Model Simulations of Infection of Douglas-Fir Seedlings by *Fusarium oxysporum*

W. J. Bloomberg

Forest pathologist, Environment Canada, Canadian Forestry Service, Pacific Forest Research Centre, Victoria, B.C. V8Z 1M5.
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ABSTRACT

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A simulation model of Fusarium root rot of Douglas-fir seedlings was used to predict seedling infection, mortality, root growth in various temperature regimes, root growth rates and sizes, and concentrations of inoculum. The most important factors in simulated root infection were those affecting size and number of infection sites (root tips), size and concentration of inoculum particles, and rate of lesion elongation. More and longer root tips per seedling, more infections, more rapid spread of lesions in roots, and more seedling mortality were predicted by simulations with warm regimes than by those with moderate or cool regimes. Simulations with fast root growth rates also predicted more and longer root tips and infections than did those with slow or moderate root growth rate but no increase in rate of lesion spread or seedling mortality. Simulations with relatively long or thick inoculum particles or relatively dense inoculum concentrations predicted more root infection and seedling mortality than did those with small particles or sparse concentrations. According to model predictions, density of inoculum in the upper 10 cm of soil had a greater effect on infection and seedling mortality than density in the lower 10 cm. The rapidity with which the taproot became infected and the proximity of infections to the upper part of the taproot were the most important factors in seedling mortality. Predicted root length was affected most by rate of root elongation, number of infections and rate of lesion elongation.

Additional key words: Computer, late damping-off, nursery disease.

A function of simulation modeling of plant diseases is the extrapolation of relationships derived from experimental data to more general and thus more useful guidelines for disease control. By integrating the results of a number of experiments, the modeler aims at developing a system that is more useful than the sum of its components. Confidence in the accuracy of a model depends primarily on the frequency with which predicted results fall within a range of acceptable accuracy relative to observed results and depends secondarily on the correctness with which it represents the mechanisms that determine disease development, because in practice the accuracy of a model cannot be tested against all possible disease situations.

A simulation model of root rot of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Fr.) seedlings by *Fusarium oxysporum* Schlecht. was developed from relationships of root and lesion elongation to temperature and root and inoculum distribution to soil depth (5). The model, called NURDIS, was written in FORTRAN and was mounted on a Digital Electronic Corporation PDP 11/45 computer. The model represents seedling root systems comprising vertical taproot with elongating and branching secondary roots. In the model, contact between root tips and immobile inoculum particles may result in infection, followed by lesion elongation along roots and eventually spread of infection to the taproot and other roots. The model predicted root length, distribution, and infection with 70–80% accuracy over 3 yr of comparison with nursery records of the disease. I now report the results of using the model to predict seedling root growth, infection, and mortality over a range of temperature regimes, root growth rates, and inoculum particle sizes, concentrations, and distributions in the soil. The objectives were to evaluate the usefulness of the method in formulating disease controls and to gain insight into possible disease mechanisms. The results are analyzed in terms of the relationships in the model and are compared with the experimental results. General implications for control of Fusarium root rot are drawn from simulation results.

METHODS

Values necessary to execute the model were supplied as regression equations, functional values, constants and factors (5). For all simulation runs, the following constants were used: number of seeds sown (50 per 40 × 40 cm plot); length of growing season (1 May to 31 October); seedling emergence threshold (4,500 degree-

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hr); emergence coefficient (17.5% per 1,000 degree-hr); slow emergence percentage (85%), and slow emergence factor (0.5) (4). Initially, runs were based on 100 seeds sown, but 50 seeds did not reduce the accuracy of the results. The following functional values were varied: temperature, seedling root elongation rate, inoculum particle diameter and length, and concentration and distribution of inoculum particles in soil.

Temperature was expressed as heat sum (accumulated degree-hr above 0 C) daily for the germination period and for 5-day periods over the 180-day growing season to coincide with the temperature units and time divisions of the model. To simulate annual variation, runs were performed with temperature regimes of 1973, 1974, and 1975 derived from a continuous weather record station at Koksilah, British Columbia forest nursery. The regimes differed in total heat sums (53,326, 55,817, and 56,389 degree-hr, respectively) and in distribution of degree-hr over the growing season; ie, 1973 was consistently cooler than the other years; 1975 was warmer than for 1974 for 120 days and then became cooler. Inoculum particle sizes (range 1–20 mm long × 3 mm dia.), concentration (0.2–0.7 per cubic centimeter of soil) and percent distribution by 2-cm soil depth class (approximately equal in all depth classes) were obtained from nursery samples (3). Root elongation rates were obtained from experiments (5). Predictions were based on the average for 3 yr. Disease was expressed as: (i) seedling infection (one or more roots infected) or mortality (percent of seedlings killed); (ii) root growth (number and length of taproots and secondary branch roots, number of tertiary branch roots); and (iii) root infection (number, length, and percent of each type of roots infected). Estimates of least significant differences were based on five replications each for 1973, 1974, and 1975.

