A Model of Damping-off and Root Rot of Douglas-Fir Seedlings Caused by Fusarium oxysporum

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ABSTRACT

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The mathematical relationships required to construct a model of damping-off and root rot of Douglas-fir seedlings caused by *Fusarium oxysporum* were derived from the literature, unpublished data, and experiments. A time and space frame of 180 days from sowing, in plots 0.1–0.2 m^2 × 20 cm deep containing up to 100 seedlings, was selected. Simplifications and assumptions in the model included use of temperature as the main environmental factor, subdivision of time into 5-day periods and space into 2-cm intervals, with one vertical and one horizontal dimension, and natural variation based on pseudo-random selections from normal distributions. Using chi-squared goodness-of-fit, model predictions of germination, root growth and root rot mortality were not significantly different from nursery results in 4 yr. Predictions of number of seedlings and seedling roots infected ranged from 72 to 120% of nursery results.

Additional key words: control, disease, simulation.

More than 90% of damping-off and root rot in British Columbia coastal nurseries is caused by *Fusarium oxysporum* Schlecht. (2). The diseases are initiated when propagules of the fungus in the soil infect the roots and ramify through the root system, causing lesions in cortical and vascular tissues (6). Invasion of the radicle in young seedlings is nearly always fatal and results in damping-off (8). Invasion of older seedlings results in progressive root rot, leading to death.

The use of modeling to integrate climatic, pathogen, and host relationships in disease forecasting has been demonstrated for crop plants (28,29). This report describes the construction of a Fusarium root disease model applicable to forest nurseries in coastal British Columbia. Prediction of root growth, infection, and disease development required the calculation of relationships with reference to space and time (Table 1). The data necessary to express the relationships mathematically were obtained from the literature, unpublished reports, and experiments.

Damping-off is confined to the cotyledonary stage of Douglas-fir seedlings, usually to 30 days after germination (2). Damage from root rot is confined to the first growing season, occurring from June to the end of October. Spatial distribution of damping-off is more or less random throughout the nursery; that of root rot is random within patches (3). Plots 0.1–0.2 m^2, containing 30–100 seedlings, provide representative samples of both root rot and damping-off (*unpublished*). Until the end of October of the first year, most of the Douglas-fir roots occur at soil depths less than 20 cm and shoot length is 6–10 cm (9,25).

Temperature is considered to be the most important environmental factor determining the incidence of damping-off and the root rot of conifer nursery seedlings caused by *F. oxysporum*. As temperature increases, incidence of damping-off increases, disease onset advances, and disease curves rise more steeply (21,24). Root rot incidence is greatest in the hottest nurseries and during years with the hottest summers (3,30). Reducing nursery bed temperatures by shading or irrigation decreases the incidence of root rot. In Douglas-fir seedlings, mortality from Fusarium root rot is four to five times greater at 36 than at 4–28 C constant temperature (21) and four times greater in temperature regimes exceeding 23 C for more than 6 hr per day during the first month after sowing than in regimes with lower temperatures during that period (3). Seed germination and seedling emergence in Douglas-fir is a function of: (i) threshold heatsum, ie, number of degree-hours above 0 C that must be accumulated at seed depth in the soil before emergence commences, ranging in different seed lots from 4,500 to 4,900 degree-hours, (ii) emergence coefficient, ie, percentage emergence per thousand degree-hours above the threshold, ranging from 15.7 to 21.4%, (iii) a slow-emergence percentage, ranging from 62 to 82, at which the emergence rate is reduced, and (iv) a slow emergence factor (0.14–0.29) by which the emergence coefficient is reduced when emergence reaches the slow emergence percentage (7).

Douglas-fir seedling root growth (dry matter production) is a function of temperature with optimum at 432 daily degree-hours, decreasing to 30 and 40% of maximum at 200 and 700 degree-hours, respectively (11). Relative production of total seedling dry matter is 100% at 30 and 20 C constant air and soil temperatures, respectively, decreasing to 40% at 0 and 30 C or at 10 C for both air and soil temperatures (13). Total seedling growth follows the law of compound interest (26).

In coastal British Columbia forest nurseries, propagules of *F. oxysporum* are associated with particulate organic matter in the soil, which is distributed more or less randomly (6). The particles range from less than 1 mm to 20 mm length × 3 mm diameter. Small particles have reduced infectivity. Average concentration ranges from 0.2 to 0.5 particles per cubic centimeter of soil. Root invasion of host plants by *F. oxysporum* generally takes place only when contact or near contact is made between a propagule and an actively growing host root tip (12,14,18,19). Lesion distribution on roots indicated that this limitation also applies to Douglas fir seedlings (3,6, *unpublished*). The rate of lesion elongation from the point of invasion averages 1 mm/day. Lesions of tertiary branch roots invariably extend into parent secondary branches. Cross infection does not occur among seedlings. Minimum, optimum, and maximum temperatures for hyphal growth of *F. oxysporum* in vitro are approximately 10, 25, and 30 C, respectively (20,24). Temperature of 10–30 C does not, however, affect infection (6), suggesting that it is influential only after the fungus is established in the root.

