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# Canopy Light and the Distribution of Hemlock Dwarf Mistletoe (*Arceuthobium tsugense* [Rosendahl] G.N. Jones subsp. *tsugense*) Aerial Shoots in an Old-growth Douglas-fir/Western Hemlock Forest

## Abstract

Hemispherical photography was used to quantify the relationship between canopy light and the distribution of hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones subsp. *tsugense*) aerial shoots in an old-growth Douglas-fir/western hemlock forest to determine if aerial shoots only occur in higher light environments in the upper canopy. The Wind River Canopy Crane provided three-dimensional access by lowering a gondola into gaps between trees and stopping at 5 m intervals and sampling all trees around the gap at that height. A total of 89 dwarf mistletoe infections in live branches were sampled on 14 trees from 18 to 60 m. Forty-one infections had no aerial shoots whereas 48 had aerial shoots. All infections above 50 m had shoots, while all infections below 30 m (except one) had none. There were no aerial shoots at infections exposed to estimated insolation (yearly insolation = diffuse light * indirect site factor + direct light * direct site factor) of 1,000 MJ $m^{-2}yr^{-1}$, while all infections above 3,200 MJ $m^{-2}yr^{-1}$ had aerial shoots. Height and light were highly correlated but between 30 and 50 m the light environment became especially heterogeneous, with a 50% probability of aerial shoots occurring at 40 m, or at 2,200 MJ $m^{-2}yr^{-1}$. A complex of biotic and abiotic factors may account for the correlation of high light and aerial shoot occurrence in the field because laboratory studies have shown dwarf mistletoe produces the most aerial shoots in low light and high temperature. In this tall, multi-layered canopy, the source of the seed rain from western hemlock dwarf mistletoe was above the bulk of the western hemlock foliage, perhaps another explanation for the fast spread and intensification of mistletoe in old-growth forests.

## Introduction

Dwarf mistletoes (*Arceuthobium* species, Viscaceae) are flowering plants that parasitize conifers, primarily members of the Pinaceae (Hawksworth and Wiens 1996). These perennial, dioecious parasites are endophytic within branches of the host tree. Infected branches often become swollen and with age may become deformed and highly branched. Aerial shoots appear within 2-7 years of infection and the female plant may produce single seeded fruit, which explosively discharges the seed (Smith 1971, Hawksworth and Wiens 1996, Mathiasen 1996). Although dwarf mistletoes are well studied, there is still much to know about their response to physical factors such as light, temperature, and humidity. These physical factors vary with height in forest stands and individual tree crowns (Parker 1995) and may affect several aspects of the life cycle of the mistletoe plant including; seed dispersal, seed germination, haustorium development, early growth of the endophyte, aerial shoot production, flowering, and pollination (Wagener 1961, Beckman 1964, Scharpf 1970, 1972, Wicker 1974, Knutson 1984, Hawksworth and Wiens 1996).

The influence of light on dwarf mistletoes has attracted limited study. Because partial thinning appears to favor rapid intensification of dwarf mistletoe, Weir (1916) suggested that dwarf mistletoes benefit from high light levels. Wagener (1961) has questioned this conclusion and demonstrated greater production under partial light than higher levels. Dwarf mistletoes may depend on light for seed germination (Wagener 1961, Beckman 1964, Scharpf 1970, Knutson 1984, Hawksworth and Wiens 1996), early growth of the plant (Wagener 1961, Scharpf 1972, Knutson 1984), and aerial shoot production (Knutson 1984) and light levels may be too low in some parts of the canopy for successful completion of the plant life cycle.

Knutson (1984) conducted 2 greenhouse experiments on several species of *Arceuthobium* to examine the influence of light and temperature on aerial shoot production. Mistletoe infected seedlings were exposed to various light and temperature regimes, and the development of the aerial shoots was observed under three levels of shading. The greatest number of aerial shoots was produced in low shade, but greatest cumulative length of aerial shoots was produced at low to medium shade. In a second experiment two light levels and three temperature regimes were used. The best development of aerial shoots was produced under high temperature and the lower light regime, leading Knutson to conclude that the effect of light seems indirect.

