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A model of spread and intensification of dwarf mistletoe infection in young western hemlock stands

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The following relationships were quantified in a mathematical computer model to predict spread and intensification of dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G. N. Jones) infection, originating from residual trees, in regeneration of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.): distribution of dwarf mistletoe infections in residual source trees, dwarf mistletoe seed production, escape from crown and dispersal, interception of seeds by neighboring trees, distribution of seeds within crowns, development of dwarf mistletoe infections, mortality of plants, and tree crown growth. The model included options for thinning or sanitation by removal of infected residual or regeneration trees. Predictions by the model for a 10-year period did not differ significantly ($p = 0.05$) from results of a field plot with respect to average number of infections per tree, percentage of infections at 1-m distances from the residual tree, and percentage of infections in each quadrant centered on residual source tree. Predictions of the effects of stocking density and sanitation or thinning on infection agreed with results obtained from experiments with other tree species.

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On a quantifié les rapports suivants à l'aide d'un modèle mathématique par ordinatrice dans le but de prédire la dispersion et l'intensification de l'infection par le Faux-gui (*Arceuthobium tsugense* (Rosendahl) G. N. Jones) provenant d'arbres résiduels, dans une régénération de Pruche occidentale (*Tsuga heterophylla* (Raf.) Sarg.): distribution des infections par le Faux-gui chez les arbres résiduels d'origine, production de graines du Faux-gui, échappement de la cime et dispersion, interception des graines par les arbres avoisinants, distribution des graines à l'intérieur des cimes, développement des infections du Faux-gui, mortalité des semis et croissance de la cime. Le modèle comprenait aussi les effets de facteurs environnementaux sur l'infection, puis l'éclaircie et l'hygiène par enlèvement des arbres infectés. Les prédictions fournies par le modèle sur une période de 10 ans relativement au nombre moyen d'infections par arbre, le pourcentage d'infections à une distance de 1 m de l'arbre résiduel et dans chaque quadrant centré sur l'arbre résiduel d'origine n'ont que peu varié ($p = 0.05$) des résultats d'une placette sur le terrain. Les prédictions quant aux effets de l'infection sur la densité et l'hygiène du matériel sur pied, de même que l'éclaircie ont été conformes aux résultats obtenus d'expériences effectuées avec d'autres essences d'arbres.

Introduction

Hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G. N. Jones) is a damaging parasite of coastal western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) stands. Baranyay and Smith (1972) reported that infection spreads by explosive discharge of seeds from plants on source trees for distances of about 15 m. They recommended silvicultural control of the disease in immature stands through sanitation, i.e., by felling old, infected residual trees which constitute the primary source of infection, and by felling or otherwise killing young infected trees, preferably in combination with thinning or spacing operations. Owing to variation in stand composition and age, and disease incidence and pattern, it was not possible to specifically recommend the precise area, number of trees, and timing for sanitation operations.

In view of the dearth of permanent plot data on which to base more comprehensive control recommendations, we adopted a simulation model approach to estimate the spread and intensification of the disease for a range of stand and infection conditions and sanitation procedures. Simulation models of dwarf mistletoe infection have been developed for lodgepole pine (Myers *et al.* 1971) and ponderosa pine (Dixon and Hawksworth 1979; Myers *et al.* 1976; Strand and Roth 1976). None was considered suitable to immature western hemlock because of host and pathogen differences. In addition, these models did not provide the disease estimates required to formulate detailed sanitation guidelines. Available information on the biology of western hemlock dwarf mistletoe and the factors affecting seed production and dispersal and the infection process was considered sufficient to provide many of the mathematical relationships for a model designed to develop guidelines for silvicultural control.