Under conditions prevailing in coastal British Columbia nurseries, other factors appear to be less important than temperature in the incidence and severity of Douglas-fir root disease caused by *F. oxysporum,* probably because of relatively

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stable soil conditions. Irrigation systems maintain moisture tensions at less than 1 bar during the growing season (5), pH averages 5.5–6.5 and organic matter content ranges from 5.5–8.5% (27). Soils are free of stone and moderately to well drained (16).

EXPERIMENTS

Fungus growth. The following experiment was conducted to measure growth of *F. oxysporum* longitudinally in seedling roots. Douglas-fir seedlings were grown aseptically in pots of autoclaved peat-sand medium sown with seeds surface-sterilized with 30% H_2O_2 for 0.5 hr. After 60 days, seedlings were gently washed out of the pots with sterile distilled water and their root systems, consisting of taproot and several secondary branches, were spread in an acrylic-bead observation box with a removable faceplate, modified from Bloomberg (1) (Fig. 1). Individual branch tips were inoculated with 5-mm root fragments naturally infected by *F. oxysporum* placed on the root tip (6). The faceplate, lined with a tissue-paper wick, was replaced over the root system, which was held in place by the acrylic-bead rooting medium. Irrigation was by sterile distilled water through the tissue wick. Nutrients were added weekly as a 0.05% (w/v) solution containing 20% available, N, P, and K. The boxes were contained in a closed Perspex chamber placed in a controlled environment room at 21 C with 16 hr day length supplied by 19,375 1x cool white fluorescent lights. At intervals of 30–50 days, seedlings were removed from the boxes. Each inoculated root branch was aseptically subdivided into 5-mm segments, which were plated on soil extract agar medium to determine the presence of *F. oxysporum*. Average and range for rate of longitudinal fungus movement in roots were 1.1 and 0.8–1.7 mm/day, respectively, approximately the same as that of lesion elongation.

Root growth. The following experiment was conducted to determine root elongation rate during a growing season. Pots, 20 cm in diameter and 20 cm deep, were lined on the base with pea

TABLE 1. Relationships, data required to quantify them, and source of data in a model of damping-off and root rot of Douglas-fir nursery seedlings caused by *Fusarium oxysporum*

Relationship	Data for quantification	Source of data[a]
Number of seedlings germinated and emerged	Daily heatsum at 0.5 cm soil depth, threshold heatsum, emergence coefficient, slow emergence factor, slow emergence percentage	(7)
Radicle length	Random selection from a normal distribution	Experiments
Periodic total root	Number of days since germination, periodic heatsums in shoot and root zones, relative seedling dry weight production rates at different air and soil temperatures, correlation of total root length and seedling dry weight	Experiments, Fig. 2, (13)
Total root length	Sum of periodic root growth	(26)
Taproot	Fraction of periodic total root growth	Experiments,
Periodic growth		Fig. 3
Secondary branch roots		
Number	Total root length	Experiments, Fig. 5
Location on taproot	Number of days since germination, percent distribution of branches by taproot depth	Experiments, Fig. 6
Initial length	Random selection from a normal distribution	Experiments
Periodic growth	Number of days since germination, relative growth rate at different soil depths, fraction of periodic total root growth	Experiments, Fig. 4
Total length	Sum of periodic growth	(26)
Angle of growth	Depth of taproot, total branch length, competition	Experiments, Table 2
Length of root tip	Latest 5-day periodic growth	Unpublished
Tertiary branch roots		
Number	Regression on length of secondary branch	Experiments
Initial length	Random selection from a normal distribution	Experiments
Location on secondary branch	Number of days since germination, percent distribution along secondary branch	Experiments, Fig. 7
Angle of growth	At right angles to secondary root	Experiments
Inoculum particles		
Distribution and concentration	Soil depth	(6)
Size	Observed frequency distribution	(6)
Infectivity	Particle size	(6)
Root tip infection	Root tip size, inoculum particle size and concentration, random selection from a set of inoculum particle-root tip contact positions	Experiments, Fig. 8
Lesion growth	Periodic heatsum in root growth zone, linear growth of *F. oxysporum* in secondary branches, relative growth rate of *F. oxysporum* at different temperatures	Experiments, (20,24)

[a]Figures in parentheses refer to cited literature references.

gravel, 1 cm deep, and filled with a mixture of 3:1 nursery soil and washed sand. Pots containing soil were autoclaved 1 hr at 121 C, then arranged in four blocks in a growth room with day/night temperatures of 25/18.5 C and 16-hr illumination at 19,375 lx, the optimum temperature and light conditions for Douglas-fir seedling growth (11). In each pot was transplanted either a single Douglas-fir seedling placed centrally or three seedlings in a row, to represent competitive effects. Seedlings were selected for planting from axenically germinated stock (8). They were watered daily to soil saturation with tapwater at room temperature.