In a study at the Wind River Canopy Crane Research Facility, southern Cascade Mountains of Washington State, on adult sex ratio of hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones subsp. *tsugense*) Mathiasen and Shaw (1998) sampled 239 branches for mistletoe infections along the vertical axes of six western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) trees. Below 20 m in height, 53% of the infections did not have aerial shoots, while above 45 m, only 3% did not have aerial shoots. These data from Wind River suggested that there is a strong vertical gradient, along which production of aerial shoots from dwarf mistletoe infections increased with height. This supports observations by Smith (1969) that the quantity and vigor of shoots increased with increasing height in coastal western hemlock forests of British Columbia, Canada. Smith suggested that low light levels are responsible for reducing shoot production from infections in the lower canopy.

Plants higher in the canopy may not necessarily be receiving more light because light is heterogeneously distributed in time and space. To determine whether this is so, measurements or estimates of the forest light environment at each plant are necessary. This requires a means for reaching each plant and for quantifying the light environment in a meaningful way. Hemispherical photography provides a method for rigorously quantifying light environments in complex forest canopies (Anderson 1964, Rich 1990). From a single photograph of an evergreen forest, it is possible to measure overall canopy openness and openness along the sun track through the entire year. These measures of canopy structure can be directly transformed into relative amount of light, or absolute amounts if radiation data are available.

Hemispherical photography has been used to map fine scale horizontal variation in forest light environments (Becker and Smith 1989, Clark et al. 1996) but complete vertical access has proven problematic except in short forests (Lerdau at al. 1992). The Wind River Canopy Crane, a 75 m tall construction crane placed in an old-growth forest reserve to function as a canopy observatory, has been particularly useful in the study of dwarf mistletoes (Mathiasen and Shaw 1998, Shaw et al. 2000). The three-dimensional access provided by the Wind River Canopy Crane allows for sampling of numerous mistletoe infections even in the tops and outer canopy of 50 m tall trees. This canopy access technology is particularly suited for using hemispherical photography.

The objective of this study was to determine whether the observed vertical occurrence of aerial shoot production was related to the light environment associated with individual mistletoe infections. Hemispherical photographs allow several measures of the light environment in the forest canopy to be used to build predictive models of the presence/absence of aerial shoots. The results are then discussed with regard to the relative effectiveness of predictor variables, and some potential mechanisms and consequences of those relationships.

## Study Site

The study site is located at the Wind River Canopy Crane Research Facility (Parker 1997) in the T.T. Munger Research Natural Area (Franklin and DeBell 1988), Wind River Experimental Forest, southern Cascade Mountains, Washington State (Latitude 45° 49' 13.76", Longitude 121° 57' 06.88") at an elevation of 355 m. A weather station was located 2 km south of the crane site at the now defunct Wind River Ranger Station, raw data was obtained from National Climate Data Center (1994) for the period 1931-1977. Annual precipitation was 2,467 mm, and is strongly seasonally distributed with summer precipitation averaging ~5% of the annual total. Average annual snowfall was 180 cm. Mean annual daily minimum temperature was 0.5°C, while mean annual maximum daily temperature was 12.3°C.

The forest is a tall stature Douglas-fir (*Pseudotsuga mensiezii* (Mirb.) Franco), western hemlock, and western redcedar (*Thuja plicata* Donn.) dominated stand with Douglas-fir reaching 65 m (average ht 52.2 m) and western hemlock reaching 55m (average ht 19.0 m). Stand density is 435 stems/ha with a basal area of 82 $m^2$/ha (Harmon et al. 1998). The understory vegetation is dominated by vine maple (*Acer circinatum* Pursh), salal (*Gaultheria shallon* Pursh), and Oregon grape (*Berberis nervosa* Pursh), while the site is classified on the border of Western Hemlock/Oregon grape-Salal/Western Hemlock/Salal Plant Association complex and Pacific Silver Fir (*Abies amabilis* (Dougl) Forbes)/Salal Plant Associations (Meyer and Fredricks 1993). Soils are deep and well drained, derived from volcanic ejecta (Franklin 1972), and tentatively classified as medial, mesic Entic Vitrands (J. Klopatek, personal communication).

