Simulation Model for Spread and Intensification of Western Dwarf Mistletoe in Thinned Stands of Ponderosa Pine Saplings

M. A. Strand and L. F. Roth

Present address: Department of Plant Pathology, University of California, Davis, CA 95616; and Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331.

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ABSTRACT

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A mathematical model was formulated to describe the population increase of western dwarf mistletoe (*Arceuthobium campylopodum*) in a young ponderosa pine stand. The model predicts numbers and locations of new infections on evenly spaced (2-6 m) trees of uniform height (3.0 m initially). Submodels were used to estimate probabilities of occurrence of events which lead to infection. Rules of probability were used to combine the submodels. Two routes to a new infection were considered: reinfection, the infection of a branch on an infected tree by inoculum from the tree; and contagion, infection by inoculum from an outside source. The simulation predicted 2.83 new infections at the end of 5 years for a typical tree in a stand with spacing of 2.7 m and an average initial infection level of 1.2 infections per tree. For stands with similar initial infection levels, the expected new infections were about halved for every 1.5 m increase in spacing. Where the initial infection level was 2.4 mistletoe plants per tree, 6.46 new infections were expected after 5 years for trees spaced 2.7 m apart. Trees spaced 2.7, 3.9, and 5.4 m apart received about 55%, 22%, and 12%, respectively, of their new infections through contagion.

Additional key word: epidemiology.

Western dwarf mistletoe (*Arceuthobium campylopodum* Engelm.) is a serious pathogen of ponderosa pine (*Pinus ponderosa* Laws.) in the northwestern United States. Silvicultural control depends on selective thinning or complete removal of the infected stand (2). Pruning of residual mistletoe plants from trees left in thinned stands is sometimes practiced (6). Mistletoe eradication, short of stand destruction, appears impossible; infected stands that are not destroyed must be managed. Therefore, it would be useful if we could reliably predict infection trends for damage estimates and silvicultural considerations.

Our objectives were: to formulate a mathematical description of the process of dwarf mistletoe increase in the pine stand, and to use this description for prediction of mistletoe spread. The description is a simulation model that predicts the location of new infections on typical trees in thinned stands. It is based on hypothetical plots thinned to various even spacings (2-6 m) in managed stands of naturally regenerated, ponderosa pine saplings. The trees were of uniform height (3.0 m initially) and had a light level of infection (less than three infections per tree).

Dwarf mistletoe is a dioecious, seed-bearing plant and is an obligate parasite. It produces a crop of seeds each autumn. The adhesive seeds are forcibly ejected from single-seeded fruits. Needles are the primary interceptors of the seed (5). Seeds stick at points of interception until wet by rain, when their sticky coating becomes slippery. Under the influence of gravity the seeds slide. If the intercepting needles are oriented upward, the seeds will lodge on the fascicle sheath or the stem in the axil of the fascicle (5). In the spring the seed germinates and the primary rootlet forces its way through the bark to establish an absorption (endophytic) system in the host tissues. Penetration is seldom possible on old or thick bark; thus, infections are usually initiated on 1- to 3-year-old wood (the foliated part) of twigs (4). After penetration, several years may elapse before the emergence of aerial shoots which flower and bear fruit. Wagener (8) reported that the majority appeared after 4 years.

Seed production and the subsequent events that result in seedling establishment were quantified by experiments conducted during an extended period of study. These experiments took place in thinned stands of ponderosa pine saplings at Pringle Falls Experimental Forest near LaPine, Oregon.

DEVELOPMENT OF THE MODEL

Based on the above life history, dwarf mistletoe propagation was partitioned into nine events (Fig. 1). The probability of occurrence of each event and other necessary information are computed in submodels. These submodels are discussed under six headings: crown structure, mistletoe seed production, seed dispersal, reinfection, contagion, and infection establishment. Relevant equations are listed below and are cited later in the text by number. For complete derivations consult Strand (7). The authors suggest that the text be read first.

The probability notation used in this paper should be read as $P(A)$, the probability of event A occurring; $P(A|B)$, the probability of event A occurring given that event B has occurred; and $P(A \cap B)$, the probability of both events A and B occurring.

Crown structure.—The dynamic population of susceptible branchlets (suscepts) is arranged in a geometrical configuration that comprises the surface of the modeled tree crown. The crown structure submodels describe the number and positions of the suscepts.

