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MARY ANN SALL STRAND for the DOCTOR OF PHILOSOPHY
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Lewis F. Roth

Western dwarf mistletoe (*Arceuthobium campylopodum* Engelm. f. *campylopodum*) is a parasite of ponderosa pine (*Pinus ponderosa* Laws.). The objectives of this investigation are: (a) to formulate a mathematical description of the process of dwarf mistletoe disease spread in a pine forest, (b) to use this description to predict the spread in a few cases of interest, and (c) from the result to make some general hypotheses concerning the process. The simulation is based on a young-growth, managed ponderosa pine stand, where the trees are evenly spaced (9 to 18 feet apart), are of uniform height (10 to 25 feet), and have a light to moderate infection level.

The model consists of four major submodels: tree growth, mistletoe seed production, seed dispersal, and infection establishment. The tree growth submodel provides information concerning size, position, and number of susceptible branches. The seed production submodel relates the amount of inoculum present to plant age. The process of disease spread is partitioned into a series of sequentially operating events. The probabilities associated with the events from mistletoe seed production to seed interception by a susceptible branch are computed in the seed dispersal submodel. The probabilities of subsequent events leading to infection are in the infection establishment submodel. Each submodel provides information for the next one, forming an interlocking set.

Seven cases are examined using the complete simulation model. These include three tree spacings (9, 13, and 18 feet) with two moderate levels of infection (2 and 4 plants per infected tree) simulated for five years and one with a heavy infection level (15 plants and 9 feet spacing) simulated for ten years. The results are examined to assess changes in (a) the probability of infection with respect to tree spacing within a hypothetical stand, branchlet height, infection level, and time, and (b) the expected number of new infections.

The model shows that the probability of reinfection decreases as the crown volume around a given height becomes larger and the foliage becomes sparser. The probability of infection due to contagion is found to decrease by about half for an increase in stand spacing of five feet. In a stand with an initial infection rate of 0.60 and a spacing of 9 feet, the expected number of new infections per 100 trees at the end of the fifth year is found to be 283 plants where there is an initial level of 2 plants per infected tree and to be 644 plants where there is a level of 4 plants per infected tree.

Based on examination of the behavior of the model, five hypotheses concerning the disease spread process are formulated. (1) Plants high in the crown of the pine trees are the most important ones with respect to disease spread. (2) Where infection levels are moderate (fewer than 5 infections per tree) and where spacing is greater than 8 feet, vertical spread is accomplished primarily by reinfection. (3) It is possible for a tree to "outgrow" its infections. (4) In stands with spacing distances greater than 8 feet and a sparse mistletoe population, new infections are more likely to occur as a result of reinfection than as a result of contagion. (5) Increasing the spacing between trees reduces the probability of mistletoe infection from both reinfection and contagion. These hypotheses have a practial importance to the management of young pine forests. They indicate that selective thinning should discriminate against trees with infections at greatest heights. Also, in young stands with moderate infection levels, the chances are favorable for the trees to outgrow their infections, if they are spaced such that growth conditions are optimum.

Simulation of Population Changes of Western Dwarf Mistletoe on Ponderosa Pine

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Head of Department of Botany and Plant Pathology

Redacted for privacy

Dean of Graduate School

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INTRODUCTION

The species of Arceuthobium (dwarf mistletoe) are important economic pests of coniferous trees in western North America. In Oregon and Washington, dwarf mistletoe accounts for the loss of 148 million cubic feet of wood annually in the form of poor growth, reduced wood quality, and tree mortality (Childs and Shea, 1967).

Various aspects of the relationships between dwarf mistletoes and their hosts have been investigated. These include seed germination and nutritional requirements of the mistletoe, physiological impact on the host, and ecological and taxonomic relationships. The research has not led to effective methods of control. Where complete destruction of the stand followed by reforestation is not employed, managers are still dependent upon thinning with removal of badly infected trees and pruning of mistletoe plants from the trees left after thinning. Control is costly and is often unsatisfactory, since mistletoe infections may undergo latent development ranging from one to many years; therefore, many plants are not detected at the time of treatment.

Foresters now consider that eradication of mistletoe from stocked areas is not possible and are resigned to live with some degree of mistletoe present. It would, therefore, be useful to be able to predict future infection distributions for purposes of damage estimates and decisions concerning silvicultural practices, as well as to make general statements about the expected progress of the parasite.

My investigation concerns *Arceuthobium campylopodum* Engelm. f. *campylopodum* on ponderosa pine (*Pinus ponderosa* Laws.). I propose to describe in mathematical terms the process of mistletoe seed production and flight, and infection establishment. The description will take the form of a simulation model written in Fortran IV computer language. It will trace the distribution of new infections occurring on typical trees through time. The tree population suitable to the model is released young-growth pine, ranging from 10 to 30 feet in height. The resulting simulation model is used to predict infection distributions for several cases of interest and to make inferences about the process of mistletoe disease spread and intensification.

LITERATURE REVIEW

The name mistletoe properly refers to members of the European genus Viscum, but it is loosely used to indicate any member of a group within the family Loranthaceae. According to Gill (1953), there are 35 species of this family in North America, five in the genus Arceuthobium (dwarf mistletoe) and the remainder in Phoradendron, commonly referred to as mistletoe. Arceuthobium is currently undergoing taxonomic revision (Hawksworth, and Wiens, 1972).

The name Arceuthobium is derived from the Greek words meaning "juniper living." Although no species are found living on juniper in North America, in the Mediterranean region where dwarf mistletoe was first described, juniper is the most common host (Gill and Bedwell, 1949). In North America we find: A. pusillum Peck mainly on eastern spruce, A. americanum Nutt. on lodgepole and jack pine, A. douglasii Engelm. on inland Douglas-fir, A. vaginatum (Willd.) Presl. on three-needled pines of the southwest, and A. campylopodum Engelm. (western dwarf mistletoe) on ponderosa and other pines, spruce, true firs, larch, and hemlock (Boyce, 1961).

Ranging from British Columbia to Baja California, the typical western dwarf mistletoe (A. campylopodum Engelm. f. campylopodum) is a common parasite of the hard pines. It occurs on Coulter, digger, Jeffrey, Monterey, and knobcone pines but most extensively on ponderosa. Six other forms of this species occur on western conifers (Kimmey and Mielke, 1959).

Dwarf mistletoe is a seed-bearing plant and an obligate parasite. The genus is characterized by yellowish or brownish plants with fragile, jointed stems, often four-angled. The leaves are decussate and reduced to connate scales (Peck, 1941). Dwarf mistletoe is dioecious with staminate and pistillate plants commonly occurring on the same host tree. Pollination in western dwarf mistletoe occurs from late July through August. In the autumn of the following year, the female plant matures fruit ready to discharge seed (Gill, 1935).

Seed dispersal is accomplished by an explosive fruit mechanism. Each fruit contains a single seed and is mounted on a pedicel which, when ripe, is elongated and recurved so the perianth end points downward. Between the pedicel and the fruit, an abscission zone develops. A layer of cells between the seed and the hull of the fruit breaks from the stem, the hull contracts and hurls the seed upward (Hawksworth and Hinds, 1965).

Seeds are teardrop-shaped and are ejected round end forward. They are covered with a sheath of viscous liquid which falls off within the first 5 cm of flight. Soon after separation from the fruit, they begin to tumble primarily in the vertical plane (Hinds, Hawksworth and McGinnies, 1963). Hinds and Hawksworth (1965) reported that the initial velocity of _A. americanum_ averaged 2600 cm per second in their experiments.

The distance of seed flight varies with the height of the seed source and exposure to the wind. Maximum spread from exposed trees which averaged 120 feet in height was reported to be 130 feet with the prevailing winds for _A. campylopodum_. However, the heaviest concentration of seed was found within 35 feet of the base of the infected tree (Roth, 1953). Hawksworth (1961) found an average horizontal distance of flight of 17.4 feet with a maximum of 42 feet for _A. vaginatum_.

Needles rather than stems have been observed as the primary interceptors of the western dwarf mistletoe seed. A viscin layer forms an adhesive outer coating around the seeds allowing them to adhere to surfaces. The widely spreading needles present a resilient and receptive target surface to the sticky seeds. Naked stems have small target surfaces and being rigid, striking seeds tend to ricochet rather than to adhere. Seeds remain stuck at points of interception until the first rain, then the viscin coating of the seeds absorbs water and becomes slippery. Under the influence of gravity the seeds slide. If the intercepting needles are oriented upward, the seeds become lodged against the open end of the fascicle sheath or against the stem in the axil of the fascicle (Roth, 1959).

The seeds must survive the winter in place to successfully infect in the spring. Many are removed by snow, wind, rain, insects, and molds (Wicker, 1967). Dormancy is apparently regulated by a chemical inhibitor associated with the persistent endocarp (Beckman and Roth, 1968). In the spring, after germination, the primary rootlet forces its way through the bark to establish an absorption system within the host tissues. Penetration is seldom possible on old or thick bark; thus, infections are usually initiated on 1- to 3-year-old twigs (Kimmey and Mielke, 1959). Several years may elapse prior to the time when the infection may be recognized by the appearance of aerial shoots. Wagener reported (1962) that from 3 to 6 years elapsed from seeding until shoot appearance for western dwarf mistletoe with the largest number of shoots appearing after 4 years. He found no correlation between growth vigor of the host and length of the latent period.

Control methods, where destruction of the entire stand is inappropriate, have been generally limited to thinning out of infected trees and pruning of remaining infections (Korstian and Long, 1922; Hawksworth and Andrews, 1961; Herman, 1961; Childs, 1963). Biological control by fungal pathogens has been suggested and several fungi have been reported on dwarf mistletoe, but success with this method has not been reported. No successful chemical treatments have been found.

In comparison to fungal diseases, the rate of spread of dwarf mistletoe is extremely slow. Localized spread is accomplished by the explosive seed mechanism which ejects the seed only a few feet. The greatest spread of infection is from an overstory source to the understory with infections being more numerous on the side of the understory trees facing the overstory source of infection (Roth, 1953). Beyond the limits of the overstory seed shower, spread through the even-aged stand is much slower. The average rate of spread through an even-aged lodgepole pine stand was reported to be 1 to 1.5 feet per year. Spread was 1.5 times greater through stands in which the canopy had not closed than in those with closed canopies (Hawksworth, 1959). Complete burns reduce the forest area affected by dwarf mistletoe because the return of the trees is usually much faster than the return of the pathogen. Clearcuts have the same effect; however, partial cuts or incomplete burns may stimulate the mistletoe in the residual opened stands (Hawksworth, 1961). The past history of the stand largely determines its mistletoe distribution.

To put together a mathematical description of a biological system, in this case the population dynamics of western dwarf mistletoe on ponderosa pine, a model is formulated. A model is simply a thought concept of a real situation, i.e., a "set of hypotheses representing a class of phenomena as a particular combination of elementary mechanisms" (Chapman, 1969, p. 73). It is built by a

> process of abstraction which defines a set of sufficient parameters on the level of study, a process of simplification which is intended to leave intact essential aspects of reality while removing distracting elements, and by addition of patently unreal assumptions which are needed to facilitate study (Levins, 1968, p. 6).

Models may be classified in several ways. The first division of types could be inductive (empirical) and deductive (theoretical) models. The theoretical models are developed by deducing general mechanisms from a series of simple premises. If these premises are formulated prior to consideration of experimental results, the model is called an *a priori* model; whereas, those based on premises derived from observations are designated *a posteriori* models (Watt, 1962). Deterministic and stochastic forms of *a priori* and *a posteriori* deductive models and inductive models can be formulated.

A stochastic model is one which specifies the joint probability distribution of a number of different occurrences at each point in time. Such a model may be defined by the simple relation:

$$\Pr(\underline{Y} \leq \underline{y}) = (\underline{\psi}, \underline{X}\,;\, \underline{y})$$

where:

$\underline{Y}$ = a vector of random variables,

$\underline{\psi}$ = vector constant over a class k of situations,

$\underline{X}$ = vector which varies over the class k,

and where:

$\underline{\psi}$, $\underline{X}$ are parameters of a probability distribution with argument $\underline{y}$ (Chapman, 1969, p. 75)

Bailey (1964) and Bartlett (1960) have developed a set of a priori stochastic models dealing with dynamics of populations, for example, in predator-prey interactions, competition, and epidemic situations. In several cases the transition probabilities (e. g. probability of going from uninfected to infected) are non-linear functions of population size. This leads to mathematical analysis of extreme complexity from models which are descriptively very simple. Indeed, in the case of the general epidemic model, no explicit solution is known (Bailey, 1964).

Deterministic models, on the other hand, assume that every variable in the system is a function of the others. An example of an a priori deterministic model is the one used by van der Plank (1963) in describing the occurrence of new fungal infections on plants. Using the basic idea of the intrinsic rate of natural increase, he relates new infections to the amounts of inoculum and susceptible tissue and to the infection rate. His model has been used by several plant pathologists working with fungal diseases (Adegbola and Hagedorn, 1969; Burleigh, Romig and Roelfs, 1969). Animal ecologists have also developed deterministic models for a wide variety of biological phenomena. These are reviewed by Watt (1962) including the a priori models of Lotka and Volterra and of Nicholson and Bailey as well as the a posteriori models of Fujita.

It is generally conceded that a deterministic model can be expected to give a satisfactory description of a process as long as the number of individuals is sufficiently large. If the numbers are small, the effects of chance occurrences become appreciable in any particular instance and stochastic modeling may be necessary. For large populations the deterministic model is sometimes the same as the mean function of the stochastic form; however, this is not generally true (Rushton and Mautner, 1955).

Empirical-deterministic models often use the standard statistical techniques of data description particularly regression analysis. An example of the use of such techniques is Morris's (1963) work on the spruce budworm. This type of modeling is particularly valuable for making predictions. The techniques of regression analysis both linear and non-linear are reviewed by Draper and Smith (1966).

With simulations, a building block approach is taken. Rather than constructing a single algorithm to describe a process, it is modeled as a sequence of consecutively operating components. The resulting submodels are fitted together to form a simulation. By using the result of one submodel as input for the next, a great number of variables may be incorporated and different modeling schemes may be employed to suit the situation. Deterministic and stochastic models, therefore, may be included in the same simulation, depending on the nature of the operating components. The main disadvantage of simulation models is that it is not generally possible to estimate their accuracy due to lack of data or to the intricacy of the model which may prevent statistical tests.

By altering an initial condition, it is possible to investigate the consequences of the single alteration on the entire process of interest. There have been several successful simulations developed which have been used to evaluate various schemes. A review of simulation models used in forest management and harvesting was written by Newnham (1968). They included simulated sampling models for comparing efficiency of various sampling techniques, management models to test the effects of rotation length and allowable cuts on the volume harvested, fire protection models to evaluate detection schemes, and stand models used to evaluate spatial patterns. A simulator of an aquatic ecosystem including biotic components of phytoplankton, *Cladocera*, and kokanee salmon was used to assess the consequences of various levels of phosphate pollutants (Parker, 1968). Insect population simulation models exploring pest control strategies have also been developed (Watt, 1963). A comprehensive simulation model of a plant disease system was written for *Alternaria* blight on tomato (Waggoner and Horsfall, 1969). This simulator (called EPIDEM) successfully mimicked several actual epidemics of past years and was used to assess the importance of characteristics of the fungus, the weather, and the host with respect to the course of the disease. No simulation models for a dwarf mistletoe population have been reported.

PROCEDURES

Modeling

Even simple biological systems containing few components may be descriptively complex. The system under consideration consists of only two populations--dwarf mistletoe and ponderosa pine. There are a large number of combinations of stand characteristics and infection levels that would be interesting to simulate. These cases are diverse enough that many submodels would be required to handle them all. To simplify the problem to one for which a meaningful simulation can be developed, there are two ways a modeler may proceed: definition and assumption. Conceptual definitions are converted into operational ones. The populations of interest must be defined in a precise manner to prevent confusion concerning applicability and to provide a basis from which to work. Assumptions are also necessary either to remove aspects where data gathering would be impossible or to prevent mathematics from becoming too difficult to handle. During the discussion of the submodels of this simulation, the assumptions will be pointed out and a justification for their use will be given.

In formulating operational definitions for the component populations, consideration of the purpose of the model must be made. If this simulation is to aid pine foresters in making management decisions where mistletoe is present, cases must be considered where decisions will have an impact. In very old stands, the mistletoe story is past history. No silvicultural practices can significantly change the infection distribution. Consequently, attention is focused on the young manageable stand. In the constructed case chosen for this model, the trees are growing at a constant rate on a site of quality IV, are between 10 and 30 feet tall, and are evenly spaced. A light mistletoe infection level exists in the stand. One of the simplest cases was deliberately chosen with the hope that enough data would be available to make the simulation feasible. The definition will be further elaborated in the section concerning assembly of the simulation.

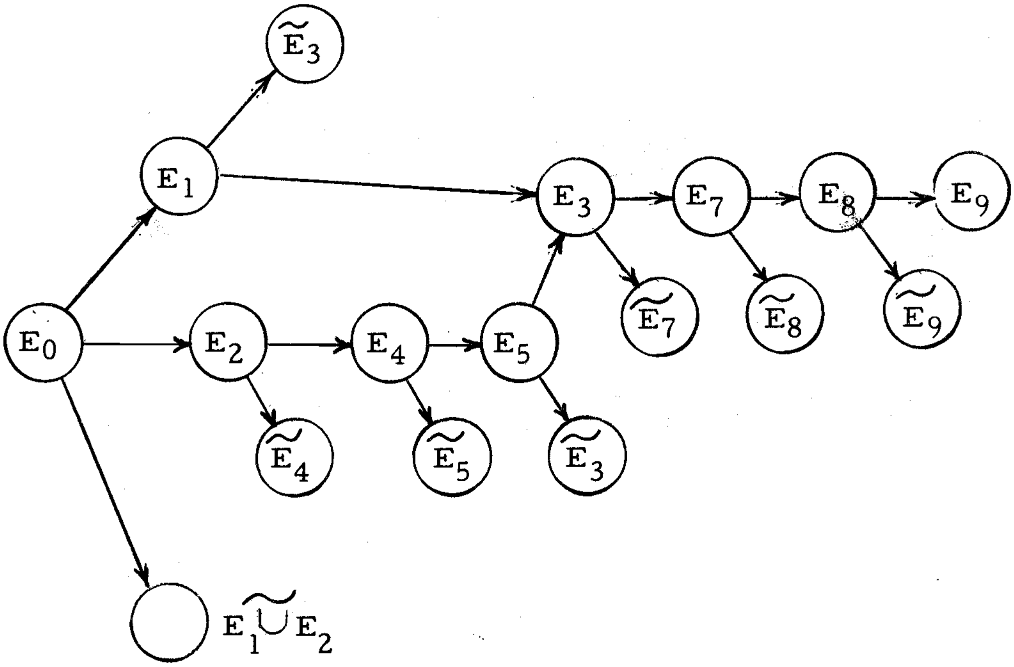
The mistletoe population of interest here contains only the female plants. These plants produce the inoculum (seeds) enabling the parasite to spread to other branches or to other trees, whereas male plants play a role in contagion only if pollen is a limiting factor, a condition not known to occur. The sex ratio for _A._ _campylopodum_ plants is 1:1 (Roth, unpublished report).

The production of mathematical descriptions for the processes of seed production, dissemination, interception, emplacement, germination, and infection is a formidable task in data collection alone. Most of the information used to generate the models was provided by Dr. Lewis F. Roth, who has been working on the problem of western dwarf mistletoe population dynamics for the past 16 years. Being formulated after the experimentation, the models in many cases were necessarily limited by the availability of information. Besides providing raw data, Dr. Roth has provided his unique biological insights on which I relied heavily where no information was obtainable.

The simulation model describes the change in distribution of mistletoe infections on a typical tree. The first step in developing this simulation was the partitioning of the process of infection into a series of subprocesses which could be modeled separately. It was assumed that the infection process could be decomposed into a series of independent events: E_i, $i = 1, 2, \ldots, n$, such that the intersection of these events forms the event of infection of a given suscept (susceptible terminal branchlet) by a seed from a particular plant. There are two general ways a suscept may become infected, the inoculum producing the infection may either be produced by a mistletoe plant hosted on the same tree as the given suscept (reinfection) or be produced by a plant on another tree (contagion). The series of events leading to infection therefore is dependent upon the inoculum source. The chains of events are defined and diagrammed in Figure 1.

The probability of occurrence of each event is estimated in a submodel. In the discussion of submodel synthesis, it will be shown how these probabilities may be combined to give the probability of infection for a given suscept and inoculum source. In succeeding sections, it will be shown how this basic equation can be used to simulate the infection distribution over any tree.

Figure 1. Diagram of the chain of events from seed production to infection of a suscept.



E_0 is the event that a seed is discharged from a particular plant.

E_1 is the event that a seed lands on the tree that is host to the plant bearing the seeds.

E_2 is the event that a seed escapes the crown of the host tree in free flight.

E_3 is the event that a particular target branch tip (suscept) intercepts a seed.

E_4 is the event that a seed leaves the crown with an azimuth such that it can strike the green suscept.

E_5 is the event that a seed leaves within a velocity and elevation range such that it can strike the given suscept.

E_7 is the event that a seed is retained overwinter and is transported to an infective position.

E_8 is the event that a seed germinates.

E_9 is the event that a seed infects a susceptible host.

$\tilde{E}_i$ is the event E_i does not occur.

The submodels will be discussed under four main headings: tree growth, mistletoe seed production, seed dispersal, and infection establishment. The tree growth submodel provides the structural information concerning suscept size, position, and number; the seed production submodel relates the amount of inoculum present to the ages of the mistletoe plants; the probabilities of events leading to the susceptible branch tip receiving a mistletoe seed are calculated in the seed dispersal section; and the subsequent fate of the suscept is described in the infection establishment section.

Tree Growth

The tree is modeled as a dynamic population of susceptible branch tips (suscepts). Because the simulation proceeds through time, the model must show how the positions and numbers of suscepts change from year to year. The population is arranged in an idealized geometrical configuration on the surface of the modeled tree crown.

Crown silhouettes were recorded in 1969 for the 79 trees on a plot on Pringle Butte (near LaPine, Oregon) that had been thinned in 1958 to an 18.7 foot spacing (Roth, unpublished report). The tree heights ranged from 2.25 to 21.25 feet with a mean height of 12.25 feet. 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 from the top of the tree.

Simple linear regression was used to relate the various dimensions to the height of the trees. The resulting relations were found to be strong (Table 1). To simulate the conical crown of an open-grown pine, the regression equations were used to form a silhouette of the tree crown (Figure 2). Knowing the height of the tree, radii of the crown at various locations may be computed. The silhouette is formed by connecting the radii with straight lines. To produce the rounded outline of the lower crown, the crown radius at the base of the crown was assumed to be half as great as the radius at one-third of the crown length above the base and the crown outline was assumed to make an angle of 45° from the lower radius to a radius equal to the radius at one-third of the crown length above the base. The equations for the connecting lines are listed in Table 2.

Because the dimensions of the crown may be related to the tree height, changes reflecting tree growth can be simulated by adding a growth increment to the tree height and recalculating the other dimensions. For simplicity and because data are lacking, trees are assumed to grow at a constant rate relative to their spacing which is the mean distance between trees. In Barrett's papers (1965, 1968), the tree heights were within the range of those included in the previous tree crown information and the mean growth increment for three spacings was given (Table 3). Trees with spacings less than 13.0 feet are assumed to grow at 0.2 foot per year, between 18.0 and 26.0

Table 1. Regression equations describing the empirical relation between tree height and other dimensions.

Equation	Coefficient of determination R^2
$WI = .373 + .126 \cdot THT$	.904
$WII = .276 + .163 \cdot THT$	.914
$CL = -.726 + .718 \cdot THT$	.826

THT = Total tree height (range 2.25 to 21.25 feet)
WI = Crown radius at one-third of crown length from top of tree
WII = Crown radius at two-thirds of crown length from top of tree
CL = Total foliated crown length

Table 2. Equations describing the silhouette (lateral Cartesian projection) of the modeled pine tree crown. The ordinate (vertical direction) is represented by y, the abscissa (horizontal direction) is represented by x.

Equation	Boundaries
$y = THT - (\frac{TCL}{WI})x$	$THT - TCL \leq y \leq THT$
$y = THT - TCL + [\frac{TCL}{(WI-WII)}](WI-x)$	$THT - 2TCL \leq y \leq THT - TCL$
$x = WII$	$THT - [2TCL + (\frac{WII}{2})] \leq y \leq THT - 2TCL$
$y = THT - CL - \frac{WII}{2} + x$	$THT - CL \leq y \leq THT - [2TCL + (\frac{WII}{2})]$

THT = Total tree height
CL = Crown length
TCL = One-third of crown length
WI = Radius of crown at THT - TCL
WII = Radius of crown at THT - 2TCL

Figure 2. Crown silhouette projected on Cartesian coordinates showing straight lines (1, 2, 3, 4) representing crown outline and a simulated branch (5).