Two seed lots collected from central Vancouver Island at 500 and 630 m elevation above sea level, respectively, were used. Single seedlings of each seed lot were transplanted to 36 pots, and competitive seedlings of one seed lot to 24 pots. Every 20 days, one singly grown seedling and every 30 days, one seedling from the middle of a row (competitive seedling) were washed out of one pot from each block and their total root lengths measured. Seedling shoots were excised, and roots and shoots were oven-dried at 75 C for 24 hr and then weighed. Correlations of total root length and root or total seedling dry weight were calculated. The experiment lasted 120 days. Mean total root length for each seed lot was plotted over time starting with germination, and a curve was fitted through the points. Confidence limits were calculated for each mean. Individual curves for seed lots were compared and their confidence limits were found to overlap. Curves for competitive seedlings overlapped those for single seedlings. Therefore, data from all seedlings were pooled and a single curve was drawn through the means of total root lengths at each measurement time (Fig. 2). Total root length was significantly correlated ($P = 0.05$) with root dry weight ($r = 0.92$) and total seedling dry weight ($r = 0.83$).

To determine the relative growth of taproot and secondary branch roots, data were collected from weekly measurements on three Koksilah nursery seed lots sown in adjacent beds. At each collection, a randomly selected section of bed containing about 10

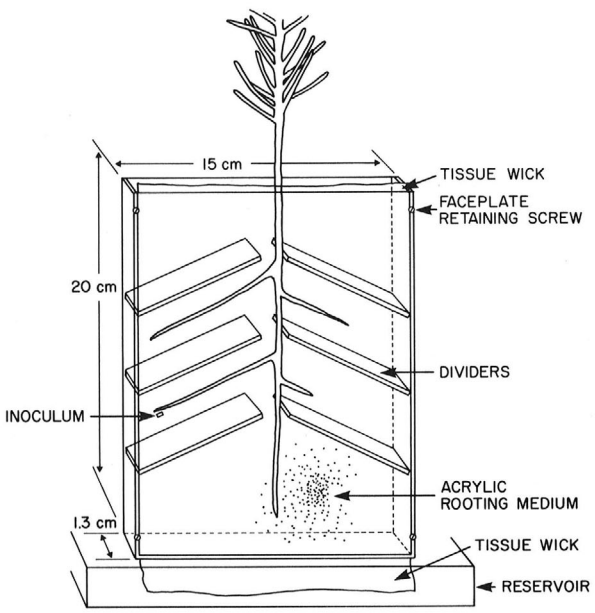

Fig. 1. Translucent observation box for measurement of growth of *Fusarium oxysporum* in Douglas-fir seedling roots.

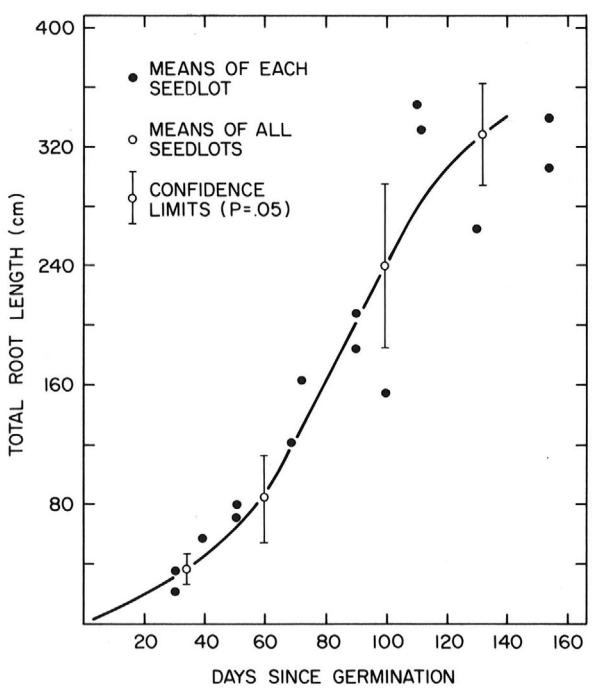

Fig. 2. Growth of Douglas-fir seedling roots at constant day-night temperatures of 25–18.5 C.