The light environment of this forest has been characterized by Parker (1997) and reflects the vertical structure of the forest, which is bottom heavy. He divided the canopy into three vertical zones: 1) a bright zone above 40 m in height where the light is 90% or more of available incoming light. 2) a transition zone from 40 m to about 8 m where available light drops steeply to about 10% of the incoming. 3) a dim zone below 8 m where light is less than 10% of the above canopy incoming. Western hemlock dominates the foliated portion of the canopy from 15 to 35 m, whereas western hemlock and Douglas-fir codominate the foliated canopy from 35 to 45 m, and Douglas-fir dominates above 45 m, with 80% of the stand foliage below 40 m (Parker 1997, Song 1998, Van Pelt and North 1999).

## Methods

### Infection Sampling

Infections were surveyed and sampled on 4 and 5 June 1998. Completely random sampling was not feasible given constraints on crane operations. A modified point-centered system was used. The gondola was placed over a gap between infected hemlock trees. At 5 m height intervals, the nearest infection on each tree was sampled. A total of 87 mistletoe infections on 14 trees were sampled, and heights ranged from 18 to 60 m. Sampling was restricted to mistletoe infections on live branches, implying the plant associated with the infection would also still be alive.

Mistletoe aerial shoot status was scored on a 0-3 scale. 0 meant no visible aerial shoots, 1 meant small poorly developed shoots <1 cm length, 2 meant many shoots, and 3 meant numerous robust shoots. For analysis purposes in logistic regression, 0-1 were considered "No Shoots", and 2-3 were considered "Shoots."

### Hemispherical Photography

Hemispherical photographs were taken with standard procedures described in Rich (1989, 1990). Photos were taken through a Nikkor 8mm lens attached to a self-leveling platform (gimbals) on a monopod. Kodak TriX PAN 400 ASA black and white film was used. The gondola was maneuvered within reach of the chosen mistletoe infection and the camera assembly placed above the branch within 0.3 ms of the infection. A self-timer allowed the camera to steady at a level position, and the photograph was taken. Crane azimuth, hook height, and jib distance were recorded. Most photos were taken under dawn and overcast conditions, which allowed for acquisition of high quality images in which sky and foliage were well differentiated.

Photographs were analyzed with the program CANOPY 2.1 (Rich 1989), using standard procedures. Because the steel cage of the gondola precluded accurate compass measurements to orient the photos to true north, the azimuth of the crane jib was used for orientation. Following orientation of the negative to true north, the editing capabilities of CANOPY were used to remove the jib, cables, and other components of the crane and gondola. All photos were analyzed by one person (SBW).

### Determination of the Light Environment

Standard "site factors" were calculated. Indirect Site Factor (ISF) is the proportion of sky visible from the photo point, and measures the penetration of diffuse radiation through the forest canopy. Direct Site Factor (DSF) is the proportion of the sunpath not obscured by foliage, weighted by a function of solar elevation angle to account for atmospheric transmissivity. Both ISF and DSF can be cosine corrected to a horizontal surface. In practice, cosine corrected and uncorrected site factors are highly correlated, and both were used in the initial analysis to find the best predictors of mistletoe shoot production.

Site factors can be converted into an estimate of total yearly (or monthly) radiation, if measures of direct and diffuse insolation are available (Rich et al. 1993). Shortwave insolation has been measured at Portland, Oregon, approximately 65 km east southeast from the study site (National Renewable Energy Laboratory 1999). Insolation at the study site may differ slightly from that in Portland. The mean insolation for the year was calculated as a weighted sum of ISF and DSF:

1) Insolation = Dif*ISF + Dir*DSF

Yearly direct and diffuse shortwave insolation on a horizontal surface at Portland were 1779 and 1783 MJ $m^{-2}yr^{-1}$, respectively, and daily mean normal beam radiation was 4815 W $m^{-2}d^{-1}$. Global site factor for a horizontal collector (GSFC), therefore, is an equal weighting of ISFC and DSFC, while GSFU (uncorrected) is more heavily weighted by DSFU.