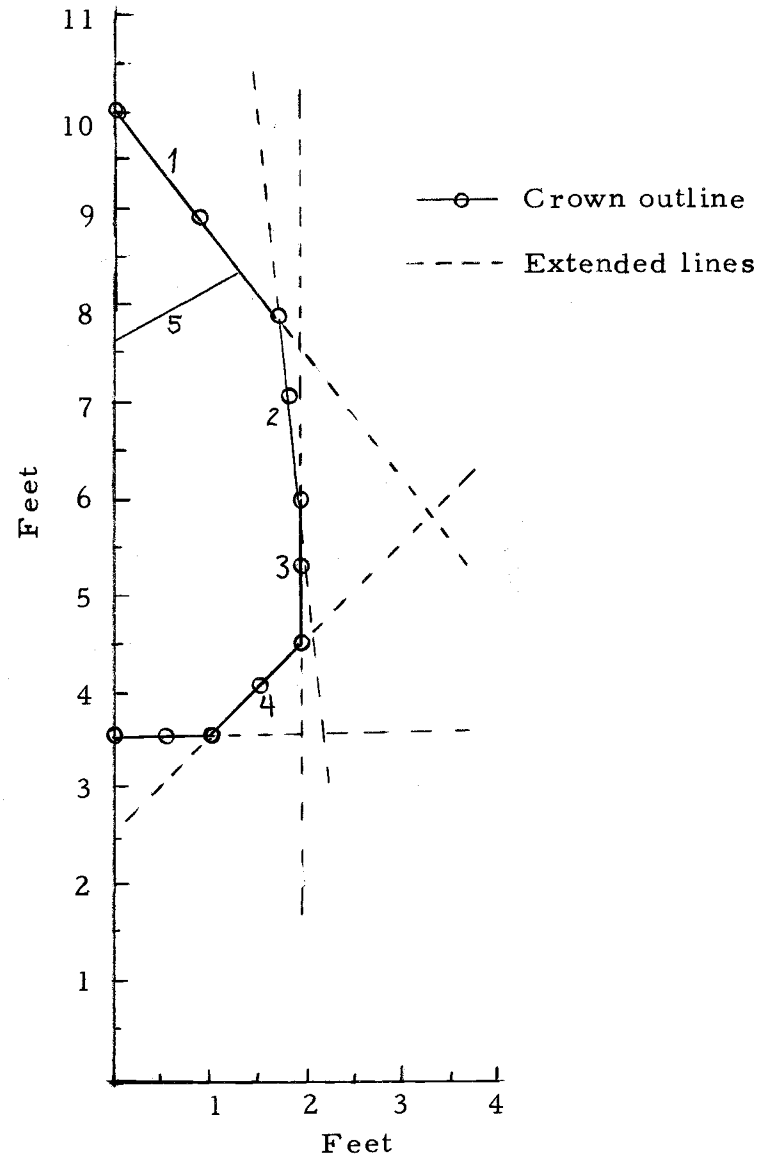


Table 3. Mean yearly height growth for three different stand spacings.

Mean tree height (ft)	Spacing (ft)	Annual growth increment (ft)
10.9[a]	13.2	.26
13.2[a]	18.7	.30
11.7[a]	26.4	.32
23.4[b]	13.2	.64
25.7[b]	18.7	.72
28.5[b]	26.4	.82

[a] Barrett, 1965

[b] Barrett, 1968

increase is at a rate of 0.3 foot per year, and with spacings greater than 26.0 feet the increment is 0.32 foot per year. The growth increments (ADD) are therefore assumed to be dependent upon stand spacing. The light mistletoe infection level is assumed not to influence tree growth.

The crown shape model and assumptions concerning height growth are combined with a branch model to find the spatial coordinates of a branch tip. No direct information on the angle made by the mainstem and the branches was available. By observation, it was noted that the angle is acute in the upper portion of the crown and becomes progressively larger further down the tree, so it is assumed that the amount of increase of the angle from one whorl to the next is equal for all whorls. The maximum angle is assumed to be 150° (2.618) radians). Thus, a simple formula is found:

$$\mathrm{ANG}_i = \mathrm{IAGE}_i \cdot 2.618/\mathrm{WHNUM} \tag{1}$$

where

ANG_i = angle in radians between a branch of the i^{th} whorl and the mainstem,

IAGE_i = age of the i^{th} whorl,

WHNUM = total number of whorls within the live crown.

It was further assumed that the branches are straight from the mainstem to tip.

To find the coordinates of a branch tip, the modeled branch must be intersected with the crown outline. In the plane of the silhouette, the equation of the branch would be:

$$y_i = WHT_i + B \cdot x_i \tag{2}$$

where

WHT_i = height of the i^{th} whorl, the height of the attachment of the branch to the mainstem,

B = tan (1.571 - ANG_i),

y_i = the height of a branch tip in the i^{th} whorl,

x_i = the perpendicular distance from the mainstem to the branch tip.

To find the height of the whorl, the amount of growth since the whorl was produced is subtracted from the present tree height. When the age is greater than the number of years since the stand was thinned, the equation is:

$$WHT_i = THT - (ADD \cdot YRSTH) + [0.2 \cdot (IAGE_i - YRSTH)] , \tag{3}$$

where

THT = total tree height,

ADD = constant growth increment after thinning,

YRSTH = number of years since the stand was thinned,

0.2 = constant growth increment before thinning.

When the whorl is produced after stand thinning, the whorl height is simply calculated by:

$$WHT_i = THT - (ADD \cdot IAGE_i). \tag{4}$$

The modeled tree crown is divided into four sections by the four straight lines which form the silhouette. Intersecting the equation (2) for the modeled branch and the crown outline, the x-coordinate (perpendicular distance from the mainstem) of the branch tip may be found. There are four equations for finding the x-coordinate based on tree height, whorl height, branch angle, and crown section (Table 4). Substituting into equation (2), the height of the branch tip may also be found (y-coordinate). Thus, the position of the population of suscepts on the surface of the tree crown may be found. The height and distance from the mainstem for each suscept in a given whorl are assumed to be constant.

To follow the changes in the number of suscepts for whorl, 20 trees were examined. These trees had a mean height of 11.6 feet and were selected from various places on Pringle Butte. All had been growing in a released condition long enough to exhibit a typical conical crown. The number of branches arising from the mainstream, the number of branch tips, and the number of new buds were recorded for each whorl. For five of the trees, complete dissections were made and the number of tips was traced through time by counting bud scale scars.

The assumption was made that the number of new buds produced by a whorl is related to the physiological age of the whorl and to the number of buds previously produced. A bud increase factor (F) was computed for each whorl and for each year for the five dissected trees

Table 4. Equations describing the radius of the modeled pine tree crown at the tips of branches in whorls of different heights. The ordinate (vertical direction) is represented by y, the abcissa (horizontal direction) is represented by x.

Equation	Boundaries
$x = \dfrac{\text{THT} - \text{WHT}}{[\tan(1.571-\text{ANG}) + (\frac{\text{TCL}}{\text{WI}})]}$	$\text{THT-TCL} \leq y \leq \text{THT}$
$x = \dfrac{\text{THT-WHT-}[\frac{\text{TCL} \cdot \text{WI}}{(\text{WI-WII})}]}{[\tan(1.571-\text{ANG}) - (\frac{\text{TCL}}{\text{WI-WII}})]}$	$\text{THT-2TCL} \leq y \leq \text{THT-TCL}$
$x = \text{WII}$	$\text{THT-}(2\text{TCL} + \frac{\text{WII}}{2}) \leq y \leq \text{THT - 2TCL}$
$x = \dfrac{\text{THT-}\frac{\text{WII}}{2}\text{-WHT}}{[\tan(1.571-\text{ANG})-1]}$	$\text{THT-CL} \leq y \leq \text{THT-}(2\text{TCL}+\frac{\text{WII}}{2})$

THT = Total tree height
CL = Crown length
TCL = One-third crown length
WI = Radius of crown at THT-TCL
WII = Radius of crown at THT-2TCL
WHT = Height of the whorl
ANG = Angle of the branches in the whorl with the mainstem (measured from the positive vertical in radians)

using the formula:

$$F = \frac{N_{i+1} - N_i}{N_i} \tag{5}$$

where

N_{i+1} = number of new branchlets produced by the branch tips present in the i^{th} year,

N_i = the number of branchlets present in the i^{th} year.

It was further assumed that branches in the same relative position to the top of the tree had the same distribution of increase factors. Thus, regardless of the number of whorls below, equal-aged whorls were said to be in comparable positions with respect to bud tip increase.

The mean relative increase factors were computed for whorls from 1 to 14 years old. Simple linear regression was used to relate the mean increase factor to whorl age; the equation had an R^2 of 0.91. It was:

$$\begin{aligned} F &= -0.014 + \left(\frac{1.93}{IAGE_i}\right) & & 1 \leq IAGE \leq 13 \\ &= 0.124. & & IAGE > 13. \end{aligned} \tag{6}$$

From the relationship generated, the change in the number of suscepts may be found. By knowing the number of branch tips in the previous year, the current number may be found:

$$\begin{aligned} N_{i+1} &= F \cdot N_i + N_i \\ &= N_i \cdot (F + 1). \end{aligned} \tag{7}$$

New whorls are added at the top of the tree and the number of branches arising from the mainstem is assumed to be two, which is approximately the mean number of mainstem branches for a whorl (which was found to be 1.72).

The tree growth submodel is used to find the position and number of susceptible branch tips in a tree crown. The suscepts in a single whorl are assumed to be at a constant height and distance from the mainstem. To calculate these position parameters, the total number of whorls on the tree, the age of the given whorl, the spacing of the trees in the surrounding stand, the years since the area was thinned, and the current tree height must be known. The number of suscepts on a whorl is assumed to be a function of the age of the whorl and the number of buds previously produced.

Mistletoe Plant

Plant fertility, as expressed by the number of seeds produced, changes as the plant ages. The purpose of the mistletoe plant model is to determine the expected amount of inoculum produced by a plant in a given year.

A study was made of the relationship of plant age to seed production. In an area on the east side of Pringle Butte, where a sapling stand had been thinned to 18.6 foot spacing, 25 infected trees were arbitrarily selected and the mistletoe plants numbered and tagged. A total of 121 plants were tagged the first year, 1967, and these were observed from 1967 to 1969. Just prior to seed expulsion, each plant was covered with an envelope-style paper bag and the bag was stapled closed (for small plants, total counts were made to determine the number of fruits). After the seeds were disseminated, usually in October, the bags were carefully removed to retain the seeds. Estimates were made to assess the number of seeds remaining on the plant unshot or adhering to the plant stalks, host limbs, or enclosed foliage. Seeds were then counted on the bags and a total number of seeds produced by the plant was determined.

An estimate of age was made for each plant. By assuming that most infections occur on the youngest wood, the plant age was approximated by the age of the wood on which the plant grew. This estimate was made by counting from the tip back, employing terminal bud scars as markers.

Weighted linear regression was used to formulate an empirical model for seed production. For each age (PLAGE) the mean and standard deviation (s. d.) of the number of seeds (SEED) produced was computed. Because the number of plants within an age group varied, a weighted regression on the seed means was required. The weighting factor was s. d. / $\sqrt{n}$, where n was the number of plants recorded in a given age group. The equation:

$$\text{SEED} = -334.06 + 100.75 \cdot \text{PLAGE} - 3.97 \cdot (\text{PLAGE}^2) \qquad (8)$$

had a coefficient of determination (R^2) of 0.81 which indicates approximately 81% of the variation is accounted for by the generated equation. Note that the function is a quadratic with a negative second power component. Annual production of seed apparently increases with plant age up to about 12 years then a decline occurs until the plant is about 21, when the computed number of seeds approaches zero. The decline is probably related to the age group of trees which hosted the studied plants. The oldest foliated branch on these trees was not more than 30 years old. It could be expected that as the host branch declines the mistletoe fertility would also decline.

After an infection occurs, the dwarf mistletoe plant undergoes a "latent period," that is, a time when aerial shoots, and hence inoculum, are not produced. According to Wagener (1962), this period averages four years for western dwarf mistletoe. Using this mean as a constant, it will be assumed that a dwarf mistletoe plant does not produce seeds until it is beyond four years old.

To calculate the inoculum produced by a given plant, the model requires that the age of the plant be known.

Seed Dispersal

In this section, the series of events from seed dispersal to interception by a susceptible branch tip will be discussed. There are two paths by which a branch tip may receive the mistletoe inoculum:

reinfection and contagion. Both pathways are important in the infection distribution pattern. Fruiting mistletoe plants are found toward the center of the crown; therefore, expelled seeds must travel between the needles of the host tree before escaping in free flight. Many seeds are deflected by branches or lack sufficient initial velocity to exit the host's crown; most are lost without initiating infections. Some of the seeds strike and adhere to the needles and stems of the host tree, whereas others escape possibly to initiate infections on other trees. The mechanism of explosive seed ejection is the only form of dispersal considered in this model. Birds probably play an important role in the long distance transport, but no documentation is available concerning this method of dispersal. Wind effects are also ignored. In the opinion of most authorities, the forcible expulsion of the seeds is the primary means of local spread and intensification.

To determine the potential inoculum available for infection intensification on the host tree and for transfer to other trees, the proportion of seeds remaining within the crown and those escaping must be known. The necessary information is available from Roth's unpublished studies on seed dispersal, where the fate of every seed produced by mistletoe plants on trees with single infections was followed. Twelve percent of the seed was found adhering to the host tree, 27% escaped the crown, and 61% had fallen out of the bottom of the crown. These percentages are used to estimate the probabilities:

$$P(E_1) = 0.12, \tag{9}$$

$$P(E_2) = 0.27, \tag{10}$$

where

E_1 = the event that a seed lands on the host tree,

E_2 = the event that a seed escapes the crown of the host tree in free flight.

The series of events leading to reinfection will be considered first. Data were available concerning these events from Dr. Roth's unpublished work. Seven saplings about 10 feet tall and with single mistletoe infections were examined. Each seed that had adhered to the tree above the source plant was recorded with respect to position. However, no information was available about seed landing below the level of the mistletoe plant.

To analyze the results, the tree crowns were divided into halves. Because it may be assumed that crown characteristics, particularly needle density, affect seed trapping, it would be expected that the more heavily needled top portion of the crown has a different interception distribution than the sparser lower region. In the experiment, the crown above a plant was divided by imaginary horizontal planes into fifths and the number of seeds within each fifth was recorded. In analysis, however, the combined information from the seven trees was adjusted to layers, each one foot thick, by assuming a uniform distribution over each fifth and apportioning the seeds into the one-foot layers. The proportion of seeds which adhered to the host tree in the one-foot units is recorded by upper and lower crown regions in Table 5. No seeds were found above six feet from the plant on the one tree where this event was possible.

Table 5. Proportions of mistletoe seed retained within the host crown distributed on one-foot bands above the mistletoe plant, where the plant is located in either the upper or lower half of the crown.

Distance above plant (ft)	Upper half of crown	Lower half of crown
6-5	0	.001
5-4	.003	.012
4-3	.051	.051
3-2	.214	.181
2-1	.394	.363
1-0	.338	.392

To find the probability that a branch will intercept a seed from a plant on the same tree, certain assumptions must be made. The proportions of seed landing in each of the one-foot bands are used to estimate the uniform probability of a seed landing within the band. If the distribution of probability within the volume of the band is uniform, then the probability of any branch receiving a seed, given that the seed has been trapped by the host tree, is proportional to the volume the branch occupies. Thus,

$$P(E_3 \mid E_1) = \frac{p_i(VB_i)}{V_i} \qquad (11)$$

where

E_3 = the event that a branch in the i^{th} band receives a seed,

E_1 = the event that a seed lands on the tree that is host to the mistletoe plant bearing the seed,

p_i = the probability that the seed lands in the i^{th} band if it is caught by the host tree (values from Table 5),

VB_i = the volume of the needled area of the branch tip in the i^{th} band,

V_i = the volume of the i^{th} band,

and using the crown model developed previously, the volume of the bands may be found (Table 6).

To estimate the target volume, results of an experiment were examined. Information regarding the fresh weights of the foliated portion of branchlets had been collected (Roth, unpublished data). Thirty trees were examined, their crowns were divided into thirds, and 311 branch tips were collected from each area. These samples were weighed and the resulting mean weights are given in Table 7.

Needles are longer in the uppermost third of the crown. The foliated portion of the branches extends for about a foot inward from the bud tips. These suscepts were defined to be the standard, and their volume was approximated by a cylinder of one foot in length and 0.25 foot radius. The target volume was assumed to be constant within a crown third. The volumes of the suscepts in the lower thirds

Table 6. Equations concerning the volumes of one-foot bands of the modeled tree crown.

Equation	Boundaries
$V_i = (\frac{\pi}{3}) \cdot [R1^2 \cdot (THT-H1) - R2^2 \cdot (THT-H2)]$ where: $R1 = (THT-H1)(\frac{WI}{TCL})$ $R2 = (THT-H2)(\frac{WI}{TCL})$	$THT-TCL \leq H1 \leq THT$ and $THT-TCL \leq H2 \leq THT$
$V_i = (\frac{\pi}{3}) \cdot [(\frac{TCL}{WII-WI}) (R2^3 - R1^2)]$ where: $R1 = (THT-H1-TCL)(\frac{WII-WI}{TCL})$ $R2 = (THT-H2-TCL)(\frac{WII-WI}{TCL})$	$THT-2TCL \leq H1 \leq THT-TCL$ and $THT-2TCL \leq H2 \leq THT-TCL$
$V_i = (\frac{\pi}{3}) WII^2$	$THT-(2TCL+\frac{WII}{2}) \leq H1 \leq THT-2TCL$ and $THT-(2TCL+\frac{WII}{2}) \leq H2 \leq THT-2TCL$
$V_i = (\frac{\pi}{3}) [R1^2(H1-CL+(\frac{WII}{2})) - R2 \ (H2-CL+(\frac{WII}{2}))]$ where: $R1 = H1-THT+CL+(\frac{WII}{2})$ $R2 = H2-THT+CL+(\frac{WII}{2})$	$THT-CL \leq H1 \leq THT-(2TCL+\frac{WII}{2})$ and $THT-CL \leq H2 \leq THT-(2TCL+\frac{WII}{2})$

V_i = Volume of the i^{th} band
H1 = Upper height of band
H2 = Lower height of band
THT = Total tree height
CL = Crown length
TCL = One-third of crown length
WI = Radius of the crown at THT-TCL
WII = Radius of the crown at THT-2TCL

Table 7. The measured weights and modeled volumes of the foliated portion of branches in three horizontal layers of the pine tree crown.

Crown third	Mean weight per branchlet (g)	Modeled volume per branchlet (ft^3)
Upper	73. 8	0. 196
Middle	62. 6	0. 165
Lower	31. 2	0. 082

were adjusted by the ratio of their fresh weights to that of the upper third. The resulting adjusted volumes are given in Table 7.

To estimate the probability of a given branch receiving a mistletoe seed from a plant on the same tree, given that the seed adhered somewhere to the host tree, equation (11) is used and values from Tables 5, 6, and 7. The height of the plant, the given branch and the tree are required to compute the interception probability.

If the seed source is on a tree other than the one supporting the suscept of interest, the concern becomes the problem of outward flight. The seeds, which escape the crown of their host, are assumed to follow the parabolic path common to projectiles. From physics comes the formula for a trajectory of an object with no other force except gravity acting on it after discharge. It ignores the effects of air friction and wind. The formula is:

$$y = (\cot \theta) \cdot x - \left(\frac{g}{2}\right) \cdot \left(\frac{x}{[(\sin \theta) \cdot V_o]}\right)^2 \qquad (12)$$

where

y and x = the vertical and horizontal Cartesian coordinates of the position of the seed in relation to the position in which it was discharged,

θ = the angle of discharge measured from the positive vertical,

V_o = the initial velocity,

g = the gravity constant (32 ft/sec^2).

To simplify calculations and to conform to available field data, the initial angles were divided into nine subunits of 10° each. The assumption was made that any seed exiting within a 10° band leaves the plant at the median angle of that band. Notice that for a given angle group the distance of horizontal flight to reach a particular height is governed solely by the initial velocity. Thus, to find whether a seed from a particular mistletoe plant will strike a particular branch, the probability distributions for the angle of discharge and initial velocity are needed.

Information concerning both distributions was available (Roth, unpublished data). The angle of discharge was approximated by the angle between the plant level and the point at which the seed was found on a crinoline-covered hemispherical dome six feet in diameter. The dome was placed so as to locate the plant at the center of the base. Nine bands each representing 10° elevation were marked on the dome; also 12 radial sectors were designated and the seeds were recorded by band and sector. Fifteen sets of data from various plants and trees were obtained from 1966 through 1969.

Because the problem of distribution according to angle of discharge concerns those seeds that escape the crown, it is postulated that the position of the plant within the crown affects this distribution. Seeds from plants located high in the crown may have a different angle pattern, due to the crown characteristics around the plant, than those located in the sparser lower crown. In order to compare the effect between plants in trees of different heights, the statistic "relative position" was defined. It is the ratio of the distance between the bottom of the crown and the plant to the total crown length, thus:

$$RP = \frac{PHT - (THT - CL)}{CL} \qquad (13)$$

where

RP = the relative position of the plant,

PHT = the height of the plant from the ground,

THT = the total tree height,

CL = the length of the crown.

A plant at the bottom of the crown would have a relative position of zero and one exactly in the middle of the crown would have one of 0.5. This statistic enables the comparison of plants with respect to the area in the crown where they are located. Some insights into the influence of the crown immediately surrounding the plant can be gained, thereby.

Proportions of escaping seed were analyzed by angle of seed discharge, orientation of the plant around the tree, and relative position of the plant. The proportion of escaping seed in the various radial sectors did not show a definite pattern with respect to the orientation of the plant. The plants with the highest standard deviation of proportion of seed found in each sector were mainstem infections. Presumably, if orientation is an important factor, then mainstem infections by their central location would have the lowest deviation from a mean value per sector. It is concluded that crown variations have more effect on the probability distribution of direction of flight than does plant orientation in the cases studied. For purposes of the simulation, a uniform distribution with respect to direction will be assumed. The probability that a seed leaves the mistletoe plant in an orientation such that it could strike a particular branch tip target (i. e., is in a vertical plane intersecting the suscept) is equal to the width of the target divided by the circumference of a circle with a radius (R) equal to the horizontal distance from the plant to the target. Thus,

$$P(E_4 \mid E_2) = \frac{0.5}{(2\pi R)}, \qquad (14)$$

where

E_4 = the event that a seed leaves the plant in such an orientation (azimuth) to strike a particular branch tip,

E_2 = the event that the seed escapes the host crown in free flight, 0.5 = the postulated target width.

To estimate the proportion of seeds exiting the crown within each of the 10° bands, an empirical model was postulated. Multiple regression was used to find the parameters of the equation:

$$SP_i = -0.032 + 0.21 \cdot AZ_i + 0.15 \cdot AZ_i \cdot RP - 0.19 \cdot AZ_i^2 \cdot RP, \tag{15}$$

where

SP_i = the proportion of seed exiting a tree crown within the i^{th} angle band,

AZ_i = the median in radians of the i^{th} angle band.

All parameters were significant and the R^2 was 0.67.

The sum of the probabilities of a seed exiting in any given angle band must add to one. Because the empirical model for SP_i, $i = 1, 2, \ldots, 9$, does not insure this total, the SP_i may not be used to directly estimate the corresponding probabilities. If it is assumed that the probability is proportional to SP_i, then the probability may be estimated by:

$$P(E_{6,i} \mid E_2) = \frac{SP_i}{\sum_{j=1}^{9} SP_j} \tag{16}$$

where

$E_{6,i}$ = the event that a seed leaves the mistletoe plant within the i^{th} angle band,

E_2 = the event that the seed leaves the plant in free flight.

Table 8 gives the $P(E_{6,i} \mid E_2)$, $i = 1, 2, \ldots, 9$, for plants with relative positions of 0.5, 0.25, and 0.75.

Experimental data concerning the initial velocity of mistletoe seeds were not directly obtainable. However, such information was indirectly provided by measurements of distance of seed flight for seeds leaving at particular angles (Roth, unpublished data). Because the approximate angle of discharge, the height of the plant, and the distance of flight are known, an approximation of the initial velocity (V_o) may be computed. The formula:

$$V_o = \sqrt{\frac{16 \cdot x^2}{[-y + (\cot\theta)x]\ (\sin\theta)^2}} \qquad (17)$$

where, in this case,

x = the horizontal distance from plant to the mistletoe seed on the ground,

y = the height of the mistletoe plant,

θ = the median angle of the exit band

is derived from the previously presented trajectory equation (12). The upper, lower, and mean velocities are given for each angle band in Table 9.

For each angle band the frequency of occurrence of each velocity was recorded. These frequencies were used to find the cumulative relative frequency (CP_i) of velocity (V_o) for each angle band (AZ_i, $i = 1, 2, \ldots, 9$). An empirical model was postulated and regression

Table 8. Probability of a seed discharging within a particular angle (from the positive vertical) group from a plant at various relative positions. The probabilities are computed from equation (16).

Angle group	Relative position		
	0.25	0.50	0.75
0-10°	0.000	0.000	0.000
10-20°	0.026	0.035	0.045
20-30°	0.060	0.072	0.086
30-40°	0.091	0.103	0.118
40-50°	0.119	0.129	0.141
50-60°	0.144	0.149	0.155
60-70°	0.167	0.164	0.160
70-80°	0.188	0.172	0.154
80-90°	0.205	0.176	0.141

Table 9. The upper, mean, and lower velocities of mistletoe seeds leaving the plant within one of the nine angle groups (measured from the positive vertical). The velocities are computed using equation (17).