The model equations.—

Crown structure submodels.—

1. $c = -0.218 + 0.718t$ $(R^2 = .83)$
2. $r_1 = 0.112 + 0.126t$ $(R^2 = .90)$
3. $r_2 = 0.083 + 0.163t$ $(R^2 = .91)$
4. $a_i = i \cdot (150/w)$
5. $f_i = -0.014 + (1.93/i); 1<i<13$ $(R^2 = .91)$
   $= 0.124 \quad ; i \geqslant 13$

Variables defined:

t = tree height (m).
c = length of foliated crown.
r_1 = crown radius at $t-(c/3)$.
r_2 = crown radius at $t-(2 \cdot c/3)$.
i = age of branch whorl in years.
w = age of oldest live whorl.
a_i = angle (measured from the vertical) of branch in the i^{th} whorl.
f_i = suscept increase factor for the i^{th} whorl (i.e. ratio of annual branchlet increase to the number already present).

Mistletoe seed production submodel.—

6. $s = -334.06 + 100.75\,n - 3.97n^2$ $(R^2 = .81)$

Variables defined:

s = number of seeds produced by a mistletoe plant.
n = age of the plant (years).

Seed dispersal submodel.—

7. $P(E_1) = 0.12$ (SD = 0.056)
8. $P(E_2) = 0.27$ (SD = 0.118)

Variables defined:

E_i = an event in the life cycle of mistletoe. See Fig. 1 and text for explanation.

Reinfection submodel.—

9. $P(E_3|E_1) = (p_y) \cdot (V_1) / (V_{2,y})$

Variables defined:

y = vertical distance between inoculum source and a given branchlet (m).
p_y = probability of a seed landing somewhere on the tree at y meters above the inoculum source (values from Table 3).
V_1 = the volume of a cylinder delimited by the needle tips of the target branchlet: 0.0054 m^3 in upper one-third of the crown, 0.0046 m^3 in the middle one-third, and 0.0023 m^3 in the lower one-third.
$V_{2,y}$ = the volume of a disk of the crown at a height $y \pm 0.15$ m above the mistletoe plant.

Contagion submodels.—

10. $P(E_4|E_2) = (0.15)/(2 \cdot \pi \cdot x)$

11. $y = (\cot\theta)\,x - (g/2)\,(x/((\sin\theta)\,(V_o)))^2$

12. $b_i = -0.032 + 0.21\,\theta_i + 0.15\,\theta_i r_p - 0.19\,\theta_i^2 r_p$ $(R^2 = .67)$

13. $P(E_{6,i}|E_2) = b_i / (\sum_{k=1}^{9} b_k)$

14. $c_{j,i} = -3.81 - 1.83\,\theta_i + 0.80\,v_{j,i}, \quad j = 1,2$ $(R^2 = .71)$

15. $$P(E_5|E_2 \cap E_{6,i}) = \frac{\exp(c_{1,i}) - \exp(c_{2,i})}{(1 + \exp(c_{1,i})) \cdot (1 + \exp(c_{2,i}))}$$

16. $P(E_5|E_2) = \sum_{i=1}^{9} P(E_5|E_2 \cap E_{6,i}) \cdot P(E_{6,i}|E_2)$

17. $P(E_3|E_2 \cap E_4 \cap E_5) = 0.865 - 0.162\,r_b$

Variables defined:

x = horizontal distance between inoculum source and target branchlet (m).
y = vertical distance between inoculum source and a particular branchlet (m).
θ = angle of discharge of the seed measured from the vertical.
V_o= initial velocity of the seed (m/sec^2).
g = gravity constant.
b_i = an estimate of $P(E_{6,i} | E_2)$, equation 13 is required to insure that $\sum_{i=1}^{9} P(E_{6,i} | E_2) = 1$.
θ_i = angle of discharge (in radians) representing $(10 \cdot (i-1) + 5)$ degrees, for $i = 1,2...,9$.
r_p = position of the plant in the crown relative to the bottom of the crown such that, if plant height = h, then $r_p = (h-(t-c))/c$.
$c_{j,i}$= a parameter related to the velocity and angle of seed discharge.
$v_{1,i}, v_{2,i}$ = range of velocities (max., min.) required for a seed having a discharge angle $\theta_i = (10 \cdot (i-1) + 5)$ degrees to reach a particular target.
r_b = relative position of the branchlet in its crown, definition is the same as r_p.
$\exp(c_{1,i}) = e^{c_{1,i}}$