The objectives for such a computer model are to provide the following disease parameter estimates: (1) horizontal spread of infection from source trees; (2) numbers and percentages of trees infected; and (3) numbers of infections and dwarf mistletoe ratings for individual trees and stands. Estimates should be provided over the period from logging until stand age 30 years when spac-

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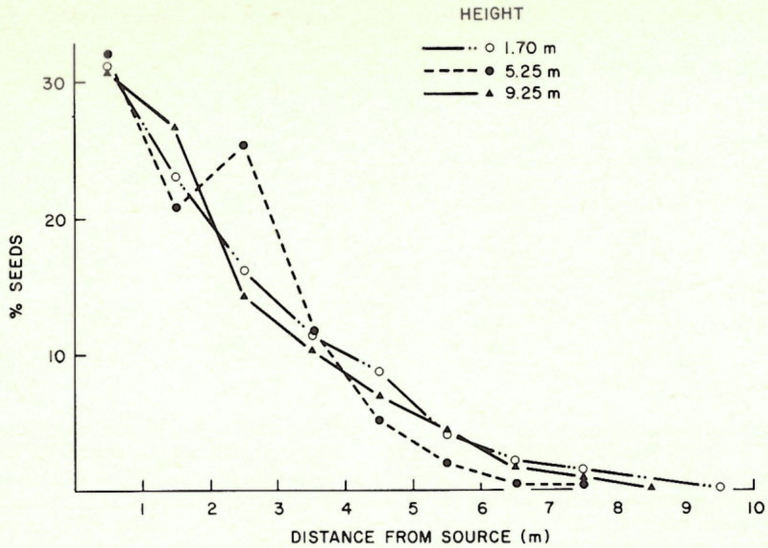

FIG. 1. Relationship of horizontal distribution of dwarf mistletoe seeds to position of plant.

ing operations generally are discontinued. To cover as wide a range as possible of stand and infection conditions, the following factors must be included: stocking, size, and spatial distribution of residual source trees and of regeneration; severity of infection of residual source trees; topographic slope; tree growth rate and environmental effects on mistletoe seed production, dispersal, and infection, e.g., early autumn frost and wind. To evaluate the effects of various sanitation strategies, the model must provide for various degrees and timings of spacing and sanitation.

Simulation model functions needed to attain these objectives include creation of a stand and growth of trees; distribution of dwarf mistletoe plants in trees; dwarf mistletoe seed production, dispersal, and distribution within trees; seed escape from crowns; interception and retention of seeds by surrounding trees; infection of trees; and tree removal by thinning or sanitation. Data required to implement some of these functions were obtained from the literature.

Additional information required to implement the functions contained in the model included: (1) effect of height above ground of dwarf mistletoe infections on the horizontal dispersal of seeds; (2) direction of seed dispersal relative to the infection; (3) proportions of seeds escaping from or retained in the crowns of source trees; (4) distribution of retained seeds within source trees; and (5) seed interception by trees adjacent to source trees. This information was obtained by experiments. Additional information required to test the model included number, age, and height of dwarf mistletoe infections on western hemlock residual trees ranging from 1 to 10 m in height.

Experiments

Effect of infection height on horizontal seed dispersal

Sections of branches with dwarf mistletoe infections were excised from young hemlock trees near Caycuse, B.C., Canada, and placed in coolers for transportation to the laboratory. Before removal, the orientation of the branch segment relative to the horizontal was measured. Each infection bore 100–200 seeds. Immediately before use, branch sections were removed from coolers and placed in clamps, oriented as on the tree facing outward on the sills of windows in the laboratory building 1.70, 5.25, or 9.25 m above the ground. Seed discharge was induced by warming the ambient air with an electric heater. Seeds were trapped on a polyethylene sheet, 3 m wide × 20 m long, laid on the level parking lot immediately below the windows. Three to four plants were used at each height; approximately 900 seeds were trapped. Anemometer recordings of wind movement were made to ensure that release of seeds occurred only during calm periods. Seeds dispersed from each height were counted on the trapping sheet; results were expressed as percentage of seeds per square metre of trap at 1-m distances from the source (Fig. 1). We concluded that no major differences in horizontal distribution were caused by height differences from 1.7 to 9.25 m. Beyond distances equal to the crown radius of a source tree, seed distribution was comparable to that recorded in field experiments (Smith 1966, 1973).