Angle group	Lower limit velocity (ft/sec)	Mean velocity (ft/sec)	Upper limit velocity (ft/sec)
0-10°	23.0	36.0	54.0
10-20°	12.6	24.9	30.8
20-30°	9.7	18.4	29.8
30-40°	8.0	20.1	30.9
40-50°	8.4	19.6	31.3
50-60°	7.8	21.3	31.2
60-70°	5.3	16.3	31.7
70-80°	5.1	18.9	30.2
80-90°	5.2	19.0	36.6

analysis was used to estimate the equation parameters. The resulting equation is

$$\ln\left(\frac{CP_i}{1 - CP_i}\right) = -3.81 - 1.83 \cdot AZ_i + 0.24 \cdot V_o, \tag{18}$$

and it has an R^2 of 0.71. This relationship is used to compute the probability of a seed leaving at a given velocity or at a lesser velocity for a specific angle of discharge. For a given angle of takeoff, the range of velocities needed for a seed from a particular mistletoe plant to fall along the target length may be estimated using the velocity formula (17), knowing the spacing between trees and the position of the target branch, and assuming that the target has a length of one foot. If the range of velocities is known, then the probability of a seed leaving the plant within the range may be estimated by:

$$P(E_5 \mid E_2 \cap E_{6,i}) = CP_{i,1} - CP_{i,2} \tag{19}$$

where

E_5 = the event that a seed leaves with a range of velocities such that it can intercept a particular target,

E_2 = the event that a seed leaves the host crown in free flight,

$E_{6,i}$ = the event that a seed leaves the mistletoe plant within the ith angle band,

$CP_{i,1}$ = the cumulative relative frequency for the upper limit velocity of the interception velocity range for a seed leaving the plant in the ith angle band,

$CP_{i,2}$ = the cumulative relative frequency of the lower limit velocity.

To determine the probability of a seed having a sufficient velocity to land on the target regardless of angle of discharge, a rule dealing with conditional probability may be applied. If $[A_1, A_2, \ldots, A_m]$ forms a partition of the universe S, if $P(A_i) \neq 0$ for all $i = 1, 2, \ldots, m$, and if A is an event in S, then

$$P(A) = P(A_1) \cdot P(A \mid A_1) + P(A_2) \cdot P(A \mid A_2) + \ldots$$
$$+ P(A_m) \cdot P(A \mid A_m). \tag{20}$$

Let the event E_2 (seed leaves the crown in free flight) be the universe under consideration. Thus, because it is not possible for a seed to exit the crown at more than one angle and all must exit at some angle, the events $E_{6,1}, E_{6,2}, \ldots, E_{6,9}$ are mutually disjoint sets forming a partition of the universe. Equation (16) is used to estimate these conditional probabilities. The event E_5 is also dependent upon the occurrence of E_2; therefore, it is an event within the universe of escaping seeds.

The probability of a seed having an initial velocity within the interception range regardless of the angle of discharge may be found by combining equations (16) and (19) and applying rule (20):

$$P(E_5 \mid E_2) = \sum_{i=1}^{9} P(E_5 \mid E_2 \cap E_{6,i}) \cdot P(E_{6,i} \mid E_2). \tag{21}$$

Branch tips and the surrounding needles do not make solid targets; therefore, entry into their range by a seed does not assure interception. The probability of a seed striking the target, given that it comes within its bounds, is assumed to be directly related to the proportion of blocked paths (i. e., paths with needles or twigs in the way) to total paths through the target area. Seeds may enter this area from many different angles and each angle will offer a different set of clear and blocked paths. A photographic study of the branch tips was used to estimate the number of such paths.

Samples were taken from three saplings in an area thinned several years previously to a spacing of approximately 18 feet. The trees had developed full conical crowns since release. Six branch tips were taken at regular intervals along each crown and tree heights and branch heights were recorded. Branches were held in their natural angles and black and white photographs were taken of each; one straight down on the bud and one at 45° with respect to the point of support. By definition, the branch targets are considered to be 0.5 foot wide and one foot along the branch. An overlay dot grid was used to measure the amount of white area (clear paths) and black areas (blocked paths) within the target area.

The results show that the proportion of open area is not significantly different ($P > 0.5$) in the 90° angle shots from that found in the 45° angle pictures. Although these two angles do not make a sufficient sample of the possible angles, they do indicate that the probability of interception is independent of angle of entry.

To compare the branch tips from trees of different heights, the position (RP) was used. Here

$$RP = \frac{BHT - (THT - CL)}{CL} \tag{22}$$

where, in this case,

BHT = the height of the sampled branch.

When the proportion of closed paths was plotted against the relative position of the branch, a linear relationship was postulated. Regression analysis was used to estimate the parameters of the equation;

$$PS = 0.865 - 0.162 \cdot RP, \tag{23}$$

where

PS = the proportion of closed paths.

The proportion is assumed to estimate the probability of a seed striking the suscept given that it enters the "air space" of the target. Thus,

$$P(E_3 \mid E_2 \cap E_4 \cap E_5) = PS \tag{24}$$

where

E_3 = the event that a given suscept intercepts a seed,

E_2 = the event that a seed exits the host crown in free flight,

E_4 = the event that a seed leaves the plant in such an orientation (azimuth) to strike a particular branch tip,

E_5 = the event that a seed leaves the mistletoe plant within a velocity range such that it may intercept a target.

To estimate the probability of a given branch receiving a mistletoe seed from a plant hosted by another tree, these values must be known: the height of the mistletoe plant, the height of the tree that is host to the mistletoe plant, the height of the tree on which the suscept is found, the height of the suscept, and the spacing between the trees.

Infection Establishment

For infection to successfully occur, the intercepted seed must be transported to the axil of the needle, be retained until the following spring, germinate, and penetrate the tissue of the tree. The probability of these events occurring is assumed to be independent of inoculum source. In this section, the factors which affect infection establishment after a seed has been intercepted by a susceptible branchlet will be discussed.

The seeds adhering to a needle or stem sooner or later are moistened by rain and become slippery. The seeds slide under the influence of gravity; therefore, needles which hang downward will not retain seed--rather the seeds will slide off the ends of the needles. The probability that a seed will remain on the needle depends on its chance of landing on an upwardly oriented needle. The number of such needles usually depends on the angle of the entire branch tip. The more acute the angle with respect to the vertical, the more needles will be pointed upward (Roth, 1959).

Measurements of branch tip orientations were available for 341 tips (Roth, unpublished data). These were divided into three sets based on the crown third occupied by the branchlet. For the upper third of the crown, 125 samples were distributed over a range from 0° to 90° from the vertical with a mean of 41° (0.721 radians), in the middle section the angles ranged from 0° to 115° with a mean of 64° (1.117 radians) from 116 samples, and in the lower third of the crown 100 samples ranged from 10° to 125° and had a mean of 78° (1.367 radians). Both ranges and means indicate the relationship between branch angle and height. In general, the angle with respect to the vertical decreases with an increase in height. The correlation is not strong, so for the purposes of this exercise the mean angle for each crown third will be used to approximate the angle of any branch tip within the section.

Information concerning the effect of a tree's foliar habit upon seed retention was available from a number of sources. However, a thinned stand in the Skyliner area near Bend, Oregon, most closely represented the model stand of the simulation and was used as a source of data (Roth, unpublished data). Data from 1967 and 1968 were employed. Twenty-one branch tips were inoculated with a known number of seeds and the branch tip angle recorded. A year later the remaining seeds were noted as to position. Seeds found either on young wood (i.e., wood with needles) or on the fascicle sheath of a needle were considered to be in a position to infect the branch. It is assumed that the years, when the data were collected, were representative with respect to climatological variables.

Linear regression analysis was used to relate branch angle in radians to the proportion of seed retained in an infective position:

$$PSR = 0.887 - 0.379 \cdot BA \qquad (25)$$

where

PSR = the proportion of seed retained in an infective position,

BA = the angle of the branch tip measured in radians from the positive vertical.

The coefficient of determination for this equation is 0.72. If the proportion is used to estimate the probability, then the branch angle assumption and the retained seed estimator may be combined to give an estimate of the probability of a seed being retained given it lands on a branch tip in a specified crown section. Therefore,

$$\begin{aligned} P(E_7 \mid E_3) &= 0.61, \text{ for seed landing in the upper third of the crown,} \qquad (26) \\ &= 0.46, \text{ for seed landing in the middle third of the crown,} \\ &= 0.37, \text{ for seed landing in the lower third of the crown,} \end{aligned}$$

where

E_7 = the event that a seed is retained overwinter and is transported to an infective position,

E_3 = the event that a seed is intercepted by a given suscept.

Insects, molds, adverse weather conditions, and infertility are probably the most important factors in germination failure. Germination frequencies were recorded in 1968 and 1969 in a total of five localities (Roth, unpublished data). All seeds observed had overwintered after dispersal in natural conditions and were subjected to many different environmental forces. A seed was classed as germinated if the emerging radical was observed in early summer. The combined percentage of germination was found to be 80.3%. It is assumed that this percentage is an estimator for the germination probability; thus,

$$P(E_8 | E_3 \cap E_7) = 0.80, \tag{27}$$

where

E_8 = the event that a seed germinates,

E_3 = the event that a seed is intercepted by a given branchlet,

E_7 = the event that a seed is retained overwinter and is transported to an infective position.

Because the many conditions of the natural environment--weather, insects, seed fertility, and fungal action--were represented in the data, it is assumed that the estimated probability approximates the mean probability of germination in nature.

Not all seeds that germinate are able to penetrate and establish new plants. Three hundred seventy-two seeds which had germinated in an infective position were examined for infection (Roth, unpublished data). By the defined standards only 6.4% had indeed infected their hosts. The criteria upon which infection was judged to have occurred included turgidity of the seedling and disturbance of the host cortex; these factors were examined with the aid of a dissecting microscope.

Although these data represent but one year, the proportion of infecting seeds will be used as an approximation of the probability of infection given germination. Thus,

$$P(E_9 \mid E_3 \cap E_7 \cap E_8) = 0.064, \tag{28}$$

where

E_9 = the event that a seed infects a host,

$E_3 \cap E_7 \cap E_8$ = the event that a seed is caught by a branch, is retained in an infective position, and germinates.

Submodel Synthesis

In this section, certain probability rules and the submodels for estimating the probabilities of the series of events leading to infection will be used to generate an expression for the probability of infection for a given suscept by a seed from a given mistletoe plant. The series of events defined earlier are:

E_1 = the event that a seed lands on the tree that is host to the plant bearing the seeds,

E_2 = the event that a seed escapes the crown of the host tree in free flight,

E_3 = the event that a particular target branch tip (suscept) intercepts a seed,

E_4 = the event that a seed leaves the crown with an azimuth such that it can strike the given suscept,

E_5 = the event that a seed leaves the crown within a velocity and elevation range such that it can strike the given suscept,

E_7 = the event that a seed is retained overwinter and is transported to an infective position,

E_8 = the event that a seed germinates,

E_9 = the event that a seed infects a susceptible host.

Note that while E_1 and E_2 are disjoint occurrences, E_3 is a subset of the union of E_1 and E_2 (written: $E_3 \subset (E_1 \cup E_2)$), also $E_4 \subset E_2$, $E_7 \subset (E_1 \cup E_2)$, and $E_9 \subset E_8$.

Several formulas from statistical theory enable the manipulation of the probabilities associated with these occurrences. The multiplication rule for conditional probability with two events is

$$P(A_1 \cap A_2) = P(A_1) \cdot P(A_2 \mid A_1). \tag{29}$$

This means that the probability of both A_1 and A_2 occurring is equal to the product of the probability that A_1 occurs and the probability that A_2 occurs given that A_1 has occurred. This rule may be extended to the general case for more than two events:

$$\begin{aligned} P(A_1 \cap A_2 \cap \ldots \cap A_n) = {} & P(A_1) \cdot P(A_2 \mid A_1) \\ & \cdot P(A_3 \mid A_1 \cap A_2) \ldots \\ & \cdot P(A_n \mid A_1 \cap A_2 \cap \\ & \ldots \cap A_{n-1}). \end{aligned} \tag{30}$$

A susceptible branchlet may receive a seed as a result of reinfection or of contagion. After the suscept intercepts the inoculum, the succeeding events leading to infection are assumed to be independent of seed source. The assembly of the submodels, therefore, will be in two parts: first the probability of receiving a seed will be considered and then the probability of subsequent infection establishment will be discussed.

The reinfection case will be assembled first, Reinfection, by definition, is the result of a seed which was produced by a mistletoe plant on the same tree as the susceptible branchlet. Using equations (9) and (11) and the conditional probability multiplication rule (29), the probability of a branch being struck by a mistletoe seed coming from the same tree is found:

$$P(E_3 \cap E_1) = P(E_1) \cdot P(E_3 \mid E_1). \tag{31}$$

For seed dissemination to other trees, a similar process is followed. The probability that a seed escapes the host tree crown is estimated by equation (10). Combining this probability with the conditional probability of E_5 (21) by the conditional probability multiplication rule (29), the joint probability of a seed escaping the host crown and having a sufficient velocity and elevation to intercept a given susceptible target is found:

$$P(E_2 \cap E_5) = P(E_2) \cdot P(E_5 \mid E_2). \tag{32}$$

Because the occurrence of event E_4 is independent of E_5, it follows that

$$P(E_5 \mid E_2 \cap E_4) = P(E_5 \mid E_2). \tag{33}$$

Using the multiplication rule (30) and equations (14) and (32), the joint probability may be found:

$$P(E_2 \cap E_4 \cap E_5) = P(E_2) \cdot P(E_4 \mid E_2) \cdot P(E_5 \mid E_2), \tag{34}$$

where

$E_2 \cap E_4 \cap E_5$ = the event that a seed enters the "airspace" of a branch target on a tree other than the one on which the seed originated.

As previously stated, the target is not solid; hence, the probability of striking the branch given the seed reaches the target is computed by equation (24). Again combining by the multiplication rule (30), the probability of a branch being struck by a seed from an outside source may be found:

$$P(E_2 \cap E_4 \cap E_5 \cap E_3) = P(E_2) \cdot P(E_5 \mid E_2) \cdot P(E_4 \mid E_2) \cdot P(E_3 \mid E_4 \cap E_2 \cap E_5). \tag{35}$$

The events E_4 and E_5 are subsets of the event E_2 and $E_2 \cap E_3$ is wholly contained in $E_4 \cap E_5$. If a seed is intercepted by a branch on a tree other than the one on which the seed originated (which is the event $(E_2 \cap E_3)$), it must have had the velocity and elevation (E_5) and the azimuth (E_4) necessary for interception; therefore,

$$E_2 \cap E_3 = E_2 \cap E_4 \cap E_5 \cap E_3, \tag{36}$$

and

$$P(E_2 \cap E_3) = P(E_2 \cap E_4 \cap E_5 \cap E_3). \tag{37}$$

The probabilities associated with events E_7, E_8, and E_9 were considered without regard to inoculum source. They are assumed to be dependent upon the receipt of a seed (E_3) and to be independent of seed source. Therefore,

$$\begin{aligned} P(E_7 \mid E_3) &= P(E_7 \mid E_3 \cap E_1) \\ &= P(E_7 \mid E_3 \cap E_2), \end{aligned} \tag{38}$$

$$\begin{aligned} P(E_8 \mid E_3 \cap E_7) &= P(E_8 \mid E_3 \cap E_1 \cap E_7) \\ &= P(E_8 \mid E_3 \cap E_2 \cap E_7), \end{aligned} \tag{39}$$

$$\begin{aligned} P(E_9 \mid E_3 \cap E_7 \cap E_8) &= P(E_9 \mid E_3 \cap E_1 \cap E_7 \cap E_8) \\ &= P(E_9 \mid E_3 \cap E_2 \cap E_7 \\ &\quad \cap E_8). \end{aligned} \tag{40}$$

Equations (38), (39), and (40) estimate respectively the conditional probabilities of: transport to an infective position (E_7) given interception (E_3), germination (E_8) given interception (E_3) and transport to an infective position (E_7), and infection (E_9) given interception (E_3), transport (E_7), and germination (E_8). These equations may be combined by the conditional probability multiplication rule (30) to give the two expressions:

$$P(E_1 \cap E_3 \cap E_7 \cap E_8 \cap E_9) = P(E_1 \cap E_3) \cdot P(E_7 \mid E_3) \cdot P(E_8 \mid E_3 \cap E_7) \cdot P(E_9 \mid E_3 \cap E_7 \cap E_8), \quad (41)$$

$$P(E_2 \cap E_3 \cap E_7 \cap E_8 \cap E_9) = P(E_2 \cap E_3) \cdot P(E_7 \mid E_3) \cdot P(E_8 \mid E_3 \cap E_7) \cdot P(E_9 \mid E_3 \cap E_7 \cap E_8). \quad (42)$$

Equation (41) estimates the probability of infection of a given suscept by a seed from a given mistletoe plant hosted on the same tree. Equation (42) estimated the probability of infection of a given suscept by a seed from a given mistletoe plant hosted by another tree. These estimates are specific for both the suscept and the source of inoculum.

Simulation Assembly

The previous section showed a way of determining the probability that a branch tip would become infected by a seed from a specified plant. This probability expression forms the basis for calculating the probability of infection for any simulated branch tip and the expected number of infected tips per whorl of branches. The primary concern of the simulation is determination of these probabilities and expected numbers for a representative tree within the constructed stand.

This discussion of the assembly of the simulation will include four parts: 1) outline of the method of assembling the probabilities, 2) discussion of the hypothetical stand, 3) inputs and outputs, and 4) a description of the programming of the simulation.

Outline of the Simulation

In the preceding section, the method for calculating the probability of infection of a particular branch by seed of a particular mistletoe plant was given. The maintenance of this level of resolution presents many problems in information storage and, indeed, interpretation. The focus of the simulation will be on the number of infected branches per whorl regardless of inoculum source rather than on the number of infections per branch.

To find the probability of infection of a particular susceptible branch, the probabilities from all the potential sources must be combined. Let the probability (41, 42) that was generated in the preceding section be represented by $p_{i,j}$. It is the probability that the given suscept is infected by a seed from the i^{th} mistletoe plant on the j^{th} tree (the j^{th} tree may be any tree in the stand including the representative tree upon which we will focus) given that the j^{th} tree is infected. Then $1 - p_{ij}$ is the probability that the branch escapes infection by an individual seed from this plant. All seeds from a plant are assumed to have the same probability of infecting or not infecting any given branch and it is assumed that these probabilities are independent between seeds; hence, the joint probability for not infecting is the product of these probabilities. Thus, the expression

$$\prod^{s} (1 - p_{i,j}) = (1 - p_{i,j})^{s} \qquad (43)$$

is the probability that none of the seeds from the i^{th} plant on the j^{th} tree infects the target branch given that the j^{th} tree is infected and where s is the number of seeds produced by the i^{th} plant on the j^{th} tree which may potentially infect the branch tip and produce a female plant (estimated by equation (8)). Let

$$PP_{i,j} = 1 - (1 - p_{i,j})^{s} . \qquad (44)$$

The probability ($PP_{i,j}$) generated by this expression will be the probability of a given branch being infected by at least one of the seeds of the i^{th} mistletoe plant. If the j^{th} tree has n plants and if the $PP_{i,j}$ $(i = 1, \ldots, n)$ are assumed to be independent, then the joint probability of none of the plants being a cause of infection for our given branch becomes:

$$\prod_{i=1}^{n} (1 - PP_{i,j}) \qquad (45)$$

and the joint probability of at least one of the plants on the j^{th} tree causing an infection on our branch is

$$1 - \prod_{i=1}^{n} (1 - PP_{i,j}) . \qquad (46)$$

The preceding arguments are based on the assumption that the j^{th} tree is infected; thus, the probability of this tree being infected is needed. A mean infection probability, r, is specified for the trees of the hypothetical stand. Contagious diseases generally form spatial patterns with respect to infection intensity. However, since the simulation is concerned with any representative tree, the tree containing the particular branch will be assumed to be infected with the mean probability r, as will all the surrounding trees. The rate of spread of this disease between trees is slow; hence, for simulations of relatively short periods r may be assumed to be constant. To find the probability that the branch is infected by some mistletoe plant on the j^{th} tree and, simultaneously, that the j^{th} tree is infected, we need only to apply the conditional probability multiplication rule (29) and multiply r by expression (46).

To extend the expression from one potential source to all sources of inoculum, all the trees in the forest must be considered. Of course, many will be too far away to provide a source of mistletoe seeds, so the probability of seed from plants hosted by these trees causing an infection on the particular branch will be zero. All trees are assumed to be independent with respect to probability of hosting a plant that can cause an infection on the branch. If there are N trees in the hypothetical stand, then the joint probability of a branch escaping infection will be

$$\prod_{j=1}^{N} [1 - r(1 - \prod_{i=1}^{n} (1 - PP_{i,j}))] \tag{47}$$

and the probability of a branch becoming infected regardless of source is

$$1 - \prod_{j=1}^{N} [1 - r(1 - \prod_{i=1}^{n} (1 - PP_{i,j}))] . \tag{48}$$

The probability of a branch becoming infected was computed by an indirect method. The probabilities of not infecting were computed first because this eliminated the problem of dealing with multiple infections. For example, if the probability of at least one seed from the i^{th} plant on the j^{th} tree infecting the given branch tip is computed directly, the probability of one seed infecting would need to be added to the probability of two seeds, to the probability of three, and so forth. The solution is much simpler if the disjoint probability of none infecting is subtracted from one simply leaving the probability of infection.

Hypothetical Stand

The particular hypothetical stand on which the simulation is based was arrived at using three criteria: 1) the general relationship between the hypothetical stand and probable future stands in nature, 2) availability of data, and 3) judgments on the degree of complexity which could be handled. As previously discussed, one of the purposes of the simulation is to help in evaluating management plans where dwarf mistletoe is a problem. This goal prompted the decision to make the hypothetical stand a young managed forest with a moderate infection level--one in which stand density and mistletoe abundance could be modified by silvicultural practices. The data for nearly all the submodels came from young pine stands on the Pringle Falls Experimental Forest southwest of Bend, Oregon. The trees were in a variety of conditions, but commonly were between 10 and 25 feet tall and growing in thinned stands with the immediate overstory removed. The degree of complexity increases rapidly when even a few variables are incorporated into a model. This problem necessitated the incorporation of average values for some variables rather than more realistic ones which would vary with varying conditions. Compromises had to be made where data were not available.

Within the hypothetical stand trees are nearly alike. It is a thinned, managed stand, the trees are evenly spaced so that a tree is equally distant from each of its six nearest neighbors. All trees are uniform in height and increase in height by a common rule. The infection is uniform over the entire stand and any tree which is infected has the same number of mistletoe infections at the same heights and ages. The stand is considered to be on level ground. A mistletoe seed which enters the crown volume of a tree other than that in which it was produced is assumed to either be caught or deflected, but not to fly on to be possibly intercepted by the crown of another tree. These conditions and relationships persist through time with tree growth occurring and the probability of infection for any branch and possibly the number of infections changing.

How realistic is this representation of a stand? Its counterpart in the real world does not, of course, exist, but it does perhaps represent in a general way a category of young forests. These forests may have arisen after fire or logging. When thinned pre-commercially, their crowns become symmetrical and well filled out. They retain a very uniform appearance and growth pattern. Initial dwarf mistletoe infections originally entering this uniform stand from a few residual overstory trees would be fairly similar in height and age. Although the hypothetical stand of the simulation is greatly simplified and somewhat stylized, reality of the managed young forest is believed to be partly retained.

Inputs and Outputs

Input variables are used to initialize the conditions for simulating special cases of interest. These variables include the first year values for tree height, the numbers of whorls, years since thinning, and mistletoe plants on infected trees, and the ages of these plants. Invariate values for the spacing, heights of the initial infections, probability that a tree is infected, and mean yearly growth increment as well as the number of years to be simulated are also input. The tree height may range between 10 and 25 feet but must be initialized such that the simulated height after the specified number of years does not exceed 25 feet. The number of whorls is closely related to the tree height, years since thinning, and the mean yearly growth rate and must be made compatible with these. A plant of a certain age must not be placed at such a height that the wood there is younger than the plant and, because the submodels were developed on thinned stands, spacing may not be set less than 9.00 feet. By specifying these initial values, many different cases may be observed. Of particular interest will be the impact of various spacings and plant numbers on the probability of infection for branches of different heights.

The output includes a set of whorl numbers for the representative tree beginning with the top whorl as number one and continuing downward to the last live whorl on the tree. For each whorl the branch tip height is given along with the probability of infection from inoculum originating on the host tree, probability of infection from inoculum originating on another tree, probability of infection regardless of source, and the expected number of infections on the whorl.