Infection establishment submodels.—

18. $P(E_7 | E_3) = 0.61$, seed landing in upper third of crown,
0.46, in middle third, or
0.37, in lower third.
19. $P(E_8 | E_3 \cap E_7) = 0.80$
20. $P(E_9 | E_3 \cap E_7 \cap E_8) = 0.064$

Submodel synthesis.—

21. $P(A_1 \cap A_2 ... \cap A_n) = P(A_1) \cdot P(A_2 | A_1) \cdot P(A_3 | A_1 \cap A_2) ... P(A_n | A_1 \cap A_2 \cap ... \cap A_{n=1})$

22. $p = 1 - \prod_{j=1}^{N} 1 - \rho (1 - \prod_{i=1}^{N} (1 - p_{ij})^{s}_{ij})$

Variables defined:

A_i= any event.
$P(A_1 \cap A_2 ... \cap A_n)$ = probability that the chain of events A_i, $i = 1,...n$ has occurred.
p = probability of a particular branch becoming infected, regardless of inoculum source.
N = number of trees in the stand.
ρ = proportion of trees infected.
n = number of infections per infected tree.
p_{ij}= probability of a seed from the ith mistletoe plant on the jth tree infecting a particular branchlet.
s_{ij} = number of seeds produced by the ith plant on the jth tree.

Crown shape was derived from measurements of 79 trees on plots of a spacing study at the Pringle Falls site (1). The trees had been thinned 10 years previously to a spacing of 5.6 m. Data recorded for each tree included total tree height, bare trunk length, and crown radii measured at one-third and two-thirds of the crown length. Relationships between tree height and other dimensions were found by linear regression (equations 1,2,3). These equations were used to simulate the crown shape of a pine in an openly-spaced stand (Fig. 2).

Suscepts are the foliated portions of branch tips. The spatial positions of a suscept on the surface of the tree crown was found by intersecting a modeled branch with the crown outline. We observed that the angle formed by a branch and the main stem increases as the tree grows. Thus, the angles of the main branches of the whorls form a progression of increasing angles from the top of the tree downward. It was assumed that the increase is constant for all branch whorls, that the main branches are straight (an over-simplification), and that the maximum branch angle is 150 degrees from the vertical. This assumption is expressed in equation 4. Using equations 1, 2, 3, and 4, it is possible to locate in a two-dimensional projection the terminal ends of branches of known whorl height.

The number of suscepts changes each year as new branchlets are produced from the previous year's buds. To examine this change, 20 well-spaced young pines were examined. For each whorl the number of buds, branch tips, and branches arising from the main stem were recorded.

It was assumed that the number of new branchlets (that is, new suscepts) produced on a whorl is related to the age of the whorl and the number previously produced. A suscept increase factor (f_i) was defined as the ratio of the increase to the number already present and was computed for each whorl. Linear regression was used to relate f_i to whorl age (i) (equation 5). Using the computed f_i and knowing the previous number of branches, the number of new suscepts on a branchlet whorl can be predicted.

Mistletoe seed production.—This submodel predicts the expected amount of inoculum produced by a female mistletoe plant. To investigate plant fertility, the seed production of 121 female plants was observed for 3 years. The age of a plant was estimated from the age of the interwhorl on which the plant grew. Weighted linear regression was used to relate seed production to plant age (Table 1; equation 6).

Seed dispersal.—There are two paths to a new infection: reinfection and contagion. Reinfection is the transfer of inoculum from a mistletoe plant to a suscept in the same crown. Contagion is the transfer to a suscept in the crown of another tree. Seed dispersal by birds and wind was excluded as not significant, only exposive seed ejection (3) was considered. To determine the potential inoculum available for reinfection and contagion, the numbers of seeds landing on the host crown and those escaping were counted for 15 trees, each with a single infection and enclosed in a hemispherical crinoline cover. These data were used to estimate the respective probabilities $P(E_1)$ and $P(E_2)$ (equation 7,8).