RESULTS AND DISCUSSION

Temperature regime. To simulate the effects of various types of temperature regimes on incidence and severity of root rot caused by *F. oxysporum*, the regimes for 1973-1975 (average heat sum 55,177 degree-hr) were designated as moderate and their heat sums were increased or decreased by 10% for all or part of the growing season, as follows (regime designation and average heat sum in 1,000 degree-hr in parentheses): increased during the first 50 days (early warm, 56.0); increased or decreased over the whole season (warm and cool regimes, 60.7 and 54.6, respectively); increased during the first half of the growing season (warm-moderate, 58.1) or second half (moderate-warm, 57.8); decreased during the first half (cool-moderate, 54.9) or during the second half (moderate-cool, 54.9); increased during the first half, decreased during the second half (warm-cool, 57.8), and vice versa (cool-warm, 57.5). The adjustment of ± 10% was based on the maximum difference during

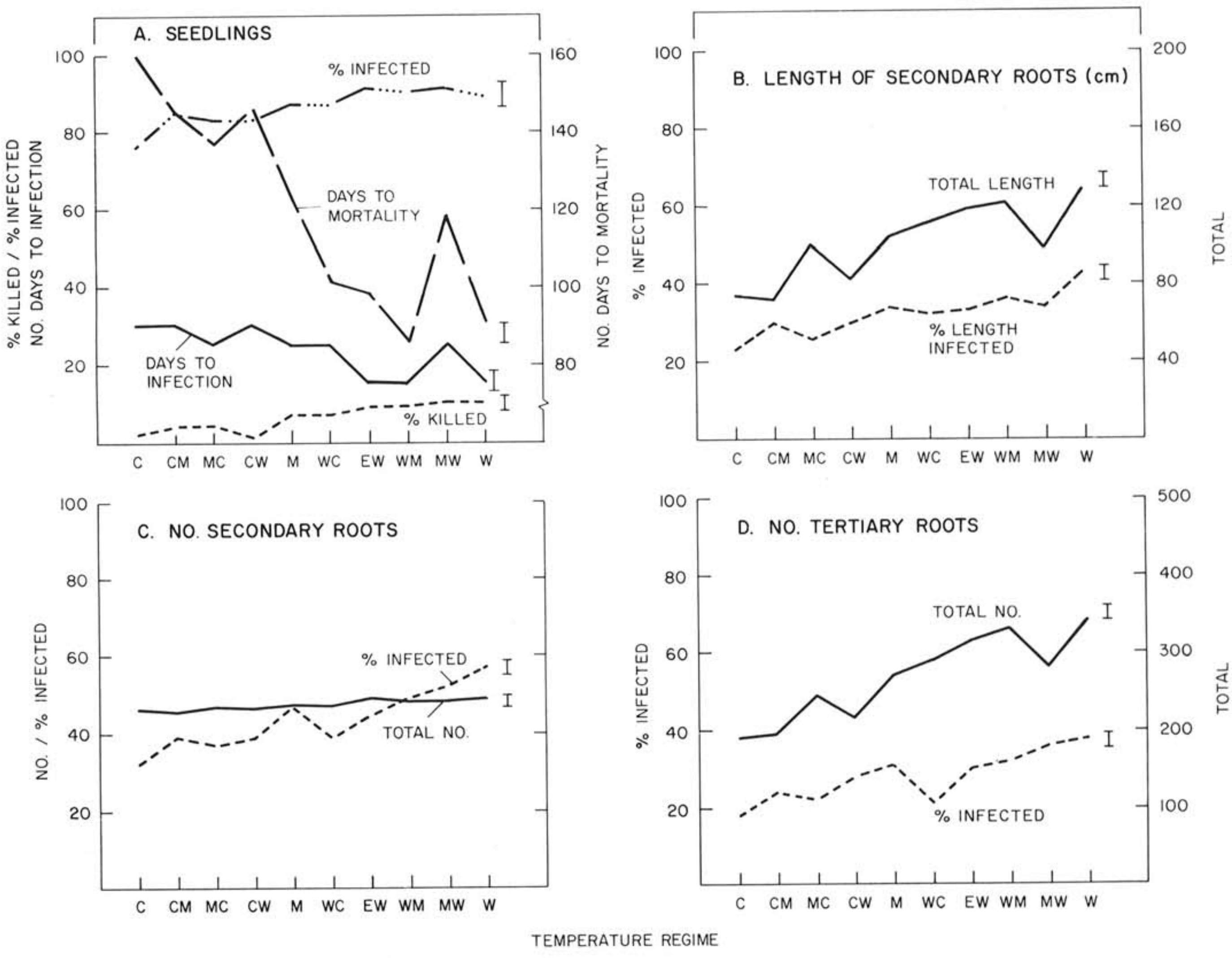

Fig. 1 Effect of temperature regime on infection and mortality of Douglas-fir seedlings caused by *Fusarium oxysporum* as predicted by model. Regimes are ordered in approximately increasing number of degree-hr as follows: C, cool; CM, cool-moderate; MC, moderate-cool; M, moderate; WC, warm-cool; EW, early warm; WM, warm-moderate; MW, moderate-warm, and W, warm. **A,** Percent of seedlings infected or killed and number of days to infection or mortality. **B,** Average aggregate length of secondary roots and percent of length infected per seedling. **C,** Average number of secondary roots and percent infected per seedling. **D,** Average number of tertiary roots and percent infected per seedling.

any 5-day period for 1973-1975.

For all regimes, the average predicted infections through secondary and tertiary roots were 73 and 27%, respectively. Less than 10% of the secondary root infections were categorized as through root tips, compared with more than 90% by spread of lesions from other roots on the same seedling. The predicted number of days to infection of the taproot by lesion spread along the secondary roots (lateral infection) was greater in regimes with cool than in those with warm periods and was greatest in the cool-warm regime (Table 1).