Simulation Programming

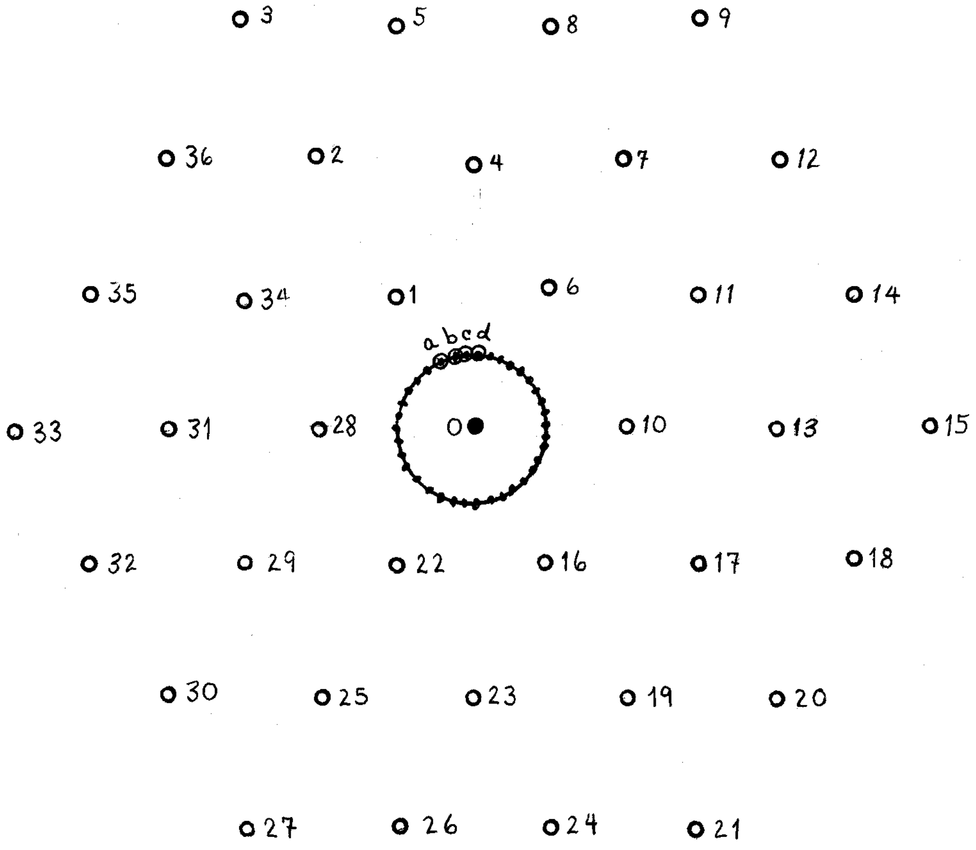
The simulation computer program is in four parts: a main calling program and three subroutines. The main program, MEPSIM, computes and combines most of the probabilities according to the plans outlined in the discussion of the submodels and the simulation assembly. It also calls the subroutines; SIML is used to calculate the target branch height and angle, INFEST computes the probability of infection from a source on the same tree, and BLOCK calculates the probability of a seed having a velocity with the range needed to clear any intervening trees and strike any given target. To facilitate programming further assumptions and simplifications were necessary.

The weighted mean plant height was used as the height of seed discharge from adjacent trees. The mean was weighted by the expected number of seeds produced by the mistletoe plants. It was shown in preliminary simulations that the mean height gave a good approximation of the results obtained by allowing each plant height to be entered separately.

A Cartesian coordinate system is used to identify the trees in the hypothetical stand with the center of the base of the representative tree at the origin (0, 0). All trees are postulated to be equidistant to their six nearest neighbors; therefore, the stand forms a regular pattern (Figure 3). It is assumed that trees at a greater distance than three spacing units from the representative tree have no effect on it. Using the maximum velocities at which seeds were found to fly, this assumption was found to be safe for spacings greater than nine feet. This assumption means that 36 trees may possibly be outside sources of inoculum.

Figure 3. Tree spacing pattern of the hypothetical stand.

The reference tree is numbered 0 and the positions of the surrounding trees are numbered 1 to 36. The circle around the reference tree represents the perimeter of its crown and the dots on this perimeter represent 36 equal spacings.



To find the probability of infection of a representative branch tip on each whorl, a sample of the possible branch tip positions is taken. If the circumference of the crown at the branch height is divided into 36 positions, it can be seen (Figure 3) that there are four unique points (A, B, C, D) with respect to vulnerability to outside inoculum and the rest are repetitions. Likewise, there are five unique trees (1, 2, 3, 4, 5) and the rest are repetitions with respect to their relationship to the tree of interest. It is assumed that a seed cannot strike a branch tip which is beyond the point where a line from the host tree is tangent to the target tree. Notice that point A is potentially vulnerable to trees 1, 2, 3, 4, 5, 6, 7, 8, 9, 11, 12, 28, 31, 32, 33, 34, 35, 36. A corresponding relationship between point A and each of the trees can be found between one of five unique trees and one of the first nine positions on the circumference of the crown starting clockwise with A as point 1. Likewise these relationships can be defined for points B, C, and D so that the vulnerability of the four unique points to any of the trees can be represented by a combination of one of the five unique trees and the first 18 positions. To calculate an estimate of the mean probability of infection over all positions, the probability for each of the four unique points is multiplied by the number of repetitions it represents and these are summed and divided by 36.

The result of each year's inoculum dispersal may be considered as an experiment with but one of two exclusive and exhaustive outcomes for each susceptible branch tip: infection or not infection. Each branch tip on a whorl may be considered a repetition of this experiment with the probability of infection equal to the generated mean probability of infection for a tip on the particular whorl. If it is assumed that these repetitions are mutually, stochastically independent, then the probability of any particular number of infections on a whorl will be distributed according to the binomial distribution. From the binomial distribution it may be found that the expected number of infections on a given whorl will be equal to the product of the number of susceptible branch tips on the whorl and the probability of infection for a tip on the particular whorl. Using the estimated number of branches per whorl and the generated probabilities, the expected number of infections for each whorl is calculated.

RESULTS

The modeling exercise described here is used not only to simulate dwarf mistletoe population changes in one-year increments on a hypothetical stand but also to focus on specific aspects of its population dynamics. Three types of partial simulations are used to gain insights into the subtle importance of mistletoe plant height and tree spacing. These simulations concern the paths of the flying mistletoe seeds, the probability of infection of one target by one seed source, and the probability of interception of a seed by a branch on the host tree. Seven cases are examined using the complete simulation model; these include three tree spacings with two moderate levels of infection simulated for five years each and one with a heavy infection level simulated for ten years. The results are examined to assess changes in (a) the probability of infection with respect to tree spacing within the hypothetical stand, branchlet target height, infection level, and time, and (b) the expected number of new infections.

To determine areas of greatest probable seed fall, the modeled trajectories of the free flying mistletoe seed are examined. This examination begins with the definition of specific discharge velocities which were thought to be important. For each of the nine angle groups (measured from the vertical $0-10^{o}$, $10-20^{o}$, $20-30^{o}$, etc.) three velocities were computed based on equation (17): the lower limit of the velocity range, the median, and the upper limit velocity (Table 9).

Using the ballistics formula, trajectories representing the paths of seed discharged at the median angle of each of the nine elevational groups and the initial velocities of each of the three computed velocities for that group, were plotted over a distance of 20 feet. From these model patterns certain inferences may be drawn concerning the fate of mistletoe seed after discharge. The paths of seed leaving with the maximum velocity (upper limit trajectories) demonstrate the potential of plants to initiate infections at heights greater than their level for a lateral distance of over 20 feet (Figure 4). By examining the trajectories of seeds leaving at the median velocity, it may be seen that, for levels above that of the source plant, seed would most likely be intercepted by targets nearer than 15 feet (Figure 5). Indeed, few interceptions would be expected at heights greater than seven feet above the level of the source plant. This inference is again supported by the calculation of the probabilities of seed discharge within the various angle groups (Table 8). The angles which are nearest the vertical and, therefore, have the highest trajectories are also lowest in probability of occurrence. Interception of seed by targets below the inoculum source would be expected to be most likely on trees greater than seven feet from the host tree (Figure 5). On trees more than 17 feet away, the majority of the resulting interceptions

Figure 4. Traces of the trajectories expected for projectiles with initial angles of 5°, 15°, 25°, 35°, 45°, 55°, 65°, 75°, 85° and initial velocities equal to the maximum velocities found for the mistletoe seeds (Table 9). The trajectories were computed using equation (12).

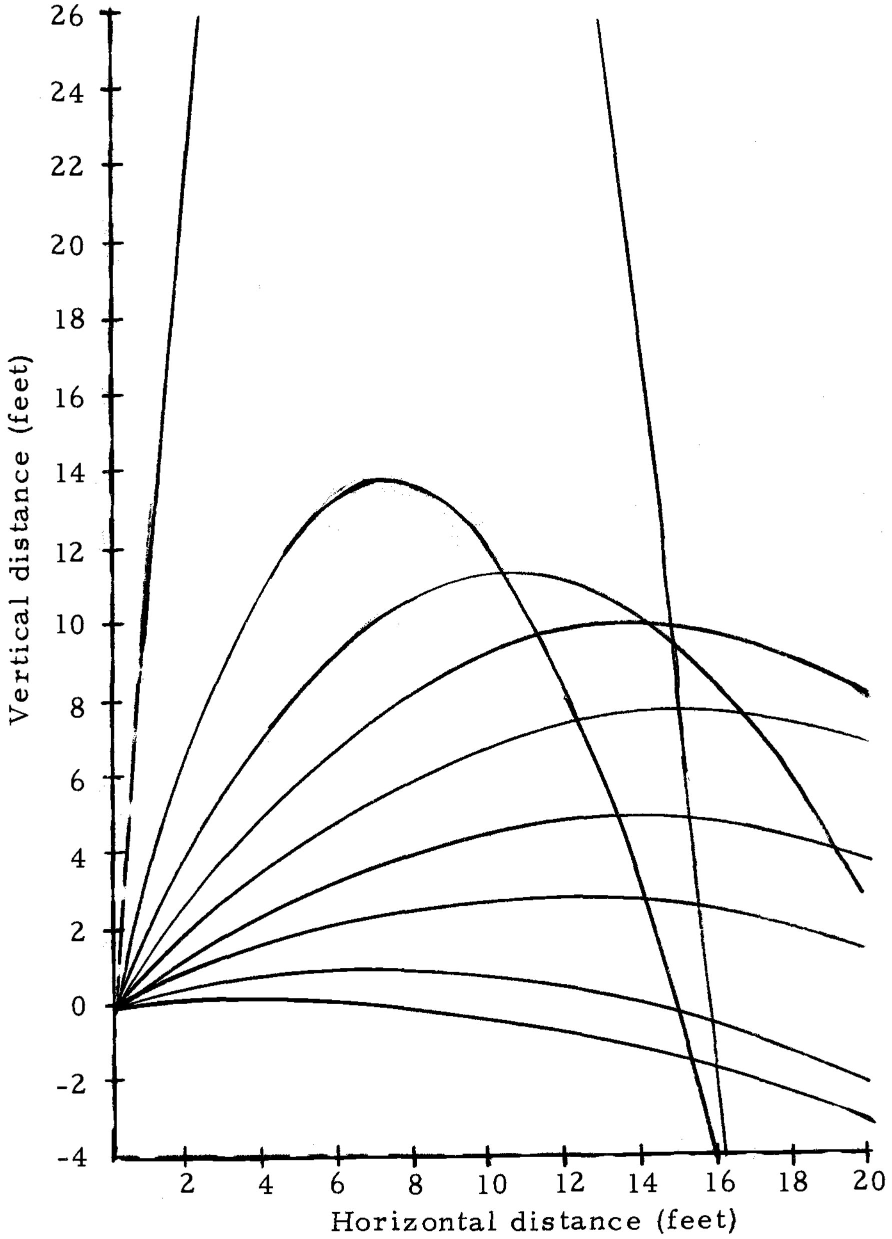
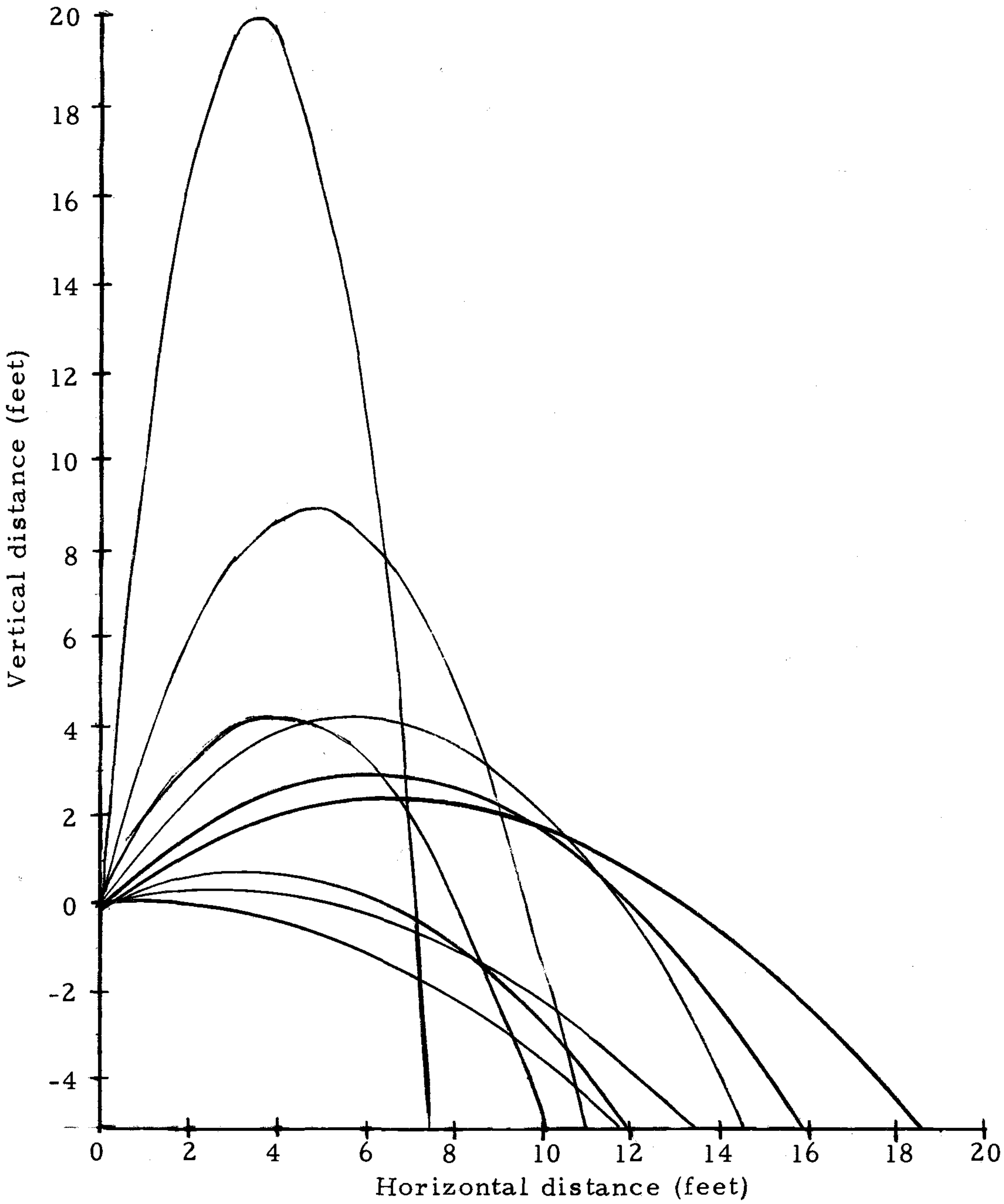


Figure 5. Traces of the trajectories expected of projectiles with initial angles of 5°, 15°, 25°, 35°, 45°, 55°, 65°, 75°, 85° and initial velocities equal to the mean velocities found for the mistletoe seeds (Table 9). The trajectories were computed using equation (12).



would be expected to be more than five feet below the level of the discharging plant. The trajectories of seeds with the minimum observed velocities show that there is little chance of a target escaping a seed by being too near the host tree (Figure 6). If the plant height were 10 feet, targets would need to be within three feet of the source tree to escape possible seed interception.

The potential radius of spread is greater for seeds from mistletoe plants of greater heights. Again using the ballistics formula (12), the horizontal distance of seed flight by seeds traveling at the maximum observed velocity for each angle group was computed for plants at heights from 5 to 20 feet (Table 10). Note, for seeds leaving at these velocities, the radius of spread increases with increasing plant height (e. g. a maximum radius of spread of 39. 39 feet for a plant 5 feet above the ground, and 47. 97 feet for a plant 20 feet above the ground). The median velocities were used to calculate the distances more likely to be expected (Table 11). The radius of spread for a plant at 20 feet above the ground is 32 feet, a distance of nearly 10 feet greater than the expected radius from a plant at 5 feet above the ground. Observations concerning the flight patterns of the mistletoe seeds seem to point to the importance of the plants high in the crown with respect to their potential for spreading seed to adjacent trees.

To assess the effects of different spatial relationships between source and target on different trees, the probability of infection of one

Figure 6. Traces of the trajectories expected of projectiles with initial angles of 5°, 15°, 25°, 35°, 45°, 55°, 65°, 75°, 85° and initial velocities equal to the minimum velocities found for the mistletoe seeds (Table 9). The trajectories were computed using equation (12).

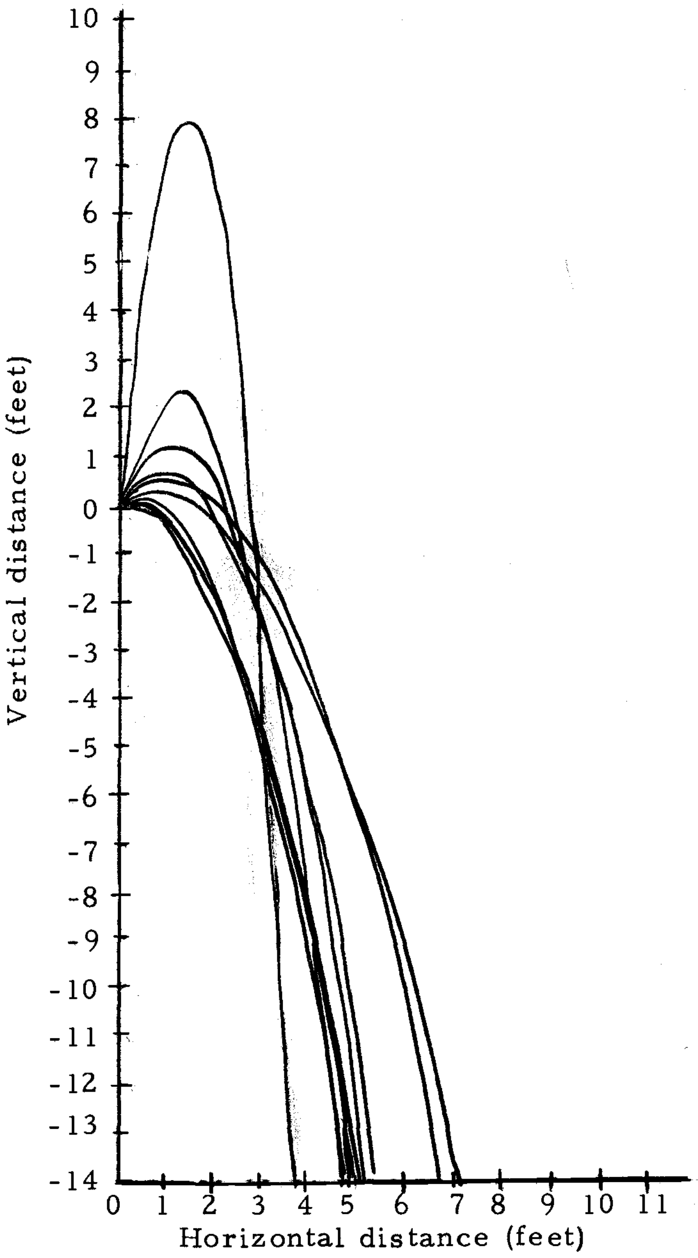


Table 10. The horizontal distance of seed flight by seeds traveling at the maximum velocity for each angle group and leaving from plants at varying heights.

Angle group	Horizontal distance (ft)			
	Plant height (ft)			
	5	10	15	20
0-10°	16.25	16.66	17.05	17.42
10-20°	16.25	17.33	18.31	19.20
20-30°	23.67	25.48	27.10	28.57
30-40°	29.56	32.18	34.48	36.55
40-50°	36.39	40.00	43.13	45.93
50-60°	36.03	40.64	44.53	47.97
60-70°	32.58	38.25	42.89	46.92
70-80°	24.69	30.99	35.96	40.18
80-90°	24.65	33.09	39.59	45.09

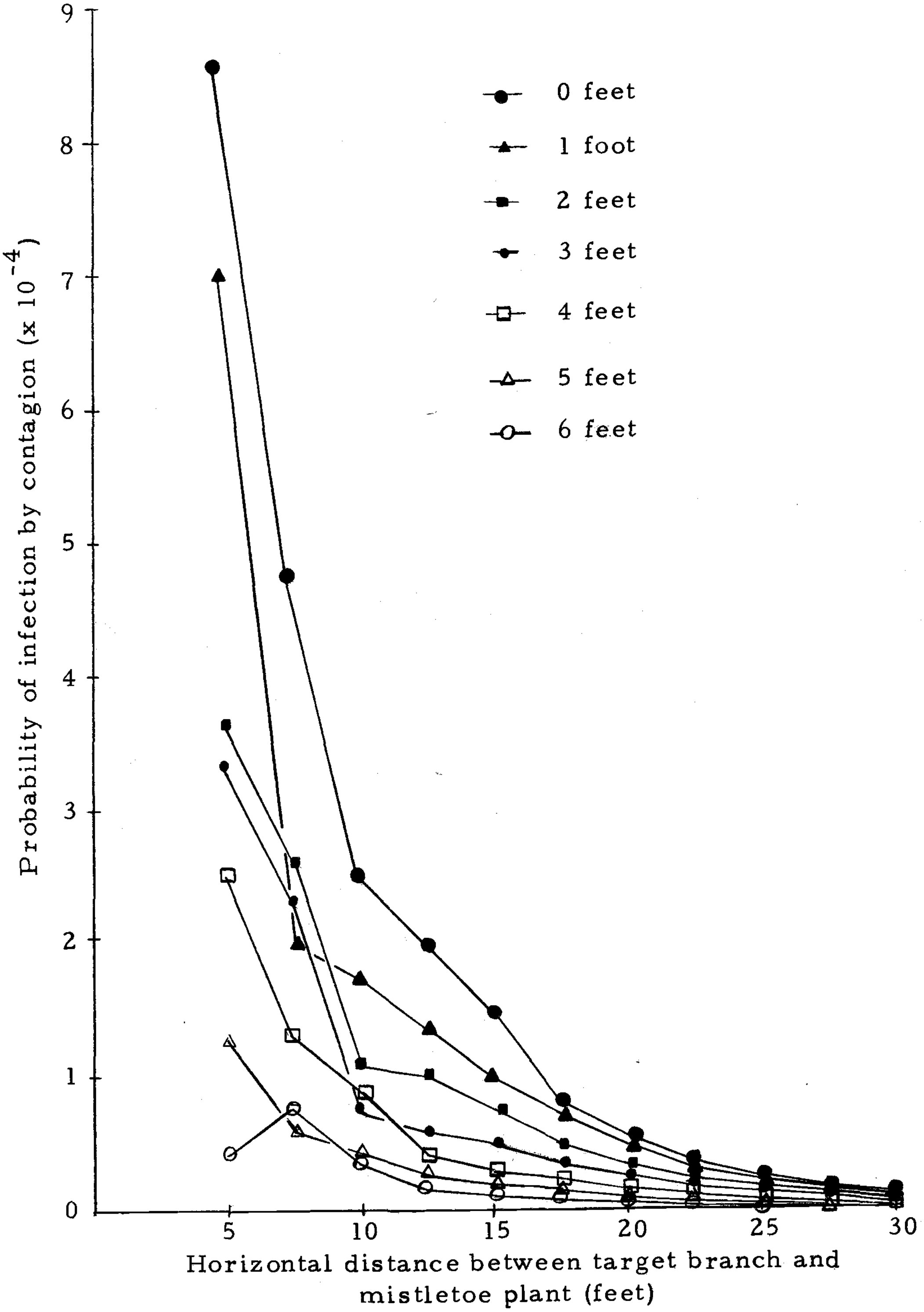
Table 11. The horizontal distance of seed flight by seeds traveling at the median velocity for each angle group and leaving from plants at varying heights (horizontal distance in feet).

Angle group	Horizontal distance (ft)			
	Plant height (ft)			
	5	10	15	20
0-10°	9.99	10.38	10.75	11.09
10-20°	13.03	14.07	14.99	15.82
20-30°	10.09	11.51	12.70	13.75
30-40°	15.82	17.99	19.82	21.42
40-50°	19.09	22.00	24.42	26.53
50-60°	22.32	26.15	29.29	32.00
60-70°	12.73	16.12	18.77	21.03
70-80°	13.02	17.05	20.18	22.83
80-90°	11.27	15.53	18.80	21.55

susceptible branchlet by inoculum from one source at varying heights and distances is computed. The height of the representative host tree is set at 15 feet and the plant height varies between 5 and 10 feet. Target suscept heights are set from four feet below to six feet above the mistletoe plant heights and spacing distances range from 5 to 35 feet. Since the number of seeds discharged by the plant is arbitrarily set at 100, the actual probabilities do not necessarily reflect the probabilities computed for a single plant in the more complete simulation model. However, it is hoped that the trends in probability with respect to the spatial relationship between the target and the plant do represent the workings of the model in simplified terms.

