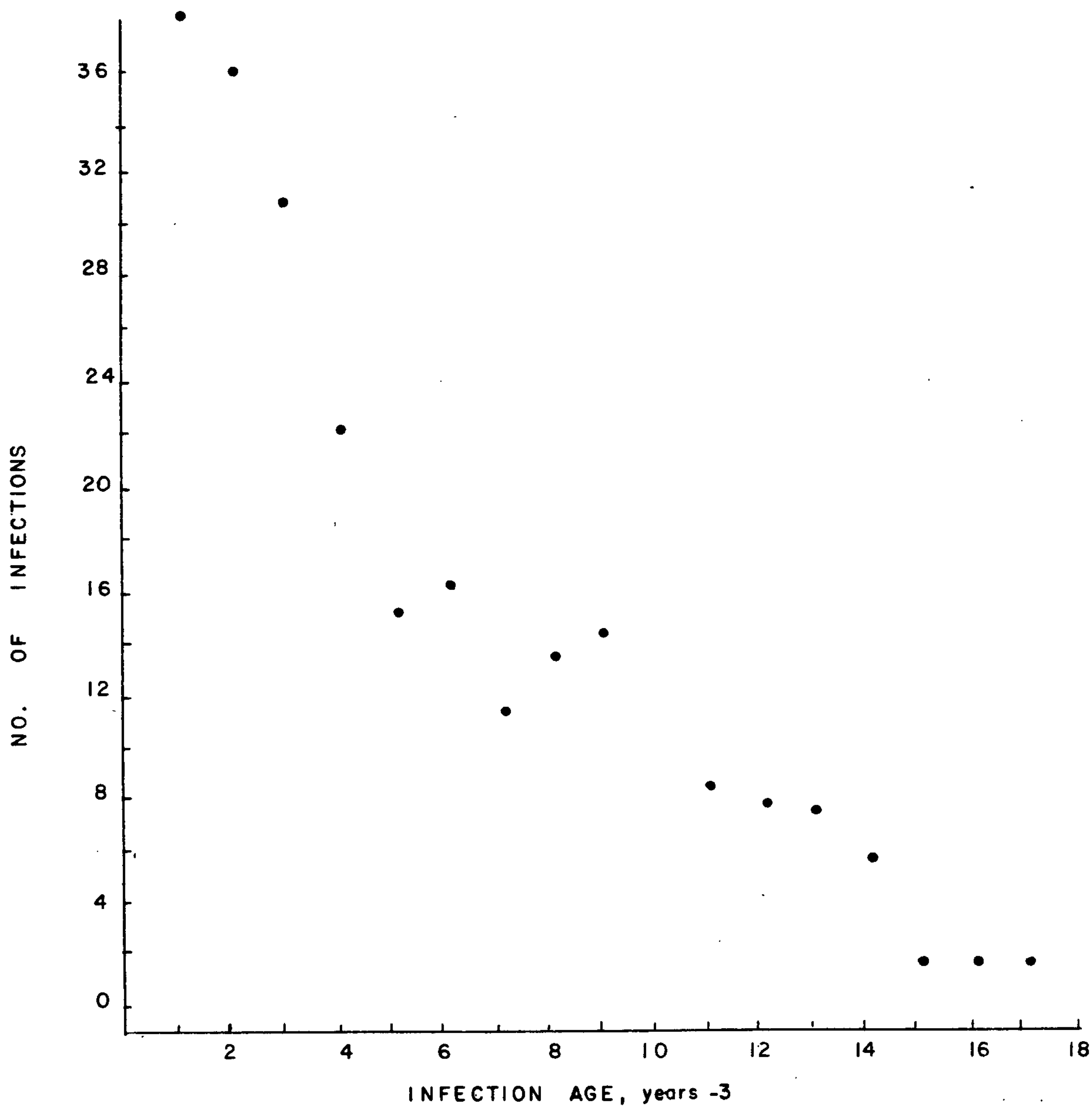

Figure 3. The number of live dwarf mistletoe infections per plot versus infection age for the immature western hemlock stand.

infection age (X) in the following forms;

$$\text{Log } Y = a + bX$$

with the doubling time (dt) of:

$$dt = \frac{\log 2}{b}$$

The log form seems to describe the young stand (and the first 14 years of the old stand) well. The dependent variable (number of infections) was examined on an area basis (per metre squared) because the study plots were of unequal size.

$$\log Y = .41434 - .06212X \qquad (1)$$

$$r = .957$$

$$\text{period} = 1962 - 1975$$

Equation 1 is based on the 238 live infections in the period of study found in the young stand. An additional 405 dead (undatable) infections were also observed. The dead infections were small and believed to be less than 10 years old at the time of death. The dead infections were below and in the live crown, and therefore not necessarily tabulated (Figure 4). (Dead branches with dead infections contributed to the litter layer below the plot trees but were not counted as part of the 405 dead infections.) The total number of infections established in the 44 year old plot was at least 683 (405 dead + 278 live).