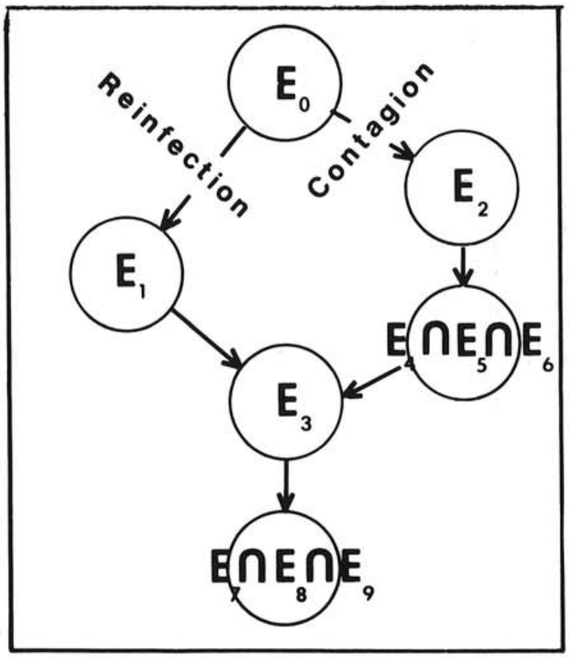

Fig. 1. Events from inoculum production to infection of a susceptible branch: E_0, a seed is discharged from a particular mistletoe plant; E_1, a seed lands on the tree that is host to the parent mistletoe plant; E_2, a seed escapes the host tree crown in free flight; E_3, a seed lands on a particular branch; $E_4 \cap E_5 \cap E_6$, a seed leaves the host crown in a way that azimuth E_4, velocity E_5, and angle E_6 all occur so that it can intercept a particular target; $E_7 \cap E_8 \cap E_9$, a seed is retained on a branch in an infective position, germinates, and infects.

TABLE 1. The observed and predicted (equation 6[a]) number of seeds produced by female mistletoe plants of various ages on thinned ponderosa pine saplings

Age (years)	Seed production (mean no.)	
	Observed	Predicted
4	9.0 ± 11.4[b]	5
5	50.3 ± 49.1	70
6	91.3 ± 127.7	127
7	300.4 ± 351.2	176
8	290.3 ± 513.2	217
9	263.5 ± 419.9	251
10	458.0 ± 643.6	276
11	321.6 ± 625.5	293
12	367.1 ± 424.6	303
13	393.6 ± 563.3	304
14	443.9 ± 653.6	298
15	221.4 ± 337.0	283

[a] Equation 6:

$$s = -334.06 + 100.75n - 3.97n^2$$

in which:

s = number of seeds produced by a mistletoe plant.

n = age of the plant (years).

[b] Standard deviation.

Reinfection.—The fate of seeds landing within the host crown is described in this submodel. The position of each adhering seed in the host crown above an inoculum source was recorded for seven trees (Table 2). Seeds that fell below an infection were considered unimportant because many slide off the lower pendent branches to the ground. These branches, also being short lived, offer the mistletoe an uncertain future. It was assumed that the probability of a seed landing on a given suscept at heights above the source plant ($P(E_3|E_1)$) is proportional to the volume of the suscept (equation 9).

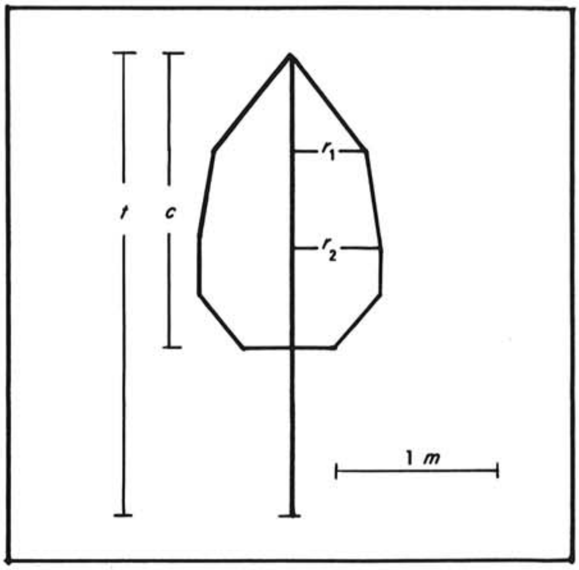

Fig. 2. Tree crown structure model. Dimensions were computed using equations 1, 2, 3:

Eq. 1. $c = -0.218 + 0.718t$ ($R^2 = .83$).

Eq. 2. $r_1 = 0.112 + 0.126t$ ($R^2 = .90$).

Eq. 3. $r_2 = 0.083 + 0.163t$ ($R^2 = .91$).

t = tree height (m).

c = length of foliated crown.

r_1 = crown radius at $t-(c/3)$.

r_2 = crown radius at $t-(2 \cdot c/3)$.