Certain inferences may be made concerning the modeled relationship between the probability of infection and the spatial position of inoculum source and target by examination of the probability trends. When the height of the target is greater than that of the mistletoe plant, the probability of infection decreases with an increase in spacing distance in a pattern resembling a decay curve (Figure 7). The probability declines rapidly until a distance of about 12 feet and then continues a slower decline until it approaches zero at 35 feet. When the target height is set at six feet above that of the seed source, the probability of infection of that target is at a low level even at close spacings. However, if the target is below the inoculum source, there is a peaked curve which broadens and flattens as the difference

Figure 7. The relationship between the probability of infection by contagion and the lateral distance between the suscept and inoculum source for suscepts at heights equal to or greater than the height of the inoculum source. The individual curves represent the height difference (suscept height - mistletoe plant height) in feet.

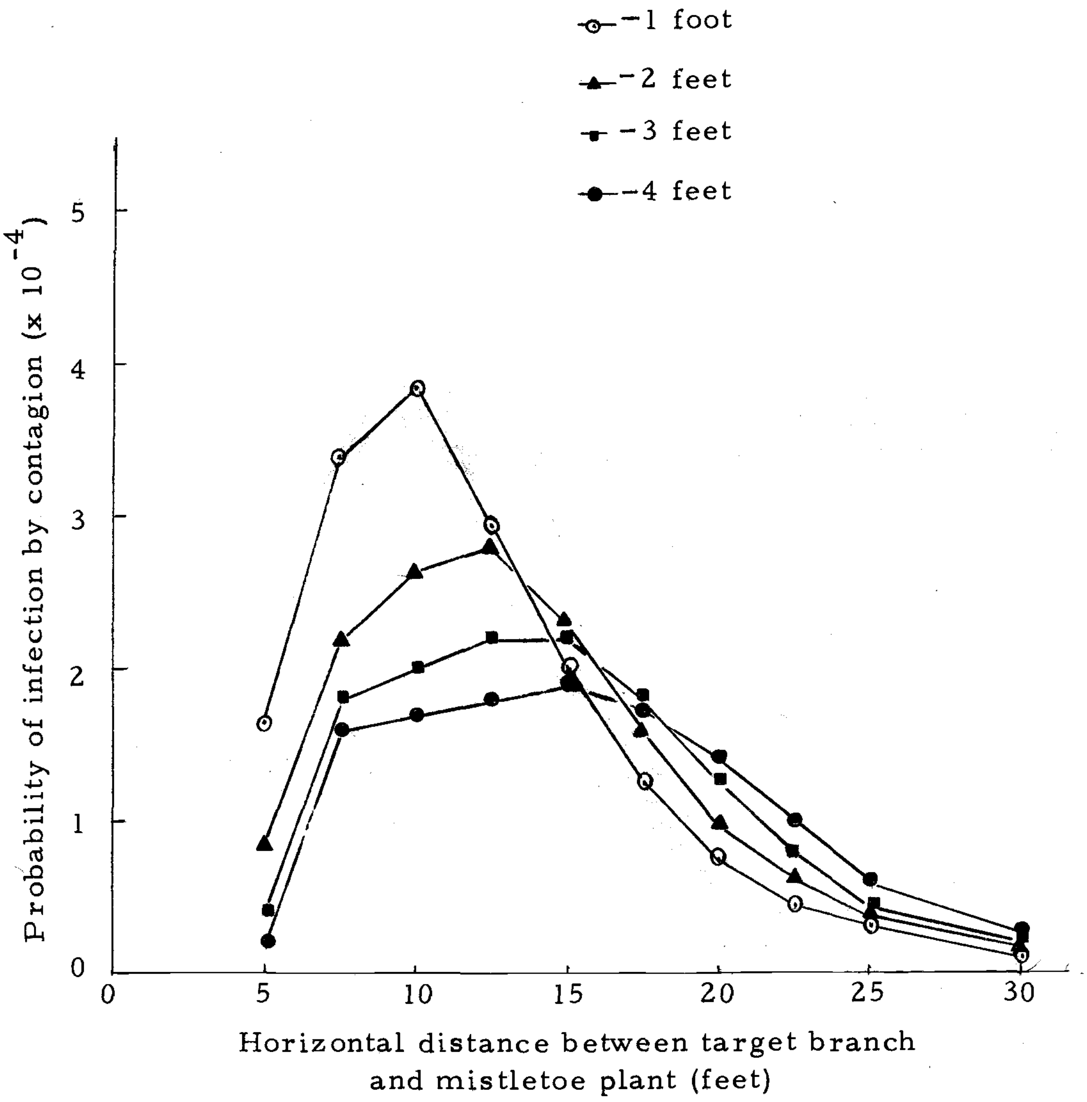


between their heights is increased (Figure 8). The probability of infection of these targets is low until the distance between the source and target trees is about seven feet. The highest probabilities are found between 7.5 and 15.0 feet spacing distances in the cases observed. After a distance of 17.5 feet is reached the probability of infection is greatest for targets at heights furthest below the source of inoculum.

It is important to note that the inferences concerning infection probability closely agree with those made when considering possible seed interception. This fact follows as a consequence of the seed interception model being a major internal part of the contagion probability submodel.

Mistletoe seeds are not only intercepted by suscepts on adjacent trees but also by ones on the host tree. The position of the susceptible target and the inoculum source with respect to each other and the surrounding tree crown determines the probability of seed interception by the suscept. To analyze the consequences of the reinfection submodel, several cases with varying branchlet and mistletoe plant heights are examined with respect to changes in seed interception probability. The height of the representative tree is input for this case at 12 feet and the target heights range from 5 to 12 feet while heights of the inoculum source range from 5 to 10 feet. The probabilities computed are the conditional probabilities that a seed

Figure 8. The relationship between the probability of infection by contagion and the lateral distance between the suscept and inoculum source for suscepts at heights less than the height of the inoculum source. The individual curves represent the height difference (suscept height - mistletoe plant height) in feet.



lands on a branch at a particular distance above the source plant given that it is indeed trapped by the host tree at some point (Table 12).

Table 12. Probability of interception of a mistletoe seed by branches of different heights and plants of different heights, where the mistletoe plants and the target branches are in the same tree crown. The interception probability is uniform over the branch height range.

Branch height range (ft)	Plant height (ft)					
	5	6	7	8	9	10
5-6	.0037					
6-7	.0044	.0035				
7-8	.0025	.0047	.0038			
8-9	.0011	.0029	.0054	.0043		
9-10		.0023	.0059	.0109	.0087	
10-11			.0046	.0115	.0215	.0171
11-12				.0319	.0797	.1495

From the model it may be seen that the ratio of volume of the target to the volume of the one-foot band in the crown which contains the susceptible target largely explains the differences between interception probabilities for branches with the same distance from mistletoe plants of different heights. This difference is demonstrated by the nearly five-fold difference in interception probability for a branch in a band from one to two feet above the inoculum source when the inoculum source is at a height of five feet than when it is at a height of nine feet (Table 12). In zones where the crown is wider the seeds have a larger volume over which to disperse. This greater volume reduces the chances that any particular branch will be struck. At the same time, in the area where the crown is widest, the foliage is sparser and, therefore, the modeled volume of the target is accordingly diminished (Table 7). However, the probability of a seed reaching a certain band height above the mistletoe plant decreases as the distance above increases while at the same time the crown width decreases (Table 5). The problems of reaching a given level above the plant and the problems of landing on a particular branch within that level are compounded, producing an irregular pattern of probability of seed interception which depends both on the distance of the target above the plant and on their relative positions in the crown.

The complete simulation is used to examine seven cases. For three of the cases information concerning a real situation is used in formulating the input variables. It is hoped not only to compare these cases with each other and the other four cases but also to compare them with future observations on the real situation. The first three runs of the simulation represent approximately the mean infection distribution and the three tree spacings found at an experimental area in the Pringle Falls Experimental Forest (Roth, unpublished report). Two mistletoe plants per infected tree represent this level of infection; the plants are located at heights of 6 and 8 feet and are 8 and 3 years old, respectively. The mistletoe plant and infection probability regimes are the same for the three runs which represent spacings of 9, 13, and 18 feet. For all seven cases the tree heights were initialized at 10 feet and the probability of infection of any tree was set at 0.60. The second set of three cases is used to see how the addition of two inoculum sources per infected tree affects the probability of infection. Four mistletoe plants are input at heights of 5, 6, 7, and 8 feet and ages 11, 8, 5, and 3 years respectively. All other inputs are the same as in the first three cases again with each case representing a different tree spacing distance. These six cases simulate mistletoe distribution changes for five years. The seventh case is used to explore the effect that an intensive infection load and close spacing has on the probabilities of infection over a period of 10 simulated years. Fifteen plants are input at heights of 5.0, 5.25, 5.5, 5.75, 6.0, 6.25, 6.5, 6.75, 7.0, 7.25, 7.5, 7.75, 8.0, 8.25, and 8.5 feet at ages of 11, 10, 10, 9, 8, 7, 7, 6, 5, 5, 4, 4, 3, 3, and 3 years, respectively. The spacing between trees is set at 9 feet and all other initializing variables are the same as in the previous six cases. The results are printed out such that the probability of a branch becoming infected by a seed from another tree and the probability that it becomes infected by a seed from a mistletoe plant on the same tree, as well as the combined probability of infection, are listed separately for each whorl of the representative tree and for each of the simulated years.

Implications of the complete model concerning the probability of infection are analyzedby examining the results of the seven simulated cases. In the first simulated year the probability of infection of a branchlet in all cases shows a general increase with an increase in the height of the target branch (Figure 9). At heights above the lowest source of inoculum, the most important contribution to the probability of infection is from internal reinfection. Whereas, the probability of infection from external sources generally decreased as the height of the branchlet target increased, this effect on the total probability of infection is not great enough to offset the effect of the increasing reinfection probabilities. Also, the effect of the external inoculum sources decreases with increased spacing distances. The results of all seven cases point at the importance of the reinfection process over that of contagion in the model.

The number of mistletoe seeds produced by plants on the infected trees in the hypothetical stands changes with time as the mistletoe plants age. The probability of infection for a branch at a particular height, therefore, also changes with time. For heights below the lowest inoculum source the pattern of change closely resembles the relationship between seed numbers and time (Figure 10). At mid-crown heights (6-8 feet) over the 10 simulated years the probability of infection is increasingly influenced by the inoculum produced by infections on outside trees (Figure 11). Branches high (9-11 feet) in

Figure 9a. Distribution of the probability of infection for branches on a representative tree in a stand where trees are spaced 9 feet apart, there are 2 mistletoe infections per infected tree, and there is an infection rate of 0.60 for the entire stand.

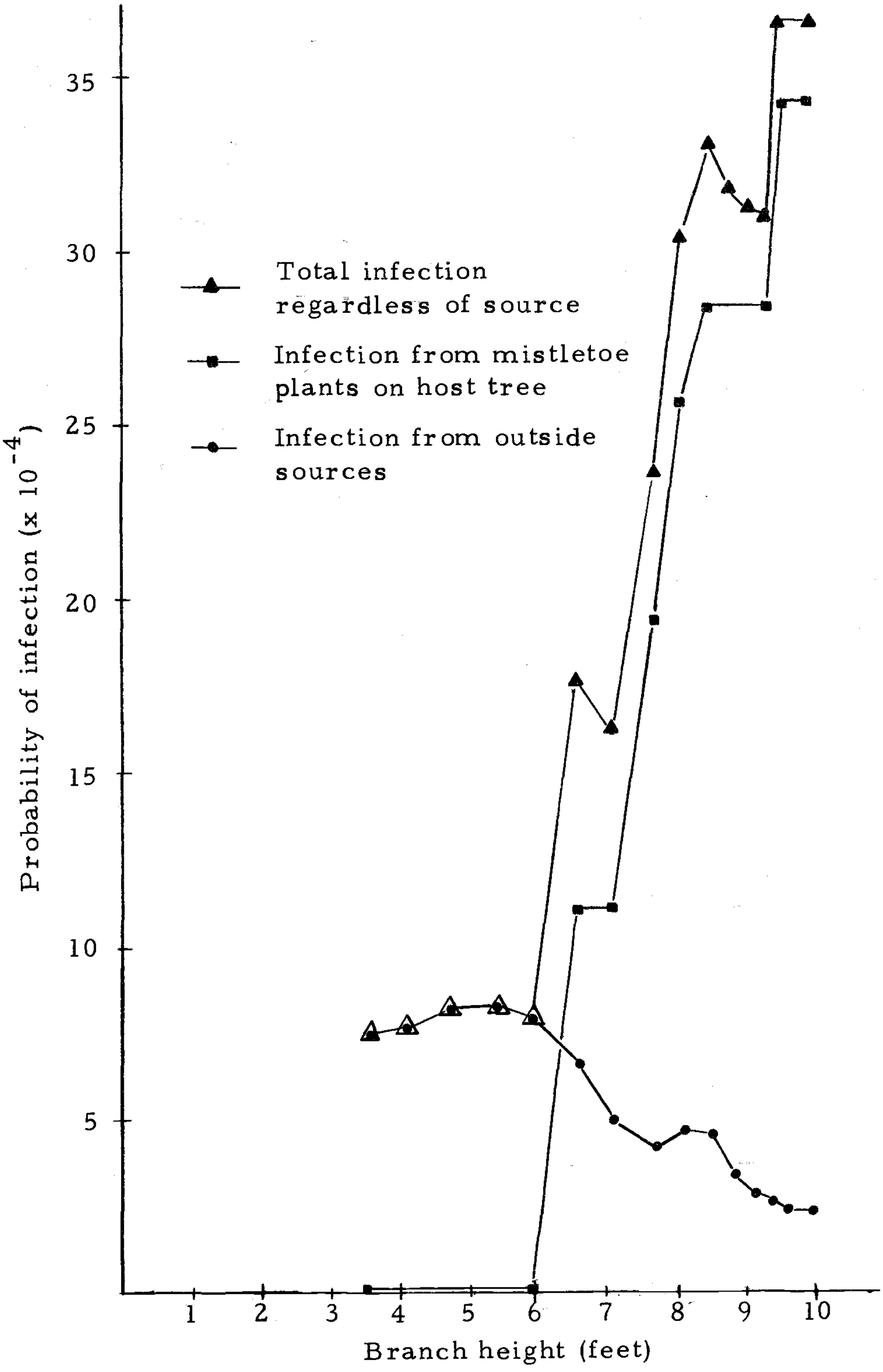


Figure 9b. Distribution of the probability of infection for branches on a representative tree in a stand where trees are spaced 9 feet apart, there are 4 mistletoe infections per infected tree, and there is an infection rate of 0.60 for the entire stand.

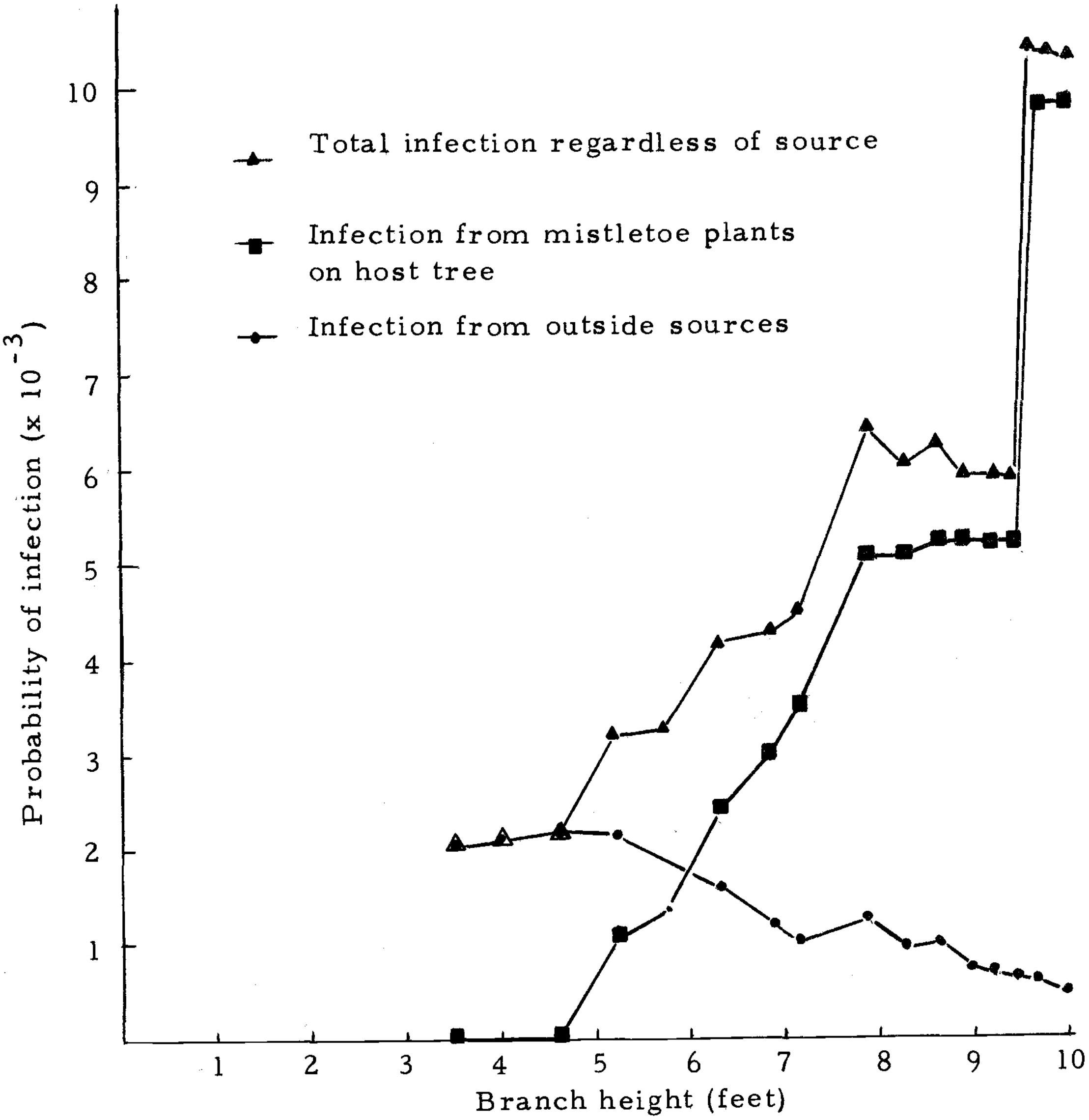


Figure 9c. Distribution of the probability of infection for branches on a representative tree in a stand where trees are spaced 13 feet apart, there are 2 mistletoe infections per infected tree, and there is an infection rate of 0.60 for the entire stand.

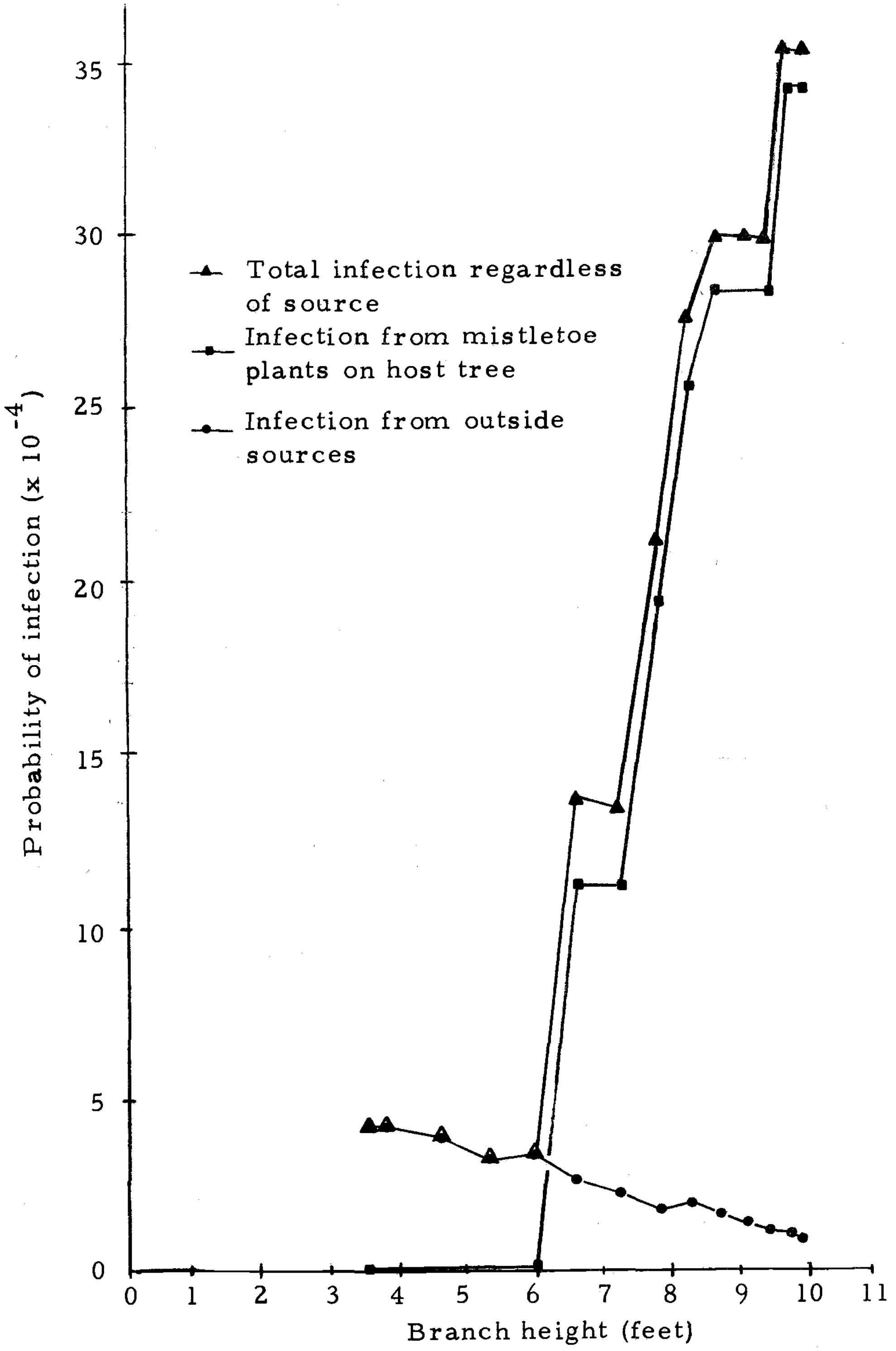


Figure 9d. Distribution of the probability of infection for branches on a representative tree in a stand where trees are spaced 13 feet apart, there are 4 mistletoe infections per infected tree, and there is an infection rate of 0.60 for the entire stand.

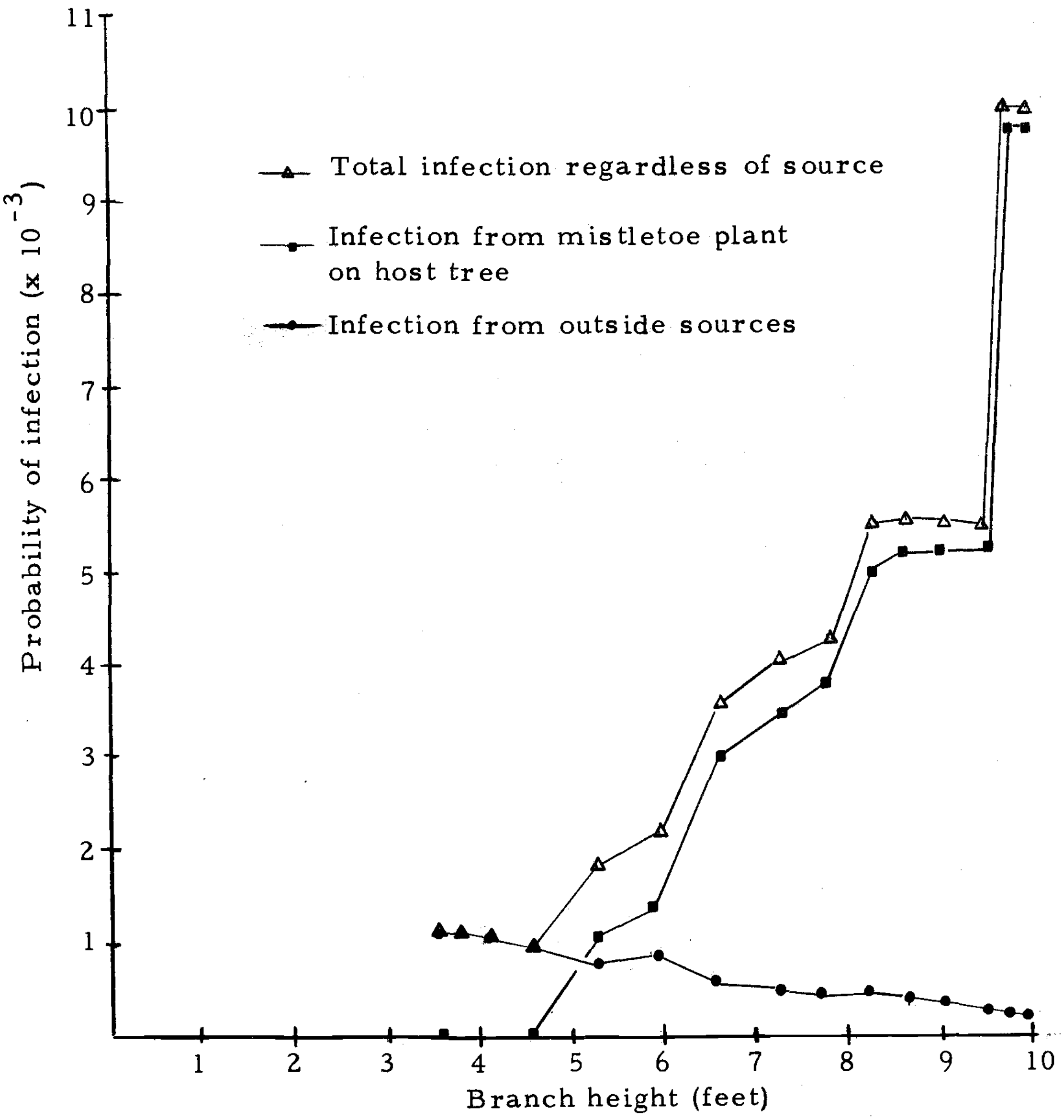


Figure 9e. Distribution of the probability of infection for branches on a representative tree in a stand where trees are spaced 18 feet apart, there are 2 mistletoe infections per infected tree, and there is an infection rate of 0.60 for the entire stand.