For Equation 1 to be correct all the dead infections must be from before or after the 1962 - 1975 study period. Equation 1 indicated only 29 infections, not 405, were established between 1936 and 1962. Moreover, most infections established before 1962 and killed within 10 years would have been lost by the collection date of 1979. And as the dead infections

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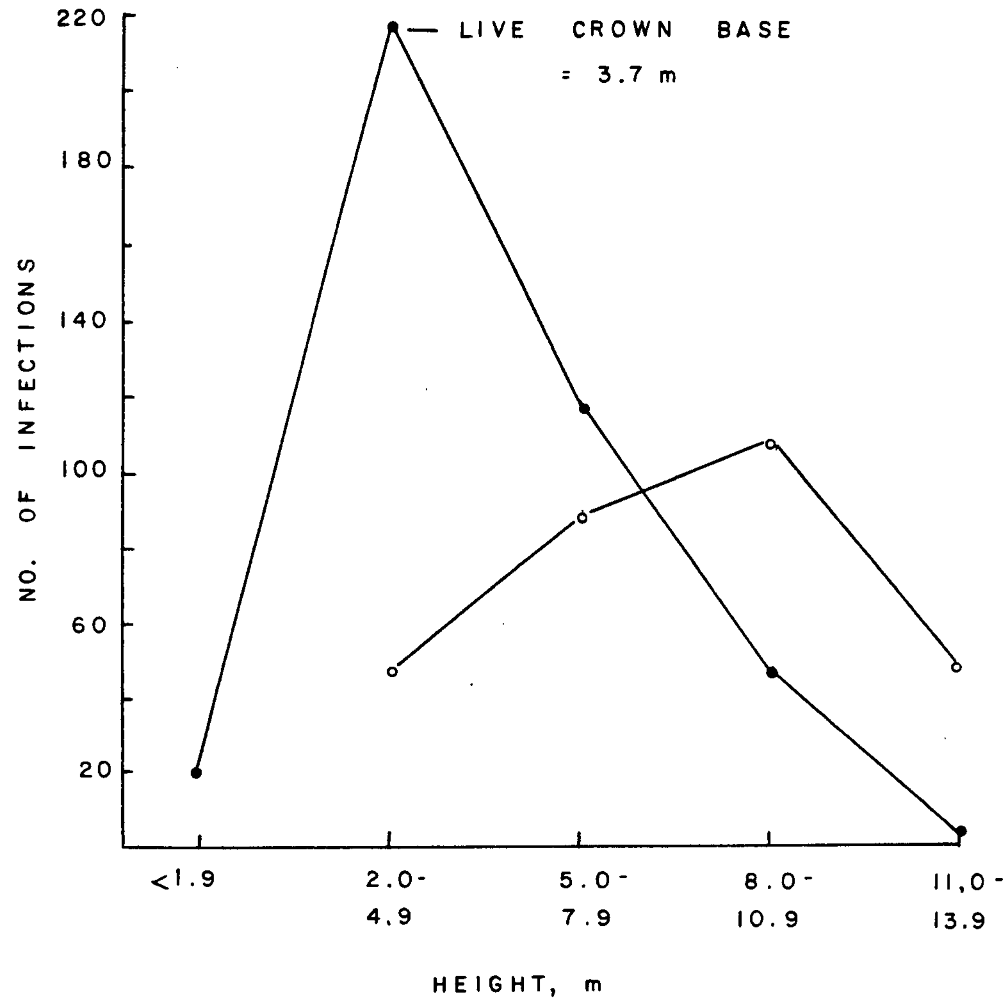

Figure 4. The number of live (o) and dead (.) dwarf mistletoe infections per plot versus infection height above ground in three metre classes for the immature western hemlock stand.

appeared to be over 3 years old, they could not have been established after 1976.

The presence of dead infections, apparently from the period between 1962 to 1975, suggested intensification and mortality occurred concurrently. Therefore, Equation 1, based solely on the live infections, is not representative of the population development.