### Statistical Analysis

Presence/absence of aerial shoots (dependent variable) was analyzed using logistic regression in JMP v. 3.0 (SAS Institute, 1995), with single predictor variables (Height, ISFC, ISFU, DSFC, DSFU, Mean yearly insolation) and goodness of fit ($r^2$) was used to compare the predictors. Logistic regression is a widely used technique for predicting presence-absence data from continuous independent variables (ter Braak and Looman 1995). Box plots were used for graphical comparisons.

## Results

Four hemispherical photographs show key features of the forest light environment (Figure 1a-d). North is indicated by the N, and all sunpaths at this latitude are in the southern portion of the sky. The crane jib is clearly visible in the bottom three photos and provides azimuth orientation. Photo 1a is of a typically dark area below 30 m, where few plants produce shoots. Photo 1b was taken higher in the canopy on the north-side of a large tree, but DSF is relatively low because much of the yearly sunpath is blocked by foliage to the south. Photo 1c was taken on the south side of a large tree at 30 m, and shows a combination of low height and high insolation, because of high DSF. Photo 1d was taken at 46.7 m on the north side of a large tree with closely spaced tall neighboring trees.

A total of 89 infections were sampled: 41 had no aerial shoots (score 0 or 1), and 48 had substantial numbers of shoots (score 2 or 3). Mistletoe shoot production was significantly related to many predictor variables (Table 1). Height alone explained 42% of the variation in the logistic regression, with higher infections far more likely to have shoots than lower infections. All measures of the light environment from photographs explained more variance than height alone. The best single predictor was Insolation U (uncorrected), which explained 49% of the variation in shoot status. No significantly better results were obtained using multiple predictors such as monthly DSFs. Uncorrected site factors were slightly better than corrected, so all analyses and discussion will from now on consider uncorrected values.

The box plots show the overall distribution of height, ISF, DSF, and Insolation for plants with (score 2-3) and without (score 0-1) shoots (Figure 2). There is some overlap in all variables, but the good separation that visually confirms the results of the logistic regression (Table 1).

The relationships between height, insolation and mistletoe shoots are seen in detail in Figure 3. All infections above 50 m had shoots, and only one infection had shoots below 30 m. On the insolation scale, all infections with annual insolation above 3200 MJ $m^{-2}$ $yr^{-1}$ had shoots, and all infections with annual insolation below 1000 MJ $m^{-2}$ $yr^{-1}$ had none. From the logistic regression, the 50% probability of shoots is at 40 m, or at 2200 MJ $m^{-2}$ $yr^{-1}$. Other probabilities are easily read off the logistic regression. In other forests, it may be easier to measure ISF and DSF, rather than using insolation data. Logistic regression parameters for ISF and DSF are presented in Table 1.

## Discussion

Light is directly related to height in the canopy crane research forest, although the standard deviation of the mean PAR transmittance is highest between 15-30 m indicating the heterogeneity of the mid canopy environment (Parker 1997). Height and light are both good predictors of aerial shoot occurrence in this forest. However, total insolation, uncorrected for a horizontal surface, was the best predictor variable for the occurrence of aerial shoots, although the improvement in predictive power was moderate (from $r^2 = 0.42$ for height to 0.49 for Insolation). Both ISF and DSF alone also predicted shoot production slightly better than height alone.