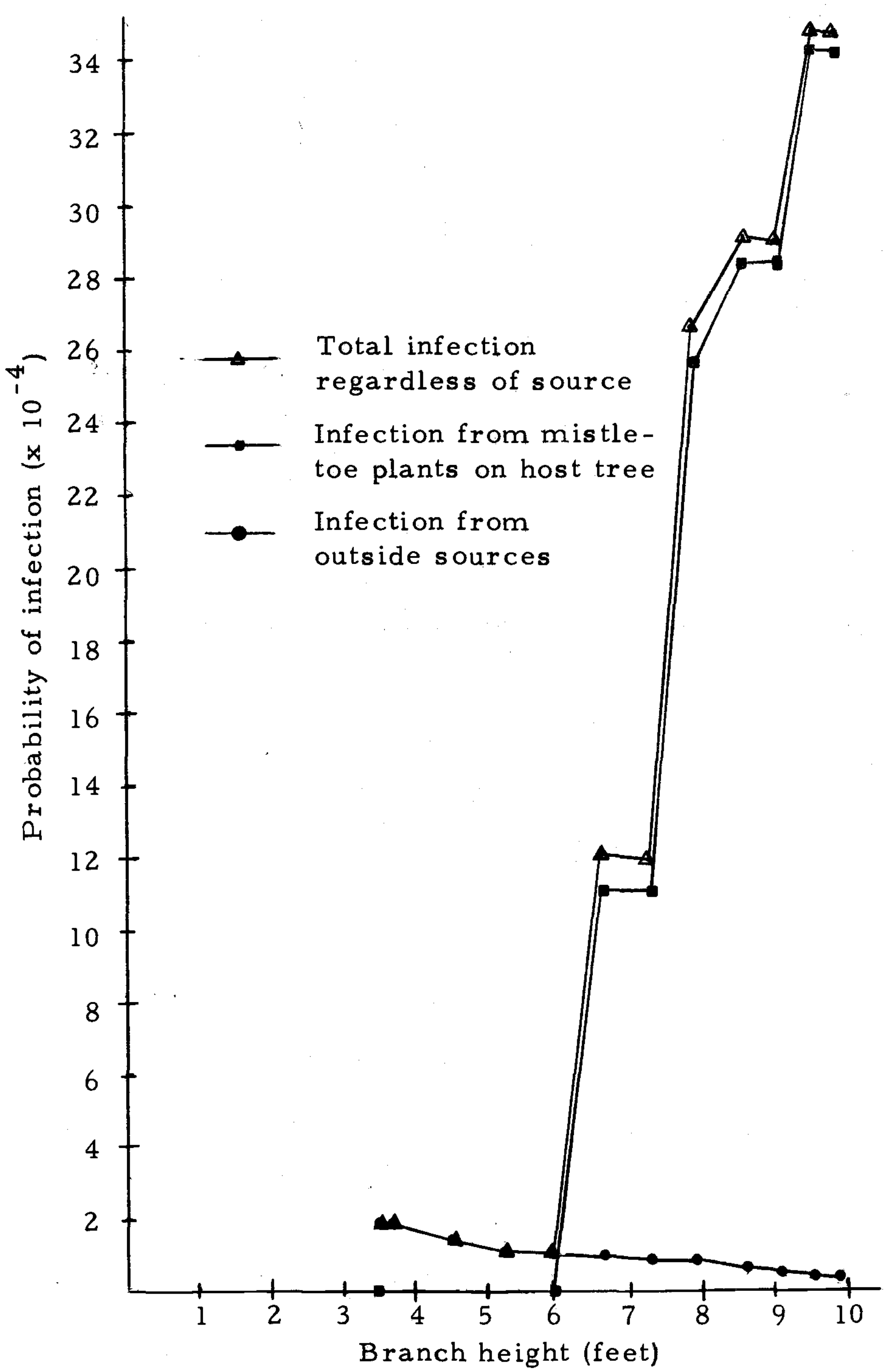


Figure 9f. Distribution of the probability of infection for branches on a representative tree in a stand where trees are spaced 18 feet apart, there are 4 mistletoe infections per infected tree, and there is an infection rate of 0.60 for the entire stand.

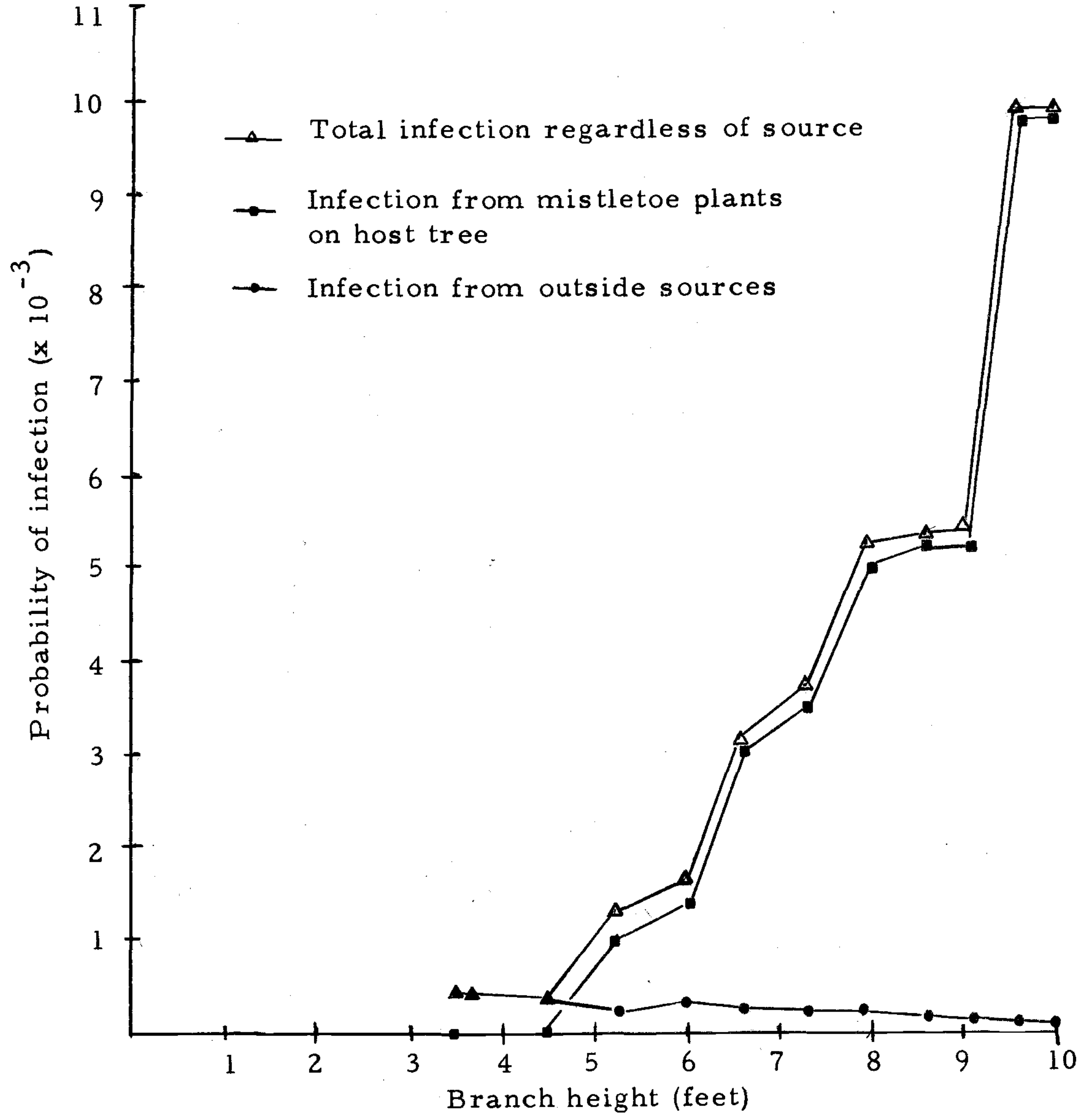


Figure 9g. Distribution of the probability of infection for branches on a representative tree in a stand where trees are spaced 9 feet apart, there are 15 mistletoe infections per infected tree, and there is an infection rate of 0.60 for the entire stand.

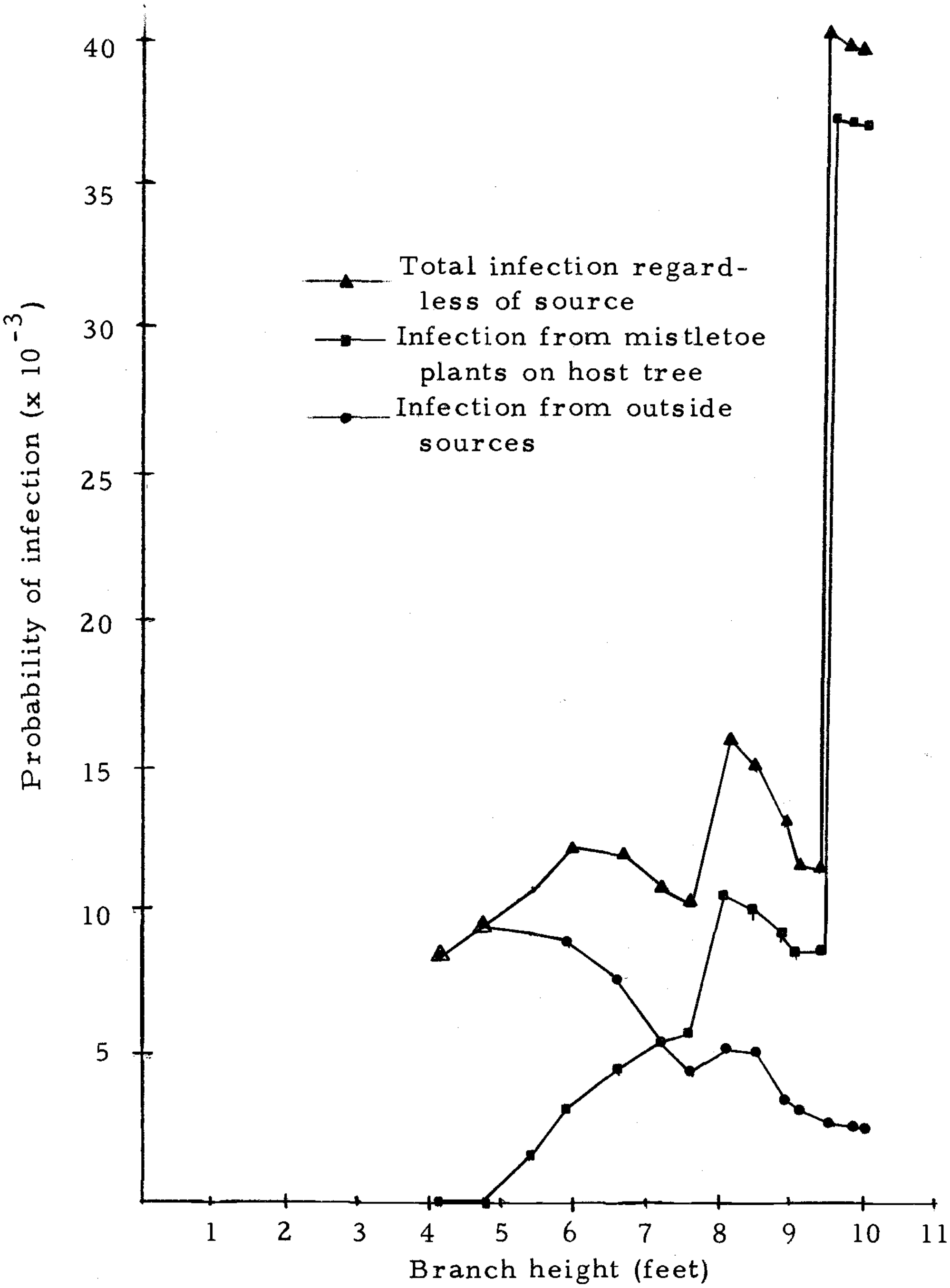


Figure 10a. Graphical comparison of the increase in seeds produced per infected tree with 2 infections over a period of 5 years and the probability of infection for a branch at 5 feet.

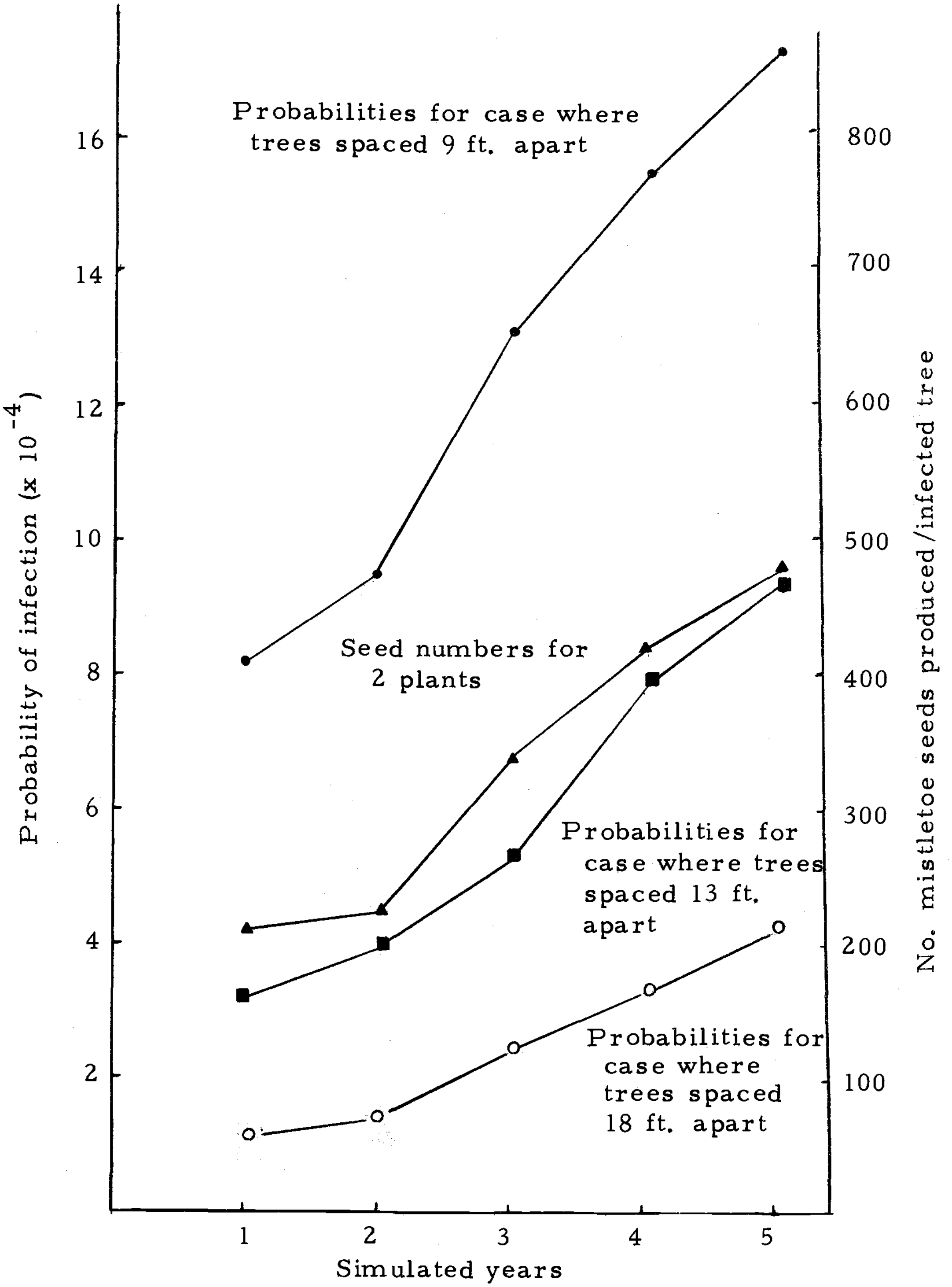


Figure 10b. Graphical comparison of the increase in seeds produced per infected tree with 4 infections over a period of 5 years and the probability of infection for a branch at 5 feet.

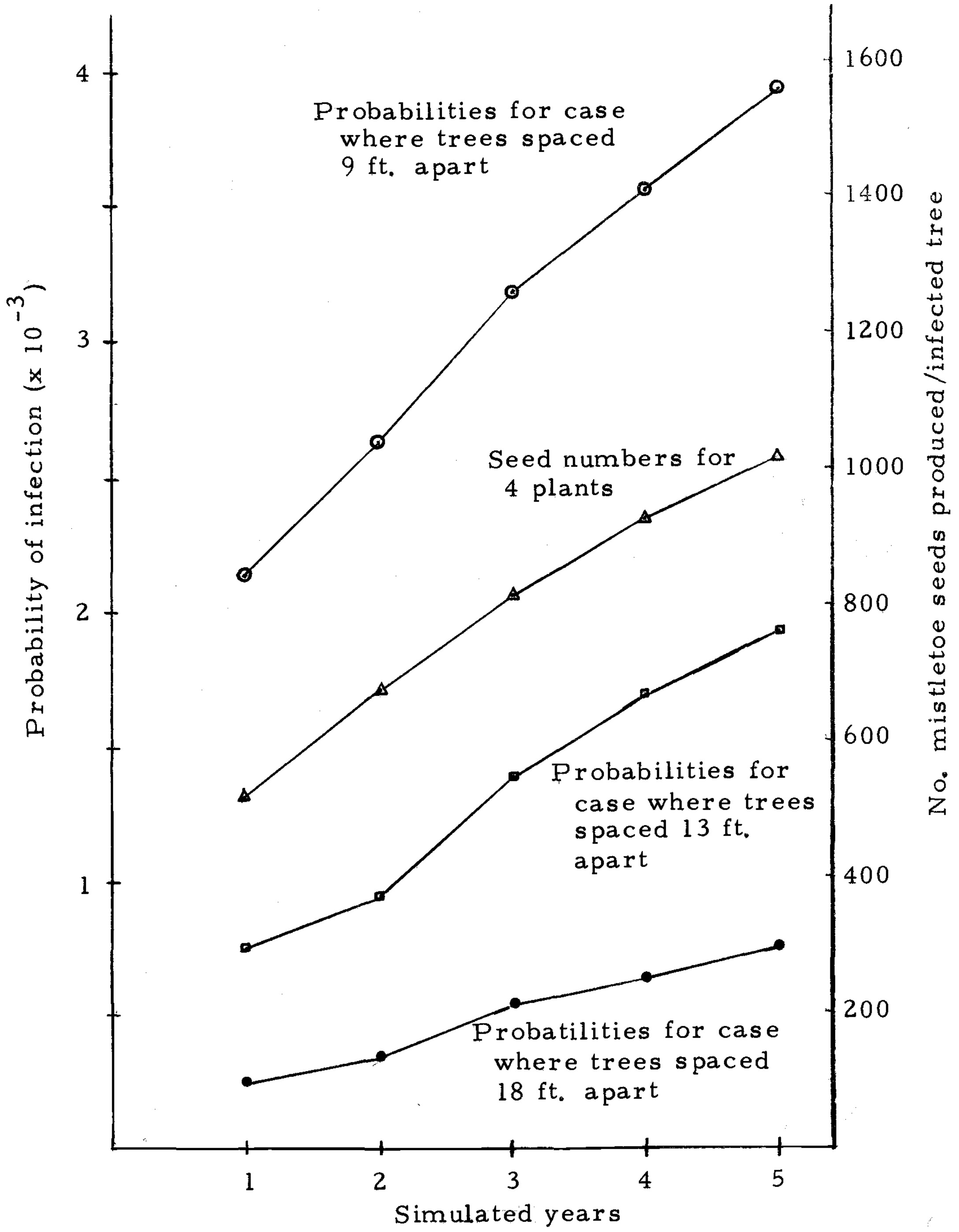


Figure 10c. Graphical comparison of the increase in seeds produced per infected tree with 15 infections over a period of 10 years and the probability of infection for a branch at 5 feet.

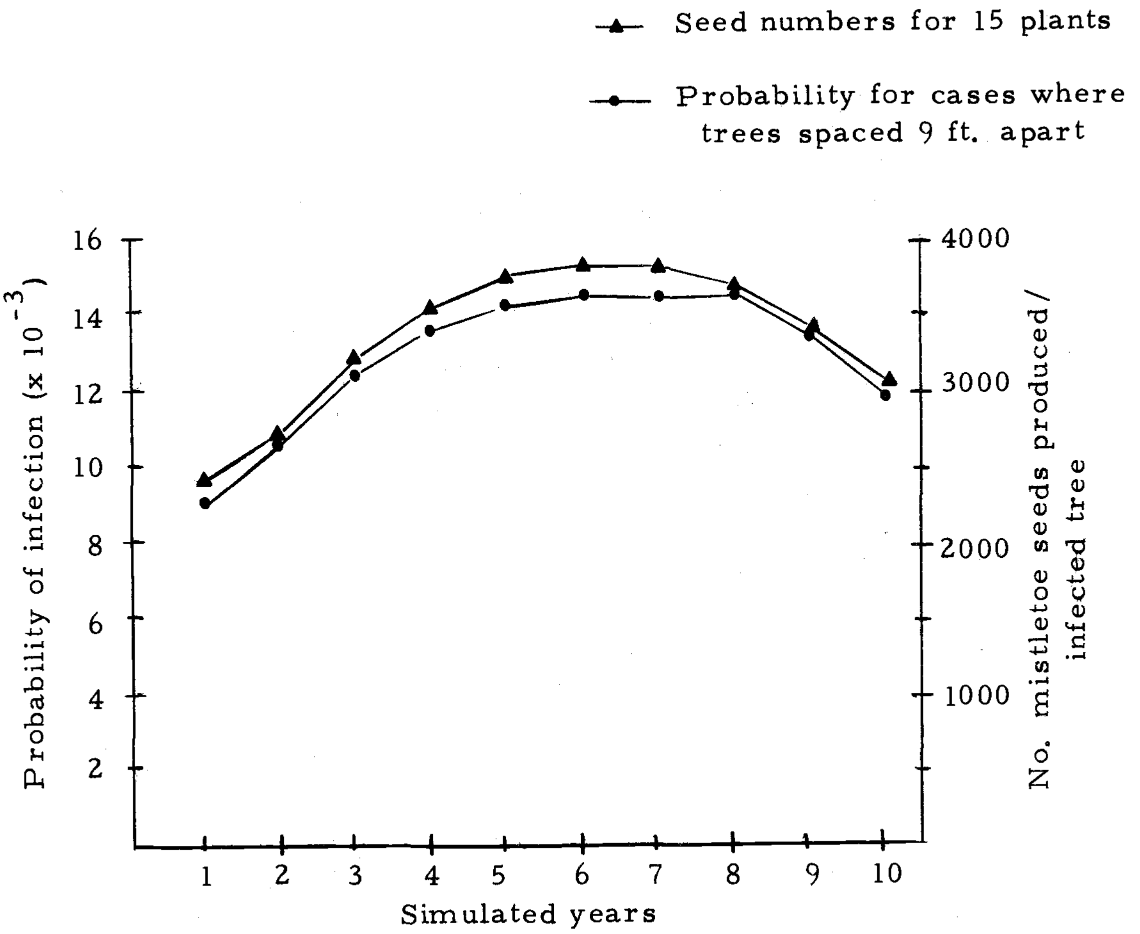


Figure 11a. Probability of infection for a branch with a height of 6 feet where trees are spaced 9 feet apart, there are 15 infections per tree, and there is an infection rate of 0.60 for the entire stand.