Infections established in 1974 and 1975 were probably alive in 1979 and if not alive, the infections would be too small to be observed and included in the 405 dead infections. Of the infections over 5 years old, some would have died and the remaining live infections would have decreased at a rate proportional to age.

If the number of infections established each year was constant, taking the number of infections found for 1975, which was 38, and multiplying 38 by 14 (the length of the study period 1962 - 1975), the number of infections expected to have been established in the study period would be 532. Therefore, accepting 643 (238 live + 405 dead) infections as the number established between 1962 and 1975 the actual number of infections had increased very little. Based on the data, Equation 1 does not give the rate of intensification but it does give an indication of infection mortality. The expression:

$$t_{1/2} = \frac{\log 2}{b}$$

gives a half-life of infections for the immature stand of 4.8 years (Table 3).

The mature stand data were then compared to the immature stand data (see Table 1). The mature stand had fewer dead and more live infections than the immature stand. Fewer dead infections could be a result of the

Table 3. Comparison of equations, infection totals and doubling times for the immature and mature dwarf mistletoe infected western hemlock stands during the 1962-1975 period.

Stand	Equation	$\hat{r}$*	$\hat{S}y.x$*	Infection Total	Doubling Time
Immature (1-14 years)	Log Y = -.3826 - .06212X	.975	3.26	238	4.8
Mature (1-14 years)	Log Y = -.8291 - .06864X	.925	4.17	200	4.4

* "Because the standard error of estimate determined from the residual mean square of a logarithmic equation cannot be transformed back to an arithmetic scale without bias, the standard errors of estimate ($\hat{S}y.x$) of all logarithimic equations were calculated from observed and estimated values of the dependent variable:

$$\hat{S}y.x = \pm \sqrt{\frac{\Sigma(y-\hat{y})^2}{n-m-1}}$$

where y and $\hat{y}$ = observed and estimated values of the dependent variable
n = number of observations
m = number of independent variables

Similarly, an estimated coefficient of determination ($\hat{r}^2$) was obtained directly from:

$$\hat{r}^2 = \frac{\text{SS total} - \hat{\text{SS}}\text{ residual}}{\text{SS total}}$$

where SS total = sum of square of untransformed Y
SS residual = $\Sigma(y-\hat{y})^2$."[1]

1. Johnstone 1976, pp. 5-7.

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greater effect of wind pruning of dead branches in older, taller stands. More live infections were found in the mature stand as a reflection of the increase in infections over time.

The similarity of Figures 2 and 3 prompted further examination. The transformation of the number of infections (1-14 years) for the mature stand to an area basis allowed for direct comparison (Figure 5). The logarithmic transformation of the number of infections corrected for plot area (m^2) preceded regression analyses of the data (Table 4). The equations for the immature and mature stands (1-14 years) were very similar. The similarity prompted further analysis of the two sets of data. Table 4 presents the results of F-tests for differences of slopes and levels of regression. No significant difference was found between the slopes but the levels of regression were significantly different. Therefore 1 equation could not describe the 2 stands, but 1 doubling time can be used for both stands (Figure 5).

A steady decrease was observed for the 15-60 year period followed by a faster rate of infection loss to only 1 93-year old infection. Sixty year old plus infections were on leafless branch stubs below the live crown (see Figure 6). Presumably, many additional infections from the 60 year old plus infections were lost through branch senescence.

Accepting the first 14 years of data to represent mortality and that following the initial period of mortality the population was relatively stable up to the 60th year, the rate of intensification could be estimated for the 1-60 year period. A logarithmic equation:

$$\log Y = 1.0534 - .01221X \qquad (2)$$

$$\hat{r}^* = .648 \quad \hat{S}y.x^* = 7.62$$

produced a doubling time of 24.0 years.