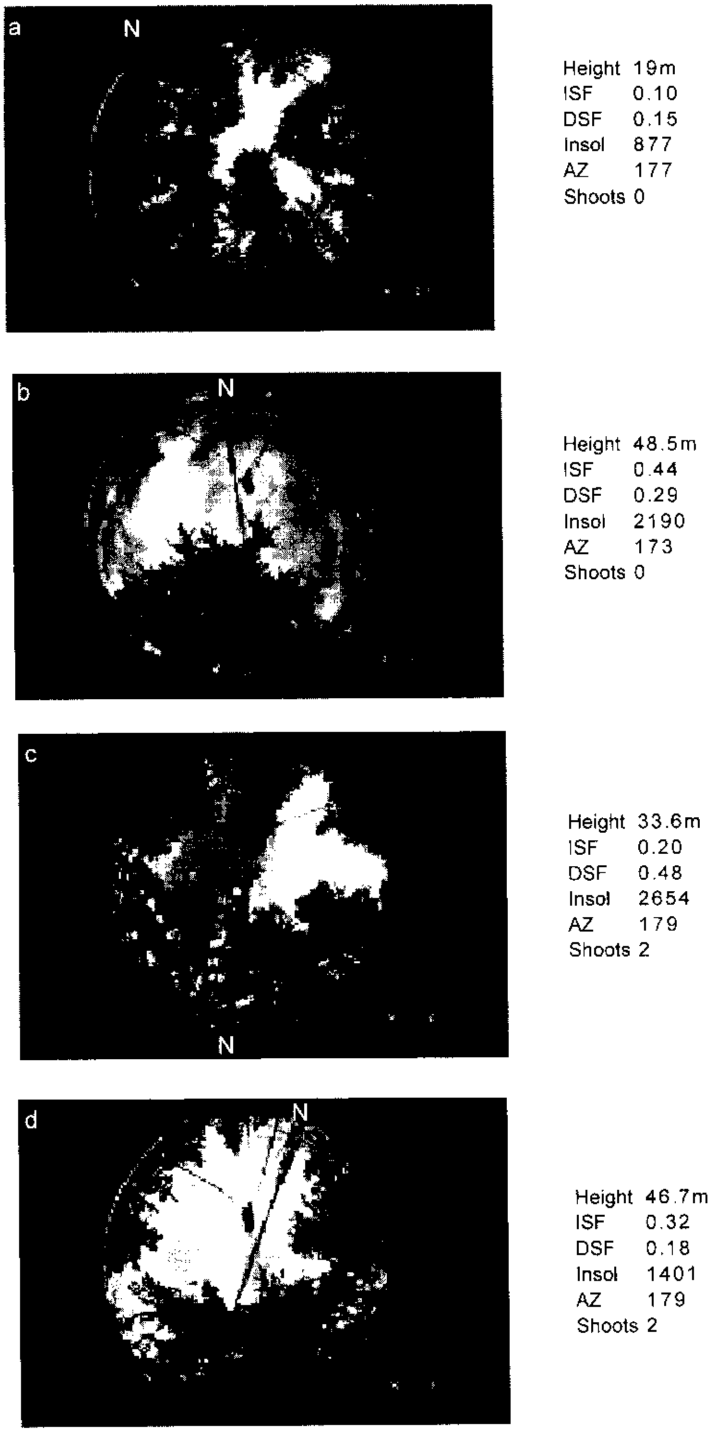


Figure 1. Four examples of photographs showing the range of conditions encountered in the study. North is indicated by the white "N". Note also that east and west are reversed on hemispherical photos taken directly upward. Height, ISF, DSF, Mean Daily Insolation, Crane Azimuth (AZ) and mistletoe score are shown next to each picture. See text for discussion of each photograph.

TABLE 1. Statistics of mistletoe predictor variables, the dependent variable is presence/absence of aerial shoots. Intercept (Int), regression coefficient (Coeff), and $r^2$ values are from nominal logistic regressions. All logistic regressions $P < 0.0001$.

| Predictor | Int | Coeff | $r^2$ | No Shoots | | Shoots | |
|---|---|---|---|---|---|---|---|
| | | | | Mean | s.d. | Mean | s.d. |
| Height | | | 0.42 | 32 | 6.7 | 47 | 9.0 |
| ISFU | 4.11 | -13.57 | 0.44 | 0.19 | 0.09 | 0.46 | 0.19 |
| ISFC | 4.80 | -11.37 | 0.44 | 0.29 | 0.11 | 0.59 | 0.20 |
| DSFU | 3.12 | -9.95 | 0.47 | 0.20 | 0.13 | 0.57 | 0.23 |
| DSFC | 3.54 | -8.92 | 0.45 | 0.22 | 0.15 | 0.59 | 0.23 |
| InsolationU | 4.01 | -0.00177 | 0.49 | 1290 | 745 | 3526 | 1418 |
| InsolationC | 4.74 | -0.0033 | 0.49 | 890 | 420 | 2077 | 723 |