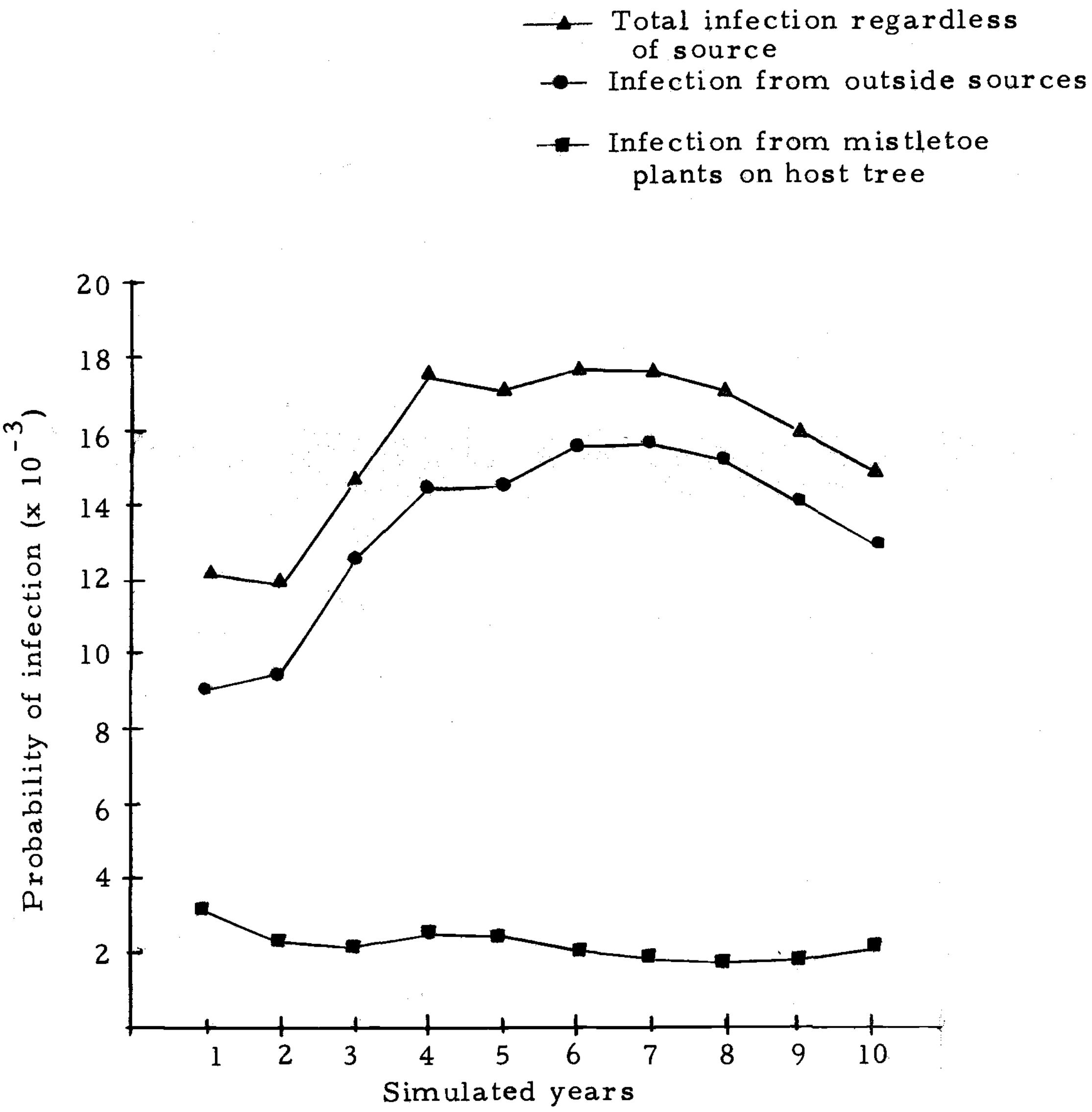


Figure 11b. Probability of infection for a branch with a height of 7 feet where trees are spaced 9 feet apart, there are 15 infections per infected tree, and there is an infection rate of 0.60 for the entire stand.

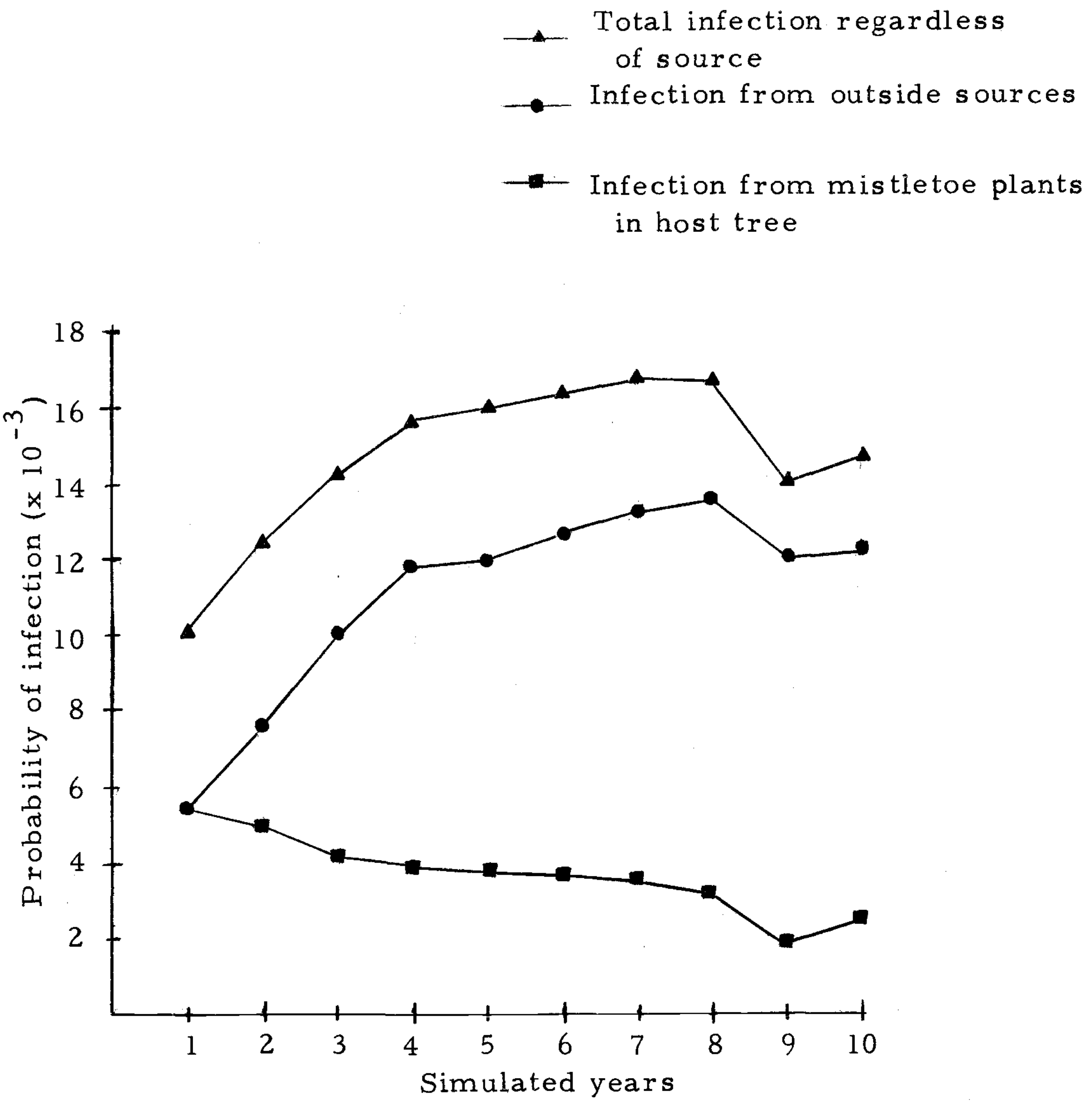
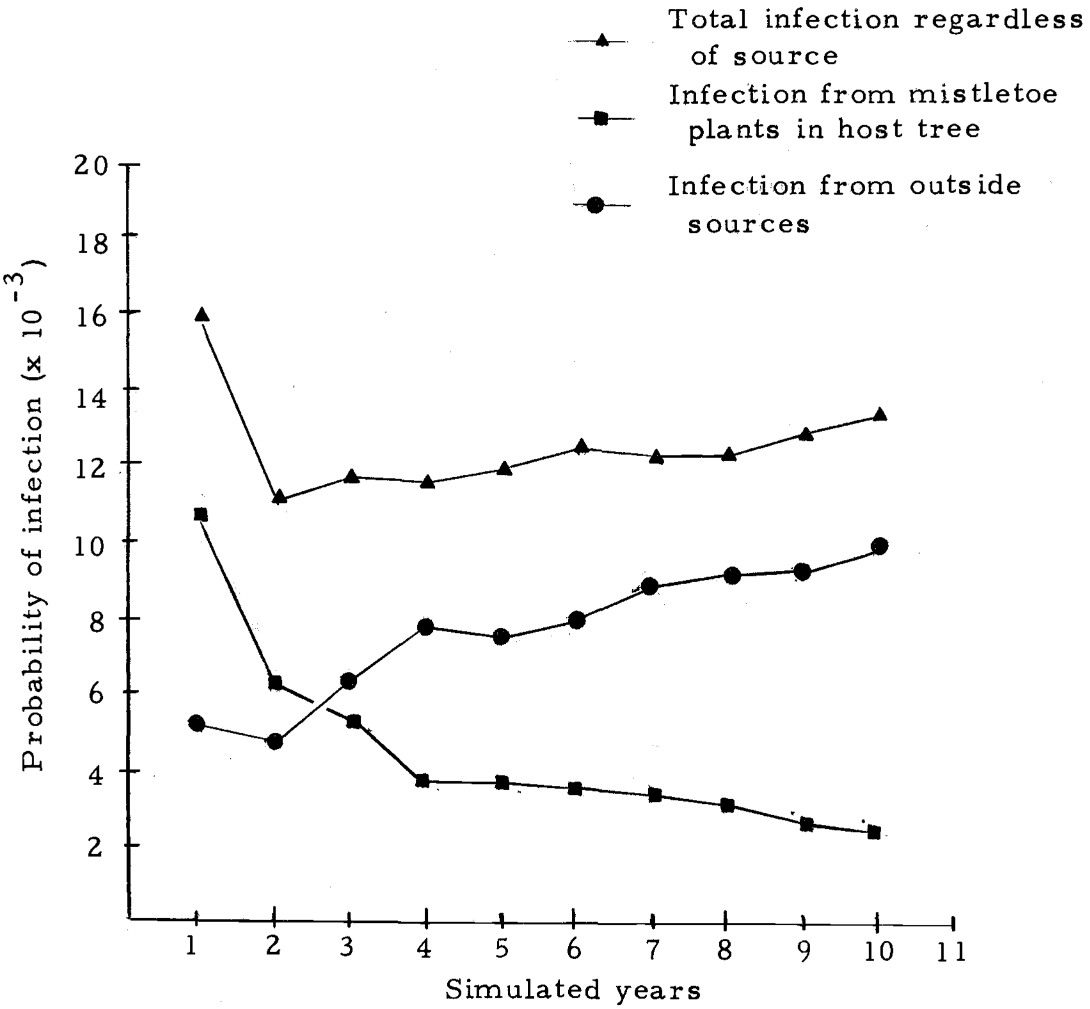


Figure 11c. Probability of infection for a branch with a height of 8 feet where trees are spaced 9 feet apart, there are 15 infections per infected tree, and there is an infection rate of 0.60 for the entire stand.



the crown decrease in probability of infection with time (Figure 12). This trend is largely due to the decrease in the reinfection probability as the crown volume around a given height becomes larger and the foliage becomes sparser. The probability of infection for the top whorl also shows an overall decrease in infection probability from which the inference that a tree can outgrow its infection might be made for the simulated case where the number of infections does not influence tree height growth (Figure 13).

The probability of infection due to contagion (the inoculum coming from an outside source) is influenced by the space between the trees. Although only three different spacing distances were used in the complete simulation, a general trend may be seen. The mean probability of contagion per branch was computed. For the case with two initial infections per infected tree the mean probabilities for the three spacings are shown in Figure 14. The probability is reduced by about half by the change in spacing from 9 to 13 feet and again in half by the change from 13 to 18 feet. A similar pattern is found in the simulated case with four initial infections. The contagion probability is not only related to spacing but also to height of the infection sources and was previously shown in Figures 7 and 8.

The simulation shows an increase in the expected number of mistletoe plants in the constructed stands. In the cases with two initial infections per infected tree, there would be a total of 120 mistletoe plants initially per 100 trees in a stand with an infection

Figure 12a. Probability of infection for a branch with a height of 9 feet where trees are spaced 9 feet apart, there are 15 infections per infected tree, and there is an infection rate of 0.60 for the entire stand.

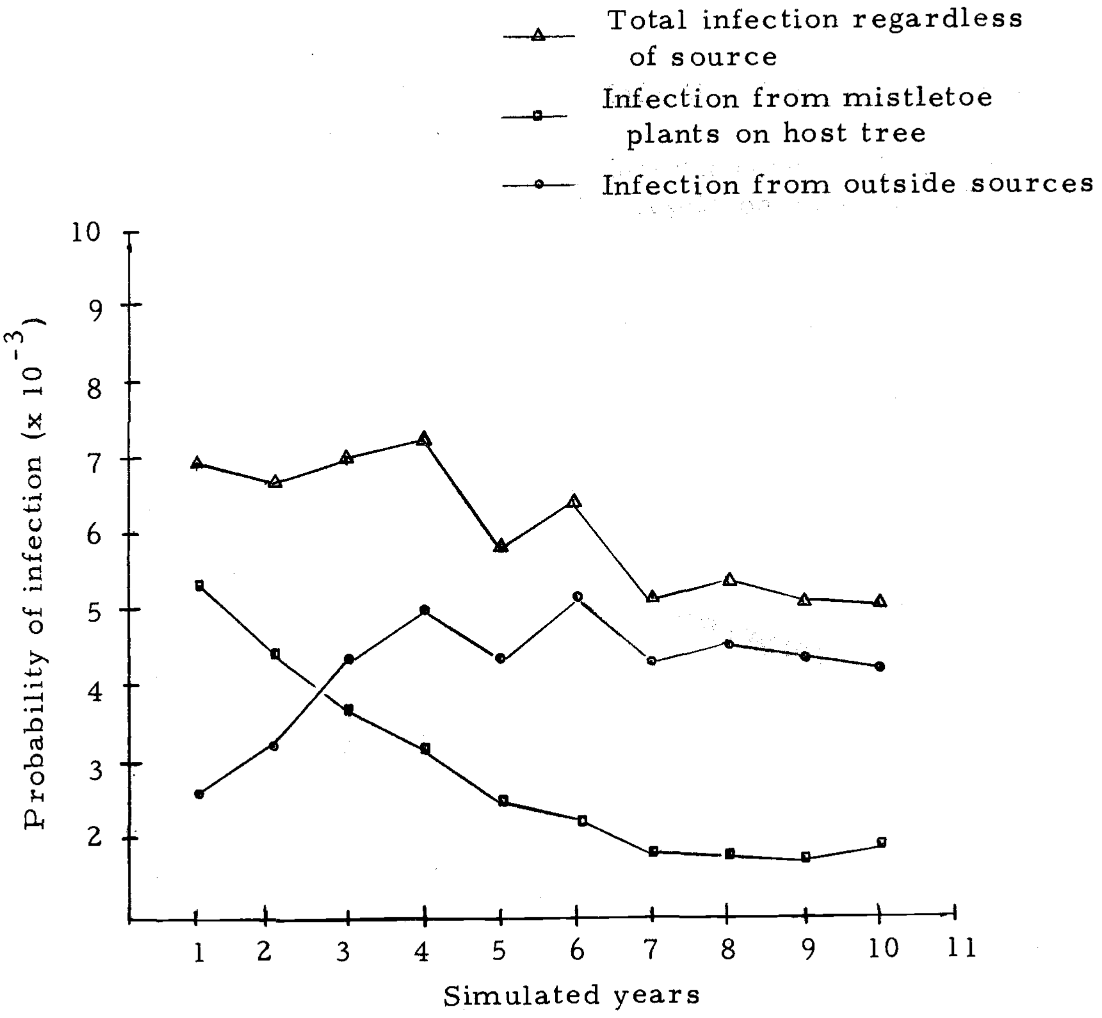


Figure 12b. Probability of infection for a branch with a height of 10 feet where trees are spaced 9 feet apart, there are 15 infections per infected tree, and there is an infection rate of 0.60 for the entire stand.

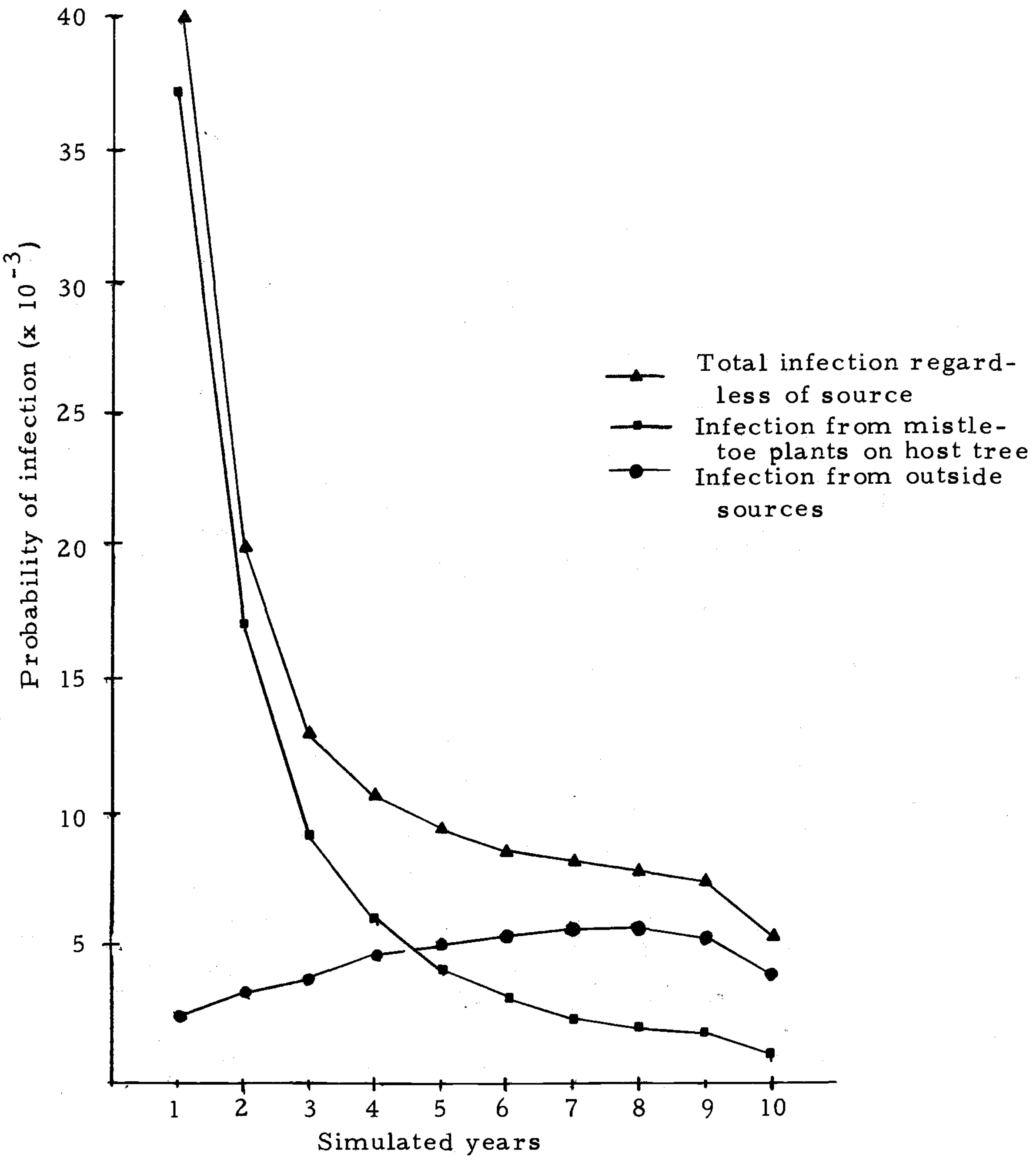


Figure 12c. Probability of infection for a branch with a height of 11 feet where trees are spaced 9 feet apart, there are 15 infections per infected tree, and there is an infection rate of 0.60 for the entire stand.

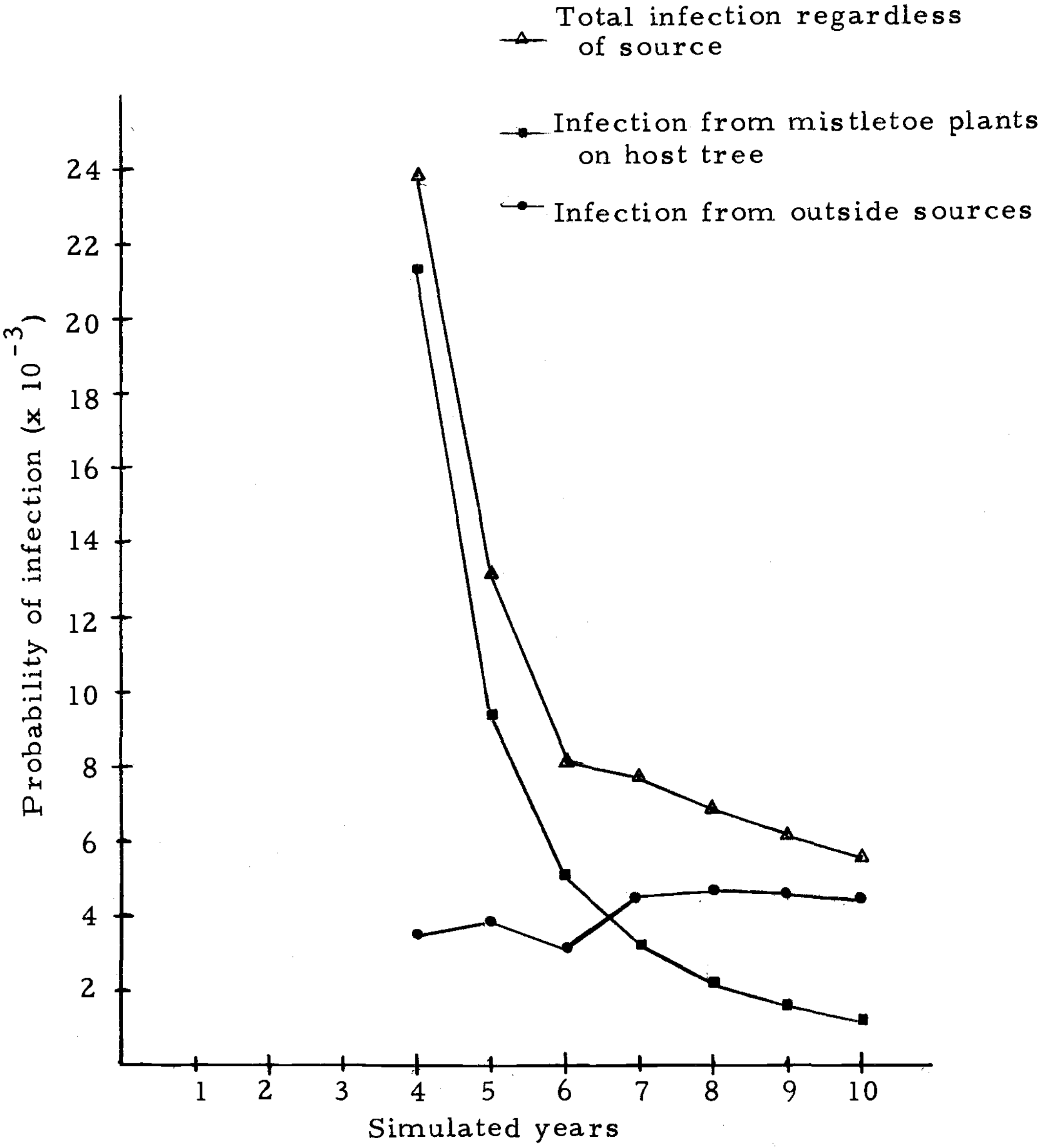


Figure 13. Probability of infection for the highest whorl on a representative tree in a stand where trees are spaced 9 feet apart, there are 15 infections per infected tree, and there is an infection rate of 0.60 for the entire stand.