Direction of seed dispersal

Sections of branches infected with dwarf mistletoe plants bearing 100–200 seeds, obtained as previously described, were clamped, orientated as on the branch, in the centre of a 1 m^3 cheesecloth cage. Seed dispersal was induced by placing cages in a warm room. Seeds adhering to the insides of the cage were recorded according to the direction relative to the original tree bole, i.e., outward or inward, and relative to the original branch, i.e., upward or downward. The experiment was replicated twice, with two infections in each cage. The results indicated consistently higher proportions of seed distribution outward and upward than inward and downward (Table 1). No consistent left or right seed movement occurred.

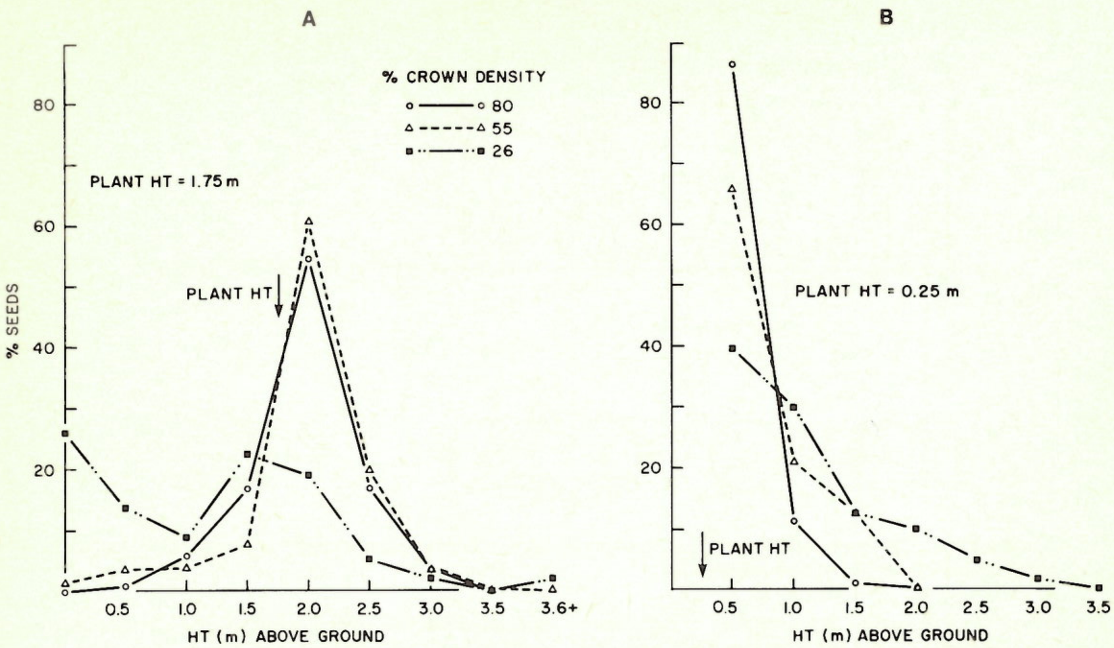

FIG. 4. Relationship of height in simulated western hemlock crown to vertical distribution of dwarf mistletoe seeds discharged from plants at different positions in crown. (A) Plant positioned between third and fourth levels from ground. (B) Plant positioned below lowest crown level (see text for explanation).

coordinate system. Seed dispersal was induced by warming the ambient air. The number of seeds trapped by the mesh was recorded by height and coordinates. Seeds were also counted on trapping cloths enclosing the base and top of the scaffold.

The percentage of seeds recovered at each height is shown in Fig. 4A, B. In downward dispersal (Fig. 4A) at the higher mesh densities, the percentage of seeds retained below the infection was less than that retained at the same distance above it. At the lowest mesh density, retention below was greater than above the infection, evidently related to the greater probability of seeds dropping back through the mesh than at the higher densities. In upward dispersal (Fig. 4B), the majority of seeds were retained 0.5 m above the infection, the percentage increasing with mesh density (40, 65, and 85% retention at 26, 55, and 80% densities, respectively). Although the experimental conditions were different, the results were consistent with those of Richardson and Van der Kamp (1972) for annual upward spread of dwarf mistletoe infections (0.30 and 0.65 m in dense and open western hemlock stands, respectively) in indicating that the majority of new infections occur at less than 1 m above the source infection and that increasing foliage density reduces upward spread.