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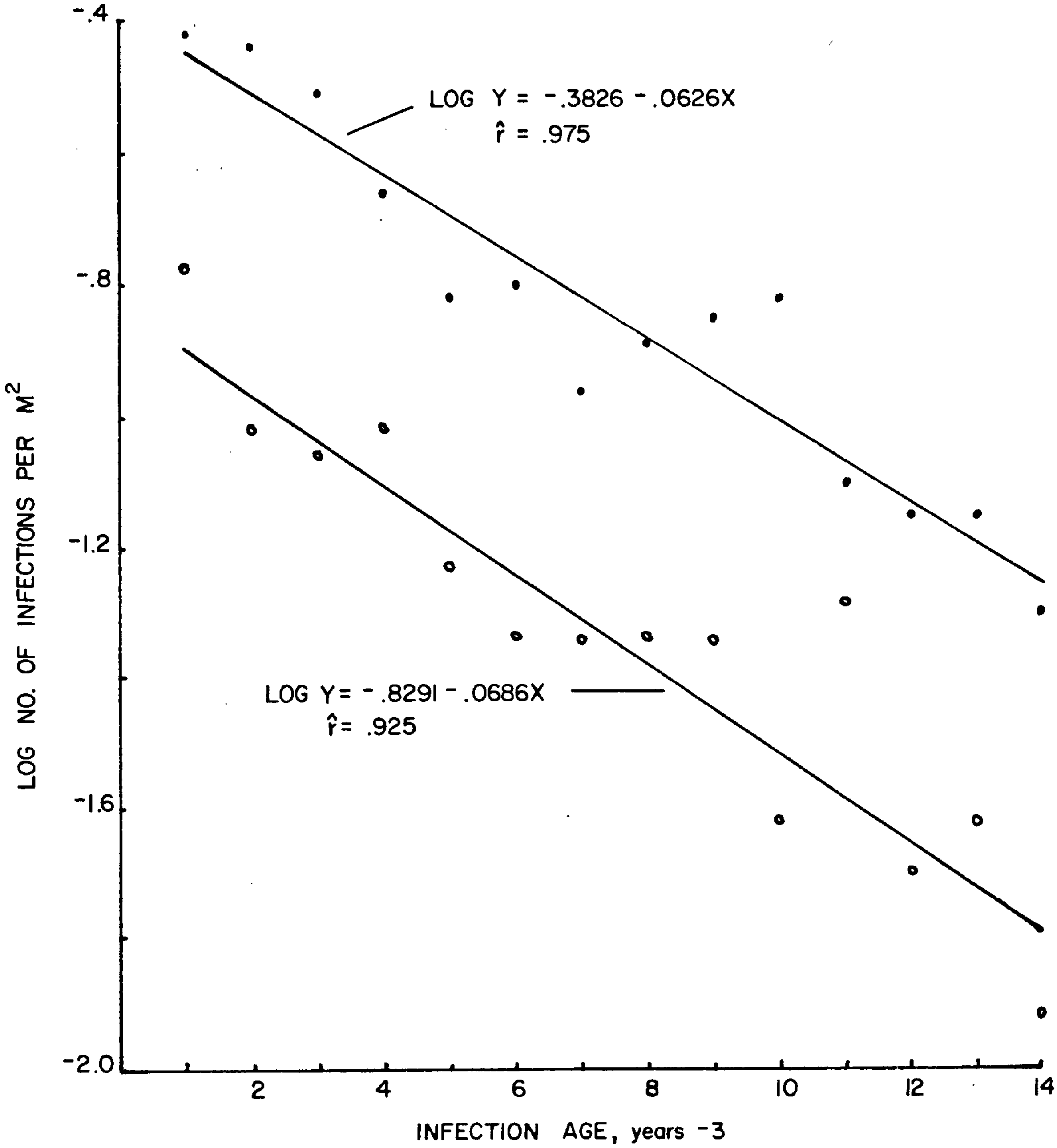

Figure 5. The log of the number of dwarf mistletoe infections per metre squared of plot area for the immature (.) and mature (o) western hemlock stands versus infection age for the 1962-1975 period (-3 years).

Table 4. Group regression analyses of the intensification rate of dwarf mistletoe in the immature and mature dwarf mistletoe infected western hemlock stands during the 1962-1975 period (Appendix III).

	Stands	
	Immature	Mature
Intercept	.41434	.14822
Regression coefficient	-.06212	-.06854
F-test of difference in slope	.42027 N.S.	
F-test of levels of regression	6.09334*	

