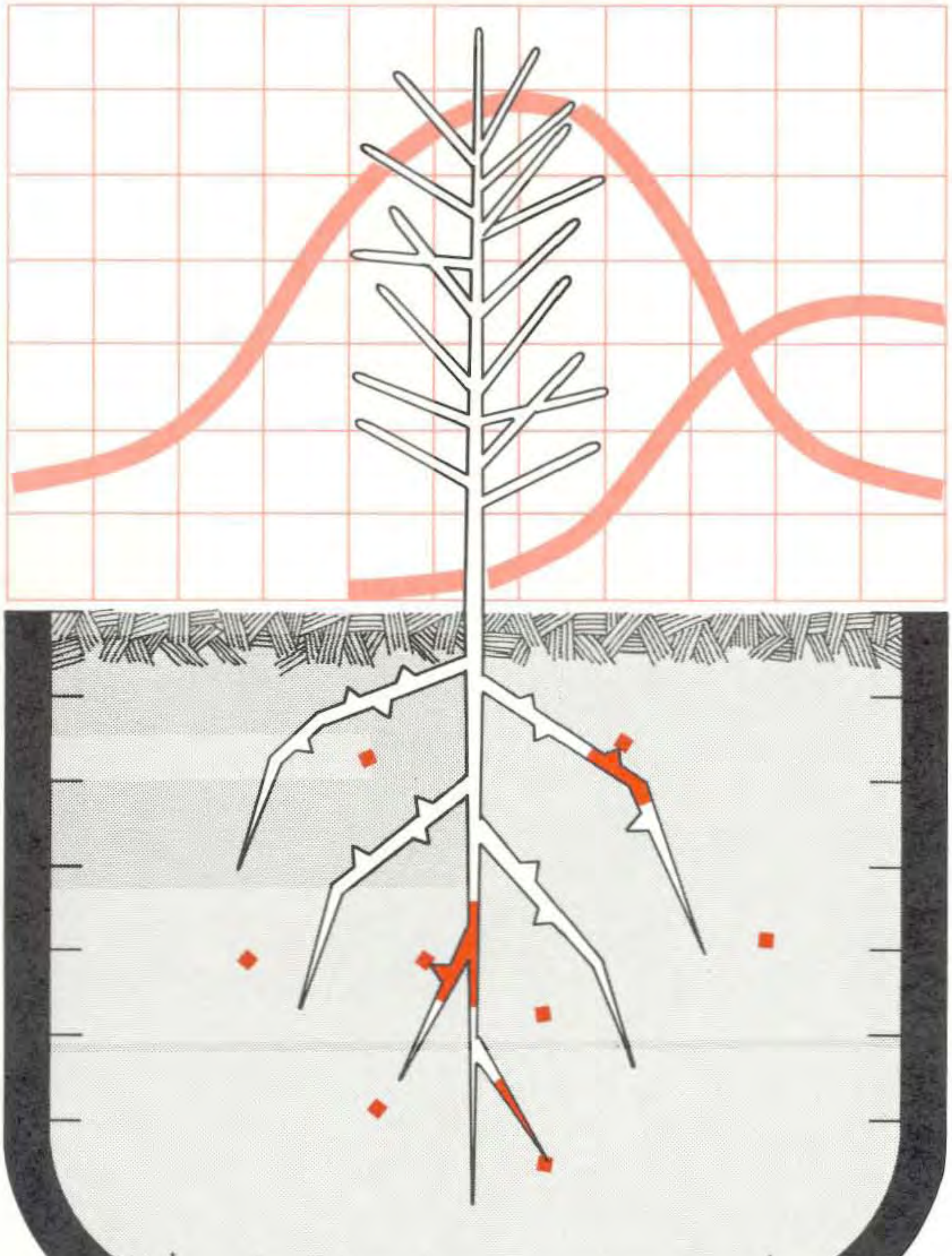
# Simulation of Douglas-fir Seedling Root Growth, Damping-Off & Root Rot

W. J. Bloomberg



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## ABSTRACT

A mathematical system was developed to describe root growth, damping-off and root rot of Douglas-fir nursery seedlings during the first growing season. Components of the system were: i) Seedling germination, including radicle initiation, ii) Root growth, including elongation of taproot, initiation and directional elongation of first-order roots and initiation of second-order roots, iii) Pathogen behavior, including distribution, size and infectivity of *Fusarium oxysporum* inoculum, and iv) Infection of root tips by fungus and growth of lesions in root. Component relationships were identified as those with consistently important effects on seedlings and fungus under coastal nursery conditions. They were expressed as regressions, tabular values or probability distribution functions and were derived from published results, experiments, logical relationships and field observations.

A computer model was constructed to integrate component relationships in logical order and in a computationally tractable form. This was achieved by subdivision of the growing season into 36 5-day periods, and the use of one vertical and one horizontal plane subdivided into 2-cm intervals of depth from soil surface and distance from taproot axis. Component relationships were modified as necessary to fit the time and space divisions of the model. A maximum population of 100 seedlings could be simulated.

Reliability of the model in predicting root growth, damping-off and root disease was tested over 2 years by applying temperature regimes for the germination, shoot growth and root zones derived from correlations with weather station records. Data on *F. oxysporum* inoculum concentration and distribution were supplied from field results or were estimated. Average accuracy of model results was better than 90% and 80% for root growth and for root disease, respectively. Accuracy in predicting root rot mortality, tested over 2 years, averaged about 80%. The model provides choice of detail in results ranging from individual root to total population parameters.

## RÉSUMÉ

L'auteur mit au point un système mathématique afin de décrire le développement du système racinaire, la fonte des semis et la carie des racines des semis de Douglas latifolie (*Pseudotsuga menziesii*) en pépinière forestière durant la première saison de croissance. Les éléments principaux du modèle sont: i) la germination incluant la naissance de la radicule, ii) la croissance de la racine pivotante, la naissance et l'allongement directionnel des racines de premier ordre et la naissance des racines de deuxième ordre, iii) le comportement de l'agent pathogène, incluant la distribution, la grosseur et nocivité (malignité) de l'inoculum de *Fusarium oxysporum,* iv) l'infection des coiffes par des Champignons et al croissance de lésions dans les racines. Les rapports entre les composantes sont identifiés selon la norme suivante: leurs effets sur les semis et les champignons doivent avoir une importance grande et soutenue dans les pépinières le long de la côte de la Colombie-Britannique. Ils sont exprimés en termes de régressions, de valeurs présentées dans des tableaux ou de fonctions de distributions des probabilités et ils furent dérivés de résultats publiés, d'expériences, de relations logiques et d'observations sur le terrain.

L'auteur construisit un modèle d'ordinateur afin d'intégrer les rapports entre les composantes dans un order logique et sous forme traitable à l'ordinatuer. Il atteignit ce but en subdivisant la saison de croissance en 36 périodes de 5 jours et en utilisant un plan vertical et un plan horizontal avec des intervales de 2 cm pour la profondeur du sol et la distance horizontale de l'axe de la racine pivotante. Il modifia les rapports entre les composantes pour les ajuster aux limites temporelles et spatiales du modele. Il put simuler une population maximale de 100 semis.

L'auteur voulut savoir si le modèle pouvait bien prédire la croissance des racines, la fonte des semis et la maladie des racines. Pour ce faire, durant 2 ans, il fit subir différents regimes de température à la germination, à la croissance des pousses et aux zones racinaires, dérivés de corrélations avec les chiffres provenant de stations météorologiques. Il estima ou mesura sur le terrain les données sur la concentration et la distribution de l'inoculum de *F. oxysporum*. Il trouva que la précision moyenne du modèle s'élevait à plus que 90% et 80% pour la croissance des racines et la maladie des racines, respectivement. Dans la cas de la mortalité causée par la pourriture des racines, il fit des tests durant 3 ans. La précision obtenue fut d'environ 80% pour des niveaux relativement éléves de sévérite de la maladie, mais de seulement à peu près 50% pour des niveaux bas. Le modèle apporte un choix de détails dans les résultats, concernant depuis une seule racine jusqu'à des paramètres de populations entières.

## INTRODUCTION

The objective of forest nursery disease research is to provide nursery managers with guidelines for minimizing disease losses, using measures compatible with other nursery operations. Recommended measures should be tested over the range of prevailing nursery conditions in conjunction with treatments, practices and type of stock likely to be used currently or in the foreseeable future. Many combinations of these can arise which significantly affect development of nursery disease.

Limitations of time and resources confine disease research to a relatively narrow range of factors and levels. This is usually achieved by a purposive or random selection of a few "representative" subpopulations of seedlings in a small portion of the nursery area for particular treatments, in what is hoped are representative climatic conditions. Extrapolation of results from a select set of experimental conditions to a wide range of actual nursery situations often leads to extreme variation in field results. Much nursery disease research has been conducted to elucidate underlying principles of disease development, but comparatively little attention has been paid to its dynamics during the development of both host and pathogen.

In studying root growth, damping-off and root rot of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings in coastal British Columbia nurseries, it was evident that simulation, rather than classical-type factorial experiments, would be more effective in evaluating the effects of fluctuating edaphic conditions, variation in the seedling and pathogen populations, changing probability of infection as seedling root systems develop, and changes or additions of treatments such as are made in the nursery while seedlings are growing. The use of simulation, or modelling, to integrate climatic, pathogen and host effects in disease forecasting has been demonstrated for crop plants (Waggoner and Horsfall 1969; Waggoner et al. 1972). The belief that simulation would be feasible for forest nursery seedling root growth and disease was based on: 1) the considerable amount of experimental and observational data that had been accumulated on various aspects of the diseases; 2) the relative ease of collecting and processing seedling material from conveniently located forest nurseries, and 3) the opportunity of quickly and easily checking the results of simulation.

The approach taken in developing a model, described herein, consisted of: i) definition of a "system", or algorithm, for representing the root growth and disease processes; ii) identification and quantification of major relationships within the system; iii) integration of relationships into a logical, computationally tractable set; iv) translation of relationships into computer language (FORTRAN); and v) evaluating the predictive reliability of the model. The predicted effects of various types of nursery practice on root growth and disease will be reported separately.

## BASIC STRUCTURE OF SYSTEM

The processes and factors determining root growth, damping-off and root rot of Douglas-fir seedlings can be considered as a system, segregated into the following major components: 1) pathogen behavior; 2) seedling attributes, and 3) climatic and edaphic effects. Their interrelationships are represented diagramatically in Figure 1. Each component comprises a number of factors and processes; e.g. pathogen distribution, infectivity and ramification; seedling germination, shoot and root growth; air and soil temperature and moisture regimes. Choice of those with most significant effects on functioning of the system is guided by definition of spatial and temporal parameters of the system, deductions from experimental results and field observations (data base) and logical relationships.

**Spatial and Temporal parameters** -- Damping-off is confined to the cotyledonary stage of Douglas-fir seedlings, usually up to 30 days after germination (Bloomberg 1971). Damage

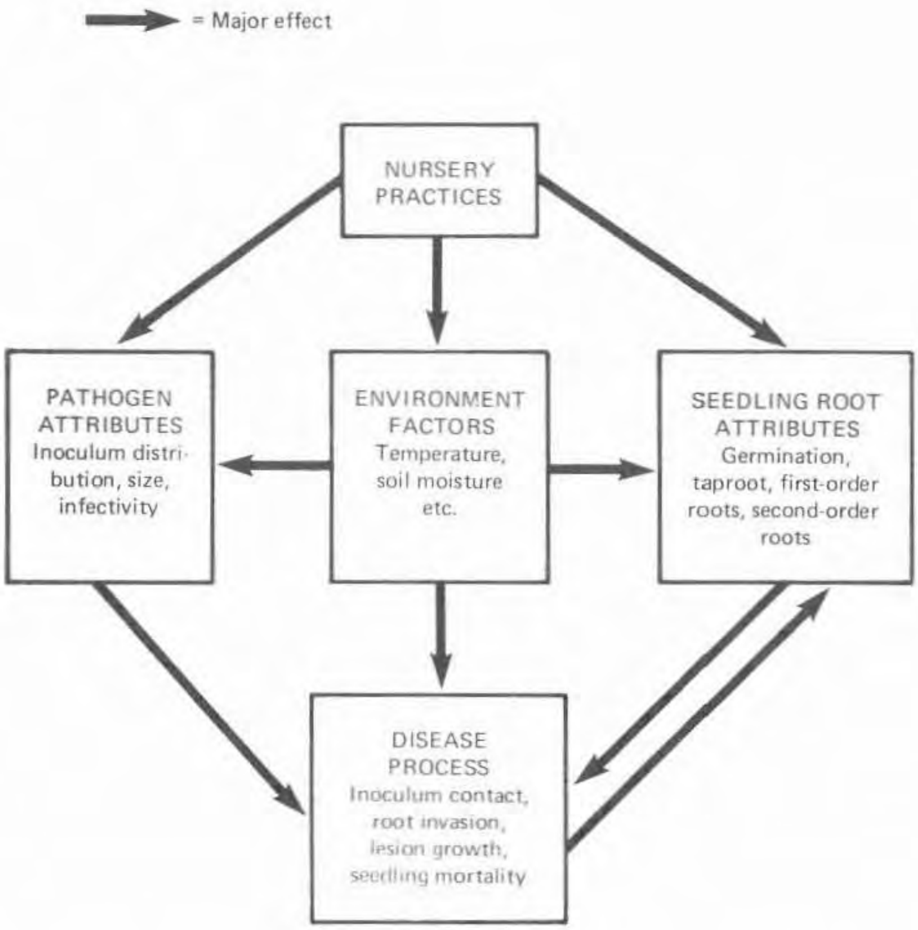



**Figure 1.** Diagram of a system for Douglas-fir seedling root growth and disease model. Note that disease process interacts with seedling root attributes by modifying root growth.

from root rot is confined to the first growing season, occurring from approximately mid-July to the end of October. Spatial distribution of damping-off is more-or-less random throughout the nursery, that of root rot random within patches (Bloomberg 1973). Plots 0.l-0.2 $m^2$ (1-2 sq ft), containing 30-100 seedlings, provide representative samples of both diseases (Bloomberg, unpublished data). Up to the end of October of the first year, the majority of roots occur at soil depths less than 20 cm and shoot length is 6-10 cm (Bloomberg and Orchard 1969; van den Driessche 1963). The system was therefore defined by the above spatial parameters, represented diagramatically in Figure 2. Time limits were set at May 1 (seed sowing) to October 31.