TABLE 2. Proportion of normally discharged mistletoe seeds retained within a host (ponderosa pine sapling) crown at heights above the inoculum source

Distance above mistletoe plant (m)	Plant in upper half of crown	Plant in lower half of crown
1.8 − 1.5	0	0.001
1.5 − 1.2	0.003	0.012
1.2 − 0.9	0.051	0.051
0.8 − 0.6	0.214	0.181
0.6 − 0.3	0.394	0.363
0.3 − 0.	0.338	0.392

Contagion.—To examine the fate of seeds leaving their host crown, crinoline-covered domes, 2 m in diameter, were lowered over 15 trees with single mistletoe infections usually on a branch near the trunk. Each dome was placed with the mistletoe plant at the center of the base. Nine bands each representing 10-degree elevations were marked on the dome and 12 radial sectors were designated. Seeds that adhered to the crinoline were recorded by angle band and radial sector. Seeds that were ejected from the host crown at angles below horizontal were assumed not to participate in infection spread because of the low probability of reaching susceptible portions of adjacent trees.

The proportion of seeds escaping the crown in the various radial sectors was not correlated with the orientation of the mistletoe plant. It was assumed that the direction of flight (azimuth) followed a uniform probability distribution; therefore the probability of interception by a given target ($P(E_4|E_2)$) was proportional to the width of the target and its distance (equation 10).

The seeds were assumed to follow the parabolic paths common to projectiles (equation 11). Therefore, two factors determine their flight pattern: initial angle (θ) and velocity of discharge (V_o).

To estimate the probability of a seed exiting the host crown at a given initial angle ($P(E_{6,i}|E_2)$), an empirical model was derived using data from the crinoline-covered domes (equation 12,13). The initial angle was estimated to the nearest 10 degrees by the position in which the seed adhered to the dome about 1 m from the center of the mistletoe plant (Table 3).

The initial velocities of the seeds were computed from measurements of distance of flight for seeds leaving 15 mistletoe plants through windows cut in the crinoline domes at known angles to the seed source (equation 11, Table 4).

If the coordinates of the branch tip, length of the needled area, and the angle of seed discharge are known, the range of velocities necessary for a seed to intercept the susceptible area of a branch can be calculated from equation 11. An empirical equation was derived to estimate the probability of a seed being discharged at a given angle and within a given velocity range ($P(E_5|E_2 \cap E_{6,i})$, equations 14,15). This probability, and that associated with the initial angle (equation 13), are combined in equation 16 to give the probability of a seed having a trajectory such that it can intercept a given target branchlet (suscept) ($P(E_5|E_2)$).

TABLE 3. Probability of the initial angle of seed ejection for mistletoe plants at various positions in the tree crown, computed by equation 13[a]

Angle from vertical (degrees)	Origin of seed		
	Lower crown	Mid crown	Upper crown
0 – 10	0.00	0.00	0.00
10 – 20	0.03	0.04	0.04
20 – 30	0.06	0.07	0.09
30 – 40	0.09	0.10	0.12
40 – 50	0.12	0.13	0.14
50 – 60	0.14	0.15	0.16
60 – 70	0.17	0.16	0.16
70 – 80	0.19	0.17	0.15
80 – 90	0.20	0.17	0.14

[a]Equation 13:

$$P(E_{6,i}|E_2) = \frac{b_i}{\sum_{k=1}^{9} b_k}$$

in which:

$P(E_{6,i}|E_2)$ = the probability that a seed is ejected with an initial angle of $(10\cdot(i-1)+5)$ degrees and given that it leaves its host tree crown.

b_i = an estimate of $P(E_{6,i}|E_2)$, computed by equation 12 for $i = 1, 2, \ldots 9$.

Because a target branchlet (suscept) is not a solid body, the entry of a seed into its airspace does not guarantee interception. Each of 18 branchlets from different locations on tree crowns were photographed from three angles (0, 45, and 90 degrees) representing the range of trajectories of incoming seeds. The photos were studied with the aid of grid overlays to determine the proportion of space occupied by needles. These data were used to estimate the probability of interception ($P(E_3|E_2 \cap E_4 \cap E_5)$, equation 17).

The contagion submodels, which estimate the probability of a seed having an azimuth (equation 10), angle, and velocity to intercept (equation 16) and strike a given suscept (equation 17), are combined by the probability rule (equation 21). To compute the combined probability, height of the mistletoe plant, height of the host tree, and the vertical and horizontal distance between the mistletoe plant and the target branchlet must be known.