N.S. not significant

* significant at the .05 probability level

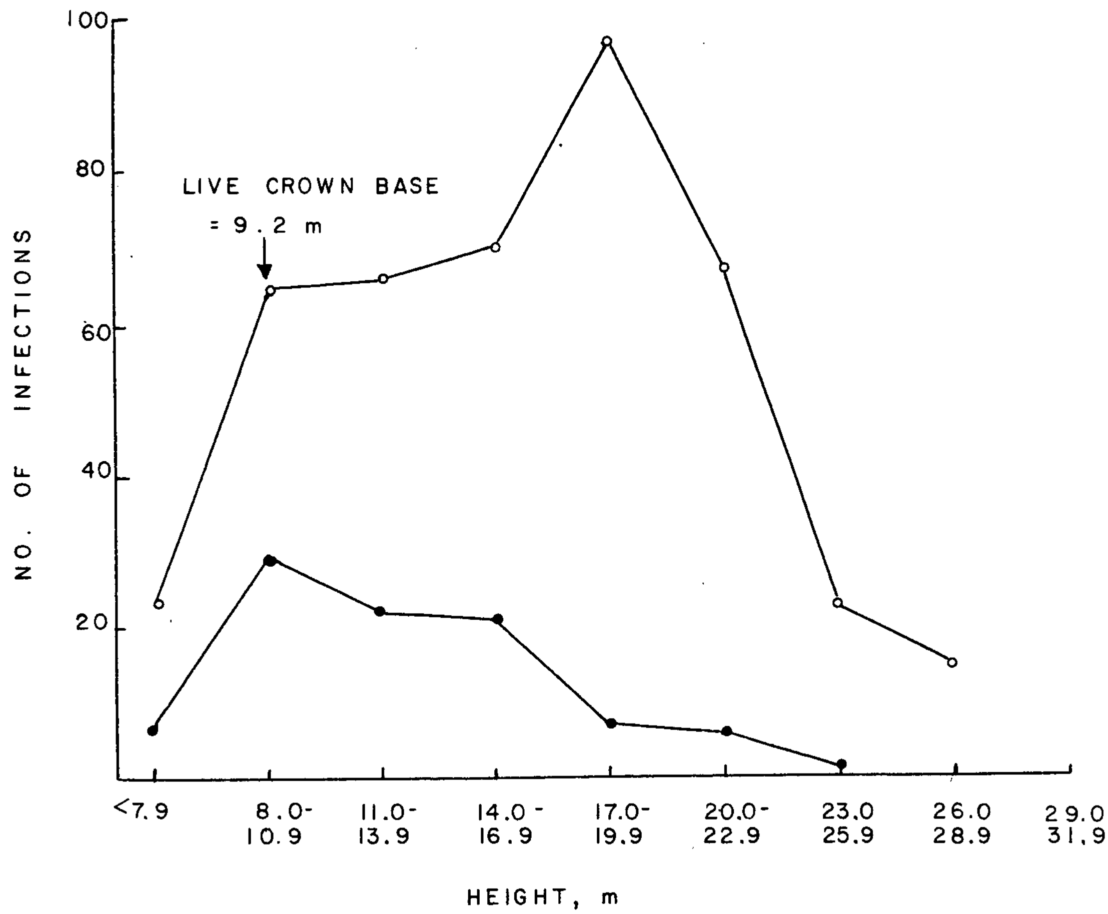

Figure 6. The number of live (o) and dead (.) dwarf mistletoe infections per plot *versus* infection height above ground in three metre classes for the mature western hemlock stand.

Infections that occur on young high order branches are expected to be lost early (before 10 years) due to branch senescence. Infections established on major branch axes are likely to become brooms and survive for a long period of time. As there are more high order fine branches than major axes, if one infection is established on each small branch and on each axis, the result is a rapid decrease in the numbers of infections for any year until the fine branch infections are mostly gone and only infections at major axes remain. Therefore, the oldest infections are found on major branch axes.

If the decrease in infections with time is due solely to mortality then Figure 2 represents a lifetable from which an equation can be developed to describe the probability of an infection surviving another year. The equation developed was:

$$P_{survival} = 1 - \frac{1}{(age-3)^{1.12} + 2} \qquad (3)$$

Equation 2 describes the situation represented by Figure 2 as well as the probability of survival increases as a function of infection age.

Equation 3 can be used to derive a distribution of numbers of infection over infection age as follows:

Starting with 100 infections at age 4, the number of infections at age 5 would be:

$$n = 100 \text{ X } \left[1 - \frac{1}{(1)^{1.12} + 2}\right] = 66.67$$

and at age 6:

$$n = 66.67 \text{ X } \left[1 - \frac{1}{(2)^{1.12} + 2}\right] = 50.69$$

. . . etc.