**Data Base** -- Relationships describing system processes were derived from published experimental results and the author's unpublished results from a variety of experiments not specifically related to modelling. In addition, experiments were conducted specifically to provide data for system relationships. Generally, preliminary experiments and field samples were conducted to obtain approximate relationships over a range of nursery conditions and practices, both in B.C. and in various Scottish nurseries. These were followed by more precise experiments and samples over a narrower range of factors and levels at the B.C. Forest Service, Koksilah, coastal Douglas-fir nursery. Physical characteristics of this nursery have been described by Keser and Devitt (1962). The nursery has been in

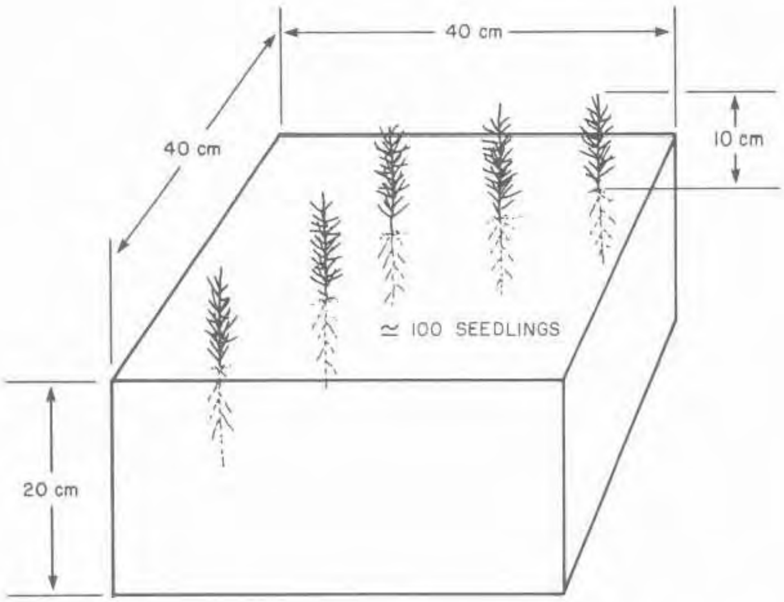



**Figure 2.** Spatial dimensions of Douglas-fir seedling root growth and disease model. Dimensions are based on average growth and spatial distribution of shoot and roots from germination to end of first growing season, approximately 180 days.

continuous production of Douglas-fir seedlings for 12 years, cropped at 2-year intervals. The soil is a sandy to silty loam, pH 5.5. Seedlings are grown in drills 5 cm apart in 15 x 1.1 m beds. Three adjacent beds, each sown with a different Douglas-fir seedlot (provenance), were used to provide the experimental data. Unpublished field observations by the author and forest nursery experts were used to substantiate and generalize from experimental conclusions.

**Logical Relationships** -- If published information directly applicable to the system was unavailable and there was anticipated difficulty in obtaining it because of experimental complexity or logistic limitations, extrapolations were made from published data derived from conditions closely related to those in the system.

## SYSTEM RELATIONSHIPS

### Pathogen Behavior

Over 90% of damping-off and root rot in B.C. coastal nurseries is caused by *Fusarium oxysporum* Schlect. (Bloomberg 1971). The diseases are initiated when infectious propagules of the fungus in the soil invade the roots and ramify through the root system, causing lesions in cortical and vascular tissues (Bloomberg 1976). Portions of root distal to the lesion are considered to be physiologically cut off from those proximal to it. Invasion of the radicle in recent germinants is nearly always fatal and results in damping-off (Bloomberg and Lock 1972). Invasion of older seedlings results in progressive root rot, leading to death. Cross-infection does not occur among seedlings (Bloomberg 1973).

**Distribution of Pathogen** -- All infectious propagules of *F. oxysporum are* believed to be associated with particulate organic matter in the soil which is distributed more-or-less randomly (Bloomberg 1976). Particle size ranges from less than 1 mm to 20 mm length x 3 mm diam. The majority are less than 4 mm (Fig. 3). The infectivity of the inoculum varies with size. Concentration of inoculum ranges from 0.2-0.5 per cc of soil.

**Environmental Effects on Pathogen** -- Temperature significantly affects hyphal growth of *F. oxysporum* (Salisbury 1952), its ability to cause mortality of Douglas-fir seedlings from root rot (Bloomberg 1973; Shea and Rediske 1961), and damping-off of other conifers (Tint 1945b). Temperature, however, did not affect lesion initiation (Bloomberg 1976), suggesting that its influence prevails only after the fungus is established in the root.

Soil moisture has not been observed by the author to be a factor in root-rot mortality of Douglas-fir seedlings in coast nurseries, a conclusion also reached by Shea and Rediske (1961). Irrigation in the nursery maintains soil moisture at 75-100% of field capacity (0-1 bars) during the first growing season (van den Driessche 1969). According to Manandhar and Bruehl (1973), linear growth to *F. oxysporum* f. sp. *vasinfectum* was little affected between 0-10 bars.

Adjustment of soil pH over the range 4.8-5.6 had no consistent effects on damping-off of Douglas-fir seedlings by *F. oxysporum* (Buckland 1942). Hyphal growth of the fungus was little affected between pH 5.0-8.0 (Salisbury 1952; Manandhar and Bruehl 1973). Range of soil pH in coastal nurseries is 5.0-6.5 (Bloomberg and Orchard 1969; Keser and Devitt 1962).

Application of nitrogen to seedbeds (20-80 lb/acre) increased mortality of Douglas-fir seedlings due to root rot (van den Driessche 1963; Bloomberg, unpublished data), but there was no evidence of effects of other major nutrients on the disease. Tint (1945a) concluded that severe nutrient imbalance had more effect on growth of *F. oxysporum* than specific excesses or deficiencies. Current practice in coastal nurseries maintains a balanced nutrient status and omits application of nitrogen to beds during the first growing season.

Use of different cover soils and organic amendments resulted in different amounts of damping-off and top-blight caused by *F. oxysporum* (Bier 1942). Present practice in coastal nurseries calls for standard amounts and types of cover soil and organic amendments (van den Driessche 1969).

On the basis of the above evidence, the only consistently important relationship between environmental factors and pathogen behavior under coastal nursery conditions was the effect of temperature on lesion growth.

Invasion of various host plants by *F. oxysporum* took place only when contact or near contact was made between inoculum and actively growing host root tip (Griffin 1969; Messiaen et al. 1965; Nyvall and Haglund 1972). Lesion distribution on roots indicated that the same limitations applied to Douglas-fir seedlings (Bloomberg, unpublished). Lesion growth rate along roots from the point of invasion at various time intervals after inoculation was estimated by measurement of lesion length (Bloomberg 1973) and deriving average growth rate. It was noted

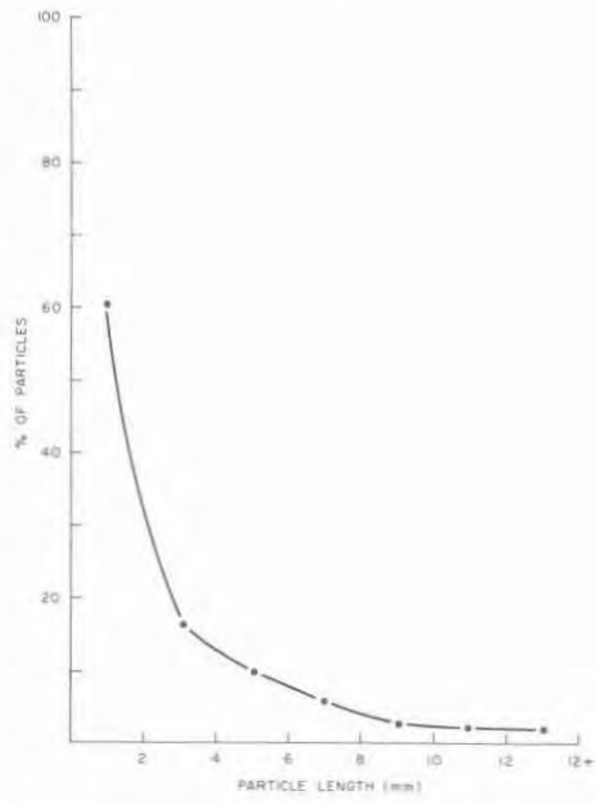



**Figure 3.** Size distribution of organic particles in a nursery soil.

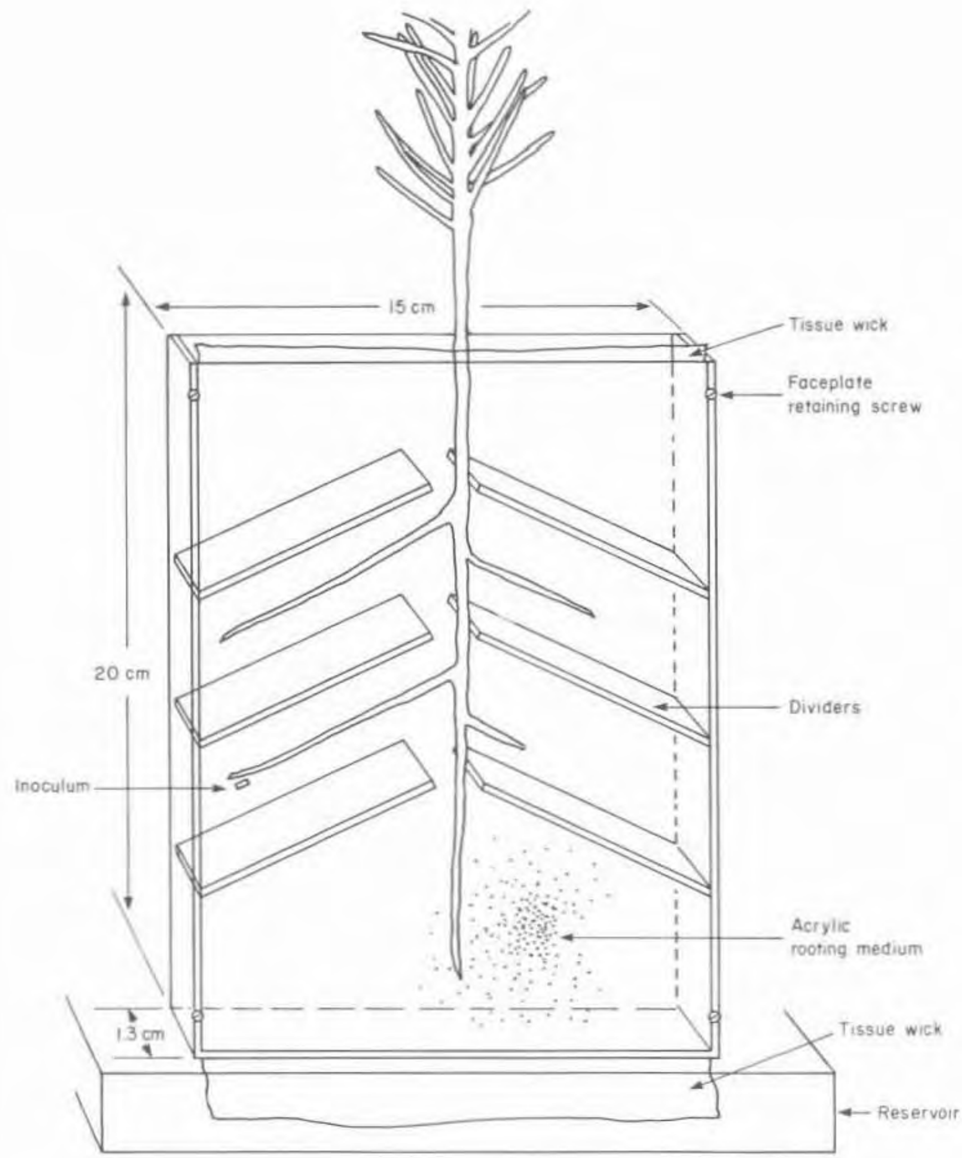



**Figure 4.** Translucent observation box for inoculation of Douglas-fir seedling roots.

that lesions on second-order (2°) roots invariably extended into the parent first-order (1°) root. In nursery soil artificially infested with an average macrospore population, average linear growth rate for all roots was 1 mm/day at average 21 C. Additional growth rate estimates were obtained from the following experiment.

Douglas-fir seedlings were grown aseptically in pots containing autoclaved peat-sand medium sown with seeds surfaced-sterilized with 30% $H_2O_2$ for 0.5 hr. After 60 days, they were gently washed out of the pots with sterile distilled water and their root systems, generally consisting of taproot and several first-order branches, were spread out in an acrylic-bead observation box with a removable face-plate, modified from Bloomberg (1963) (Fig. 4). Individual branches were inoculated with *F. oxysporum*, using the inoculum and procedures described by Bloomberg (1976). The face plate, 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 daily addition of sterile distilled water to the surface of the rooting medium and continual moistening of beads incontact with roots by the tissue wick. Nutrients were added weekly as a .05% (wt/vol) solution of Green Valley 20-20-20, high solubility fertilizer. Approximately 200 ml of the solution were added to each observation box. 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 1800 fc cool white fluorescent lights. At 30-50 day intervals, seedlings were removed from the boxes. Each inoculated root was aseptically subdivided into 5-mm long segments which were plated on soil extract medium to determine the presence of *F. oxysporum*. Re-isolation procedures are described by Bloomberg (1976). A total of 6 roots from 4 seedlings were tested.

Average and range for rate of fungus movement in roots were 1.1 and 0.8-1.7 mm/day, respectively, approximately the same as that of lesion elongation. The effect of temperature on this rate was estimated from Salisbury's data (1952) showing the relationship of temperature to hyphal elongation (Fig. 5). This was transformed to give growth rates at each temperature relative to the maximum at 25 C. Relative rates were then applied to the observed lesion growth rate of 1 mm/day at 25 C.

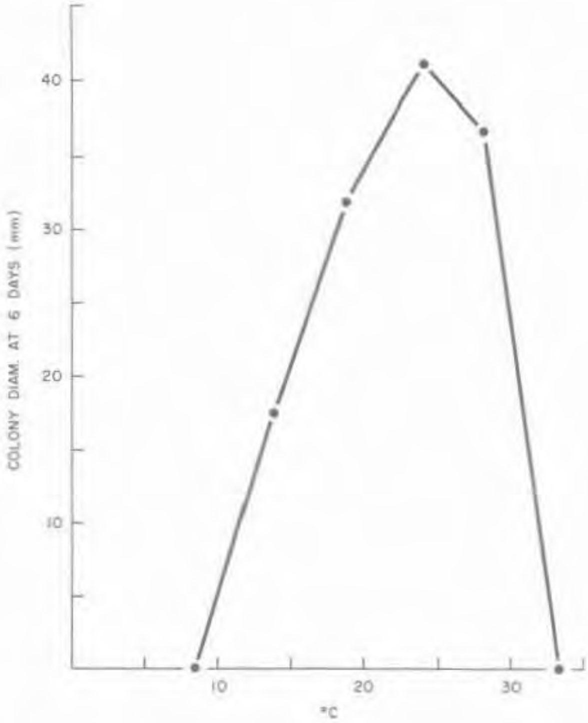



**Figure 5.** Effect of temperature on hyphal growth of *Fusarium oxysporum*. Data from Salisbury (1952).

The relationship of broad inoculum levels of *Fusarium inoculum* concentration to disease severity has been demonstrated (Cook 1968). Also, a general mathematical algorithm has been proposed for this relationship, postulating pathogen behavior and root attributes as for *F. oxysporum* (Baker et al. 1967). Both approaches were too general for application to a system involving varying inoculum size, infectivity, spatial distribution, and changing tip length and depth of individual roots. A more clearly defined algorithm was developed for predicting probability of root-tip - inoculum contact.

The algorithm assumed a matrix of inoculum particles in the soil arranged as a cubic lattice distance equal to the cube root of inoculum density. Lattice orientation could be in any direction without affecting probability of infection. It was assumed that the root tip could occupy any one of the set of positions along the X, Y or Z axes of the lattice (Fig. 6). The number of positions in the sets depended on how many times the diameter of the root tip went into the X and Y axes, or its length went into the Z axis. The root tip was said to make contact with an inoculum particle if it occupied lattice positions adjacent to or super-imposed on that occupied by the particle. The selection of X, Y and Z positions for the root tip was made by a random draw from each set. For infection to occur, it was necessary that root tip positions along all three lattice axes were in contact with the inoculum. Lattice positions were recalculated for each root tip and infection attempt.