Infection establishment.—The number of seeds retained in the needle axil the spring after seeding with a known number of seeds was determined for 21 inoculated branch tips. From these data, estimates of the mean probability of retention ($P(E_7|E_3)$) were made for branches in each third of the crown (equation 18).

Germination frequencies were recorded in 1968 and 1969 in five localities at the Pringle Falls site; 5599 seeds were examined. The probability of germination given interception and retention ($P(E_8|E_3 \cap E_7)$), was estimated from these data (equation 19). Also, 375

TABLE 4. The upper, mean, and lower velocities of mistletoe seed discharge, computed by equation 11[a] from observations of the angle of ejection and distance of seed flight

Angle from vertical (degrees)	Lower limit velocity (m/sec)	Mean velocity (m/sec)	Upper limit velocity (m/sec)
0 – 10	6.90	10.80	16.20
10 – 20	3.78	7.47	9.24
20 – 30	2.91	5.52	8.94
30 – 40	2.40	6.03	9.27
40 – 50	2.52	5.88	9.39
50 – 60	2.34	6.39	9.36
60 – 70	1.59	4.89	9.51
70 – 80	1.53	5.67	9.06
80 – 90	1.56	5.70	10.98

[a]Equation 11:

$$y = (\cot \theta)\, x - (g/2)\,(x/((\sin \theta)\,(V_o)))^2$$

in which:

y = vertical distance (meters) between inoculum source and a particular branchlet (m).

x = horizontal distance (meters) between inoculum source and target branchlet (m).

θ = angle of discharge of the seed measured from the vertical.

g = gravity constant.

V_o = initial velocity of the seed (m/sec^2).

germinated seeds were examined for evidence of infection, that is disturbance of the host cortex and turgidity of the mistletoe seedling. This probability ($P(E_9|E_3 \cap E_7 \cap E_8)$) was estimated (equation 20).

Submodel synthesis.—The submodels for contagion and reinfection were combined with those for infection establishment by a probability rule (equation 21) to give two expressions: the probability that a particular branchlet is infected by a seed from a mistletoe plant in the same crown ($P(E_1 \cap E_3 \cap E_7 \cap E_8 \cap E_9)$), and the probability that a particular branchlet is infected by a seed from a mistletoe plant on a different tree ($P(E_2 \cap E_3 \cap E_7 \cap E_8 \cap E_9)$). These probabilities were computed for each mistleote plant to which a given branchlet was vulnerable. Equation 22 was used to combine these estimates into a general expression for the probability of a branchlet becoming infected regardless of source.

RESULTS

Two cases were simulated to show the influence of the spatial relationship between the inoculum source and suscept on establishment of new infections. In each case, only one mistletoe plant and one target branchlet were included in the model and their relative positions were varied. The probability of infection of the suscept was computed for each position. The first case simulated reinfection and the second simulated contagion.

The probability of reinfection is related to the distance between the mistletoe plant and the target suscept, and to their positions in the tree crown. When the position of the inoculum source is held constant and the source-to-target distance is increased, a corresponding decrease in reinfection probability is observed (Fig. 3). However, when the distance between the source and target suscept is held constant and their vertical positions in the tree crown change, an increase in reinfection probability accompanies their increasing height (Fig. 3). This increase occurs because the branches in the top of the tree crown have a larger target volume, are more densely foliated, and are more erect (all features that enhance seed interception and retention).

In the contagion simulation, the probability of infection was computed for targets at various distances and heights (Fig. 4). Where the target is at heights greater than the inoculum source, the probability declines as horizontal distance increases. However, for lower targets,