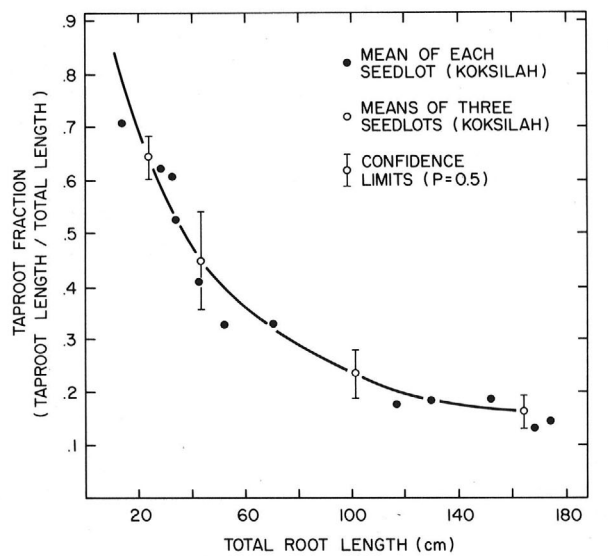

Fig. 3. Relationship of total root length and taproot length fraction in Douglas-fir seedlings.

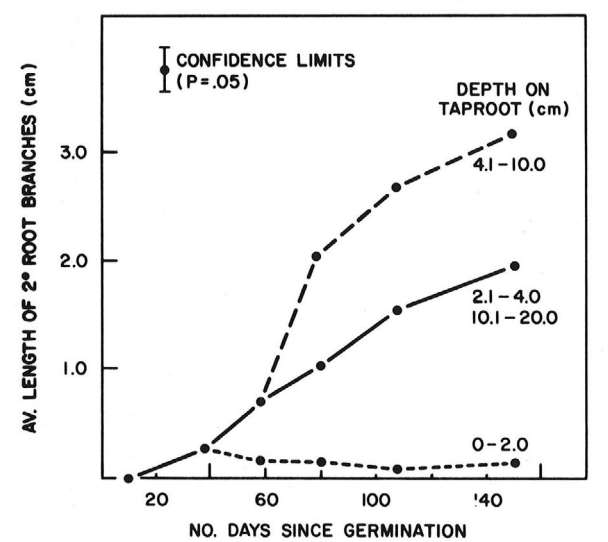

Fig. 4. Relationship of growth of secondary (2°) root branches to depth on taproot of Douglas-fir seedlings.

seedlings was dug up with root systems intact, to a depth of at least 20 cm. The seedlings plus adhering soil were transferred to the laboratory, with precautions to avoid root breakage. Weekly collections of bed sections were staggered by seed lot so that each was sampled every 3 wk. In the laboratory, soil was removed from roots by gentle hosing, followed by suspension of the roots in a column of water agitated by bubbling with compressed air. Five seedlings were randomly selected. The following measurements were taken: length of radicle or taproot from groundline to tip, distance along taproot to origin of each secondary branch, length of each branch, distance of each tertiary branch along the secondary branch and its length, position of root-rot lesions with respect to depth and distance along root. Roots with lesions were excised, surface-sterilized, and cultured for presence of *F. oxysporum*.

Frequency distributions of radicle length and initial lengths of secondary and tertiary branches, tested by chi-squared goodness-of-fit (22), were not significantly different ($P = 0.05$) from a normal distribution. Taproot growth was calculated as a fraction of total root growth (Fig. 3). Mean lengths of secondary branch roots were computed in each 2-cm soil depth class at each sampling date. Analysis of variance showed no significant ($P = 0.05$) difference among seed lots, but a highly significant ($P = 0.01$) interaction of collection dates and soil depth classes. Duncan's new multiple range test of means (22) showed that mean secondary branch length was greatest at 4.1–6.0 and 6.1–8.0 cm depths and least at 0–2.0 cm depth. Root length did not vary significantly at other depths (Fig. 4). Elongation rates were computed for branches in each depth class and expressed as percentage of total rate of root growth.

Number and distribution of roots. The number of secondary branches was plotted over total root length for each seedling and curves were fitted through the seed lot means at each collection date. Confidence limits for each mean were calculated and curves for each seed lot were compared. All had overlapping confidence limits at all collection dates and were therefore pooled to form a single curve (Fig. 5). Distribution of secondary branches along the taproot during the growing season was expressed as a percentage of branch origins occurring in each 2-cm soil depth class at each collection date (Fig. 6).

The number of tertiary roots was plotted over the length of each secondary branch for all seedlings and collection dates. Comparisons of regression lines for different collection dates and depth classes showed no clear effects of these factors. All data for each seed lot were therefore pooled and a single regression was computed for number of tertiary branches on length of parent secondary branch. Regressions were highly significant for each seed lot (b = 2.4, 3.0 and 3.1, respectively). More than 90% of tertiary roots were less than 5 mm long at the last collection date.

Distribution of tertiary branches was expressed as a percentage occurring in each 2-cm segment of the secondary branch. This was computed for all branches by 2-cm soil depth class and collection date. Trends were identified by inspection for different depth classes and collection dates (Fig. 7).

To ascertain vertical angle of secondary root branch growth, the experiment described under "Root growth" was duplicated, with the following modifications: Pots were fitted with root cages (4) prior to planting. The experiment was conducted in a greenhouse equipped with 16-hr supplementary lighting. One seedling was selected from each block every 30 days and the positions of all its roots were recorded by root plotter (4). The results showed that taproots were generally vertical and that secondary branches had angles becoming more obtuse with depth of origin and root length (Table 2). Angles were generally more obtuse in competitive seedlings. Tertiary roots branched at 90° from parent secondary roots.