Inoculum diameter was randomly selected from a normal distribution of given mean and standard deviation. Inoculum length was

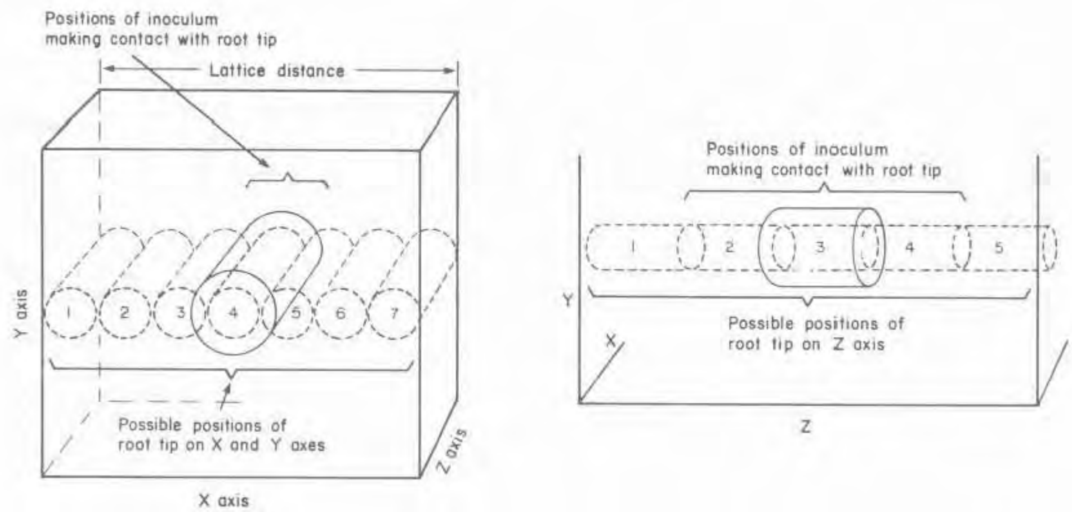



**Figure 6.** Relationship of inoculum lattice, root tip and inoculum positions in determining probability of contact. Broken lines denote possible root tip positions, solid line denotes particle position. Left, as for X and Y axes; right, Z axis.

selected from the sampled distribution (Fig. 3). The larger the diameter, the more root tip contact positions within the lattice; thus, the greater the probability of contact. Particle lengths shorter than the lattice distance were located at the centres of the X and Y axes and extended equally to both sides of the center of the Z axis. Root tip lengths equal to the lattice distance occupied the entire Z axis, the probability of contact along this axis being 100%. If the root tip was long--er, it was assumed to enter the adjacent lattice. The lattice dimensions were then recalculated if the inoculum density had been changed by the root tip passing from one soil depth to another. The more or larger the inoculum fragments, the greater the probability of root contact.

**Seedling Attributes**

Since infection cannot occur unless there is contact or near contact between root and inoculum, the dynamics of root development must be correctly represented in the system. The main determinants of these are assumed to be the characteristic growth behavior of Douglas-fir and modifications due to environmental factors. To define the root system in space and time, it must be created by germination, then its changing geometry must be represented as a series of three-dimensional relationships with time as the independent variable. The geometrical pattern must be quantified by correctly assigning initiation points, growth rates and directions to the major components of the root system; i.e., radicle, taproot, first and higher order branches.

**Germination** -- The germination process generates a seedling population distributed in time and space. The time spread between germination of the first and last seedling may be 30 days or more and greatly affects the probability of infection through the range of exposure times and seedling sizes. Radicle length influences probability of infection through its effects on subsequent root growth and the depth to which the radicle penetrates the soil, thereby encountering different inoculum concentrations. Distribution of radicle length in germinating seedlings is essentially normal (Bloomberg, unpublished).

Douglas-fir seedling germination is principally affected by provenance (seedlot), seed treatment, moisture conditions and soil temperature (Allen 1960, 1962). Under current nursery conditions, seed treatment is standardized and soil moisture content is maintained within the optimal range for germination (van den Driessche 1969). By contrast, temperature at the germination levels in the soil is uncontrolled and exhibits seasonal and diurnal variation.

Effects of only constant or cyclic temperature on Douglas-fir germination have been reported in the literature. To reproduce all possible temperature regimes during the germination period, it was necessary to derive a temperature-germination relationship independent of fluctuation pattern. Although the heatsum concept has been applied to tree growth (Hellmers 1962), no reference could be found to its use in tree seed germination. Therefore, the results of several experiments, using constant temperatures at different levels (Bloomberg 1970, 1973; Shea and Rediske 1961), were integrated to express Douglas-fir germination as a function of accumulated degree-hours above 0°C after sowing. Highly significant (P=.01) or significant (P=.05) regression slopes were derived from individual seedlots (b = .0093 - .028) and a fairly con-

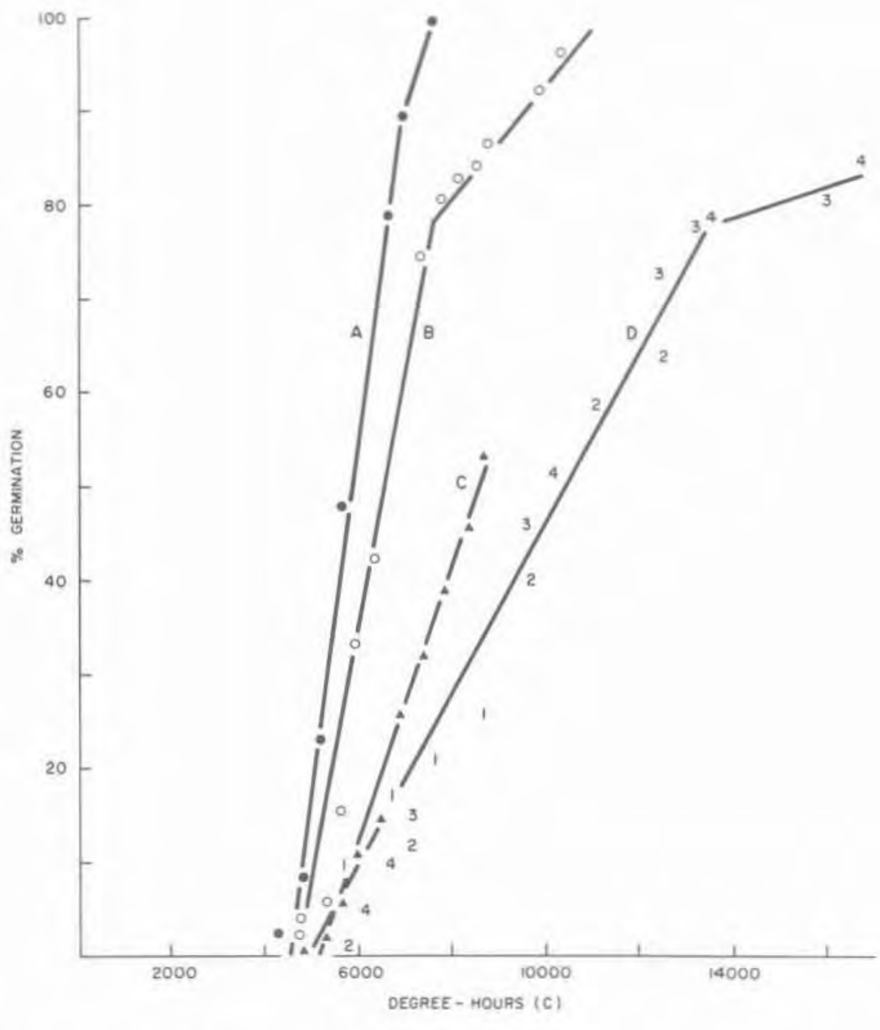



**Figure 7.** Relationship of heatsum and germination of Douglas-fir under various temperature regimes. A, seedlot 1 after 6 years storage, growth room, constant 21-18C, day-night temperature. B, seedlot 1, after 9 years storage growth room, daily cycle, 2-15 C. C, seedlot 2, field plots, min-max, 2-20 C. D, seedlot 3, growth room, various constant temperatures: 1,2,3,4 represent 4,12,20,28C respectively. Data of Shea and Rediske (1961).

stant threshold value was derived for all seedlots for which data were available (Fig. 7). Regression slopes may consist of two parts, the first representing the normal and the second, the slower-germinating fraction. The proportion of the latter may vary with seedlot and is indicated by height of the inflection point between the two parts of the curve. If the proportion is nil, there is no inflection point, since the whole seedlot has a uniform heatsum response. Germination of stratified Douglas-fir seeds in the nursery virtually ceases 30-35 days after initiation, regardless of the level achieved by that time (Hamilton, personal communication).

**Total Root Growth** -- Of the main factors in seedling root growth — soil quality, moisture and temperature (Brix 1967; Lavender et al. 1968; Steinbrenner and Rediske 1964), the first two are subject to much more control by nursery management than the last. At Koksilah nursery, fertilizer application, tillage practices, soil amendment and fixed irrigation systems maintain soil conditions near optimum for seedling root growth (van den Driessche 1969). Irrigation systems maintain soil moisture between 0-1 bars. Soil structure also appears to be suitable for root growth (Keser and Devitt 1962). Bulk density was below the limits of penetrability which could inhibit root elongation (Minore et al. 1969). Clay pan at 25- to 30-cm depth, outside the range of the model, was reached by the main part of the root system at the end of the first growing season and thus had little influence on developments during the season.

By contrast, temperature is relatively difficult to regulate. Although some control can be exercised by cooling irrigations, shading and soil mulching, it is subject to much natural variation. It was assumed, therefore, that under prevailing management practices in B.C. coastal nurseries, temperature was the major environmental variable in determining root growth.

Since total root length (aggregate of taproot and all branches) was significantly correlated with seedling dry weight (r=0.83, Bloomberg, unpublished data), it was assumed that root linear growth followed the law of compound interest, as does seedling weight (van den Driessche 1968). Although root length was also correlated with root dry weight (r=0.92), the latter did not maintain a constant proportion of seedling weight over the temperature range 8-28°C (Brix 1971) and was more variable (Lavender and Overton 1972), due to variable density of root systems. For these reasons, linear root growth was considered best related to seedling weight. Therefore, during any period, root elongation ( $\Delta$ L) was considered to be a function of total root length at the beginning of that period (L) and the rate ( $\Delta$ L/L) was maximal at temperature conditions optimal for seedling weight increase. Lavender and Overton's (1972) data for Douglas-fir seedling weight were compiled by Cleary and Waring (1969) to express growth at various air and soil temperatures as a percentage of maximum. These percentages, extrapolated to cover the nursery temperature range, were used to modify root-growth rate at near-optimum temperature for seedling dry weight increase.

To determine actual root elongation rate, experiments were conducted to record the linear extension of disease-free Douglas-fir seedling roots at the near-optimum temperature regime of 25°C by day, 18.5°C by night (Brix 1971), using different seedling stand densities. Pots, 20 cm diam. x 20 cm deep, were lined on the base with pea gravel, 1 cm deep, and filled with a mixture of 3:1 Koksilah nursery soil and washed sand. The addition of sand was necessary to offset soil compaction in the pots. Soil and sand were mixed by passing through a shredder in alternate shovelfuls, thus breaking up lumps and removing pebbles. Pots containing soil were autoclaved 1 hr at 15 psi, then arranged in four blocks in a growth room with 16 hr illumination at 1800 f-c. The soil was watered to field capacity and each pot was sown either with a single seedling placed centrally or three seeds in a row, to represent competitive conditions. Seedlings were selected for planting

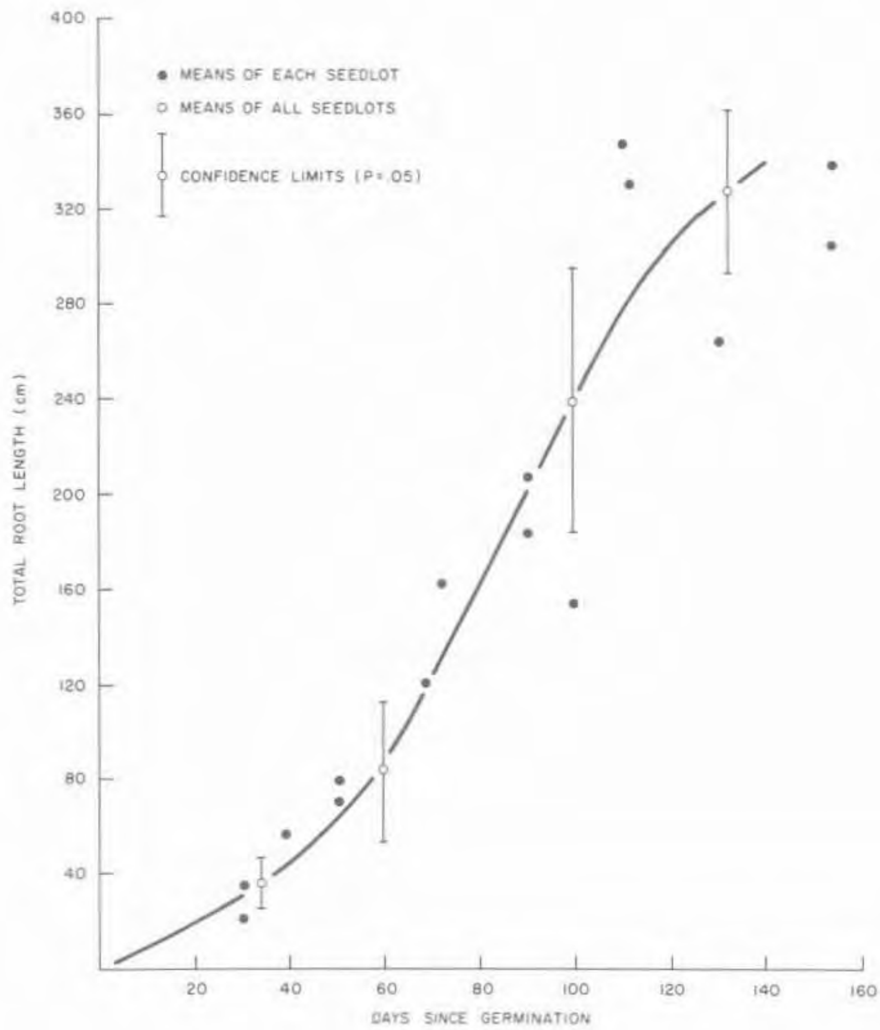



**Figure 8.** Total linear growth of Douglas-fir seedlings at constant day-night temperatures of 25-18.5C.

from axenically germinated stock (Bloomberg and Lock 1972). They were watered daily with tapwater at room temperature to field capacity.

Two seedlots collected from central Vancouver Island at 500 and 630 m elevation above sea level, respectively, were used. Single seedlings of each seedlot were sown in 36 pots, and competitive seedlings of one seedlot in 24 pots. Every 20 days, one singly-grown seedling and every 30 days, one seedling from the middle of the row (competitive seedling) were washed out of one pot from each block and their total root lengths were measured. The experiment lasted 120 days. Mean total root length for each seedlot was plotted over time since germination, and a balanced curve was drawn. Confidence limits were calculated for each mean. Individual seedlot curves 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. 8).

**Taproot Growth** -- Observations of nursery and pot-grown Douglas-fir seedlings indicated that, in the absence of injury or obstructions, a single, well-defined taproot develops from the radicle and grows approximately vertically to at least a depth of 20 cm. The taproot forms the axis from which first order ($1^{o}$) roots originate; therefore, its growth must be correctly modelled so that subsequent development of the root system will be realistically distributed in time and space. Prior to the emergence of $1^{o}$ roots, the taproot is the sole root system of the seedling. Infection at this time is usually fatal, as in early damping-off (Bloomberg 1973).