Simulation runs at temperature regimes containing cool periods predicted lower levels for infection and mortality than at those containing warm periods (Fig. 1). The warm-cool regime simulation predicted the same seedling infection and mortality levels as the moderate regime (Fig. 1A) but predicted lower secondary and tertiary root infection (Figs. 1C,D). The cool-warm regime simulation predicted least mortality. In the moderate, early-warm, cool-warm, and warm-cool regimes, the predicted percent of infected secondary root length did not differ significantly (Fig. 1B), but the number of taproot infections predicted and the percentage predicted in the upper 6 cm of taproot varied and was less in the cool-warm regime (Table 1). The cool regime simulation predicted the lowest number of taproot infections. Generally, predicted number of days to seedling infection and mortality was greater in regimes with cool than in those with warm periods (Fig 1A). Predicted infection and mortality in the cool-warm regime began 5 and 46 days later, respectively, than in the warm-cool regime.

The results of simulating the effects of temperature regime on seedling mortality can be explained by the differential effects of temperature on elongation rates of lesions and roots, based on relationships in the model. Simulated runs using regimes with warm periods in the first half of the growing season, when root length was relatively short, predicted a greater number and earlier occurrence of lateral infections of taproots than did those of regimes with cool periods in the first half. According to the model, seedling mortality occurred when the taproot was completely destroyed, since all other roots originated from it. Therefore, regimes that resulted in increased number of taproot infections, especially on the upper part and early in the growing season, also contributed to greater mortality. The general increase in predicted percentage of infection and decrease in number of days to infection of secondary roots with increased warmth of regimes could be attributed to the effect of increasing the rate of spread of lesions from root to root. The greater percentage of tertiary roots infected during regimes with warm periods in the second half as opposed to the first half, viz, cool-warm vs. warm-cool, warm-moderate vs. moderate-warm (Fig. 1D), could be attributed to the initiation in the model of most tertiary roots in the second half of the growing season. The predominance of infections predicted by lesion spread rather than through root tips was explained by the low probability, based on distribution in soil samples (3), of root tips making contact with inoculum particles, relative to the probability of infection by lesion spread. Although tertiary roots outnumbered secondary roots by approximately 6:1 (Fig. 1C, D), their later initiation and assignment of much shorter lengths in the model resulted in much lower probability of infection.