The sum of the number of infections from age 1 to 60 is 940.77. The actual number of infections observed between 1 and 60 was 379. The predicted number of infections is determined by dividing the observed infection total

(379) by the trial number total 940.77 and multiplying the dividend by the original estimate. For example, the predicted number of 1 year old infections is:

$$100 \times \frac{379}{940.77} = 40.29$$

and the 2 year old infections:

$$66.67 \times \frac{379}{940.77} = 26.86 \ldots \text{etc.}$$

In comparison equation 3 is significantly better than 2 in describing the data of the mature stand (Table 5). This study indicates that the apparent increase in infection over time is actually a decrease due to mortality. Most of the mortality occurs by 14 years of age. While the doubling time cannot be derived directly, this study shows the method used by earlier studies to be inaccurate. A doubling time of 40 or more years is suggested by this study. The 40 years plus doubling time is confirmed by the increase in infections per tree from the young (46.3) to the old (83.6) stand. A doubling time of 4 or 5 years should have resulted in the per tree infection total many orders of magnitude greater than observed. There is also a decrease in the infections per metre squared of 2.78 to 1.64 from the immature stand to the mature stand. The model developed by Bloomberg et al (1980) produces doubling times of 2 to 4 years. While the model does use a mortality equation developed by Smith (1977), the equation was recommended not be extrapolated beyond 12 years. The model should not be used until research can develop doubling times accurately by including infection mortality.

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Table 5. Comparison of logarithmic and probability equations for the prediction of numbers of dwarf mistletoe infections in the mature dwarf mistletoe infected western hemlock stand.

	Equation	d.f.	Residual sums of squares	Residual mean of squares	$F_{.05, 60, 60} = 1.96$
(2)	Logarithmic	59	1,697.10	28.76	
(3)	Probability	59	248.74	4.22	
	F value				6.82

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3.2 Vertical Spread Rate of Dwarf Mistletoe

The rates of vertical spread were .49 (range 0 to 1.6) and .42 (range 0 to 1.2) metres per year for the immature and mature stands respectively (Figures 7 and 8).

The height growth rates were .54 and .30 metres per year for the immature and mature stands respectively. The growth rate of the immature stand was keeping ahead of the parasite and the mature stand was not keeping up (Figures 7 and 8).

Projecting the vertical spread rate for the immature stand (.49 metres per year) for 86 years (to reach the age of the mature stand) the infection level is predicted to be 42.14 metres, considerably higher than the observed level of 25.4 metres and the height of the mature stand (38.1 metres). It appears that infection mortality has affected the vertical spread rate. If older infections experienced mortality throughout the vertical range of normally distributed infections in the crown, the highest and lowest older infections have likely been lost while all the younger infections are likely still present. Therefore, the estimate of vertical spread is from the centre of the range of older infections to the top of the vertical range of the latest infections. The data was re-examined. The height of the highest average infection was divided by the stand age (Table 2) and produced vertical spread rates of .28 (immature stand) and .19 metres per year (mature stand). Alternatively, for the infection level of the immature stand to reach the level of the mature stand the rate could be only .15 metres per year (difference between the infection levels of the two stands, 12 metres, divided by the age difference of the stands, 86 years).

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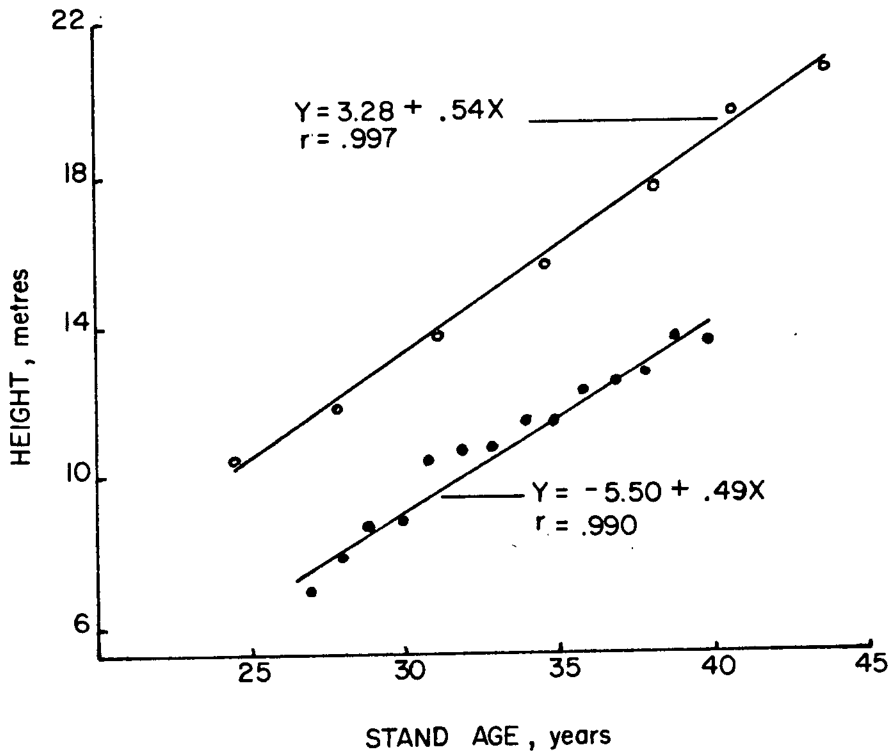

Figure 7. The average host height (o) and the height of the advancing front of the parasite (.) *versus* stand age in the immature western hemlock stand.