A well-defined relationship between taproot length and total root system length (Fig. 9) was found to exist over a range of seedlots and nurseries. This was used to apportion total root elongation to the taproot.

**First Order Roots** -- Field observations and previous experiments indicated that $1^{o}$ roots comprise over 90% of the total root length in Douglas-fir seedlings between 1-6 months. Thereafter, higher order roots contribute an increasing share to the total length. First-order roots are the main determinant in the distribution of root-rot infection sites; i.e., $1^{o}$ and $2^{o}$ root tips. This distri-

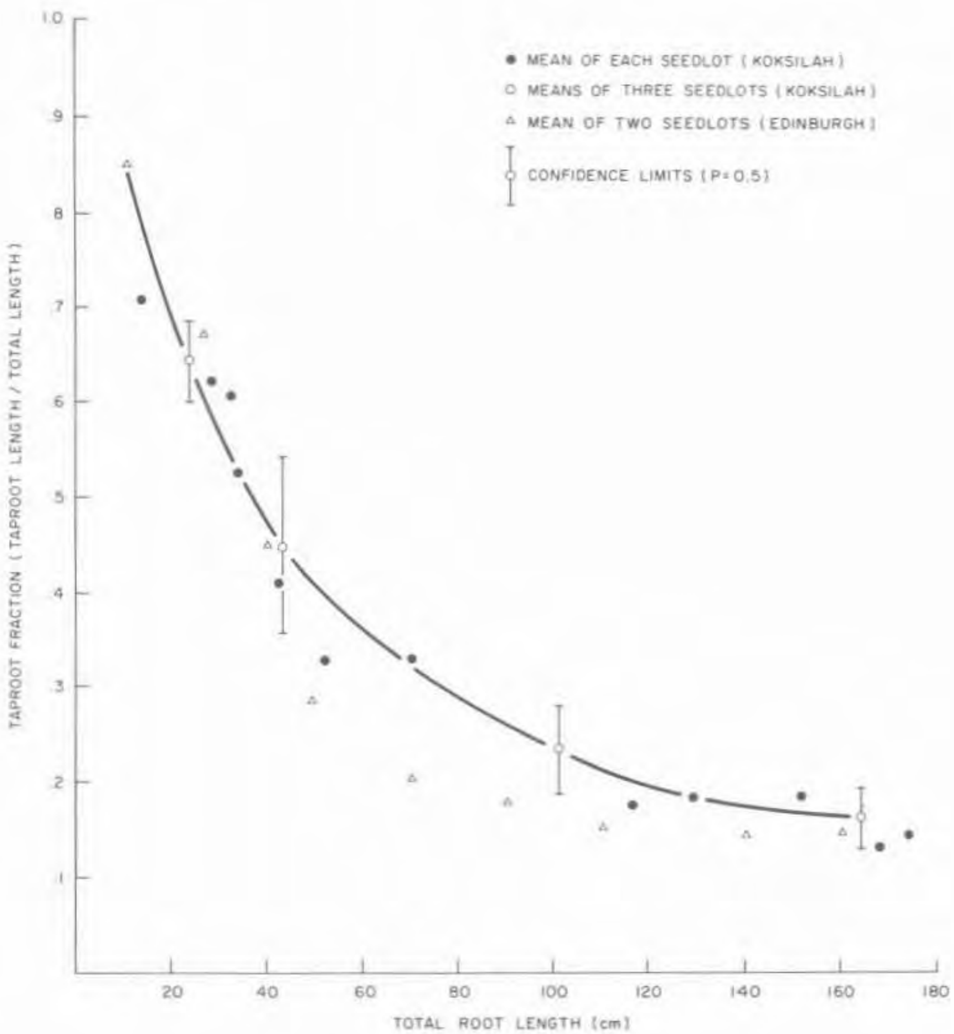



**Figure 9.** Relationship of total root length and taproot length fraction in various Douglas-fir seedlots and nurseries.

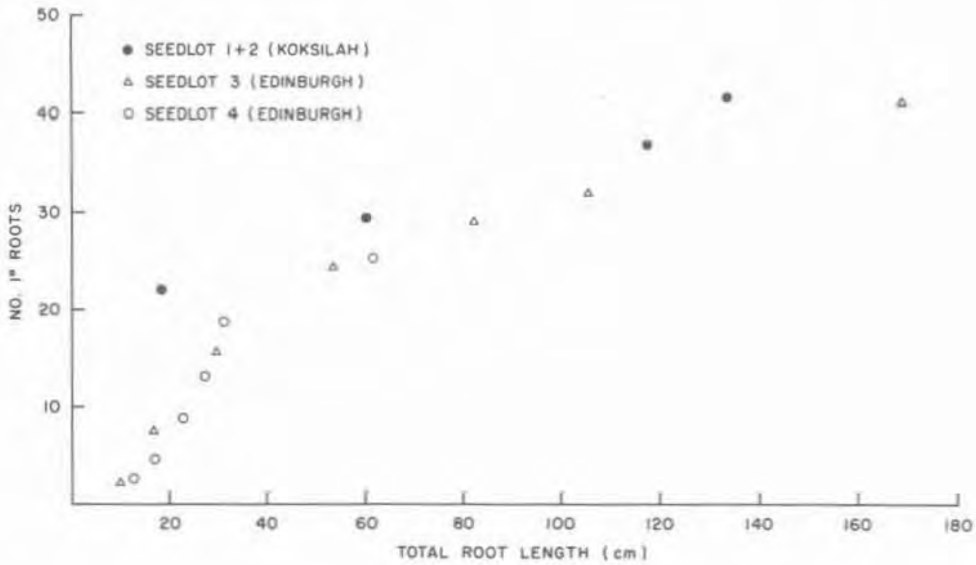



**Figure 10.** Relationship of total length and number of 1° roots in various Douglas-fir seedlots and nurseries. Measurements were made at 6-10 weeks after germination.

bution is a combined function of number of 1° roots, depth at which they originate, and extent and angle at which they elongate.

Data from experiments in a variety of conditions indicated a general relationship between total root system length and number of 1° roots, based on measurements after 6- to 10-week growth periods (Fig. 10). To substantiate the above relationship over the whole growing season, data were gathered from weekly measurements on three of Koksilah nursery seedlots, representing the average for the nursery (Mueller, personal communication). They had been collected from central Vancouver Island at 400, 500 and 630 M.A.S.L., respectively. Each seedlot was sown in separate but adjacent beds.

At each collection, a section of drill containing approximately 10 seedlings was dug up with root systems intact to a depth of at least 20 cm. Sections were taken at randomly selected positions along the length of each bed, from one of the five inside drills which contained an average linear distribution of seedlings. The seedlings, plus adhering soil, were transferred to the laboratory, with precautions to avoid root breakage. Weekly

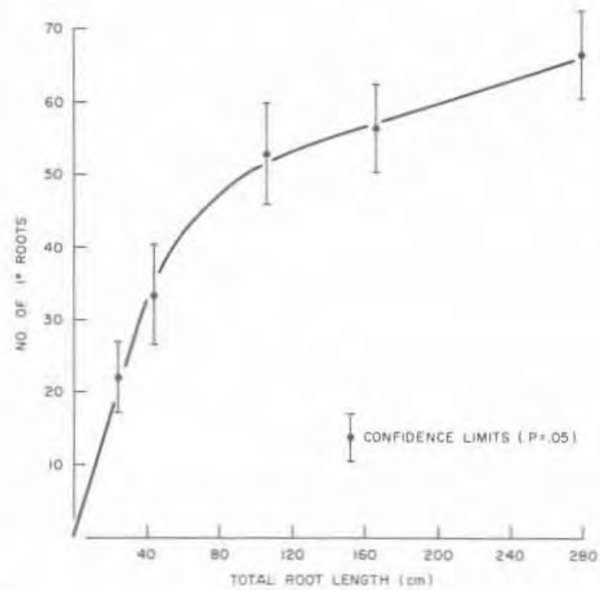



**Figure 11.** Relationship of total root length and number of 1° roots in Douglas-fir seedlings. Measurements were made weekly up to 20 weeks after germination on three seedlots at Koksilah nursery.

collections of drill sections were staggered by seedlot so that each was sampled every 3 weeks. In the laboratory, soil was removed from roots by gentle hosing, followed by suspending them in a column of water agitated by bubbling with compressed air. Five cleaned seedlings were randomly selected; their shoot lengths were measured and their roots laid out on a glass plate underlain by a measurement grid. The following measurements were taken: length of taproot from groundline to tip, distance along taproot to origin of each 1° root, length of each 1° root, distance of each 2° root along 1° root and its length, and position of root-rot lesions with respect to depth and distance along root. Roots with lesions were excised, surface-sterilized and tested for *Fusarium oxysporum* by previously described methods (Bloomberg 1976).

The number of 1° roots was plotted over total root length for each seedling and balanced curves were fitted through the seedlot mean at each collection date. Confidence limits for each mean were calculated and curves for each seedlot were compared. All were found to have overlapping confidence limits at all collection dates and were therefore pooled to form a single curve (Fig. 11).

From previous, observations, it appeared that spatial rooting patterns of Douglas-fir seedlings during their first year of growth were fairly well defined and if the governing relationships could be quantified, it would be possible to predict individual root length and spatial distribution. Analysis of root systems at the end of 6- to 10-week growth periods in preliminary experiments suggested that there was a specific distribution of 1° roots along the depth of the taproot (Fig. 12) and that these had differential rates of growth according to depth of origin and total root length (Fig. 13). Vertical angle of growth also appeared to be influenced by both depth of origin and length of root.

To determine the pattern of 1° root distribution along the taproot during the growing season, data from the nursery seedling collections described above were expressed as per cent of 1° root origins occurring in each 2-cm depth class at each collection date. The following trends were identified by averaging data for all seedlots (Fig. 14). First-order root initiation along the length

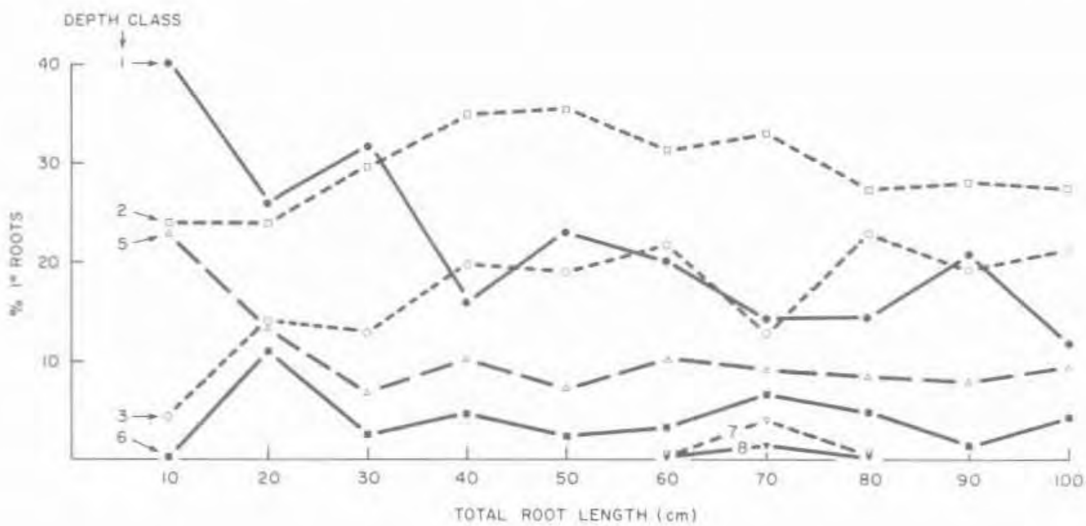



**Figure 12.** Distribution of 1° root origins by 2-cm soil depth classes in Douglas-fir seedlings. Depth classes 1,2,3,5,6,7,8 represent 2-4,4-6,6-8,10-12,12-14,14-16,16-18 cm depth respectively. Note that, excluding class 1, per cent roots decreases with depth.

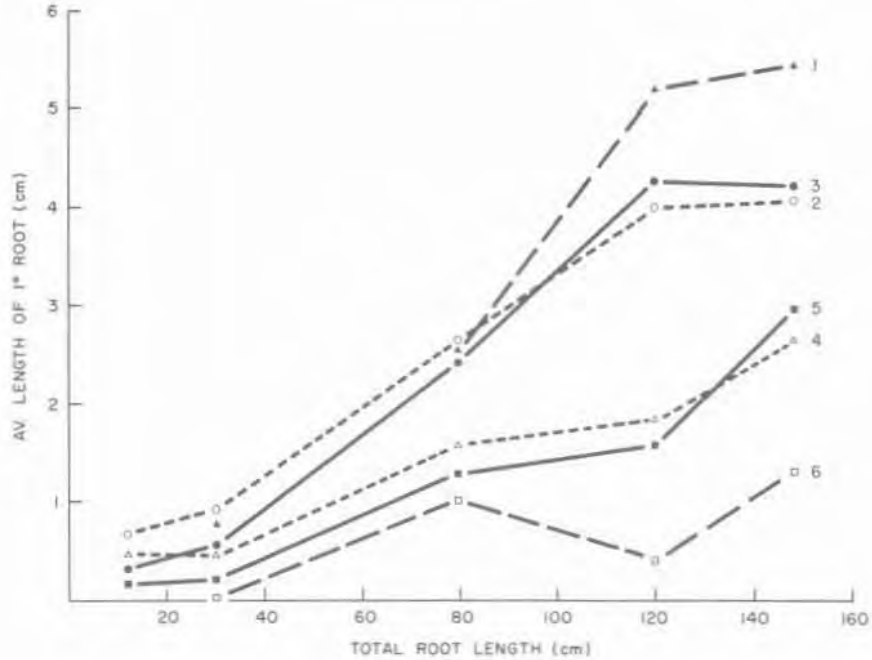



**Figure 13.** Relationship of total root length to depth of origin and length of $1^{o}$ roots in Douglas-fir seedlings. Depth classes 1,2,3,4,5,6 represent origin depths of 4-6,6-8,8-10, 10-12,12-14,14-16 cm, respectively.

of the taproot began 5-10 days after germination, the greatest percentage of roots being produced at the 4- to 6-cm depth. Up to about 50 days, roots became more equally distributed by 2-cm levels until, at 60-140 days, their distribution remained approximately equal from 4-18 cm depth, with a sharp decrease in percentage of roots above and below that range. Although collection date was confounded with seedlot, the distributions at successive dates formed a logical succession as roots were produced acropetally along the taproot, then became relatively stable as fewer roots were initiated. In view of the overlapping distributions of each seedlot after 60 days, there was no basis for treating each separately, thus data from three seedlots were combined to calculate per cent $1^{o}$ root distribution for each 2-cm depth class at each collection date.

Rate of root elongation was obviously not constant and equal for $1^{o}$ roots originating at different depths since most of the roots at some depths appeared later than in others, but were longer by the end of the growing season. Mean $1^{o}$ root lengths in each 2-cm depth of origin class were computed for five randomly selected seedlings from each of the three nursery seedlots at each sampling date. Analysis of variance of the means showed no significant ($P=.05$) difference among seedlots, but a highly significant ($P=.01$) interaction of collection dates and depth classes. Duncan's new multiple range test of means (Snedecor and Cochran 1967) showed that mean $1^{o}$ root length was greatest in depth classes 4-6 and 6-8 cm, and least at 0-2 cm. Other depth classes did not differ significantly from each other (Fig. 15). Elongation rates ($\triangle L/L$) were then computed from the mean of the three nursery seedlots at each collection date for the three significantly different depth class groups. Rates were expressed as percentage of total root growth rate to give relative elongation rates.