In general, the simulation results agreed with observed increase in mortality percentage and decrease in time to start of mortality in Douglas-fir seedlings caused by *F. oxysporum,* especially with a warm first part of the growing season (2,7). The implication of simulation for practical control of Fusarium root rot is the need to maintain cool temperatures in nursery beds in the first part of the growing season through shading, irrigation, mulching, or other methods. Nurseries with relatively moderate growing season temperatures probably need to confine cooling measures to early season heat waves, and those with warm temperatures throughout the season, according to simulation results, require cooling measures for the first half of the season. Such measures in the second half of the growing season appear to have no effect on reducing mortality.

TABLE 1. Relationship of temperature regime to number of infections by *Fusarium oxysporum* on taproots of Douglas-fir seedlings, as predicted by model

Regime[a]	Infections (No.)	Infections at 0–6 cm (%)	Days to lateral infection (No.)
Cool	50	40	50
Cool-moderate	52	40	55
Cool-warm	59	31	65
Moderate	67	46	45
Warm-cool	81	54	45
Early warm	72	57	35
Warm	68	62	30

[a]Based on soil and air temperatures for 1 May to 31 October 1973, 1974, and 1975 at Koksilah forest nursery. Total daily degree-hr were increased or decreased during the entire season by 10% to represent warm and cool regimes, respectively, and during the first or second half of the season to represent combined regimes.

Root growth rate. To simulate the effects of root growth rate on development of Fusarium root rot, the growth rate, determined experimentally from three seedlots in sterilized soil under optimal temperature and light conditions (5), was designated as normal. The rate, expressed as percent increase in root length during each 5-day period, was raised or lowered by 5% to represent fast or slow growth, respectively. The adjustment was based on maximum differences in growth rate of roots among the three seedlots.

Simulations using slow root growth rate predicted less seedling infection and mortality than did normal or fast growth rates (Table 2). The predicted percent of secondary root length infected was less; the number of days to infection of secondary and taproots and the number of taproot infections also were fewer. Simulations using fast growth rate predicted no difference in seedling mortality but more infected seedlings and greater length of infected secondary root than did normal growth rate. There was a trend (not significant) for increase in number of days to taproot infection with increasing growth rate.

The results from these simulation runs can be explained by the effect of the model in reducing the size and number of infection sites (secondary root tips) at slow compared with normal growth rate (Table 2), resulting in lower probability of infection, as indicated by the longer period before infection occurs. Runs with a faster growth

TABLE 2. Relationship of root growth rate of Douglas-fir seedlings to infection and mortality caused by *Fusarium oxysporum*, as predicted by model

Growth rate[a]	Seedlings		Secondary roots				Taproots	
	Infected (%)	Killed (%)	Av. length (cm)	Root length infected (%)	Av. tip length (mm)	Days to root infection (No.)	Lateral infections (No.)	Days to lateral infection (No.)
Slow	82 x[b]	2 x	2.0 x	27 x	1.1 x	40 x	57 x	40 x
Normal	87 y	7 y	2.2 y	34 y	1.3 y	25 y	67 y	45 xy
Fast	93 z	5 xy	2.4 z	35 y	1.7 z	30 y	71 y	50 y

[a]Based on root growth under optimum light and temperature conditions. Rate was decreased or increased by 5% to represent slow or fast rates, respectively.
[b]Values in each column are significantly different ($P = 0.05$) if followed by different letters.

rate predicted more and larger infection sites than those with slow or normal growth rate, but sites were further from the taproot, as indicated by the longer average root length and time required for lesions to pass to the taproot. Thus, the predicted percentage of infected seedlings and secondary roots was greatest at the fastest growth rate, but seedling mortality was not significantly different.

TABLE 3. Relationship of inoculum particle size to infection of Douglas-fir seedlings by *Fusarium oxysporum*, as predicted by model

Particle size distribution[a]	Days to infection (No.)	Roots infected through tip (No.)
Sample	25	128
Diameter × 2	20	183
Diameter × 4	15	279
Length × 4	20	184
Length × 8	20	191

[a] Based on sampled distribution at Koksilah forest nursery.