MODEL

The following simplifications and assumptions were made in the model. The 180-day growing season was subdivided into 36 5-day periods. This period was chosen to allow significant development in germination, root growth, and lesion elongation, while maintaining continuity. No provision was made for growth of tertiary root branches beyond their initial length. One horizontal dimension was used to represent the azimuth around a seedling, assuming that horizontal effects were the same in all directions.

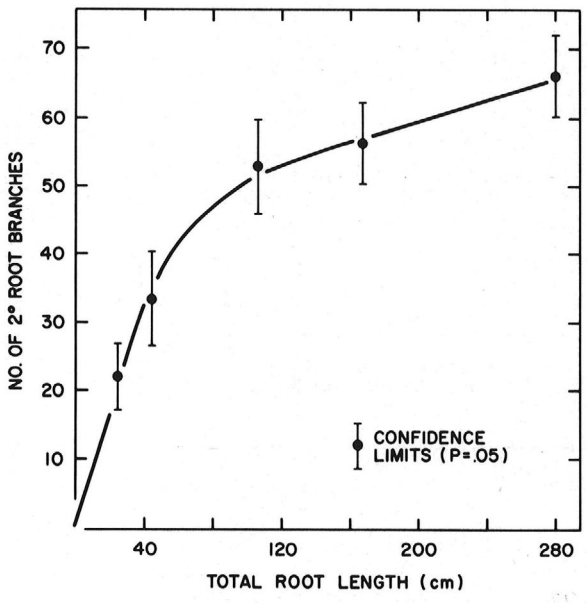

Fig. 5. Relationship of total root length to number of secondary (2°) root branches in Douglas-fir seedlings.

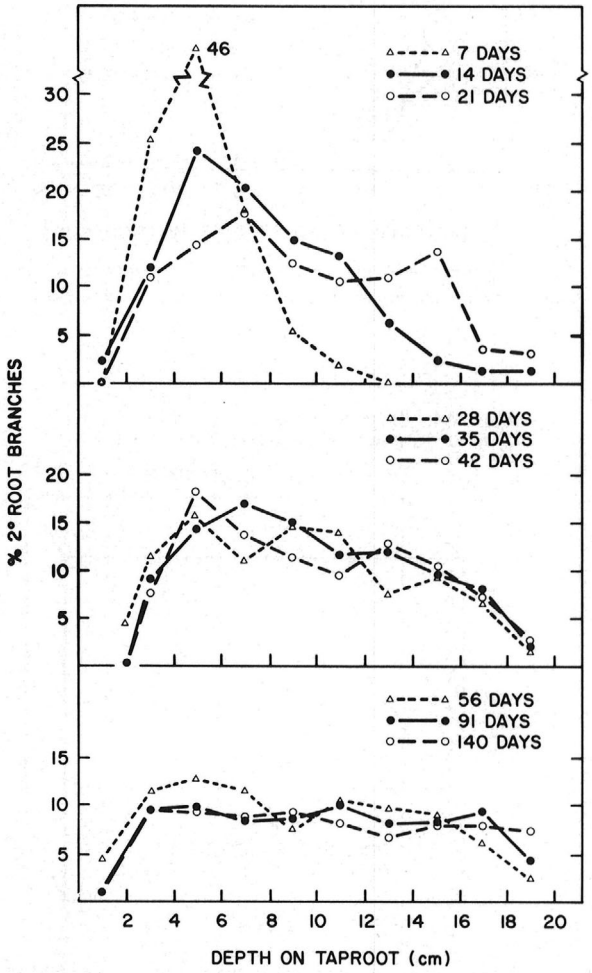

Fig. 6. Relationship of distribution of secondary (2°) root branches to age of seedling and depth on taproot in Douglas-fir seedlings.

This was not strictly true of seedlings at the edges of seedbeds. Horizontal and vertical distances were subdivided into ten 2-cm units for using distance-dependent relationships and summarizing results.

Infection was calculated as a random event of a root tip contacting an infectious organic particle by occupying the same cells of a lattice. Size of the lattice was determined from concentration of particles in the soil. Size of lattice cells was determined from diameter of organic particles (Fig. 8).

Temperatures were expressed as accumulated degree-hours above 0 C (heatsum) for each 24-hr period during germination and for each 5-day period during root and lesion growth. Most graphic relationships were applied by linear interpolation between sample points rather than by equations, because of difficulties in defining the latter. Random variation was generated by pseudo-random selection of values from normal distributions of given means and standard deviations (15) derived from experimental results.

The structure and sequence of events in the model are shown in Fig. 9. Procedures for computation of variables from the model relationships are shown in Table 1.