The depth of each root tip is determined by the root origin, length and vertical angle of growth. To ascertain the latter over the

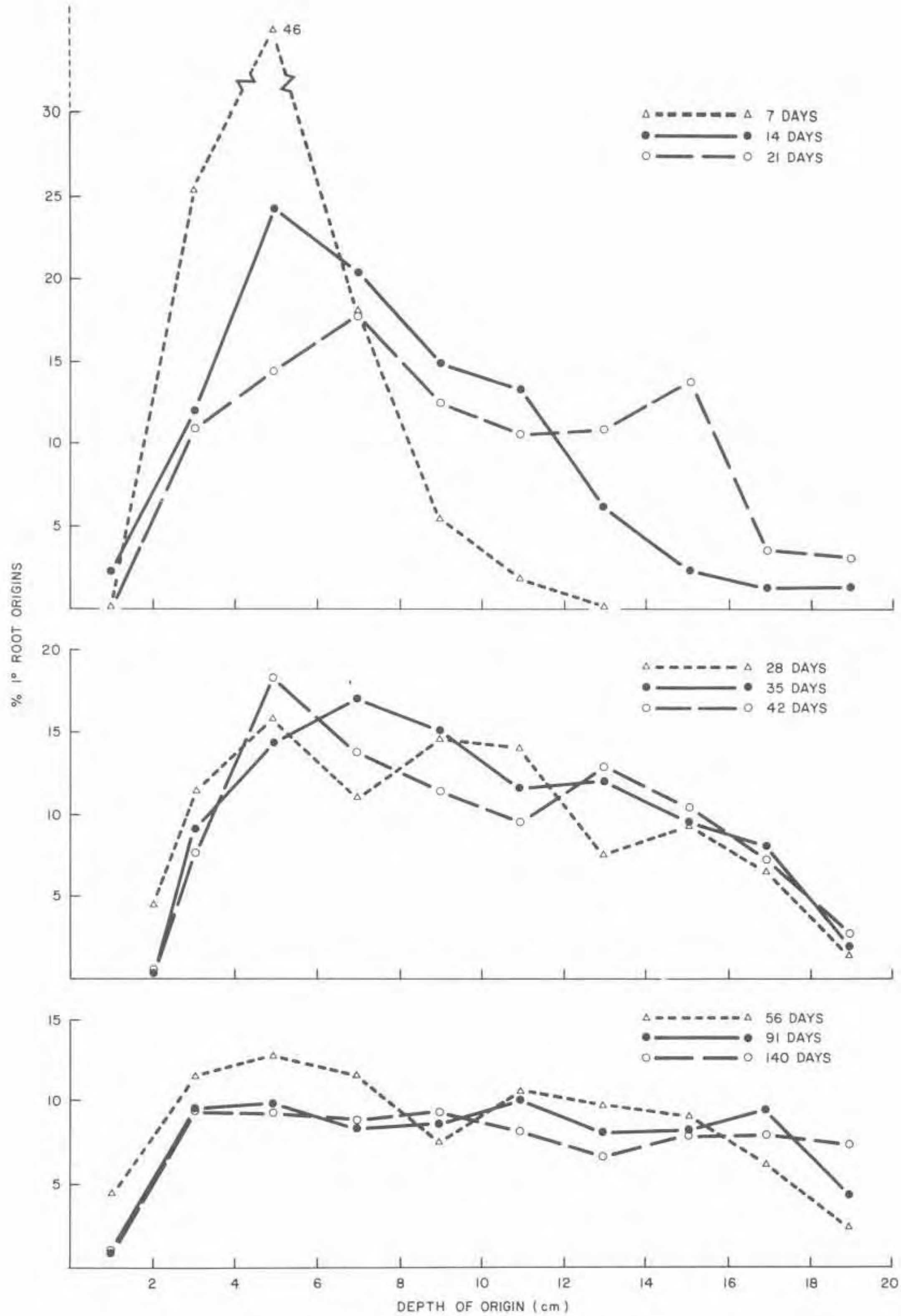



**Figure 14.** Relationship of age and depth to distribution of $1^{0}$ root origins in Douglas-fir seedlings. In youngest seedlings (7 days) nearly all roots originate above 10 cm depth. With increasing age, more roots originate at greater depths until at 56 days root origins are distributed quite evenly at 4-16 cm depth.

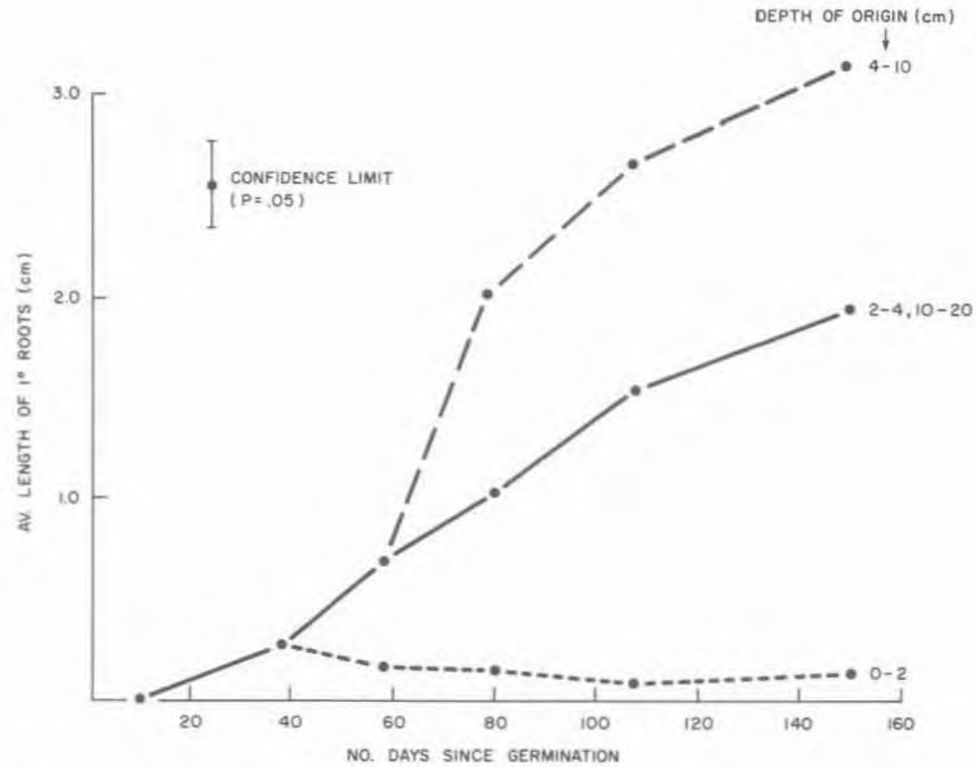



**Figure 15.** Relationship of depth of origin and elongation rate of 1° roots in Douglas-fir seedlings.

growing season, the experiment described under "Root Growth" was duplicated, with the following modifications. Pots were fitted with root cages (Bloomberg 1974) 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 (Bloomberg 1974). Roots were grouped by 2-cm length classes within 2-cm depth of origin classes. Angles subtended from the root tip to origin were measured and averaged for each group. Data from seedlings grown singly or competitively were analyzed in the same way. The results (Table 1) showed a fairly well-defined trend of root angle becoming more acute with depth of origin and root length. Angles were generally more acute in competitive seedlings.

**Second Order Roots** -- By the latter part of the first growing season, 2° roots outnumber 1° roots and constitute the major proportion of infection sites. Thus, their number and distribution on the parent 1° root are major determinants of infection probability. Field examination over a range of nurseries and conditions showed that 2° roots rarely exceed 5 mm in length during the first 6 months of growth. Thus, infections of 2° tips soon pass into the 1° root and by girdling it at that point, effectively cut off the portion distal to the infection.

The number of 2° roots was plotted over the length of each 1° root for all seedlings and collection dates used for 1° root measurement. Comparisons of regression lines for different collection dates or depth of root origin within each seedlot showed no clear effects of these factors. All data for each seedlot were therefore pooled and a single regression computed for number of 2° roots on length of parent 1° root. Regressions were highly significant for each seedlot (b=2.4, 3.0 and 3.1, respectively).

TABLE 1 - Relationship of competition, length and depth of origin to growth direction of 1° Douglas-fir seedling roots

| No. Seedlings Per Pot | Root Length (cm) | Depth of Origin (cm) 0-2 | 2-4 | 4-6 | 6-8 | 8-10 |
|---|---|---|---|---|---|---|
| | | Angle subtended from origin to tip (°) | | | | |
| 1 | 0-2.0 | 90 | 93 | 98 | 98 | |
| | 2.1-4.0 | 93 | 94 | 103 | 99 | |
| | 4.1-6.0 | 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 | |

Distribution of 2° roots was expressed as per cent occurring in each 2-cm segment of the 1° root. This was computed for all roots by depth of origin and collection date. By inspection of the data, separate trends could be seen in the distribution for different groups of origin depths and collection dates. Trend lines joining the means in each group are shown in Fig. 16.

**Summary of System Relationships**

**Pathogen Behavior** -- Inoculum particle size distribution is negatively skewed (Fig. 3). Smaller ones are less infectious. Particles are randomly distributed in the soil.

Probability of root tips contacting inoculum depends on the concentration of inoculum in the soil, size of inoculum and size of root tip (Fig. 6). Lesion growth rate is a function of temperature. Lesions on 2° root tips grow into the parent 1o root.

**Germination** -- Germination commences when heatsum reaches about 4500 degree-hours and is determined by heatsum and seedlot. Germination ceases after 35 days. Radicle lengths of the seedling population follow a normal distribution, with 0.5 cm as a typical mean.

**Total Root Growth** -- Periodic total root elongation is a function of total root length. Maximum elongation rates for each period were computed from the average rate of two seedlots grown under near-optimum growth conditions (Fig. 8). The rate is modified at sub- or superoptimal temperatures.

**Taproot Growth** -- Taproot growth is a fraction of total root growth (Fig. 9).

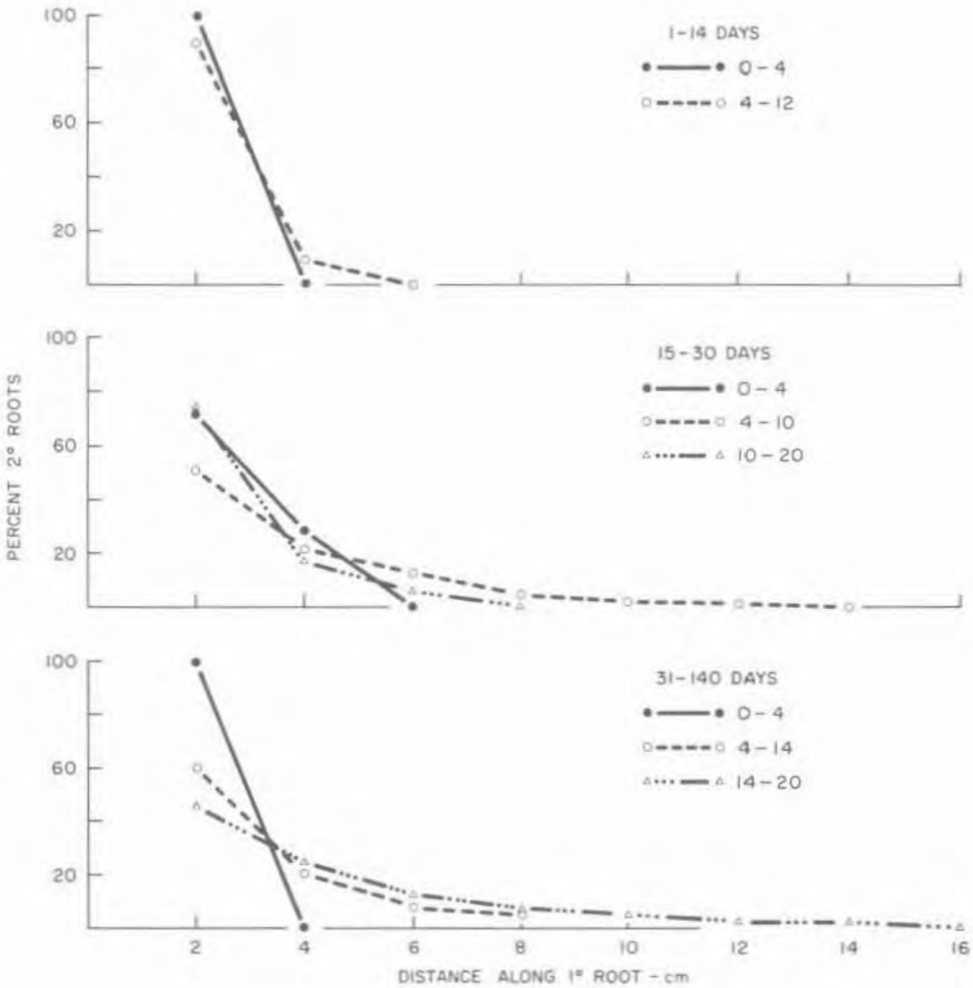


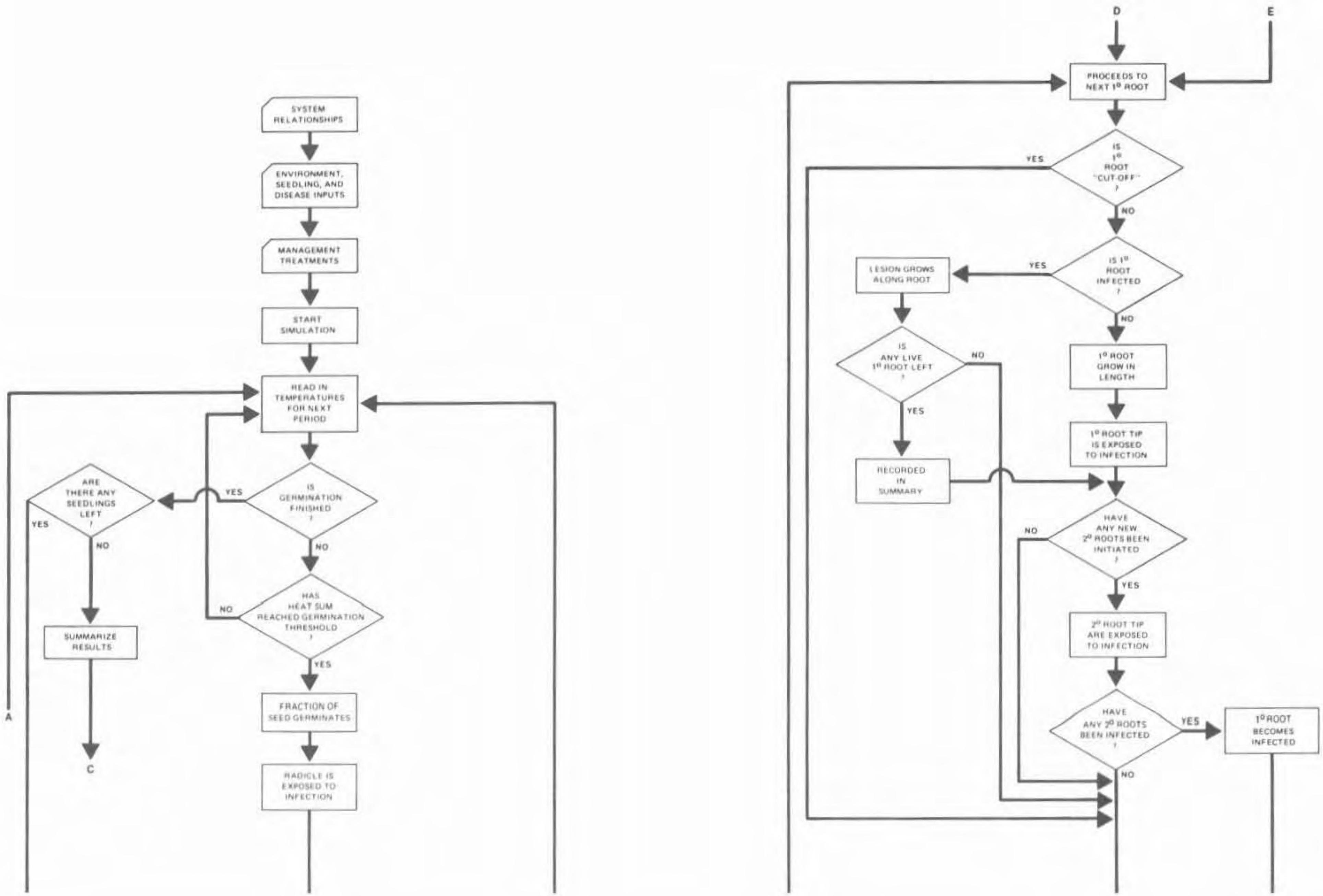

**Figure 16.** Relationship of seedling age (days) and depth of $1^{o}$ root origin (cm) to lateral distribution of $2^{o}$ roots in Douglas-fir seedlings.