The predictions from simulations are in partial agreement with the observed lack of correlation between seedling mortality caused by Fursarium root rot and root length (2), assuming that only seedlings of normal or fast growth rates as defined were examined. Observed increase in seedling mortality with application of nitrogenous fertilizers, which also increased root dry weight, were attributed to the effect of nitrogen per se (9). The implications of simulation predictions are that increased seedling growth rate exacerbates the percentage of infection; decreased growth rate reduces seedling mortality, but increased growth rate has little effect on mortality.

Inoculum particle size. Inoculum of *F. oxysporum* is associated mainly with organic particles in the soil, especially fragments of roots infected in previous croppings (3). To determine the effects of particle size on Fusarium root rot, simulations were done using various size distributions by doubling and quadrupling particle diameter, holding length distribution constant, and quadrupling or increasing particle length eightfold, holding diameter constant, based on measurements from nursery soil samples (see Methods).

The simulations predicted increased percentage of seedlings

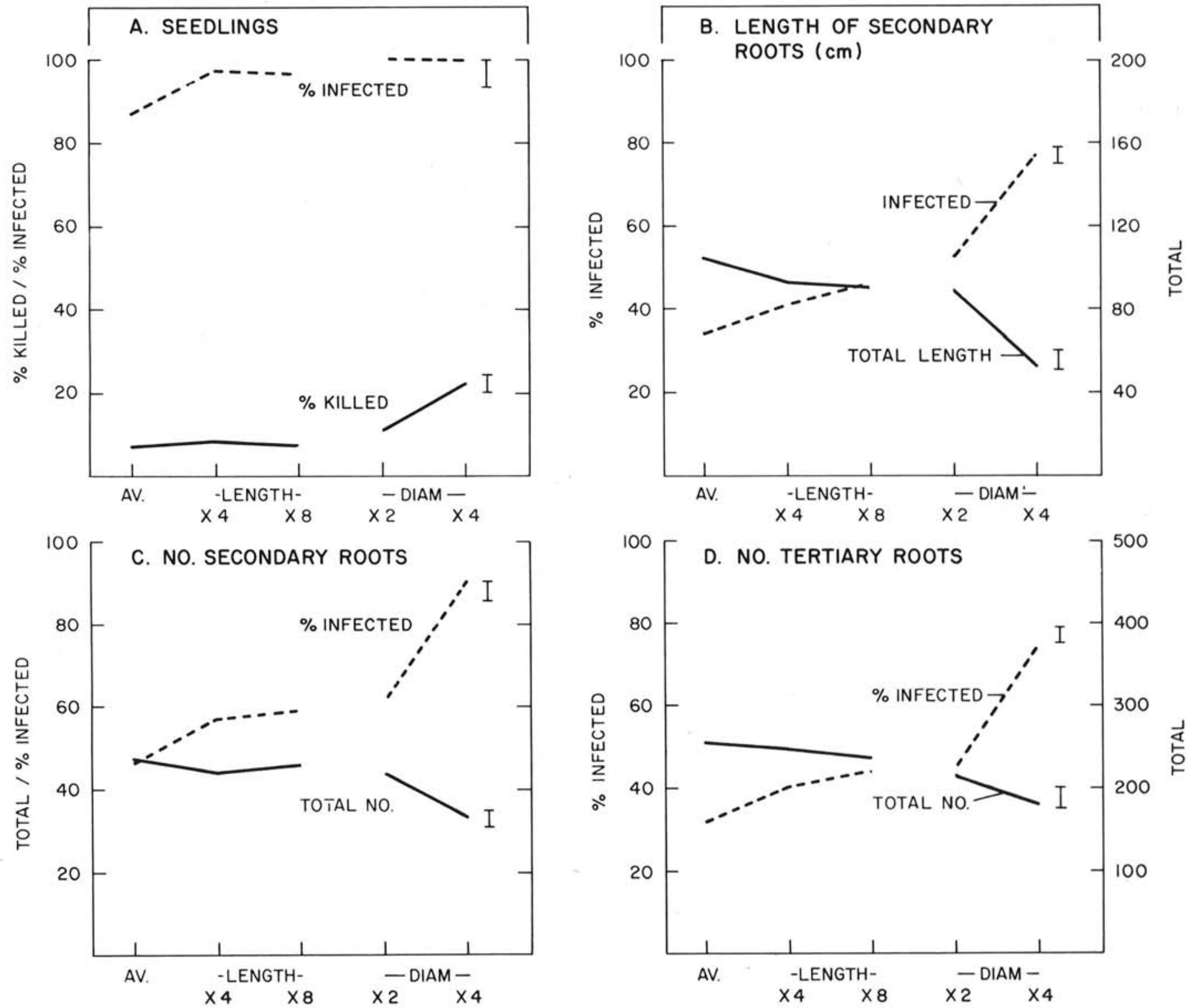

Fig. 2. Effect of inoculum particle size on predicted infection and mortality of Douglas-fir seedlings caused by *Fusarium oxysporum* as predicted by model. Inoculum particle sizes ordered in approximately increasing volume of infection lattice occupied as follows: AV, length and diameter distribution as sampled; length or diameter distributions of sample increased by factors of 4 or 8 and 2 or 4, respectively. **A,** Percent of seedlings infected or killed. **B,** Average aggregate length of secondary roots and percent infected per seedling. **C,** Average number of secondary roots and percent infected per seedling. **D,** Average number of tertiary roots and percent infected per seedling.