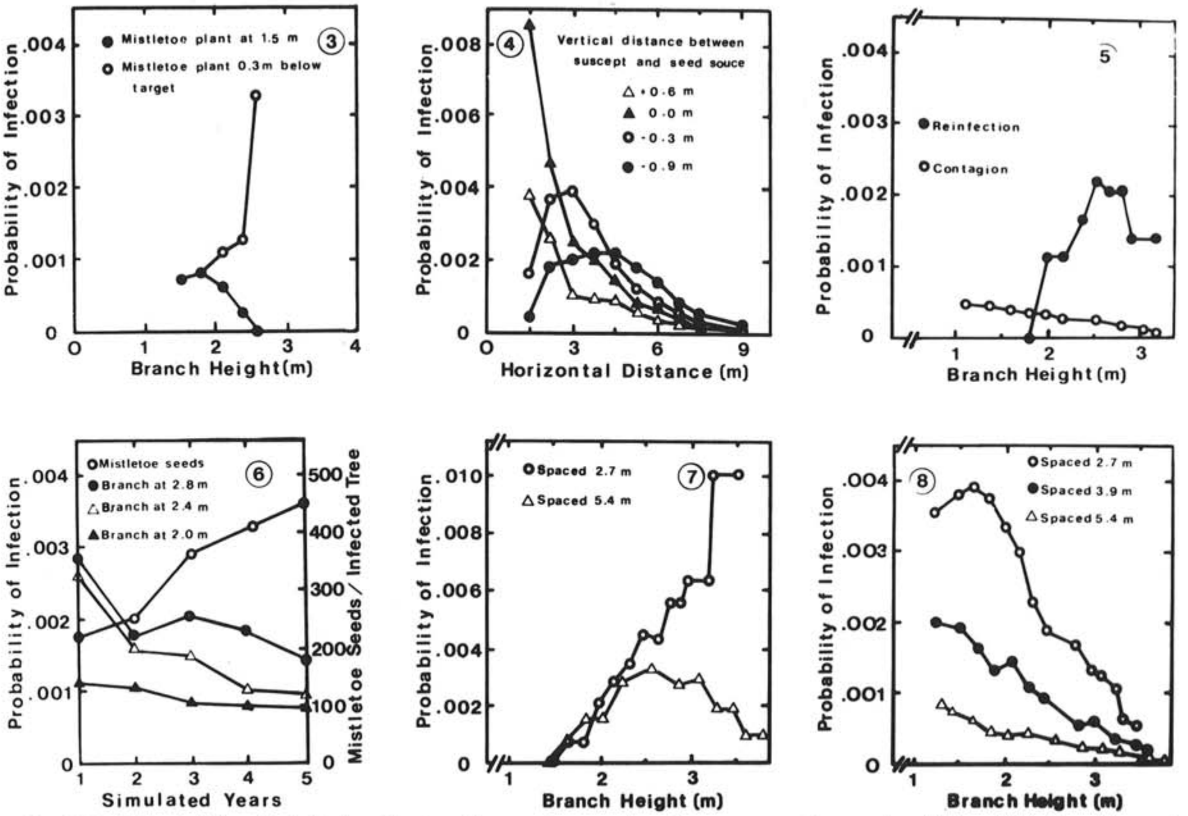

Fig. 3-8. 3) Probability of reinfection (a) when distance between inoculum source and target is varied, and (b) when distance is constant and vertical position in the tree is varied. **4)** Probability of infection by contagion for suscepts at various horizontal and vertical distances from a mistletoe seed source. **5)** Probabilities of reinfection and infection by contagion on a modeled tree crown. Initial conditions for the simulation were: tree height, 3.2 m; spacing, 3.9 m; percent of trees infected, 60; infections per tree, 1.2; height of infections from 2.4 to 1.8 m. **6)** Probability of reinfection by inoculum produced within the host crown for branches at various heights, and the amount of inoculum produced per infected tree. Initial conditions for the simulation were: tree height, 3.0 m; spacing, 5.4 m; percent of trees infected, 60; infections per tree, 1.2 from 2.4 to 1.8 m. **7)** Probability of reinfection, and **8)** probability of infection by contagion at the end of the fifth simulated year for branches on trees in stands of different spacings. Initial conditions for the simulation in both cases were: tree height, 3.0 m; percent of trees infected, 60; infections per tree, 2.4 from 2.4 to 1.5 m.

the probability forms a somewhat peaked curve that broadens and flattens as the difference in height is increased. Most new infections resulting from contagion will be at heights below old infections for trees spaced more than 3.0 m apart.

The complete simulation was used to predict new infections in stands with spacings of 2.7, 3.9, and 5.7 m and 1.2 or 2.4 infections per tree and where 60% of the trees were initially infected. These conditions are representative of infection levels common in newly thinned stands at the Pringle Falls study site. For each whorl on a representative tree, the probability of reinfection and contagion, as well as the expected number of new infections, were computed. Five years were simulated and it was assumed that only the plants initially present produced inoculum during the simulated time.