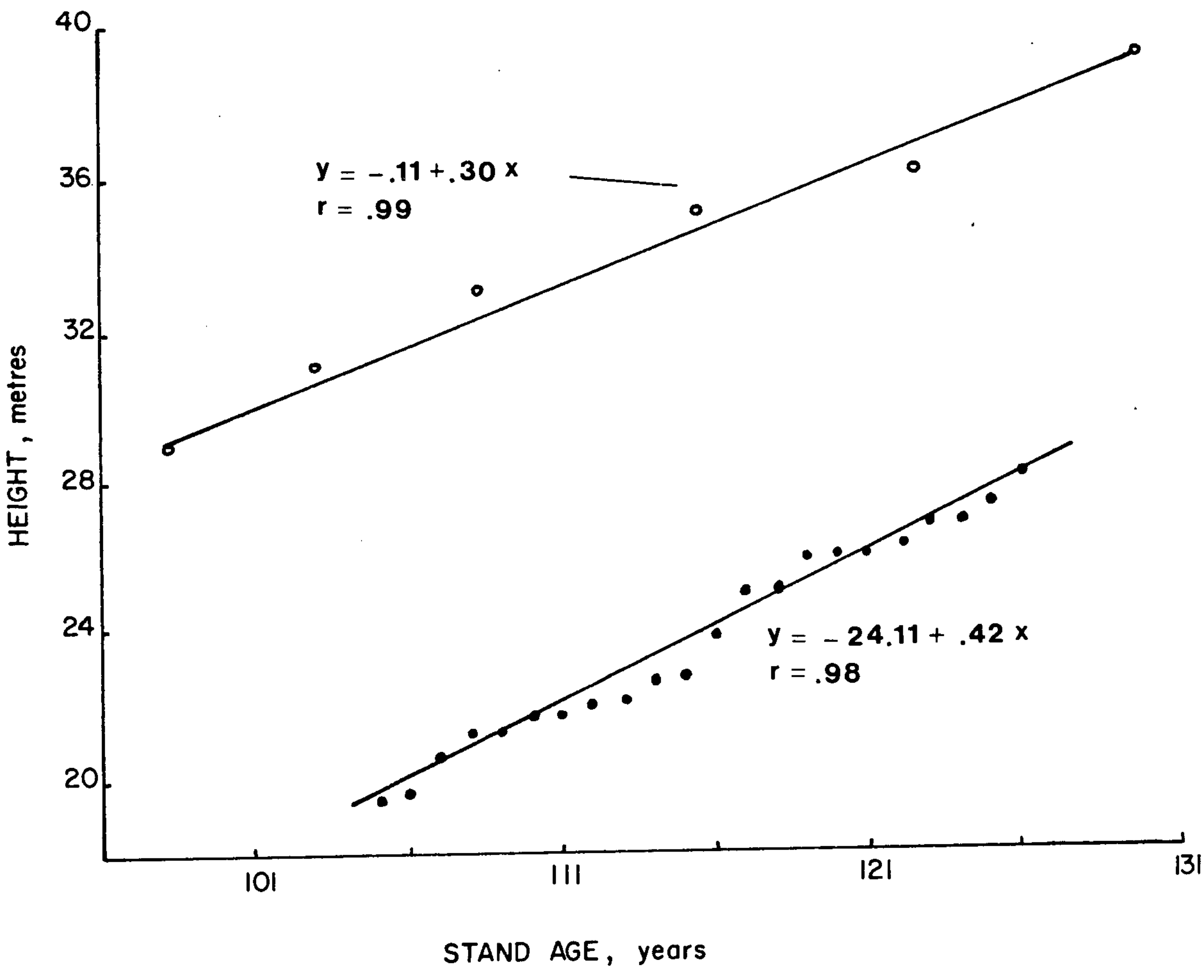

Figure 8. The average host height (o) and the height of the advancing front of the parasite (.) versus stand age in the mature western hemlock stand.