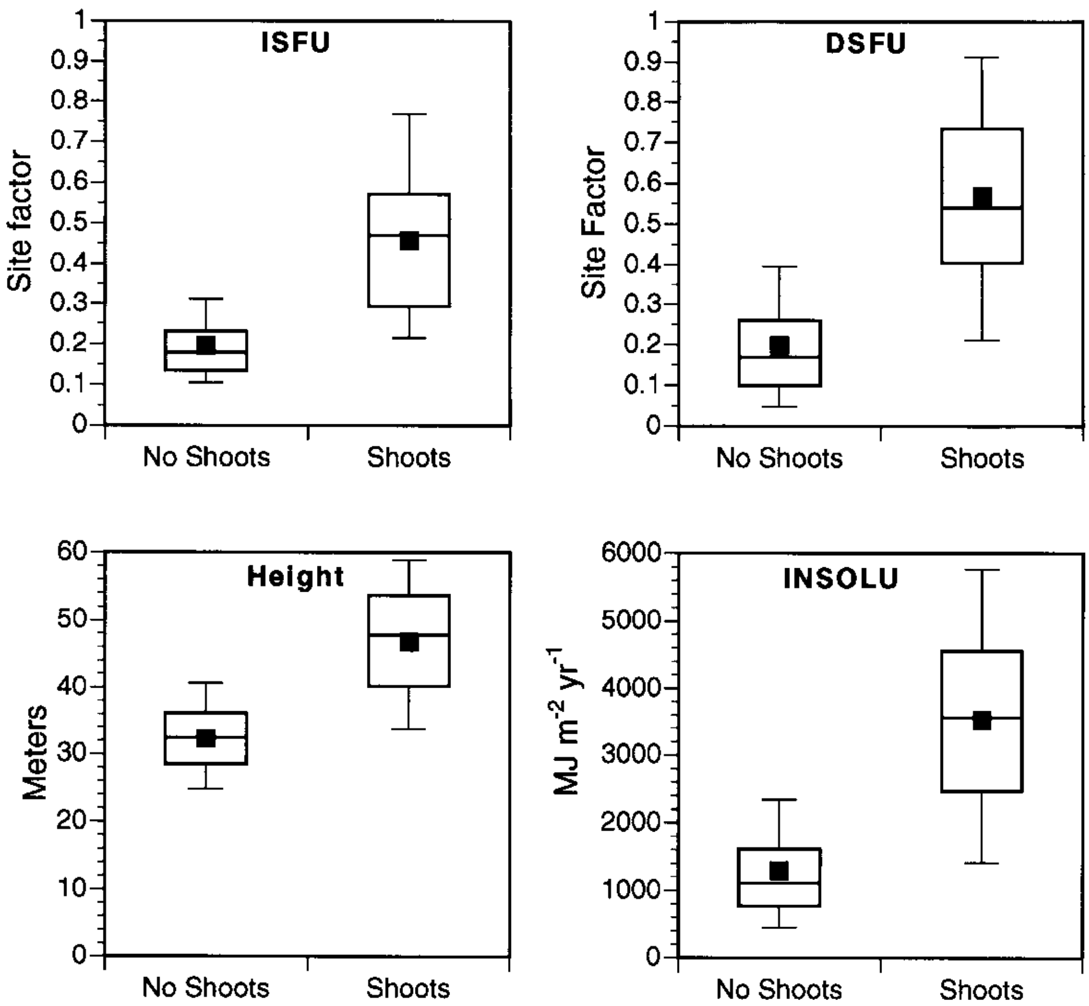


Figure 2. Box plots of predictor variables at 48 non-aerial shoot and 41 aerial shoot producing mistletoe infections. The square represents the mean, the middle line is the median, the outer lines of the box are the quartiles, and the outer bars are the 10th and 90th percentiles.