**First-Order Roots** -- The number of $1^{o}$ roots is a function of total root length (Fig. 11). Their distribution along the taproot is determined by the seedling age and their depth of origin (Fig. 14). Elongation rate of $1^{o}$ roots depends on age of the seedling and depth of root origin (Fig. 15). Angle subtended from $1^{o}$ root origin to its tip varies with root length and depth of origin (Table 1).

**Second-Order Roots** -- The number of $2^{o}$ roots is determined by the length of their $1^{o}$ root and they are distributed along the root according to age of seedling and depth of $1^{o}$ root origin (Fig. 16).

## COMPUTER MODEL OF SYSTEM

The purpose of developing a system is to predict root disease outcome from a variety of combinations of natural and man-modified conditions operating on the system. This objective involves entering and modifying different sets of conditions in the system, calculating their effects on individual processes in the model, arranging the processes in logical order, then producing results from the interaction of all processes. This procedure, represented by the flow-diagram in Fig. 17, is too complex for hand-calculation and can only be handled by computer, in the form of


SYSTEM RELATIONSHIPS
ENVIRONMENT, SEEDLING, AND DISEASE INPUTS
MANAGEMENT TREATMENTS
START SIMULATION
READ IN TEMPERATURES FOR NEXT PERIOD
IS GERMINATION FINISHED ?
YES
NO
HAS HEAT SUM REACHED GERMINATION THRESHOLD ?
NO
YES
FRACTION OF SEED GERMINATES
RADICLE IS EXPOSED TO INFECTION
ARE THERE ANY SEEDLINGS LEFT ?
YES
NO
SUMMARIZE RESULTS
A
C
D
E
PROCEEDS TO NEXT 1º ROOT
IS 1º ROOT "CUT-OFF" ?
YES
NO
IS 1º ROOT INFECTED ?
YES
NO
LESION GROWS ALONG ROOT
IS ANY LIVE 1º ROOT LEFT ?
NO
YES
RECORDED IN SUMMARY
1º ROOT GROW IN LENGTH
1º ROOT TIP IS EXPOSED TO INFECTION
HAVE ANY NEW 2º ROOTS BEEN INITIATED ?
NO
YES
2º ROOT TIP ARE EXPOSED TO INFECTION
HAVE ANY 2º ROOTS BEEN INFECTED ?
YES
NO
1º ROOT BECOMES INFECTED

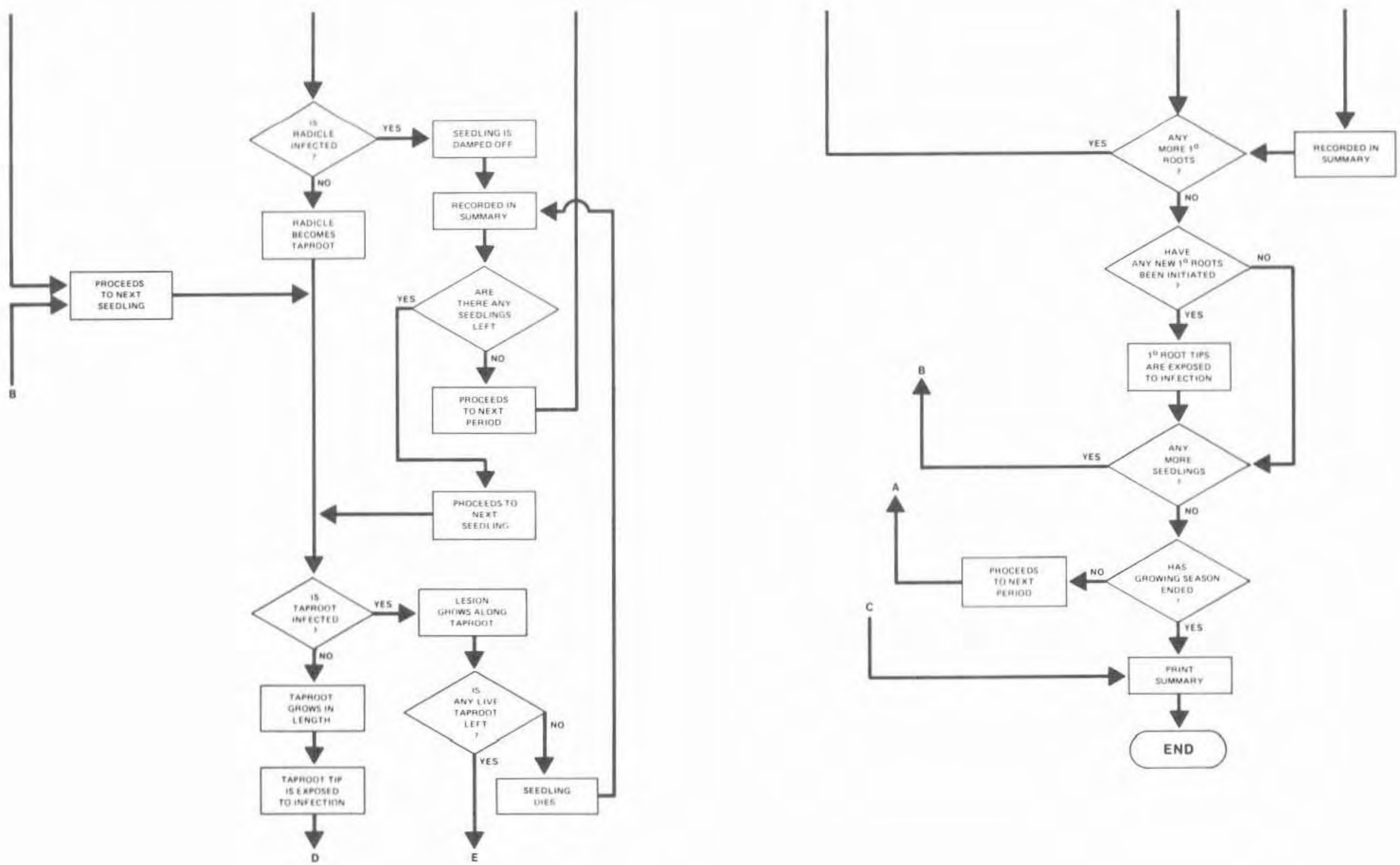



**Figure 17.** Simplified flow chart for simulation of Douglas-fir seedling root growth, damping-off, and root rot.

a simulation model.

An initial, unpublished version of a computerized nursery disease model was built by Dr. E.D. Ford, Institute of Tree Biology, Edinburgh, based on data from preliminary experiments and the author's estimates, with encouraging results. A more comprehensive version has been constructed by the author, based on the enlarged data base described above.

Size and speed of available computer facilities impose limits on the extent of size of modelled population and detail in processes. The facility available (Digital PDP-11 with 24K words of memory), could accomodate a seedling population size up to 100, 2-cm depth classes down to 20 cm, and 2-cm horizontal distance classes out to 24 cm. Thus there were no difficulties in converting (programming) most of the system relationships based on these size classes. However, only two spatial dimensions could be accommodated, one vertical and one horizontal representative of all horizontal axes. This required that there were no constraints in the horizontal direction; e.g. bed edges or gradients in soil temperature.

A further economy was achieved by subdivision of the time frame into a number of discrete periods of equal length, each long enough to allow significant change to take place in the development of events, but not so long as to encompass several events and obscure the impact of each. A time unit of 5 days (Qdays) was chosen because it conforms to the natural timetable of some of the events in the nursery; e.g. germination of stratified Douglas-fir seed commences at approximately 5 days after incubation at 25°C, peaks at 15-20 days and is virtually completed at 30. The maximum period required for infection of a root tip after contact is made with inoculum is approximately 5 days (Griffin 1969; Nyvall and Haglund 1972). Average linear growth per 1° root is 1-5 mm per 5-day period, sufficiently large to initiate events such as inoculum contact or the addition of a second-order (2°) root, but not so large as to cause major discontinuities in the growth pattern. All time-based relationships were therefore expressed by Qday subdivisions, with adjustments where time intervals of field and experimental measurements did not coincide exactly with a 5-day interval.

For computerization, system relationships were expressed by linear regression equations, interpolation between points of non-rectilinear regressions, tabular values and probabilistic (stochastic) functions. Not all regressions could be shown to be statistically significant, partly because of their shape, for which no exact equations could be found, and partly because of the amount of variation about the regression line. Tabular values were used if more confidence could be put in the means of several classes combined than in the regression line which connected individual classes. This resulted in a stepwise change in the relationship as the independent variable changed. Tabular values were also used when this was the form in which relationships were published in the literature. Stochastic relationships were used when the probability distribution of events was known or when the factors determining these events were so complex as to defy resolution. Some of the relationships in the model, therefore, were not statistically significant and the justification for their use depended on their ability to generate values which lay reasonably well within the bounds of variation of different test populations, and the realism of the final outcome of the entire simulation. A list of system processes and their model analogues is given in Table 2.

### Necessary Inputs for Operating Model

**Inputs for Environmental Conditions** -- Three sets of temperature regimes must be entered in the model. 1) Daily heatsum in the germination layer of the seedbed (0.5-cm depth) for 35 consecutive days following sowing. 2) Five-day (Qday) heatsum in the root growth zone (0.6 - 20 cm) for 36 Qdays after sowing. 3) Q-day heatsum for the shoot-growth zone (0.1 - 10 cm above soil surface) for 36 Qdays after sowing.

**Biological Inputs** -- Five seedling and pathogen parameters must be entered. Average values from previous observations are in brackets. 1) Germination-heatsum regression coefficient and regression inflection point for the seedlot being modelled (.0175 and 85%, respectively). 2) Average root-tip diameter for seedlot (.02 cm). 3) Average inoculum diameter (0.5 mm). 4) Number of inoculum particles in each 2-cm depth class in the soil (0.5). 5) Infectivity of particles in each 2-cm soil depth class (10%).

**Management Practice Inputs** -- The purpose of these inputs is to simulate effects of nursery variables which can be controlled or modified by nursery managers. They include length of growing period up to a maximum of 36 Qdays and number of seeds to be sown. For example, a shorter growth period may be required for seedlings which are to be transplanted during the summer. The number of seedlings may be increased to offset disease losses. In addition, temperature regimes, total root growth rate and inoculum infectivity at each 2-cm soil depth class can be modified during the growing season. These permit simulation of management practices such as temperature modification by shading or irrigating beds, increasing root growth by fertilizer application and reduction of inoculum infectivity by fungicide application.

**Modifications to Inputs** -- Changes in all inputs can be made prior to a simulation run by entering new sets of values. In addition, temperature regimes, total root growth rate and inoculum length can be increased or decreased by a constant factor entered before each run. These factors modify the values already entered in the model. Management interventions may be applied at any four times during a simulated growing season.

A check on all inputs is provided by the model at the beginning of each simulation run so that the run can be aborted if incorrect values have been accidentally entered.

### Results of Simulation (Output)

The model allows the user to specify degree of detail desired in the simulation results. The least detailed output is provided at the end of the simulation and consists of graphical representation of the population according to the following classification; ungerminated seeds, healthy, damped-off, root-rot-infected and root-rot killed seedlings at each Qday (Fig. 18). More detail on the seedling population may be obtained as tables at selected Qdays. These show values for 21 root parameters according to the depth of each $1^o$ root origin, or 14 parameters according to depth of $1^o$ root tip (Table 3). Tables can be requested for specific Qdays and values can be expressed as numbers and/or percentages. Tables are printed out during the simulation after the model has completed calculations for the Qday requested. The above tabular values may also be requested in graphical form. Model users can also examine selected parameters and depth classes. Graphical output is produced just before the end of the simulation run. When the model is being operated in "Interactive Mode" (see below), graphs of additional parameters can be requested at this time.

Details of individual seedling root systems can be requested by specifying the Qday and seedling numbers required. Seedlings are numbered in the order in which they germinate. Tables are produced showing the parameters listed in Table 4 during simulation after the model has completed calculations for the specified Qday.

Finally, the details of individual $1^o$ roots can be requested by Qday and seedling number. These show values for the parameters listed in Table 4.