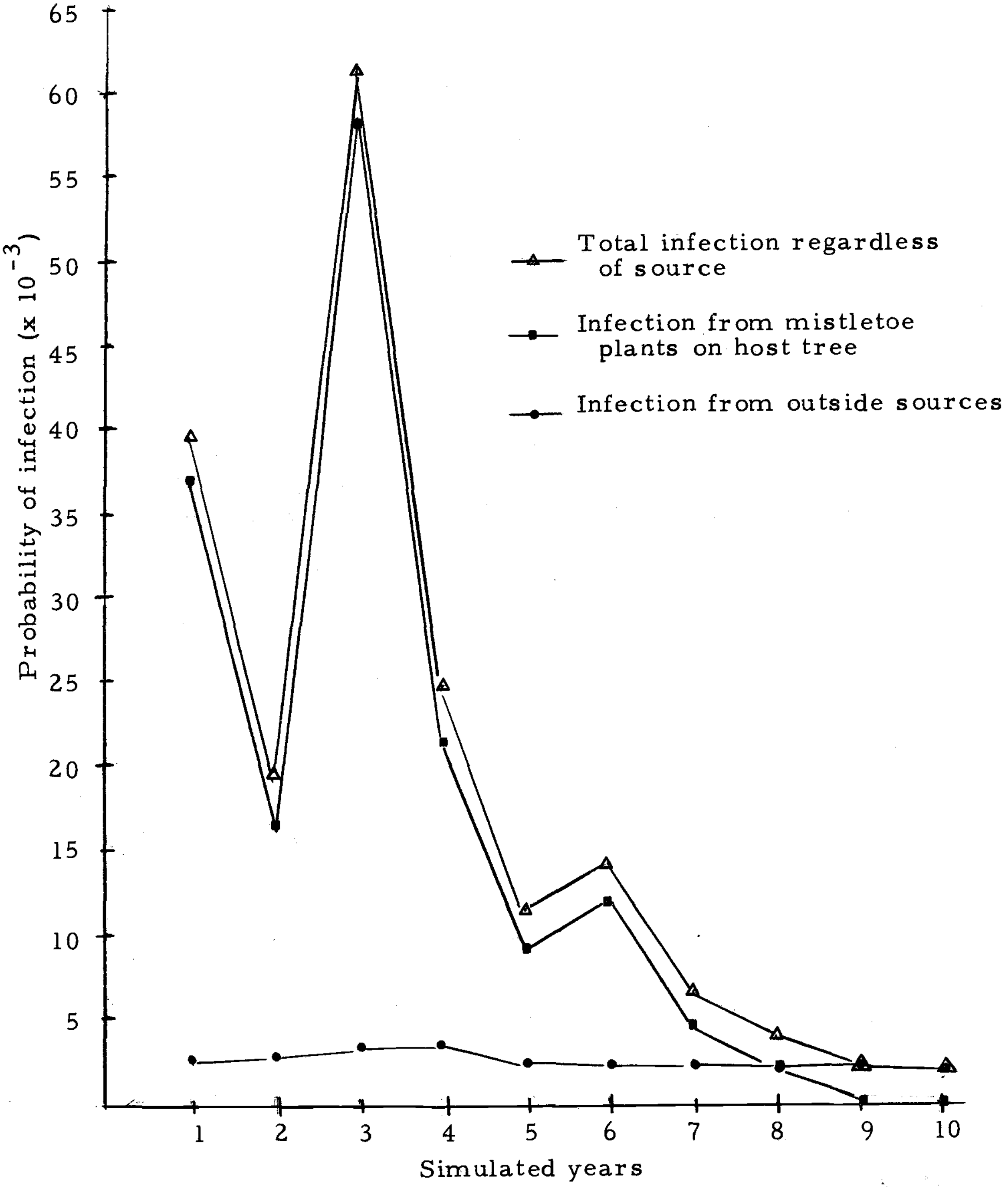
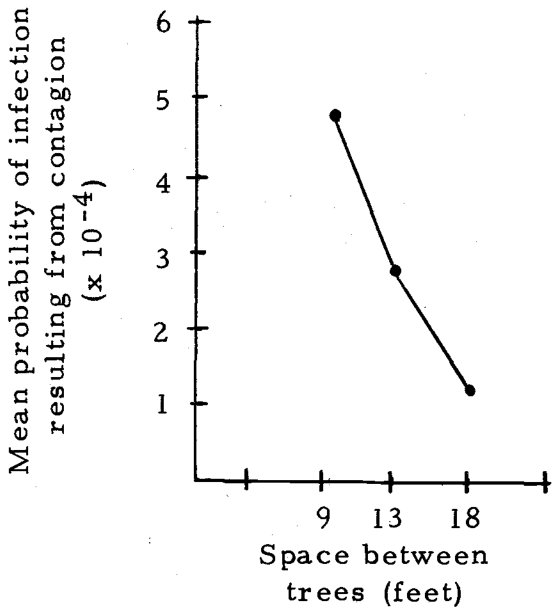


Figure 14. The mean probability of infection by contagion for stands with infection rate of 0.60 and 2 mistletoe infections per infected tree.

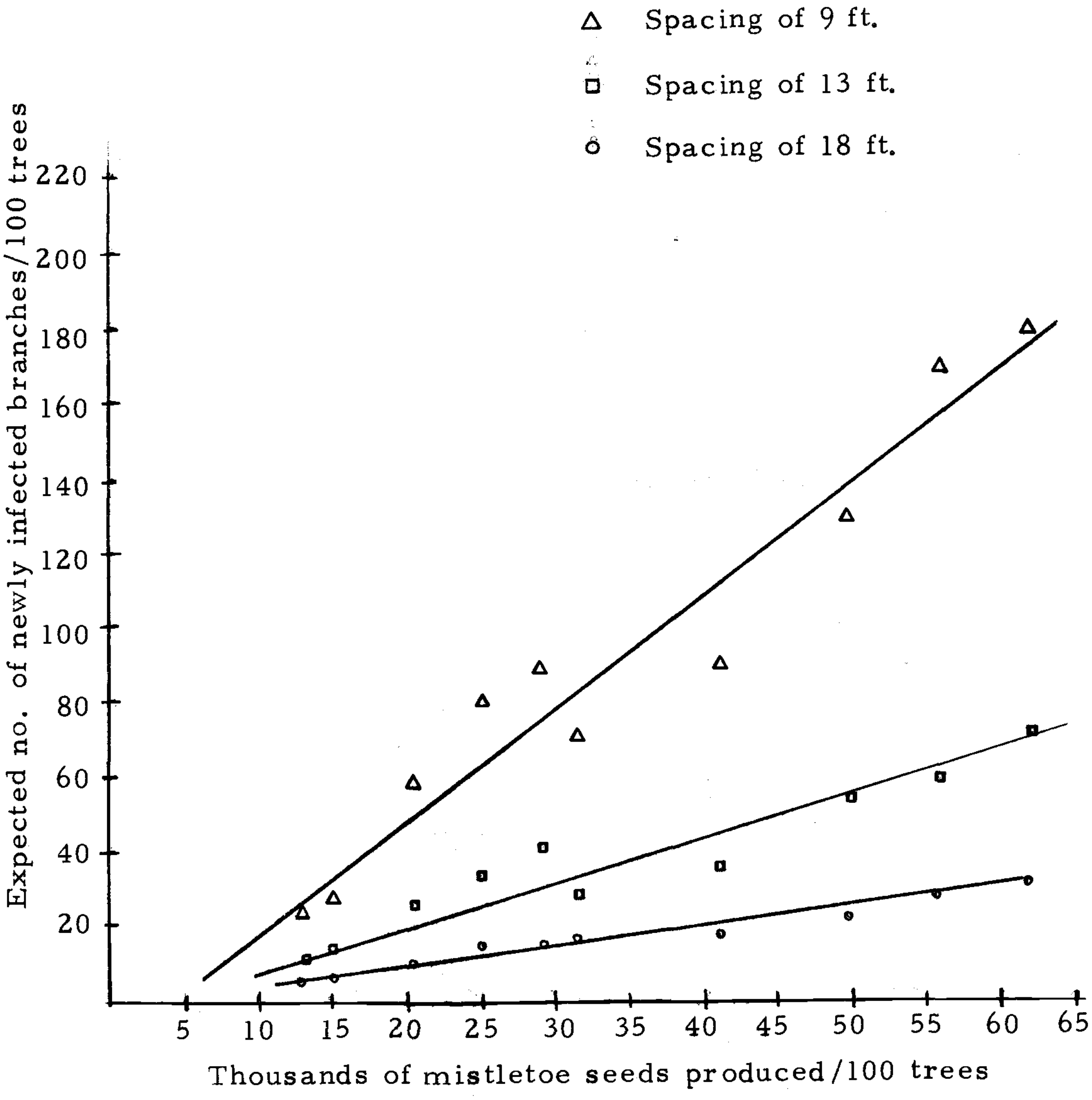


rate of 0. 6. The simulation shows that there would be 313 infections per 100 trees expected after five years in a stand where the trees are spaced 9 feet apart, 276 infections per 100 trees where trees are growing 13 feet apart, and 176 per 100 trees spaced 18 feet apart. The expected number of new infections per year is shown for the seven simulated cases in Table 13. A nearly linear relationship between the number of mistletoe seeds produced in a stand and the expected number of new infections in the stand is found (Figure 15). These results are also dependent on the height of the infections because the probabilities related to both contagion and reinfection are dependent on the position of the mistletoe plant within the pine tree crown.

Table 13. Number of newly infected branches per year expected per 100 trees in stands with an infection rate of 0.60.

Simulated year	Initial no. infections / infected tree	Total number mistletoe seeds produced/ 100 trees	Spacing between trees (ft)		
			9	13	18
1	2	12,900	24.8	11.4	6.7
2		15,000	28.9	12.3	6.2
3		20,700	59.7	26.4	11.6
4		25,200	80.5	34.0	15.1
5		28,800	89.4	41.5	16.1
1	4	31,680	72.6	29.6	17.4
2		41,220	91.6	36.1	18.3
3		49,680	130.6	54.3	23.9
4		56,220	169.7	60.1	28.6
5		61,860	179.8	72.9	31.4
1	15	145,560	188.0		
2		169,560	221.3		
3		198,540	280.8		
4		220,380	364.0		
5		235,080	456.7		

Figure 15. The approximately linear relationship between the number of expected newly infected branches per 100 trees and the number of mistletoe seeds produced per 100 trees in stands with infection rate of 0.60 and spacing between trees of 9, 13, and 18 feet.



DISCUSSION

During the attempt to mathematically describe the course of disease spread in the dwarf mistletoe-ponderosa pine system, the objectives underwent a process of evolution as the value of the development of a model was more fully realized. At the outset it was hoped that a simulation of the spread of infection might produce predictions of future infection distributions. These predictions were to be made for a few cases of interest and later to be used in field tests. Also, inferences resulting from the model were to be used to form the basis of hypotheses concerning the process of mistletoe disease spread with respect to the spatial arrangement of the trees and their infections. However, it was not until the submodels were being formulated that it became apparent that the model itself should be an objective. The process of modeling requires the careful evaluation of the problem in order to make realistic abstractions. When completed, it forms an integrated description of the system being modeled. This process of putting together bits and pieces from many observers and experiments can be a valuable contribution to the understanding of the system. It then becomes readily apparent where our knowledge is deficient or incomplete and what questions need to be asked.

This project was felt to be a worthwhile undertaking because of interest in the problem of dwarf mistletoe and because it would provide another application of modeling techniques to the procedures of plant disease investigation and control. This particular disease is economically important to the forests of the west and a backlog of information concerning its life cycle and especially its method of inoculum dispersal was available. Only a few models dealing with infection spread in a plant community have been attempted notably those of van der Plank (1963) and Waggoner and Horsfall (1969). Both employed strictly deterministic modeling methods. They were able to test the consequences of certain manipulations without experiencing them in the field and to formulate specific hypotheses from the results of the models. Waggoner and Horsfall went on to use the results to improve their model and to suggest new experiments. It was hoped that a similar process would be generated by the dwarf mistletoe modeling effort.

A brief review of modeling approaches will aid in the explanation of the reasons for choosing the approach which was ultimately used. Basically the problem of mathematically describing disease spread has been handled in two ways: single equations and simulations which are sets of equations strung together each describing a subprocess. A major drawback to the use of a single equation model is that to incorporate a realistic degree of detail, the mathematics become very difficult if not impossible to handle. Also, at the outset there is usually incomplete insight into causal pathways within the process being modeled. Hence, the equations are often based on aspects which are obvious and easily measured rather than on actual relationships. Without the inclusion of causality, predictions concerning the consequences of manipulations may not be valid. Simulations allow the inclusion of many variables and may be a realistic approach to complicated problems. They require the step-by-step analysis of every phase of the disease life cycle. The models for each subprocess, however, may be simple equations. The rationale for using the set of simple mathematical descriptions rather than one overall description is that more details may be subsumed by the model without the mathematics becoming intractable. In spite of the chance of glossing over some relationships at the subprocess level, at least part of the causal pathways may be included.

Approaching the problem of modeling the dwarf mistletoe-ponderosa pine system, it became obvious that a simulation would be necessary to describe the process of disease spread. Since it was desirable to include the effect of various spatial arrangements of the trees and their infections on the spread of disease, the required amount of detail ruled out the formulation of a single equation model. Also, one of the objectives of the modeling effort was to use the results to formulate hypotheses concerning the mechanisms of disease spread which would require an analysis of the causal pathways.

The simulation model which was formulated combined deterministic and stochastic submodels. Whenever possible, probablistic modeling was used. Compared to most diseases, the amount of inoculum produced per dwarf mistletoe infection is small. The variability of biological processes produces an appreciable effect on the outcome of reinfection and contagion. Deterministic models, which can be expected to give a satisfactory picture of a process as long as the number of observations is large, were believed to be inadequate when dealing with most phases of mistletoe disease spread. However, there was little information concerning the distribution of responses for certain events and deterministic models were employed. Mean values were used where the distributions about them were not available, where only a few responses were measured, or where the responses could not be correlated to another factor. The incorporation of a random number generator to simulate variability was considered but abandoned, since tests of the consequences of manipulations might have been obscured by the introduction of a random element.

Because it is a dangerous practice to begin to believe one's models, it is necessary to point out the problems and limitations of the simulation. During the course of model formulation, numerous problems arose which were left unsolved for many reasons. These problems may limit the reliability of the model as a simulator of reality. They concerned all phases of modeling from conceptualization to data adequacy. The simulation is strongest in terms of conceptualization and incorporation of measured values in the seed dissemination submodels and probably weakest in the seed production and reinfection submodels.

A problem of most concern to biologists is that no controlled experiments were made to test the results of the simulation. Certainly the use of actual conditions for inputs of three of the seven cases simulated will be an advantage to future testing. The simulation does predict the average number of mistletoe plants per tree to increase from 1.2 to 3.12 in five years for the stand where trees are spaced 9 feet apart, to 2.76 for trees spaced 13 feet, and 1.76 for trees spaced 18 feet apart. These infection rates do not sound unreasonable, but they will need to be compared with the actual values found on the experimental plots on Pringle Butte.

At key points in the disease spread process, there was inadequate knowledge to facilitate realistic modeling. For example, although reinfection is believed to be an important factor in disease spread, no information concerning the fate of seeds falling below the plant level was available. With 61% of the seed found to fall below the mistletoe plant, it might be expected that some infections would result. Also, the mechanism, whether by direct hit or ricochet, by which mistletoe seeds land on a particular branch is not known. Thus, the effect of differences in the tree crown can only be deduced by correlation. In the one experiment dealing with reinfection, the spatial coordinates of intercepted seed were not given by distance above the mistletoe plant but rather by designation of the band (formed by dividing the crown above the mistletoe plant into fifths) in which the seed was found. This coordinate system made combining data from more than one source difficult. Several assumptions were necessary which probably makes the resulting submodel extremely unrealistic. It was necessary to assume that the interception probability of the seed was distributed uniformly over the volume of the band in which it was found. These bands were adjusted to one-foot-wide levels and the assumption of uniform probability was maintained for these one-foot bands, because the lack of information made other assumptions unwarranted.

For plant fertility a deterministic model relating the number of seeds produced to the plant age was used. The variability of the inoculum they produce is very great. Only 311 were measured with ages ranging from 4 to 28 years. A large proportion of them produced no seed, which brought the means down to the lower end of the seed production range. The submodel does not reflect the inoculum potential of the female mistletoe plants. However, the simulation model as formulated did not allow the entry of probablistic statements concerning seed number.

It might be argued that the simulation model described here has been an attempt to model the data available rather than the system. This is probably true. The conception of the system has, at the least, been strongly influenced by the descriptive materials. At the beginning of this project, it was hoped--perhaps naively--that the simulation would be of practical value. Thus, it was my intent to include as many documentable values as possible and to avoid the necessity of including dummy functions for which there were no biological reasons or which could not be supported with experimental results. It is possible that the conceptualization of the process of disease spread has suffered for this decision. The exclusion of aspects of variability in key processes probably limits the value of the simulation as a predictive tool for expected infections. Although the predictions have not been tested, the results are felt to be realistic.

Inferences coming from the results of the partial and complete simulations enable the formulation of new hypotheses and provide evidence on a number of existing hypotheses. As discussed here, the hypotheses concerning the process of disease spread in the dwarf mistletoe-ponderosa pine system are related only to the situation which was modeled. The hypothetical stand of the simulation model is a young growth, managed ponderosa pine stand where trees are evenly spaced, are of uniform height (between 10 and 25 feet), and have a light to moderate infection level. For each general hypothesis presented, reasons will be given to justify it. These reasons are derived from the model and must, also, bear the burden of proof.

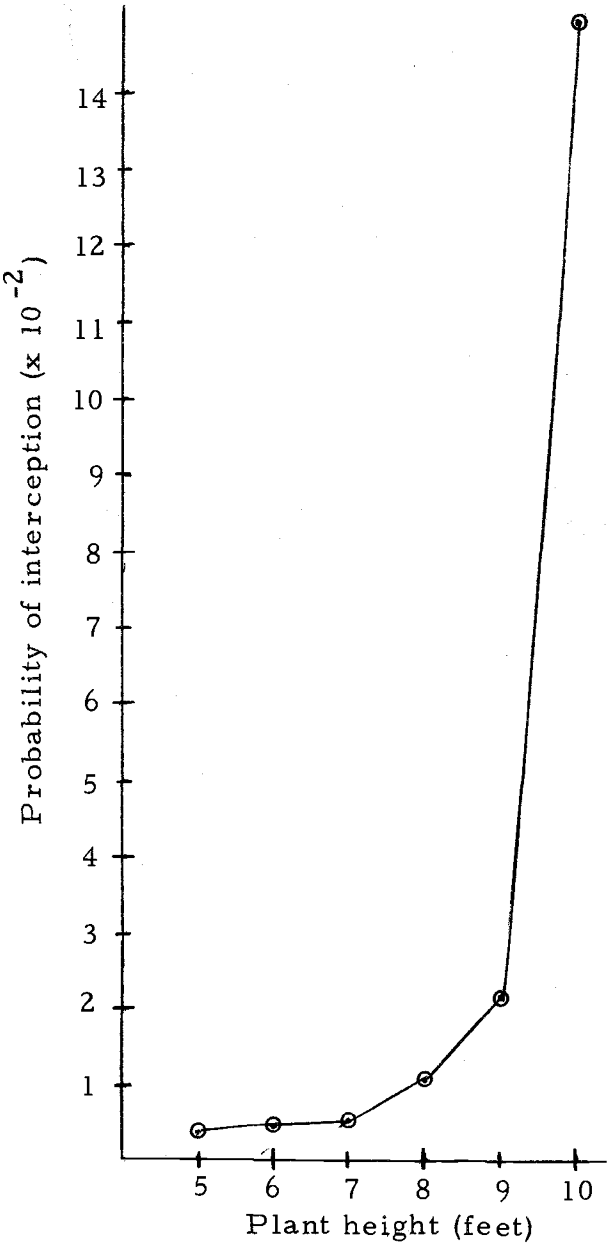
Hypotheses

1. Plants high in the crown of the pine trees are the most important ones with respect to disease spread.

The simple application of the ballistics formula shows that the radius of seed flight is greater for plants of greater heights. At maximum velocity, seeds from a plant at a height of 15 feet fly an average (weighted by probability for angles) of 9.19 feet further at ground level than those from plants at 5 feet from the ground (Table 10), and for the median velocity, the distance increases 5.92 feet (Table 11).

The probability of infection of a branch is influenced by the height of the inoculum source in both the reinfection and contagion cases. Mistletoe seeds produced by plants high in the host's crown are more likely to be intercepted by a branch in the same crown. Figure 16 shows the increase in interception probability with increased mistletoe plant height for branches from 1 to 2 feet above the plant. For contagion the probability of infection decreases quickly for branches above the level of the source of inoculum as the lateral distance between them increases (Figure 7). However, for branches

Figure 16. The relationship between the probability of a branch which is 1 to 2 feet above a mistletoe plant intercepting a seed from that plant and the height of the mistletoe plant.



below the level of the inoculum source, the probability is greatest at the intermediate lateral distances (7-18 feet) (Figure 8). Plants higher in the crown would have below their level more foliated branches on adjacent trees than those at lower heights and, therefore, a greater chance of transferring inoculum to these nearby trees.

2. Where infection levels are moderate (fewer than five infections per tree) and where spacing between trees is greater than 8 feet, vertical spread is accomplished primarily by reinfection.

In all six cases where the infection levels were moderate the probability of reinfection of branches above the highest mistletoe plant was greater than the probability of infection from outside sources (Figure 9). About 12% of the seeds produced by a mistletoe plant are trapped within the host crown at levels above the plant while 27% are discharged in free flight. The median velocity seed discharge trajectories (Figure 5) show that vertical spread is most likely to occur where trees are spaced less than 15 feet apart and about 50% of the seed exit at angles (Table 8) such that the median velocity trajectories fall below the source level at distances less than 6 feet. Indeed, at 10 feet apart there is about half as great a chance of infection for branches of equal distances above as below the mistletoe plant (Figures 7 and 8).

3. It is possible for a tree to "outgrow" its infections.

Trees spaced from 9 to 18 feet apart increase in height at rates ranging from .32 to .62 foot per year (Table 3). To maintain a constant position in the crown the mistletoe plants must produce an infection at a similar increment higher than previous infections each year. Because it takes 5 years before plants begin to produce seed (Wagener, 1962), the plants highest in the crown would not become important contributors to the inoculum for about 6 years. During this time the trees will have grown from 1.92 to 3.72 feet. However, for the 12% of the mistletoe seeds which are trapped in the crown, the average vertical distance of seed interception is 1.48 feet. The probability of a seed being intercepted at a height greater than 1.92 feet above its source plant is 0.268 (Table 12). Likewise for the 27% of the mistletoe seeds which escape the host crown, the probability of initiating an infection at heights greater than the level of the inoculum source is very small at lateral distances greater than 10 feet (Figure 7). The complete simulation also shows a decrease in the probability of infection for the top whorl over the simulated years (Figure 13).

There is little chance of a seed being intercepted at heights much greater than 2 feet above the source plant either by reinfection or contagion. With a moderate degree of mistletoe infection, trees are expected to maintain a growth rate high enough to make the possibility of the infection maintaining a constant position in the crown very small.

4. In stands with spacing distances greater than 8 feet and a sparse mistletoe population, new infections are more likely to occur as a result of reinfection than as a result of contagion.

In spite of the larger proportion of mistletoe exiting the host crown than being trapped by it, the simulations indicate that trees are more vulnerable to infection by their own plants than by the mistletoe infections on the surrounding trees. At heights above the lowest mistletoe plant, the probability of reinfection dominates the probability of infection in the six cases simulated with moderate mistletoe population levels (Figure 9). Also, in the simulated stands where there is an initial infection rate of 0.60 and two mistletoe plants per infected tree and where the trees are spaced 9 feet apart, the mean probability of contagion per suscept is 4.809×10^{-4}, while under similar conditions the mean probability of reinfection is 6.765×10^{-4}.

5. Increasing the spacing between the trees reduces the probability of mistletoe infection from both reinfection and contagion processes.

Increasing the spacing between the trees in a stand not only decreases the chances of mistletoe seeds being transferred from one crown to another, but also affects the growth rate of the tree. As the tree increases in height the crown dimensions likewise increase in size. In effect, the tree crown grows away from its infections. The faster the tree grows, the faster the decline in probability of reinfection for branches in the vicinity of an infection. The influence of spacing on the number of expected infections is shown in Figure 15. The number is decreased by half with the increase in distance between trees from 9 to 13 feet and by about half again with the increase from 13 to 18 feet.

The hypotheses concerning disease spread presented here have a practical importance to the management of young pondersoa pine forests. If the infection level of the stand is moderate, thinning to a spacing of at least 9 feet between trees will greatly reduce the chance of contagion. Reinfection, however, cannot be ignored. The most important means of increasing the height of mistletoe infections is by reinfection; therefore, allowing even a moderate infection in the residual stand may result in infections at positions which are able to increase the probability of contagion and negate the value of thinning as a control measure. Selective thinning should discriminate against trees with infections at the greatest heights and pruning of mistletoe plants in the lower part of the crown is of no particular value. Spacing trees at the optimal distance for tree growth is the best control measure for mistletoe where infection levels are moderate. If the trees are growing at their maximum rate, the chances of them outgrowing their infections are favorable, thus reducing the probability of reinfection as well as contagion.

After reviewing the results of the modeling effort, several ways of improving the simulation may be seen. The subprocesses dealing with plant fertility, branch angles for seed retention, germination, and infection might benefit by the incorporation of probability distributions rather than relying on mean values. The reinfection submodel needs a new conceptual framework which more closely reflects the mechanism of seed interception. The probability of interception for a given branch should perhaps be based on the number of branches vulnerable rather than on a modeled volume adjustment. More experimentation is called for concerning this important subprocess. The model would benefit by the inclusion of the impact of environmental variables, other diseases, and animal damage on the survival of the mistletoe. Rain- and snowfall have an important impact on seed retention and transportation to an infective site as well as on germination and infection. Wind patterns probably affect the seed trajectories. In all, the model would be most strengthened by the inclusion of inherent variability in some key subprocesses, the inclusion of causal mechanisms where known, and by taking a holistic viewpoint and allowing the mistletoe to be affected by its environment as well as by the structure of the pine trees and of the stand.

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