infected with greater particle length and diameter, and increased percentage killed with quadrupling of diameter (Fig. 2A). Other changes in inoculum particle size had little effect on predicted mortality. Simulations using quadrupled length and diameter also predicted increased percentage of root infection (Fig. 2C and D). All simulations of increased particle size predicted higher percentage of secondary root length infections (Fig. 2B). Predicted total number and length of roots were reduced by quadrupling the diameter of particles.

The results can be explained by the effect of the model in increasing the probability of root tip contact with inoculum particles as the latter were increased in size, resulting in more and earlier infections (Table 3). In the model, inoculum particles were assumed to occupy intersections of a cubic lattice centered on the root tip (5). Root tip volume increases as the square of the diameter but only as the first power of the length. Thus, increases in root tip diameter resulted in proportionally greater increase in volume of lattice occupied than with increases in length.

Because the model omitted elongation of infected roots, total length of root systems decreased with increasing infection. This result contrasted with predicted increments in root length as infection increased because of raised temperature (Fig. 1B) or larger growth rate (Table 2). The difference is explained by lack of compensating root growth as inoculum size increased, as they were assumed to be unrelated, whereas temperature or growth rate resulted in a net increase in root length even though infection also rose.

No experimental evidence can be adduced to support the simulation results, but the relationship between inoculum size and infection probability is logical. The practical extrapolations suggest that removal of large pieces of inoculum from nursery beds, eg, infected seedling roots, should result in an increment of control. Intensive rototilling at intervals during a fallowing period would probably accelerate reduction of inoculum size.

Concentration and distribution of inoculum particles in soil. Simulations were performed using the average number of inoculum

TABLE 4. Relationship of inoculum particle concentration in soil to time of infection of Douglas-fir seedlings by *Fusarium oxysporum* and number of root tip infections, as predicted by model

Particles/cm^3 soil (No.)	Days to infection (No.)	Roots infected through tip (No.)
0.25	30	92
0.50	25	128
1.00	20	134
2.00	15	191