Any combination of the above types of output can be requested and used to monitor progress of simulation run, or to examine development

TABLE 2

Modelling procedures for a system of Douglas-fir seedling root growth, damping-off and root rot

| System Process | Modelling Procedure |
|---|---|
| Germination | Each day for 35 days, number of new germinants computed from regression on heatsum at 0.5-cm soil depth. |
| Radicle development | Random assignment of radicle length from a normal distribution. |
| Taproot elongation | Assignment of a fraction of total root elongation at 5-day intervals. |
| $1^o$ Root initiation | Addition of requisite number of roots to bring total to that indicated by total root length at 5-day intervals. |
| $1^o$ Root initial length | Random assignment of root length from a normal distribution. |
| $1^o$ Root initial depth | Addition of roots sequentially down taproot to bring percentage in each 2-cm depth to that indicated by a table for each 5-day period. Initials are located randomly within 2-cm depth. |
| $1^o$ Root growth | Assignment of a fraction of total root elongation determined by age, depth of origin and length. |
| $1^o$ Root angle | Assignment of a subtending angle from origin determined by root length and depth of origin. |
| $2^o$ Root initiation | Addition of requisite number of roots to bring total to that computed by regression on $1^o$ root length. |
| $2^o$ Root initial length | Random assignment of root length from a normal distribution. |
| $2^o$ Root distribution | Addition of roots sequentially along $1^o$ root to bring percentage in each 2-cm section to that indicated by a table for each 5-day period. Roots are located randomly within each 2-cm segment. |
| $2^o$ Root angle | At right-angles to $1^o$ root angle. |
| $2^o$ Root growth | Nil |

| | |
|---|---|
| Total root growth | Relative growth rate at 5-day heatsum for 1-20-cm soil depth, multiplied by total root length at end of last 5-day period. |
| Total root length | Current total root growth added to total root length at end of previous 5-day period. |
| Inoculum distribution | Assignment of number of particles to each 2-cm soil depth. |
| Inoculum size | Random selection from a frequency distribution. |
| Inoculum infectivity | Assignment of per cent infectivity in each 2-cm soil depth. |
| Infection of taproot | 1) Random selection from a number of inoculum contact positions computed from concentration and size of inoculum particles and length and depth of taproot tip. |
| | 2) Lesion from $1^{o}$ root extending back into taproot. |
| Infection of $1^{o}$ root | 1) As for 1) in taproot infection. |
| | 2) $2^{o}$ root infected. |
| | 3) Taproot infected at a point above $1^{o}$ root initial. |
| Infection of $2^{o}$ root | 1) As for 1) in taproot infection. |
| | 2) $1^{o}$ root infected at a point proximal to $2^{o}$ root. |
| | 3) As for 3) in $1^{o}$ root infection. |
| Lesion growth | Initial growth set equal to length of infected root-tip. Subsequent growth by addition of a 5-day growth rate modified by soil temperature. |
| Damping-off | Radicle infected. |
| Root-rot mortality | Total root system infected. |

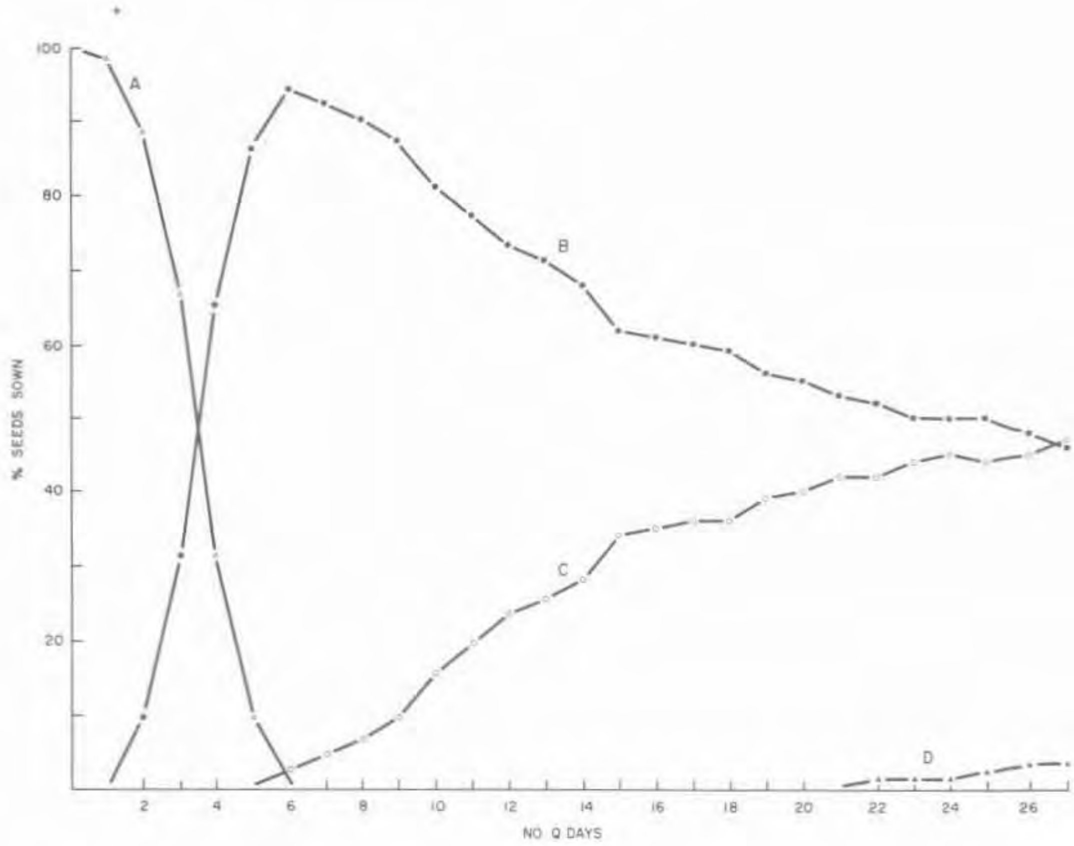



**Figure 18.** Simplest form of output from Douglas-fir seedling root growth and disease model. Line A represents number of ungerminated seeds; B,C,D, numbers of healthy, living infected, and dead infected seedlings, respectively.

of individual seedlings. Unusual simulation results can be explained by monitoring selected output information.

## MODEL OPERATION AND SPECIFICATIONS

The model is designed to run in Batch Mode; i.e., by supplying all inputs prior to the execution, or Interactive Mode; i.e., by supplying inputs during execution. The former requires inputs by punched cards and the latter by typing from a keyboard console. In Interactive Mode, the model prints requests for inputs as required, also stipulating the number and format of the inputs.

The simulation programme consists of approximately 1200 Fortran statements partitioned into 10 subroutines. Working core requirements, excluding buffers, drivers, etc., are 20K words. Direct access (disk) file requirements are for 12 files totalling 243,440 words. Current version of the programme was fitted on a Digital PDP 11, 24K words of available core, by "overlaying" subroutines. Running time on this machine is about 2 hr, for 100 seeds sown and a growth period of 36 Qdays.

A fully annotated programme listing and documentation on how to use the model will be provided on request.

## VERIFICATION TRIALS

Verification of simulation results establishes accuracy of the model in predicting parameter values of interest from given inputs. The model was tested in detail by comparing the simulated and actual values for individual growth and disease parameters and, in general,

TABLE 3

Root parameters of total seedling population calculated by model.

By depth of $1^{o}$ root origin:

| Parameter No. | |
|---|---|
| 1 | Total no. $1^{o}$ roots |
| 2 | Total no. of tip-infected $1^{o}$ roots |
| 3 | No. cut-off $1^{o}$ roots |
| 4 | No. affected $1^{o}$ (cut-off or infected) roots |
| 5 | No. healthy $1^{o}$ roots |
| 6 | Total no. $2^{o}$ roots |
| 7 | No. infected $2^{o}$ roots |
| 8 | No. cut-off $2^{o}$ roots |
| 9 | No. affected $2^{o}$ roots |
| 10 | No. healthy $2^{o}$ roots |
| 11 | Total length of $1^{o}$ roots |
| 12 | Length of infected $1^{o}$ roots |
| 13 | Length of cut-off $1^{o}$ roots |
| 14 | Length of affected $1^{o}$ roots |
| 15 | Length of healthy $1^{o}$ roots |
| 16 | Total no. of $1^{o}$ plus $2^{o}$ roots |
| 17 | Total no. of tip-infected $1^{o}$ plus $2^{o}$ roots |
| 18 | Total no. of cut-off $1^{o}$ plus $2^{o}$ roots |
| 19 | Total no. of affected $1^{o}$ plus $2^{o}$ roots |
| 20 | Total no. of healthy $1^{o}$ plus $2^{o}$ roots |
| 21 | Total no. of lateral-infected $1^{o}$ roots |

By depth of $1^{o}$ root tip:

| Parameter No. | |
|---|---|
| 1 | Total no. of $1^{o}$ tips |
| 2 | No. of infected $1^{o}$ tips |
| 3 | No. of cut-off $1^{o}$ tips |
| 4 | No. affected $1^{o}$ tips |
| 5 | No. healthy $1^{o}$ tips |
| 6 | Total no. $2^{o}$ tips |
| 7 | No. infected $2^{o}$ tips |
| 8 | No. healthy $2^{o}$ tips |
| 9 | Total no. of taproot tips |
| 10 | No. taproot tip infections |
| 11 | No. of taproot lateral infections |
| 12 | No. of affected taproots |
| 13 | No. of healthy taproots |
| 14 | No. of $1^{o}$ root lateral infections |

TABLE 4

Root parameters of individual seedlings calculated by model

By individual root systems:

| Parameter No. | |
|---|---|
| 1 | Root system length |
| 2 | No. of $1^o$ roots |
| 3 | Taproot length |
| 4 | Taproot infection indicator |
| 5 | Root system infection indicator |
| 6 | Deepest level with $1^o$ root origins |
| 7 | Age of seedling in Qdays |

By individual roots:

| Parameter No. | |
|---|---|
| 1 | Length |
| 2 | Depth of origin |
| 3 | Level of origin |
| 4 | Angle |
| 5 | Depth of tip |
| 6 | Distance of tip from main axis |
| 7 | Level of tip |
| 8 | No. $2^o$ roots |
| 9 | Infection indicator |

by comparing the overall predicted and actual outcome of disease. Inoculum size and spatial distribution and infectivity inputs were obtained from a previous experiment (Bloomberg 1976) or estimates. Germination regressions on heatsum were estimated for seedlots. Air temperature inputs were available from a weather station thermograph installed near the forest nursery. It was, therefore, necessary to derive correlations between heatsum at thermograph height (115 cm) with that in shoot growth, germination and root growth zones; i.e., 0.l-10, 0.5 and 0.6-20 cm, respectively. The following method was used.

**Temperature Inputs**--In May 1973 the W end of three N-S running experimental nursery beds was prepared in the following manner. At the end of each bed, a 1-m-wide buffer strip and an adjacent 3-m-wide zone were marked off for the installation of soil temperature measurement sensors. Each bed was instrumented with two sets of sensors, each set separated horizontally by 1 m. The sensors consisted of diode thermometers (Tang et al. 1974) embedded in resin in 5-mm-diam plastic drinking straws which were inserted in the soil at depths of 0.5 (representing the seed germination zone), 2,4,6,8,10, 14,18 and 22 cm. In inserting the diodes, a vertical face was exposed in the side of the nursery bed 20 x 25 cm. A wooden template, drilled with holes, slightly larger than the drinking straws, at the specified depths and staggered so that each was offset horizontally 1 cm from the hole above, was placed against the soil face and levelled in two planes. A brass probe of the same diameter and length of the straws was pushed through each hole, creating a horizontal tunnel in the bed to receive the diode. The template was removed and a diode was gently pushed home in each tunnel. Diode leads were soldered to the cable running along a 20-cm-deep trench between the beds. After connecting up, the trench was refilled with small bags containing excavated soil, gently and firmly placed in position to avoid damage to the leads. The bags were packed to the level of adjacent between-bed pathways. Inspection or replacement of diodes was facilitated by removing only the necessary number of bags to expose the connection. Sensors, mounted under aluminum pie-plate radiation shields (Barney 1972), were installed at 5, 10 and 115 cm above ground level, corresponding to seedling shoot height midway and at the end of the growing season, and standard instrument shelter height, respectively.

A 12-channel shielded cable, connected to each set of sensors, was passed through a protective buried polyethylene pipe to a Control Equipment Corporation Model 120 digital data logger equipped with a Tally Model P120 Paper-Tape punch (Control Equipment Corporation, Mass.) housed in a trailer sufficiently far from the beds to avoid shading or interference with nursery operations. Scanning rate of the recorder was hourly, with scan of all sensors requiring 1 min. One week after the beds, containing the diodes, had been sown with seed and irrigated daily, the accuracy of the diodes was tested in relationship to dial thermometers inserted to various depths in adjacent beds. Accuracy of input signal was + .02%. Paper-tape punched data were transferred to magnetic tape and computer-programmed to convert signals to °C and integrate them to degree-hours for the period of measurement,

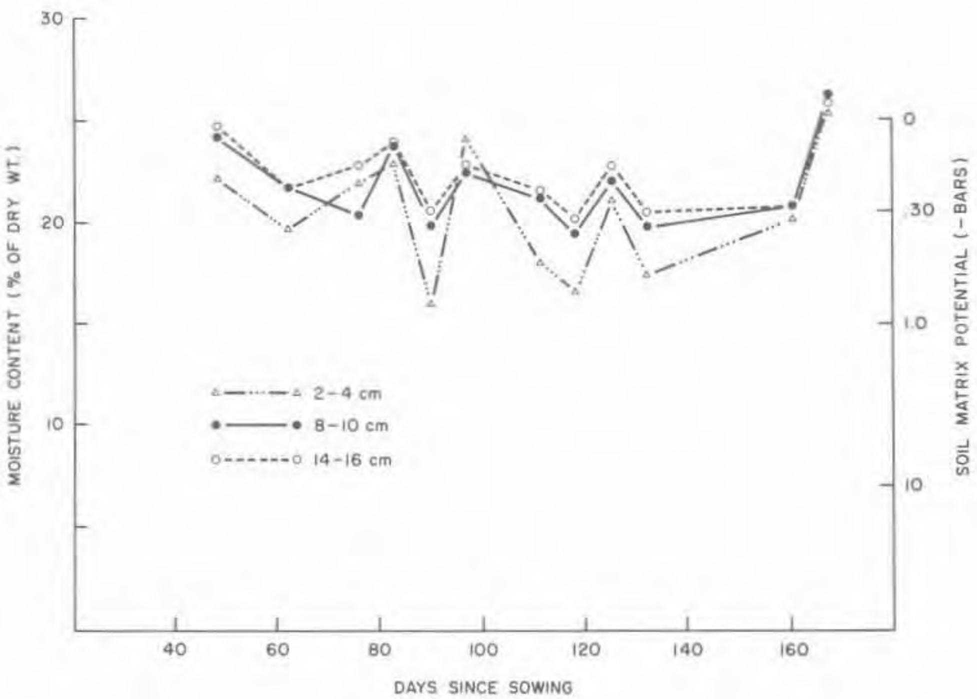



**Figure 19.** Soil moisture content by depth at Koksilah nursery.

usually 1 week.

Mechanical difficulties with paper-tape recording reduced temperature data collection to the first and last part of the growing season. However, sufficient data were collected to derive correlations between heatsum at standard instrument height and in the other strata. These relationships, based on measurement periods ranging from 1-10 days and spanning the growing season, were considered valid for the entire growing season (J.C. Turner, personal communication). Regressions of heatsum (degree-hours above $0^{o}C$) in the shoot, root growth and germination zones on that of instrument shelter height was significant (b=0.89, 0.94 and 0.98, respectively, P=.05). Heatsum at the weather station was computed and plotted over heatsum in the 115 cm stratum for each measurement period and a calibration factor was calculated. Weather station temperatures were then used to compute heatsums from the following strata: i) the average of 5 and 10 cm above ground level, representing range for temperature ambient to seedling shoots, ii) 0.5 cm below soil surface, the stratum of seed germination temperature, and iii) the average of 2-20 cm below the soil surface, the root growth zone temperatures.

**Soil Moisture** -- Soil moisture content was monitored to ensure that it fell within the limits assumed for the model. Soil cores 2 x 20 cm were removed weekly from randomly chosen locations along the length of each bed, excluding the instrumented area. Cores were taken from each inter-drill space across the width of the bed and immediately transferred to plugged polyethylene pipe to prevent moisture loss. Samples of six cores were taken at 2-hr intervals from 0900 to 1500, and immediately after and ½ hr after irrigation. In the laboratory, each core was subdivided into 2-cm segments, and moisture content of each was determined gravimetrically and converted to soil matrix potential, using desorption curves (Sutherland and Sluggett 1974). The results (Fig. 19) verified that soil moisture content during the growing season was within the limits assumed for the model.

## Results

**Germination** -- Nursery germination data were obtained from 1973 nursery germination trials (Lock et al. 1974). Because of the model assumption that all seeds were germinable, predicted germination was compared with nursery germination, based on germinable seed. Correspondence of predicted to actual germination was satisfactorily close (Fig. 20), although the nursery seedlot had a smaller slow-germinating fraction than had been estimated and maintained a linear rate up to 94% germination, compared to the 85% used in the model. The apparent later start of nursery germination at 13 days, compared to 10 days in the model, was due to the time lapse before germinated seeds emerged above the soil and could be counted. Approximately 1500 additional degree-hours are required before germinants appear above the soil (Bloomberg, unpublished).