Seed interception

Western hemlock trees about 2 m tall, with live crowns about 75 cm diameter at the base and extending the length of the stem, free of dwarf mistletoe infection, were severed at ground level and mounted upright on stands. The trees were positioned in a straight line, 1.5 or 3 m apart on a level open area, within a stand free of mistletoe infection (Fig. 5). A bagged branch section with dwarf mistletoe infection bearing approximately 400 seeds was clamped to a branch 5 cm from the tip and 1 m from the ground on one tree (source tree) facing another tree (target tree) which was draped from tip to ground with a cheesecloth seed trap. Cheesecloth, 1.5 m wide, was also laid on the ground beyond the foot of the target tree to a distance of 10 m. Either one or two trees without trapping cloth (blocking trees) were interposed between source and target trees at intervals of 1.5 or 3.0 m. As a check, no trees were interposed between source and target trees. After the trees were in place, the bag was removed from the mistletoe plant and discharged seeds were counted on the trapping cloth on the target tree and on the ground behind it. There was no perceptible wind movement during the experiment.

Results (Table 2) showed that one or two blocking trees prevented 85-95% of seeds from reaching the target tree. No seeds were trapped on the ground cloth beyond the target tree. The results indicate that the great majority of dispersed seeds do not pass beyond a crown which extends across the seed flight path. Since no seeds were found beyond the target tree, seed trajectories with an upward vector (Hawksworth 1961)

TABLE 2. Effect on dwarf mistletoe seed interception of number of trees intervening between infection source and target trees

Distance between trees (m)	No. of trees between source and target trees	No. of seeds landing on target tree
3.0	0	20
3.0	1	1
1.5	0	33[a]
1.5	1	5
1.5	1	3
1.5	2	1

[a]Estimated from Fig. 1.

FIG. 6. Example of western hemlock crown showing conical shape and whippy leader (partly visible). The latter was excluded from crown target area (from Smith 1966).

a maximum of 95%, based on observations of Baranyay (1962) and Van Sickle (personal communication). Seed reduction in years with early autumn frost was set at 90%, based on findings of Baranyay and Smith (1974), and Smith (1977). Escape of seeds from each height band in the crown of the source tree was calculated from the relationship of percentage escaped to distance from the branch tip (Fig. 2). The distance was calculated from increments in crown width since the time that infections of each age class were initiated. Distribution of seeds retained within the crown was effected by allocation of proportions of seeds to each height band using crown height - seed proportion relationships (Fig. 4A, B).

The spread of dwarf mistletoe seeds from a source to target tree was represented as a flight path defined by straight lines joining the outermost edges of source and target trees (Fig. 7A). Based on the results of the seed interception experiment, seeds escaping from the source tree crown were assumed to be intercepted within the current crown growth of target trees. No provision was made for seeds to pass through or around blocking trees. A net horizontal seed trajectory was therefore assumed between the same height bands of source and target trees. A horizontal-then-vertical trajectory was assumed for seeds dispersing from higher height bands in a source tree to lower height bands in a target tree (Fig. 7B).

The number of seeds dispersed from each height band was calculated as the product of total seed escaped from the height band and the proportion of crown circumference in the flight path weighted by factors for each quadrant of the crown.

Maximum distance of seed dispersal and distribution of seeds over horizontal distances from a source tree was derived from the experiments on horizontal seed dispersal (Fig. 1). The number of seeds intercepted by a target tree crown was calculated as the product of the number of seeds dispersed from a source tree, the proportion arriving at the distance between source and target crowns, and the area of the target crown in each height band. For horizontal trajectories, the proportion of seeds arriving at the target crown was assumed to be the sum of all proportions that would have been dispersed to or beyond the interception distance. For horizontal-then-vertical trajectories, the proportion arriving was assumed to be that dispersed to the interception distance (Fig. 1). For horizontal trajectories, the target area of the top height band was represented as a triangle and for the lower height bands, as a trapezoid with base and height equal to the lower diameter and height of the height band, respectively (Fig. 7A). For horizontal-then-vertical trajectories, the target area of the top height band was a circle and for the lower height bands, was a circular band with inner and outer diameters equal to the upper and lower diameters of the height band (Fig. 7B).