Model output. Numbers of healthy, infected but living, damped-off, and dead (due to root rot) seedlings were predicted by the model for each 5-day period. In addition, the model predicted the total number and length of secondary and tertiary root branches according to whether they were healthy or infected through their root tips or through lesion spread from other branches. Totals were produced for each 5-day period and for each 2-cm soil depth. Number, length, location, and infection status of individual branches were predicted for each seedling.

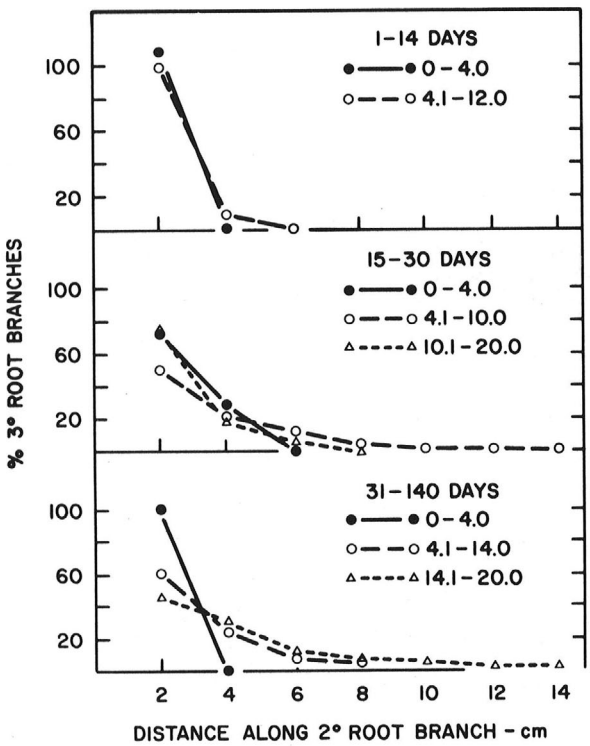

Fig. 7. Relationship of distribution of tertiary (3°) roots to age seedling and distance along parent secondary (2°) branch in Douglas-fir seedlings.

VALIDATION OF MODEL

Operation of the model was initiated by supplying values for the following variables: number of 5-day periods (maximum 36); number of seeds to be sown (maximum, 100); germination threshold heatsum, emergence regression coefficient, and slow emergence percent (averages 2,500 degree-hours, 17.5% emergence per 000 degree-hours, and 85% emergence, respectively); inoculum concentration (average 0.5 particles per cubic centimeter of soil); periodic heatsums for shoot growth, root growth, and germination zones (values derived from nursery records); and factors for changing root growth rate, inoculum size and concentration, lesion growth rate, root tip resistance to infection, and periodic heatsums (default values were 1.0).

Heatsum values were derived from continuous thermograph records at Koksilah nursery in 1973 and 1975 (5) and were estimated from climate summaries (10) for 1962 and 1963. Other initial values were derived from nursery samples in 1973 and 1975 and by estimates for 1962 and 1963. Accuracy of model predictions was tested by chi-squared goodness-of-fit to measurements of nursery seedlings ($P = 0.05$). Predicted germination did not differ significantly from germination data obtained from 1973 nursery germination trials, based on germinable seed (12). Total root length in Koksilah nursery was measured from five seedlings in each of three seed lots. In 1973, root length was measured weekly; in 1975, it was measured at 60 and 120 days after sowing. Different seed lots and seedbeds were used each year. Root length predicted by the