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3.3 Male:Female Infection Ratio Determination

The male:female ratios were 1:0.8 or (18:14), and 1:1.2 or (88:107) for the immature and mature stands respectively. For both stands the ratios are not significantly different from an equal distribution of the sexes. The 1:1 distribution supports previous studies (Hawksworth 1978).

4.0 CONCLUSIONS

The intensification and vertical spread rates of dwarf mistletoe were examined in 2 stands of western hemlock. The 2 stands were of different age but similar in site and infection history. The standard method of estimating intensification and vertical spread rates, based on the apparent number of infections established each year over a period of 10 or more years prior to the sample collection date, as used by Muir (1963) and Richardson and van der Kamp (1972), was shown to be inappropriate. Infection mortality, ignored in the standard method, was shown to be very important in the prediction of vertical spread and intensification rates of the parasite. Infection mortality is important because the loss of infections over time prevents the accurate determination of intensification and vertical spread rates. Infection mortality produces a decrease in numbers of infections over time. Additionally, if the same number of infections is established each year then intensification, as determined by the standard method, is more correctly an example of infection half-life. The real doubling time, while not directly determined, is over 40 years.

Infection mortality also affects the vertical spread rate calculation by reducing the number of older infections. Therefore, assuming the older infections experienced mortality throughout the vertical range of normally distributed infections in the crowns, the highest and lowest older infections have likely been lost while all the younger infections are likely still present. Therefore, the estimate of vertical spread is from the centre of older infection vertical ranges to the top of the latest infection vertical ranges. The data, while not directly determining the

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rate, suggested the vertical spread rate to be approximately .15 metres per year.

The implication of the study is that on sites where western hemlock grows faster than 45 centimetres per year, and where no overhead infection sources are present, infected small residuals (less than 2 metres) can be kept and infected immature stands can be spaced. The number of new infections will increase initially but will decrease again when crown closure occurs.

This work indicated continued study is required to obtain a more accurate estimate of infection mortality for computer models to avoid unjustified management decisions being made with respect to western hemlock dwarf mistletoe control in coastal British Columbian forests.

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APPENDIX I

Immature Stand Data

Infection Age	Number of Infections
1	1
2	15
3	20
4	38
5	36
6	31
7	22
8	15
9	16
10	11
11	13
12	14
13	15
14	8
15	7
16	7
17	5
18	1
19	1
20	1
21	1

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APPENDIX II

Mature Stand Data

Infection Age	Number of Infections	Infection Age	Number of Infections	Infection Age	Number of Infections
1	1	26	4	51	4
2	5	27	5	53	2
3	23	28	7	54	3
4	42	29	3	55	3
5	24	30	7	56	4
6	22	31	5	57	3
7	24	32	3	59	3
8	14	33	8	60	4
9	11	34	4	61	3
10	10	35	4	62	3
11	11	36	2	63	3
12	9	37	6	64	2
13	6	38	3	65	2
14	13	39	4	66	3
15	5	40	4	67	2
16	6	41	4	69	1
17	3	42	4	72	2
18	5	43	3	75	2
19	3	44	5	77	1
20	4	45	1	93	1
21	4	46	5		
22	8	47	2		
23	8	48	3		
24	3	49	2		
25	5	50	6		

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APPENDIX III

Group Regression Analyses (Freese 1967)

						RESIDUALS			
Line	Group	df	y^2	xy	x^2	df	SS	MS	F
1	Immature	13	.97105	-14.13348	227.5	12	.09300		
2	Mature	13	1.25635	-15.61861	227.5	12	.18408		
3				Pooled residuals		24	.27708	.01154	
4	Difference for testing common slopes					1	.00485	.00485	.42028 N.S.
5	Common slope	26	2.22739	-29.75208	455.0	25	.28193	.01128	
6	Difference for testing common levels					1	1.71788	1.71788	*6.09334
7	Single regression	27	3.94527	-29.75204	455.0	26	1.99980		

	xy	y^2	x^2	Residual SS	MS
Immature	-14.1335	.9711	227.5	.0930	
Mature	-15.6186	1.2564	227.5	.1841	
Common slope	-29.7521	2.2274	455.0	.2771	.0115

	Immature		Mature	
n	= 14			
Y	= -11.54390	+	-18.81557	= -30.69568
Y^2	= 26.54390	+	11.05226	= 37.59616
X	= 105	+	105	= 210
X^2	= 1,015	+	1,015	= 2,030
XY	= -103.23428	+	-156.73540	= -259.96968