Generally, when located at heights above the lowest infection, a branch is more vulnerable to reinfection than to contagion (Fig. 5). Reinfection is closely related to the position of the suscept in the crown. As the crown expands around a plant, the probability of reinfection for a given branch can decrease with time in spite of an increase in inoculum (Fig. 6). Rate of crown expansion is related to the spacing within the stand. For example, at the end of five simulated years trees initially 3 m tall and growing 2.7 m apart had an upper crown radius of 0.54 m while those growing 5.4 m apart had a radius of 0.59 m. Differences in spacing also were reflected in the reinfection probability (Fig. 7). At mid-crown heights, the probability was about 0.003 greater for the closer-grown 2.7 m trees.

Contagion is also related to spacing. In all cases, the probability of infection by contagion was about halved for every 1.5 m of increased spacing up to the limits of seed flight (Fig. 8). The probability decreased for branches at greater heights. For branches at a constant height, it is directly proportional to the level of inoculum.

The simulation showed an increase in the expected number of infected branches in the constructed stands (Table 5). For trees spaced at 2.7 m, about 55% of the new infections resulted from contagion. Thus, at the end of five years, 1.54 branches per tree were infected from an outside source where there were 1.2 infections initially. Trees spaced at 3.9 m received about 22% of their new infections from contagion, and those at 5.4 m received about 12% of their new infections from outside sources regardless of inoculum level. Results from this model are directly relevant only to even-spaced stands of uniform height and moderate infection levels as specified.

DISCUSSION

The results suggest some general statements concerning spread and intensification of mistletoe in ponderosa pine stands. For example, in the model, infections high in the tree crowns proved to be the most important ones with respect to mistletoe spread. In the cases we simulated, vertical spread is accomplished primarily by reinfection. However, it appears to be possible for well-spaced trees with light infections to grow in height more rapidly than the ascent of mistletoe. Reinfection appears to be more important than contagion in increasing the mistletoe population in stands with spacings greater than 3 m. Increasing the spacing between trees reduces the probability of mistletoe infection not only from contagion but also from reinfection.

The process of modeling the spread of western dwarf mistletoe in young ponderosa pine stands contributes to our understanding of mistletoe parasitism apart from the results of the simulation. The model required synthesis of the quantitative information about the mistletoe life cycle. It enabled location of deficiencies in the data set and will aid design of later studies. For example, the importance of the process of reinfection, brought out by model simulations, indicates the need for a more critical examination of this process. The assumption of uniform interception probabilities for branches at a given height above an infection source is not a satisfactory substitute for more complete information on seed interception by these branches.

The model has inherent deficiencies aside from limitations of the data base. It is not realistic to assume that the annual events in mistletoe propagation will be expressed equally each year. Seasonal variation may modify the expression. A major deficiency of the present study is the lack of control experiments specifically designed to test the results of the simulation. Such

TABLE 5. Expected number of new mistletoe infections per ponderosa pine tree in stands with 60% of the trees initially infected

Simulated year	Initial infections per tree (no.)		Expected number of new infections when spacing between trees is:		
			2.7 m	3.9 m	5.4 m
0	1.2		...	...	...
1			0.25	0.11	0.06
2			0.29	0.12	0.06
3			0.60	0.26	0.12
4			0.80	0.34	0.15
5			0.89	0.42	0.16
		Total	2.83	1.25	0.55
0	2.4		...	...	...
1			0.73	0.30	0.17
2			0.92	0.36	0.18
3			1.31	0.54	0.24
4			1.70	0.60	0.29
5			1.80	0.73	0.31
		Total	6.46	2.53	1.19

experiments are in progress. Nevertheless, because of hidden infection and other complications it is not possible in nature to exactly duplicate starting levels employed in the simulation. The use, for the initial conditions of the complete simulation, of actual infection levels rather than the 1.2 or 2.4 plants per tree and 60% frequency of infection, will be an advantage to future tests applicable to this simple case. However, an expanded data base and modification of the tree crown submodel could allow this model to simulate stands with an uneven age structure. The mechanistic approach used here, where events and associated probabilities are rigorously defined, is generally applicable to simulation of multistep processes.

In spite of limitations of our model, the simulation approach appears to hold promise as a tool for predicting mistletoe trends, especially between the time of application of first treatment for timber stand improvement (including mistletoe control) and the time of achieving commercial volume. If conservatively interpreted, our results can help managers of young ponderosa pine in the general area of central Oregon, from which our data came, to refine forestry practices for mistletoe control.

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