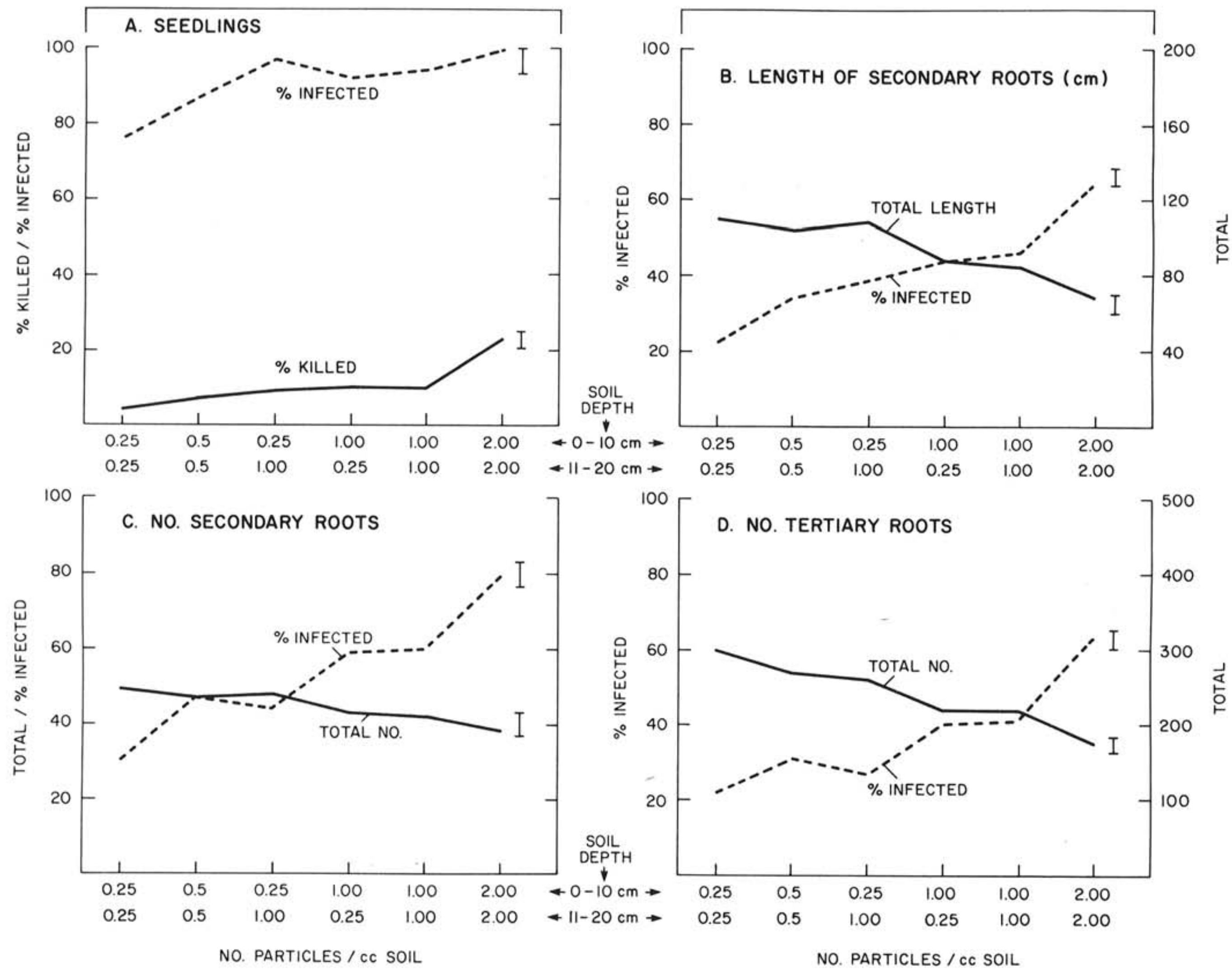

Fig. 3. Effect of concentration of inoculum particles in soil depths 0–10 and 11–20 cm on infection and mortality of Douglas-fir seedlings caused by *Fusarium oxysporum* as predicted by model. **A**, Percent of seedlings infected or killed. **B**, Average aggregate secondary root length and percent infected per seedling. **C**, Average number of secondary roots and percent infected per seedling. **D**, Average number of tertiary roots and percent infected per seedling.

particles per cubic centimeter of soil (0.5), determined from nursery soil samples (3) and also half, double, and quadruple the average number, ie, 0.25, 1.0, and 2.0, to simulate various concentrations of inoculum at all soil depths to 20 cm. Simulations also were done using half and double concentration in the upper and lower 10 cm soil depth, respectively, and double and half concentrations in the upper and lower 10 cm, respectively.

As inoculum concentration rose, the predicted percentage of seedlings infected and killed, and percentage of infected roots, increased; the total number and length of roots decreased (Fig. 3). Predicted mortality and root infection rose most sharply with a rise of inoculum concentration from 1.0 to 2.0 particles per cubic centimeter of soil at all soil depths. Predicted percentage of infected roots and percentage of root length infected were higher with inoculum concentrations of 1.0 and 0.25 than with 0.25 and 1.0 in the upper and lower 10-cm soil depth, respectively. Predicted infections with the former concentration did not differ from that with a concentration of 1.0 particle per cubic centimeter of soil at all depths.

The predictions of the simulations can be explained by the increasing probability of root tip contact with inoculum particles as the concentration of the latter increased. In the model, size of inoculum lattice, ie, distance between particles, was derived from $(\text{concentration})^{-1/3}$ giving 1.59, 1.26, 1.00, and 0.79 cm, respectively, for 0.25, 0.50, 1.0, and 2.0 particles per cubic centimeter. Because predicted root tip length approached 0.79 cm much more closely than the longer lattice distances, the probability of infection was disproportionately higher at $2.0/\text{cm}^3$ concentration. In the model, the initiation depth assigned to secondary roots on the taproot and the vertical angle assigned to root growth resulted in the majority of root tips occurring in the upper 10-cm soil depth (Fig. 4). The inoculum concentration in this depth, rather than in the lower 10 cm, affected the probability of infection most.