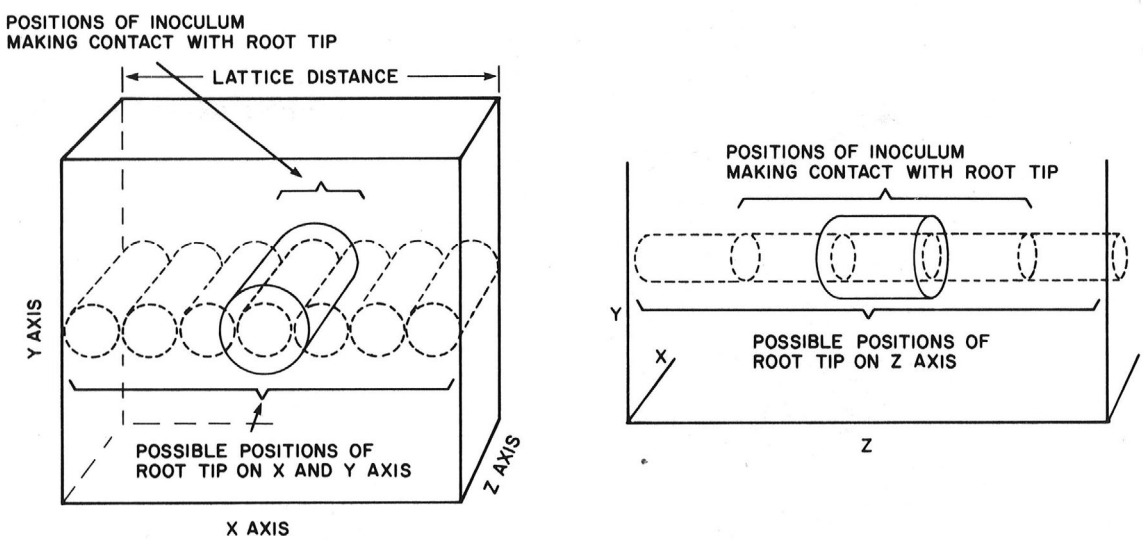

Fig. 8. Relationship of inoculum particle distribution in the soil to the root tip position in determining the probability of contact. Broken lines denote possible root tip positions within particle lattice; solid line denotes particle position at center of lattice. Actual root tip position was determined by random selection from possible positions on X, Y and Z axes.

model did not differ significantly from that measured in nursery seedlings in both years (Table 3).

Spatial distribution of secondary and tertiary root tips in Koksilah nursery was measured weekly in 1973 in three seed lots in each 2-cm soil depth, using undisturbed soil blocks containing root systems (4). The percentage of root tips occurring in each 2-cm depth class predicted by the model did not differ significantly in most depth classes from that measured in nursery seedlings.

Diseased seedlings. Number of diseased seedlings and number and length of infected roots in Koksilah nursery seedlings collected in 1973 and 1975 were compared with those predicted by the model. Model predictions ranged from 72–120% of nursery measurements (Table 3) and were within the nursery ranges for both years (22–63 and 10–31%). No damping-off or significant mortality caused by