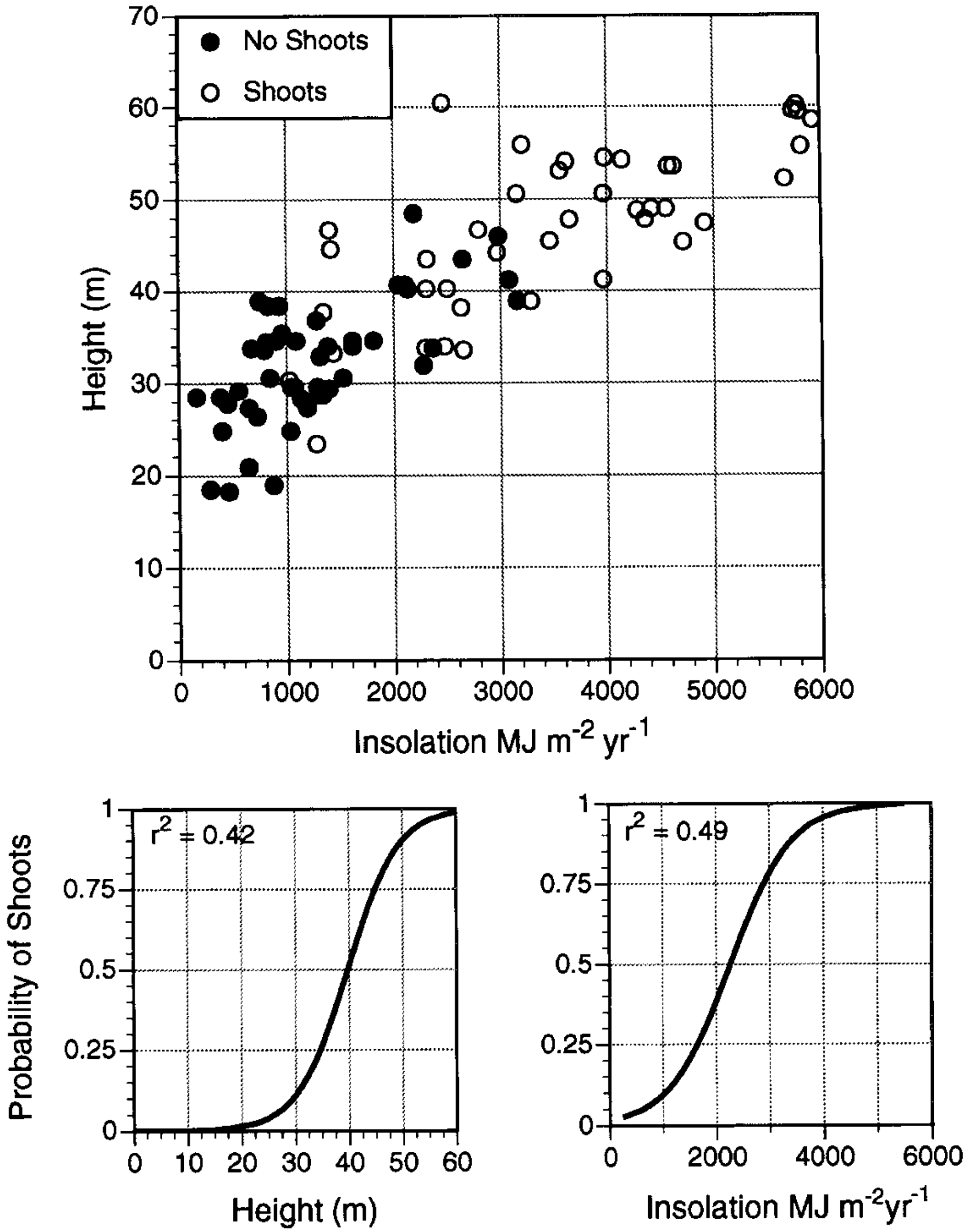


Figure 3. Insolation and Height plot showing the presence/absence of mistletoe shoots. Logistic regressions for Insolation and Height are shown below for parameters from Table 1.