Predicted reduction of total number and length of roots with increasing inoculum concentration resulted from more and earlier infections as the probability of root tip contact with inoculum increased. Because inoculum size and root growth rate were assumed to be independent, no compensating growth occurred and the net size of root systems decreased.

The simulation predictions bear out the suspicion that continuous crops of Douglas-fir without intervening fallow periods bring about increasing mortality caused by Fusarium root rot through accumulation of inoculum in the soil (2). The results also are consistent with the observed increase in mortality associated with inoculum placement at shallow depth and reduced seedling dry weight with increasing inoculum concentration (8), as well as the reduction of mortality by fungicidal soil drenches (6), even though their effect may be limited to a few cm of depth. In practical terms, the simulation results underline the importance of inoculum reduction in the upper 10 cm of soil, especially if the concentration exceeds one particle per cubic centimeter of soil. Because seedlings killed by *F. oxysporum* in previous crops appear to be the main source of inoculum (3), as much of the infected root system in the upper 10 cm as possible should be removed.

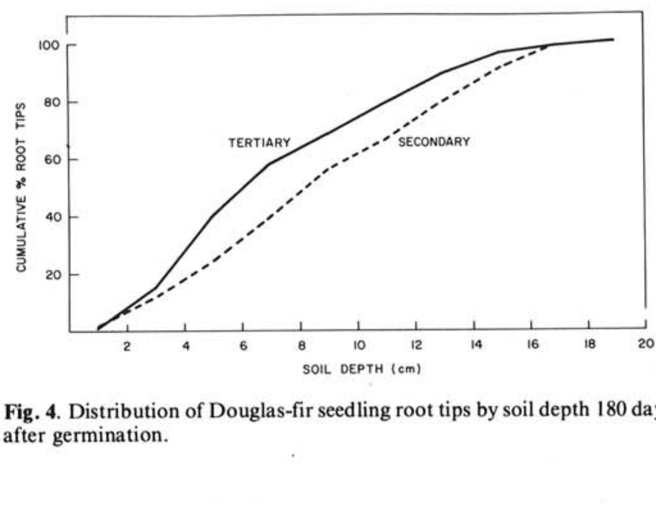

Fig. 4. Distribution of Douglas-fir seedling root tips by soil depth 180 days after germination.

Accumulation of infected roots on the soil surface, eg, in cull piles, should be avoided as these probably result in disease "hot spots" because of high concentration of inoculum. Root residues deeper than 10 cm, resulting from root pruning or seedling lifting operations, are of less concern, according to the simulation results.

Conclusion. According to the model, the most important factors affecting root infection by *F. oxysporum* are, not surprisingly, size and number of infection sites (root tips), size and concentration of inoculum particles, and rate of lesion elongation. Infection sites are related to root growth directly, or indirectly, through temperature regime. Lesion elongation is related to temperature regime. Higher temperature, therefore, increases both predicted number of infections and length of root infected. Greater growth rate, inoculum size, and density increase the predicted number of infections.

According to the model, the most important factors in seedling mortality are the rapidity with which the taproot becomes infected and the proximity of infections to the upper part of the taproot. Factors that increase the distance of infection site from the taproot or delay root tip infection also reduced predicted mortality. Fast growth rate increased not only distance but also the number, and size of infection sites. The predicted result was no increase in mortality. Cool regimes reduced distance of infection sites but also diminished the number and size and rate of lesion elongation. The net predicted result was reduced mortality. According to these relationships, nursery measures that combine fast root growth with reduction of inoculum concentration in the upper 10 cm of soil and relatively cool temperatures will reduce mortality. Simulation of these three conditons predicted nil mortality.

According to the model, opposing effects of root elongation and root infection most affected total root length. Warm regimes caused a net increase in total root length because root elongation outweighed increased infection sites and lesion elongation. Increased inoculum size caused a net decline in root length because root length did not increase to offset the larger number of tip infections.

The results of simulation were supported partly by experimental evidence and partly by principles of root infection relative to inoculum concentration (1). I conclude that the results and the simulation method, in general, are useful in prescribing control measures.

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