All pairs of trees within maximum seed dispersal distance of each other were designated as source or target trees. Intervening trees were designated as blocking if any part of their crowns lay within the source tree - target tree seed flight path. The blocked crown target area was calculated from the projection of blocking crown

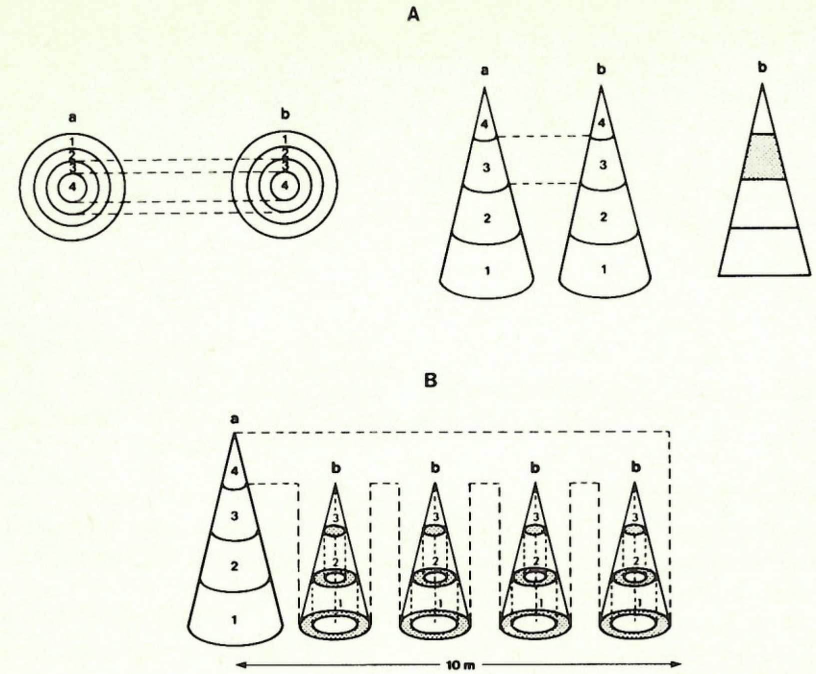

FIG. 7. Relationship of infection source tree (*a*), target trees (*b*), and seed flight path (broken line) to target crown area. (A) For horizontal seed flight trajectory, target area is triangle in top height band (4), truncated triangle (stippled) in lower height bands (1–3). (B) For horizontal-then-vertical, seed flight trajectory, target area (stippled) is a circle in top height band and a circular band in the lower height bands.

use on a Digital PDP RSX 11 computer and requires approximately 51 decimal K words of memory.[2]

The following information must be supplied to initiate model operation: periodic diameter growth; topographic slope; total number of residual trees and regeneration in stand; number, length, and width of rectangular subdivisions of the total stand area and proportions required for allocating different stocking and dbh class distributions to each subdivision; number of years after logging to be examined; number of years after logging for regeneration period; dbh of each residual tree and number of infections by age class and height in crown, and modifying factors for annual dwarf mistletoe seed production, dispersal, infection, and retention. Tree coordinates are either specified or allowed to be randomly allocated. Residual tree removal, sanitation, and thinning schedules must include timing and minimum dwarf mistletoe rating for removal and thinning distance, respectively.

Results from each execution of the model include tables of tree coordinates, dbh, number of infections, and dwarf mistletoe rating for individual trees, and stand tables showing number and percentage of trees infected according to dwarf mistletoe rating classes. Plots are produced, showing spatial distribution of trees by diameter classes or by dwarf mistletoe ratings. These results are printed at the end of each simulated year or longer periods as specified for each execution. More detailed results of the infection process in individual trees can be obtained using a special monitoring version of the model.