Although ISF and DSF are highly correlated ($r^2 = 0.89$), some sites (the north sides of large trees at intermediate heights (50-30 m) have high ISF and low DSF (e.g. Figure 1b). Conversely, DSF is higher on the south sides of trees (i.e. Figure 1c). There is likely a horizontal patterning of shoot production as one progresses from the north to south-sides of trees, and this pattern should be strongest at heights around 40 m in this forest where the overlap of shoots/no shoots is strongest (Figs 2c and 3).

There appears to be a paradox in reference to aerial shoot occurrence in the upper canopy. Our results support Weir's (1916), Gill's (1935), Smith's (1969) and Hawksworth and Wiens' (1996) observations that *Arceuthobium* "shoots seem to respond in vigor and abundance directly to the amount of light" (Gill 1935, page 216). However, experimental greenhouse studies on various *Arceuthobium* species, including *A. tsugense*, show that some light is necessary for aerial shoot development, but high light levels are not (Wagener 1961, Scharpf 1970, 1972, Tocher et al. 1984, Knutson 1984). Wagener (1961) states that, "if high light intensity is beneficial to dwarf mistletoe it must be exerted indirectly through its effect on the host tree." Why then, do aerial shoots occur mostly in the higher light levels of the transition and bright light zones of this forest?

A complex of biotic and abiotic factors associated with the vertical structure of forest canopies must be interacting to result in the observed patterns of mistletoe aerial shoot production that correlates with light and height. Knutson (1984) has determined, in greenhouse studies, that a high temperature and low light treatment resulted in greatest aerial shoot production. Because the highest temperatures are attained in the mid and upper canopy (Geiger 1965, Fitzjarrald and Moore 1995, Parker 1995), this region of the canopy may have the most optimal microenvironments for aerial shoot production.

Host plant physiology, especially the productivity of the foliage on the infected branches, may also play an important role in aerial shoot occurrence because of the nutrient and carbohydrate demands of mistletoe shoot growth. The foliage in the upper canopy has higher photosynthetic capacity and nitrogen content than foliage in the lower canopy (Holbrook and Lund 1995, Kozlowski and Pallardy 1997). Therefore, the occurrence of aerial shoots in the mid and upper canopy may be related to the capacity of the branch to "feed" the parasite. Finally, the evolutionary adaptations associated with flowering, pollination and seed dispersal in open and therefore sunny micro-environments may lead to the occurrence of aerial shoots in the upper canopy of this tall stature old-growth forest.

### Implication for Spread and Intensification

Dwarf mistletoe reproduces by explosively discharged seed. Therefore, the composition and structure of the canopy in the immediate vicinity of the female plant has a controlling influence on the distance seed is dispersed, and whether the seed strikes host foliage or twigs (Scharpf and Parmeter 1976, Mathiasen 1996). Hemlock dwarf mistletoe aerial shoots occur mostly in the well-lit middle and upper canopy, above 30 m, with a 50% probability of aerial shoots occurring on a mistletoe infection at a height of 40 m, or at an annual insolation of 2,200 MJ $m^{-2}yr^{-1}$. The source of the seed rain from dwarf mistletoe plants is above the bulk of the hemlock foliage in a relatively open portion of the canopy, and this implies an ability to rapidly spread and intensify.

Dwarf mistletoe is known to spread and intensify most rapidly in multistoried canopies (Mathiasen 1996), and hemlock dwarf mistletoe is thought to spread rapidly in old-growth hemlock forests for this reason (Shea and Stewart 1972). The additional evidence that the seed source is primarily from the more open and well lit mid and upper canopy strengthens the conclusion that hemlock dwarf mistletoe is well adapted to complex structured old-growth canopy environments. Further research on the causes and consequences of the vertical organization of aerial shoot production in dwarf mistletoes will aid our understanding of mistletoe intensification and spread, especially in managed stands with long rotations or uneven-aged silviculture.

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