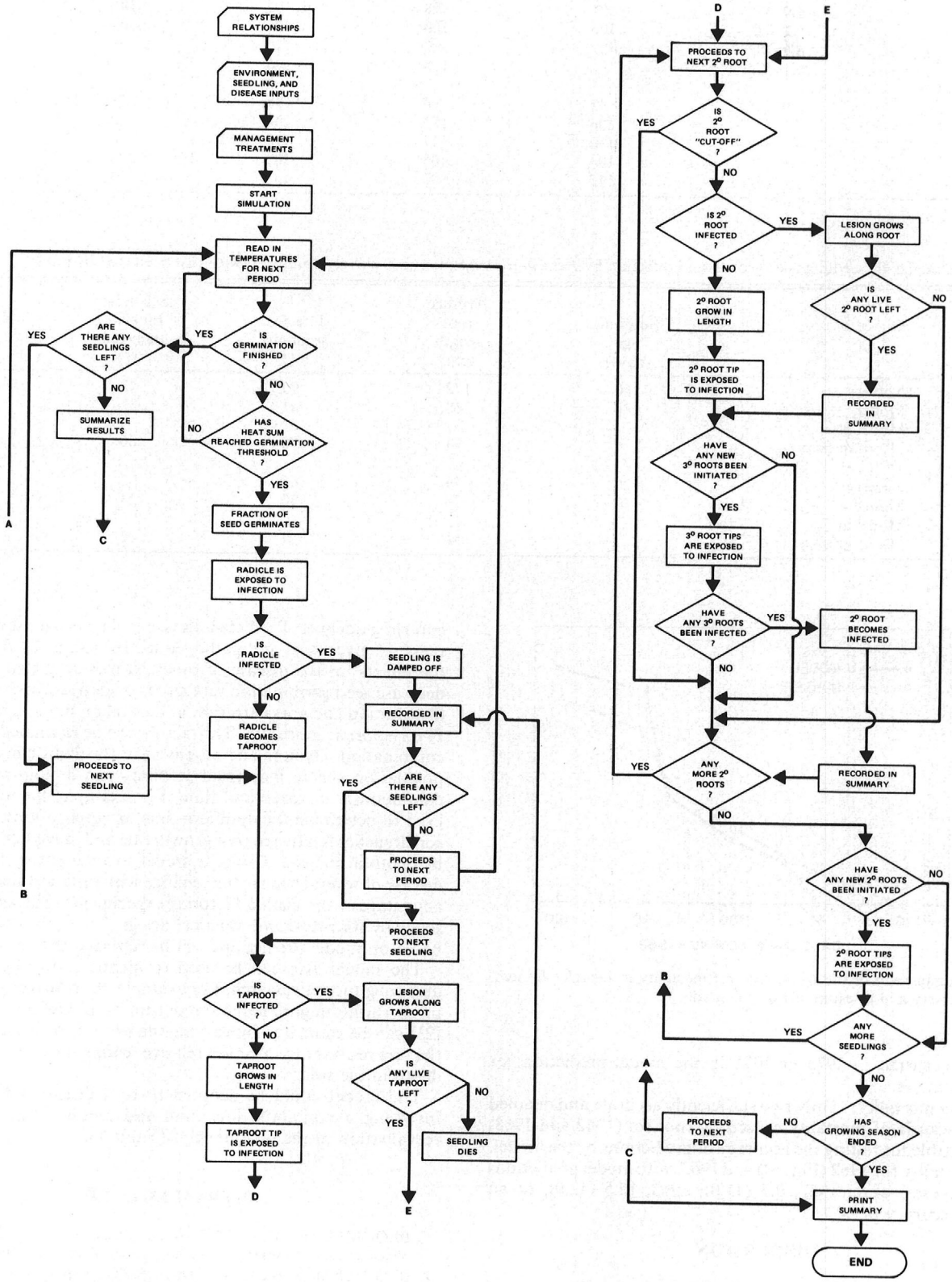

Fig. 9. Flow diagram showing sequence of events in model of damping-off and root rot of Douglas-fir seedlings caused by *Fusarium oxysporum*.

TABLE 2. Relationship of number of seedlings and length and depth of taproot to growth angle of secondary Douglas-fir seedling root branches

Seedlings per pot	Root Branch length (cm)	Angle subtended from origin to tip per depth on taproot				
		0–2.0 cm (degrees)	2.1–4.0 cm (degrees)	4.1–6.0 cm (degrees)	6.1–8.0 cm (degrees)	8.1–10.0 cm (degrees)
1	0–2.0	90	93	98	98	...
	2.1–4.0	93	94	103	99	...
	4.0–6.0	101	98	105	101	...
	6.1–8.0	106	100	105	103	...
	8.1–10.0	109	100	110	101	...
	10.1–12.0	...	114	126	...	...
3	0–2.0	98	96	98	98	104
	2.1–4.0	106	103	108	112	118
	4.1–6.0	110	117	113	114	121
	6.1–8.0	104	105	108	103	111
	8.1–10.0	115	102	131	113	...

TABLE 3. Douglas-fir seedling root growth and infection by *Fusarium oxysporum* in a nursery compared with that predicted by model

Year	Source of data	Seedling age (days)	Average root length (cm)	Infected seedlings (%)	Secondary branches infected (%)	Root length infected (%)
1973	Nursery	180	172	90	43	39
	Model	180	160	81	37	28
	Model as % of nursery		93	90	86	72
1975	Nursery	120	79	66	32	20
	Model	120	76	80	23	20
	Model as % of nursery		96	121	72	100

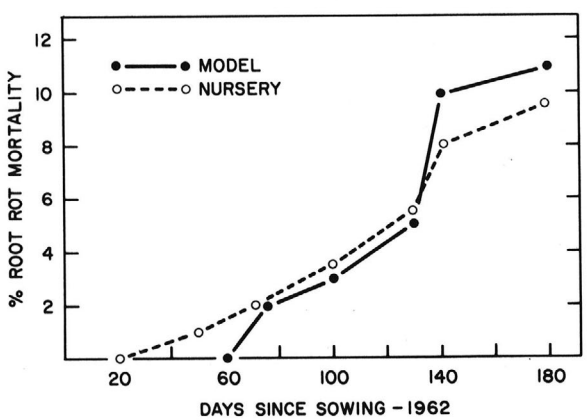

Fig. 10. Comparison of Fusarium root rot mortality in Douglas-fir seedlings in nursery and as estimated by the model.

root rot occurred in 1973 or 1975 in the model predictions or nursery samples.

Seedling mortality. Only two sufficiently accurate and detailed historic records of mortality caused by root rot (1962 and 1963) were available for testing the accuracy of predictions by the model. Total mortality for 1962 (Fig. 10) and 1963, with model predictions in parentheses, were: 1962, 9.5 (11.0); 1963, 15.5 (12.0), or an average accuracy of 80%.

DISCUSSION

Over the range of conditions in which it was tested, the model provided sufficiently accurate predictions of damping-off and root rot of Douglas-fir nursery seedlings to form the basis of disease control guidelines. Predicted disease incidence and severity over a range of given host and pathogen factors can be used to examine the effects on the disease of practical measures that increase or decrease seed germination rate and root elongation or that change distribution and concentration in the soil or size and infectivity of *F. oxysporum* inoculum. The factors can be examined singly or in combination. Dynamic development of the disease in the seedling population and in individual seedlings can be followed virtually continuously in space and time. For example, the model can be used to determine the optimum time for application of fungicidal soil drenches relative to root growth rate and inoculum distribution by depth in the soil. Use of a model to analyze the effects on the disease of several factors that change with time and space has great advantages over classic factorial experiments that are limited in scope by statistical and practical design. The results of an analysis based on model predictions will be reported in another paper.

The model also can be used to identify critical relationships deserving further research. For example, the relative importance of mycorrhizal fungi in reduction of root rot of Douglas-fir seedlings (23) can be estimated by varying the proportion of seedling roots that are resistant to infection relative to time since germination and depth in the soil.

The model could be adapted to root diseases of other hosts involving a nonmotile inoculum and motile infection court by reevaluation of the relationships (Table 1).

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