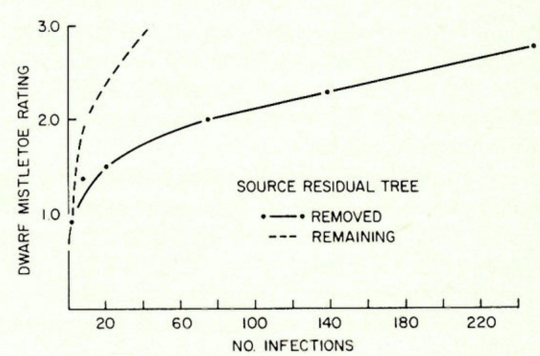

FIG. 8. Relationship of dwarf mistletoe six-point rating to number of infections per tree. Lower curve, residual tree removed 6 years after planting (data of Smith 1977). Upper curve, residual trees not removed (data of Van Sickle, personal communication).

[2]An annotated listing and flow diagram of the computer programme is available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ont., Canada K1A 0S2.

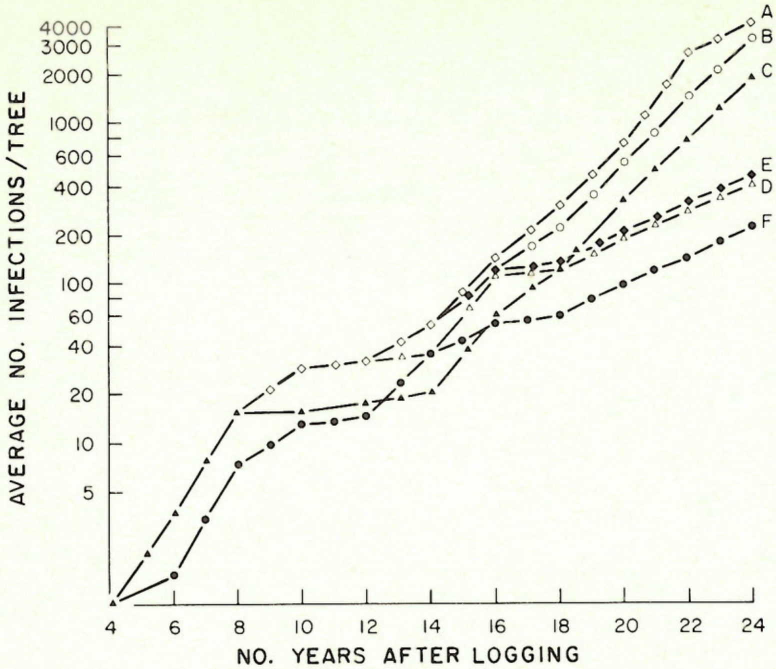

FIG. 11. Results of various sanitizing and thinning treatments of dwarf mistletoe infected western hemlock as predicted by model. Initial stand density 6666 sph, density after thinning 1400 sph. (A–E) 176 residual trees/ha, initial dbh 5.6 cm (A) Stand thinned at 12 years after logging, no selective removal of infected trees. (B) Stand thinned at 12 years after logging with source residual trees removed but no selective removal of infected regeneration trees. (C) Stand thinned at 8 years with selective removal of residual source tree and all regeneration trees with 50 or more infections (equivalent to a dwarf mistletoe rating of 1.8). (D) Residuals only removed at 12 years. No other treatment. (E) No thinning or sanitation treatments. (F) 78 residual trees/ha, no thinning or sanitation treatments.

on predicted infection and increased the predicted spread. Scharpf and Parmeter (1976) found that accelerating the height growth of red and white firs in the absence of overstory inoculum reduced infection by *Arceuthobium abietinum* Munz. because spread of infection up the tree was slower than upward development of the live crown. Thus, mistletoe infections were eventually confined to the lower crown. Results from the model indicated that moderately rapid tree growth may produce a larger amount of crown available for infection but insufficient upward crown development to outgrow the disease.

Following more extensive testing and, if necessary, refinement of the model, predictions of dwarf mistletoe infection and spread will be obtained over a range of tree stand density, tree growth, source infection levels, and site factors. The predictions will serve as a basis for constructing the guidelines for the silvicultural control of the disease in western hemlock.

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