**Root Growth** -- Total root length in the nursery in 1973 was computed weekly from five seedlings in each of three seedlots. In 1975, it was computed at 60 and 120 days after sowing in five seedlings in each of three seedlots. Different seedlots and seedbeds were used each year. Simulated total root length was computed at 10-day intervals from five seedlings randomly selected from the total model population. Agreement of simulated and field results was satisfactory (Fig. 21, Table 5).

Distribution of $1^{o}$ and $2^{o}$ root tips was measured weekly in 1973 in three seedlots by recording the number of each type present in each 2-cm soil depth, using the method of extracting and analyzing undisturbed soil blocks containing root systems (Bloomberg 1974). The soil blocks, each containing approximately eight seedlings, were removed from representative lengths of drill in three seedbeds. Root material was recovered from

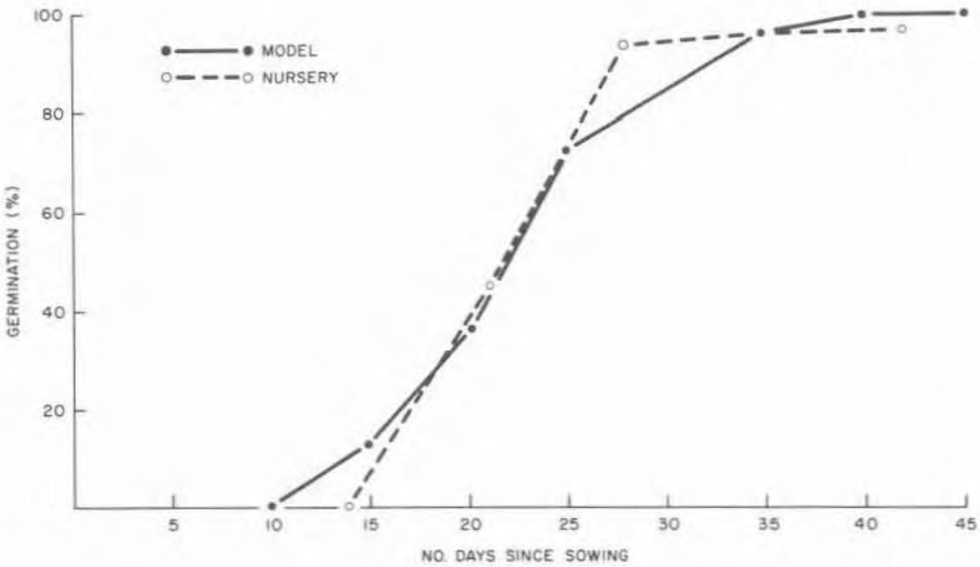



**Figure 20.** Comparison of model and nursery germination of Douglas-fir seedlings.

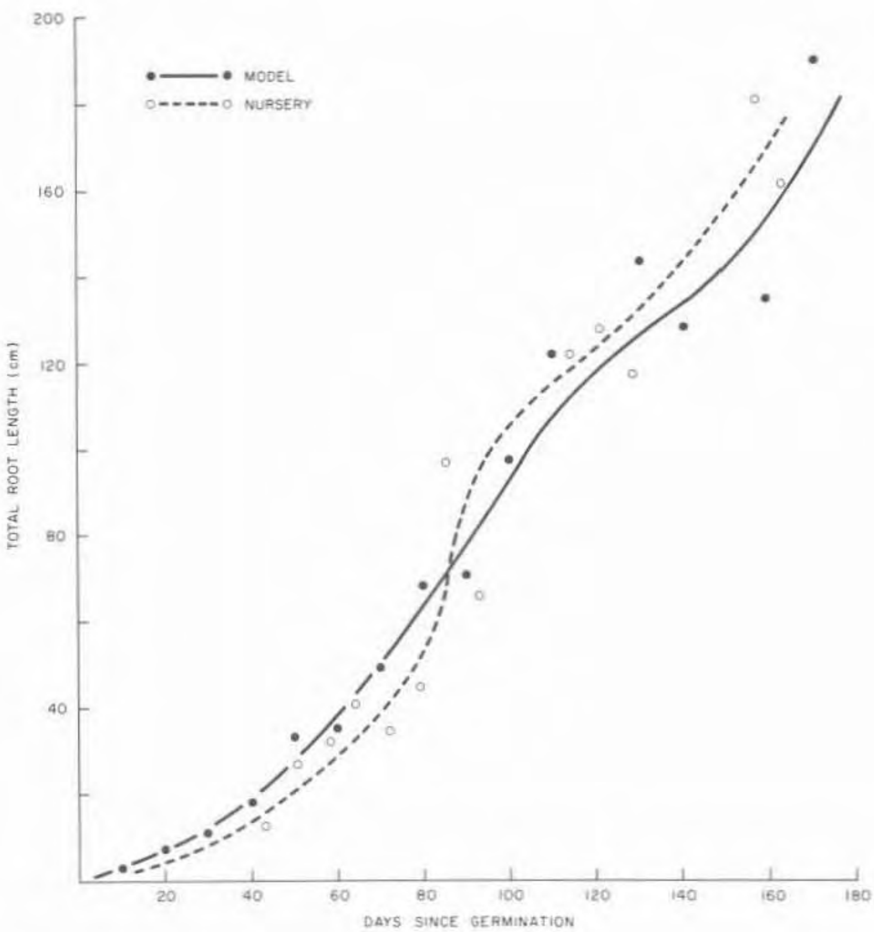



**Figure 21.** Comparison of total 1973 root growth in Douglas-fir seedlings in nursery and as predicted by model. Each point is the mean of five randomly selected seedlings.

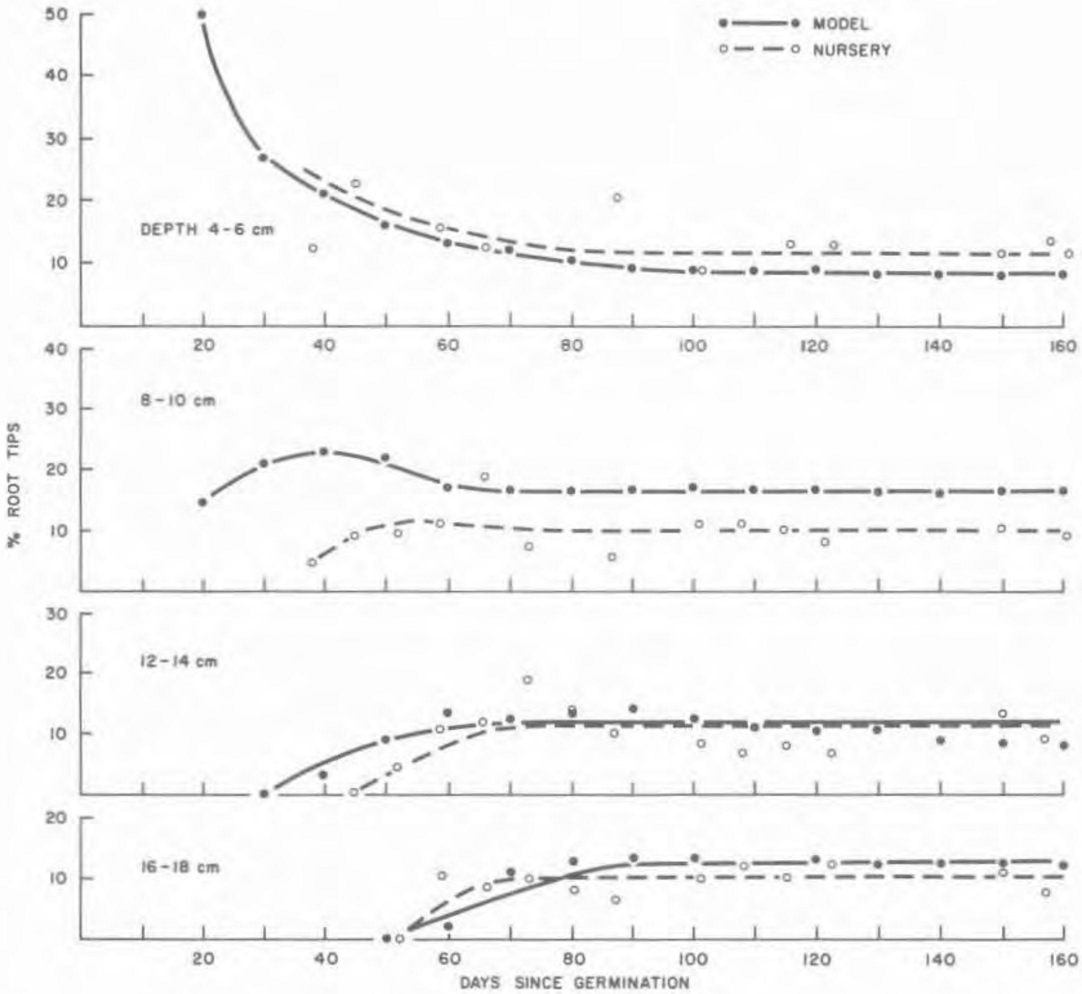



**Figure 22.** Percentage of 1° root tips by depth in Douglas-fir seedlings in nursery and as predicted by model. Each point is the mean of five randomly selected seedlings.

each 2-cm cube subdivision of the block and microscopically identified as to type. Per cent 1° and 2° root tips occurring in each 2-cm-depth level was compared with that of the total population of model seedlings.

Agreement between the two mean lines was better at some depth levels than at others (Figs. 22,23) where model values exceeded or fell below nursery values. This was to be expected in view of the great variation encountered among three seedlots and the different locations within the beds from which the soil blocks containing roots were removed. Trends in the mean lines agreed quite well and the scatter of model values was generally close to, or within, that of the nursery.

**Diseased Seedlings** -- Number of diseased seedlings and number and length of infected roots in nursery seedlings collected in 1973 and 1975 were compared with those in seedlings randomly selected from the model results. Agreement between model and nursery in per cent diseased seedlings was considered satisfactory in view of the inclusion of all seedlings with diseased roots, regardless of number or length (Table 5). Per cent length of root infected in 1973 and 1975 (28 and 20%) showed a reasonable relationship to the 20% reduction in root weight found in Fusarium-infested compared to disease-free (fumigated) Koksilah nursery

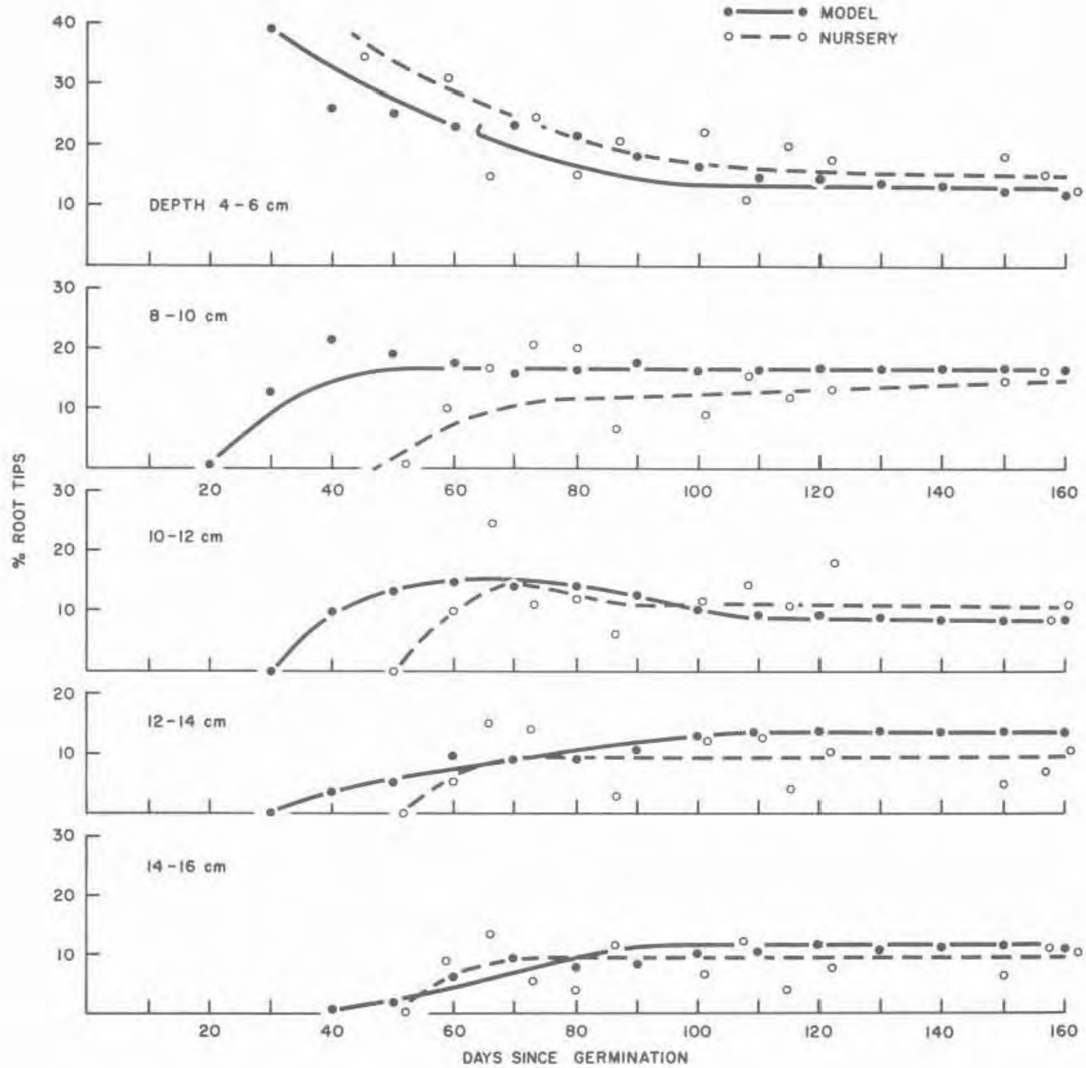



**Figure 23.** Percentage of Douglas-fir seedling $2^{o}$ tips by depth in nursery and as predicted by model. Each point is the mean of five randomly selected seedlings.

beds (Bloomberg and Orchard 1969). The model values were well within the nursery ranges for both years (22-63 and 10-31%). No damping-off or significant root-rot mortality occurred in 1973 or 1975 in the model or nursery samples, a situation typical of the sporadic nature of the diseases. Clearly, even in the absence of mortality, the disease causes serious reduction of root systems.

**Root-Rot Mortality** -- Model results for root-rot mortality were evaluated by estimating inoculum levels for other years in which root-rot records had been kept. In the absence of thermograph records, heatsum values were calculated from mean daily temperature records. The comparison of root rot development from model prediction and nursery records for 1962 is shown in Fig. 24. Total root rot mortality for two years, with model predictions in brackets, were: 1962, 9.5 (11) 1963, 15.5 (12), or an average accuracy of 80%. Considering the approximate method of estimating heatsum and inoculum, the model has acceptable accuracy in disease prediction for investigating response to environmental and biological factors.

TABLE 5

Comparison of Douglas-fir seedling root growth and Infection by root-rot in nursery and as predicted by model

| Year | Source of Estimate | Seedling Age (days) | Avg Root Length (cm) | Infected Seedlings (%) | $1^{0}$ Roots 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 |

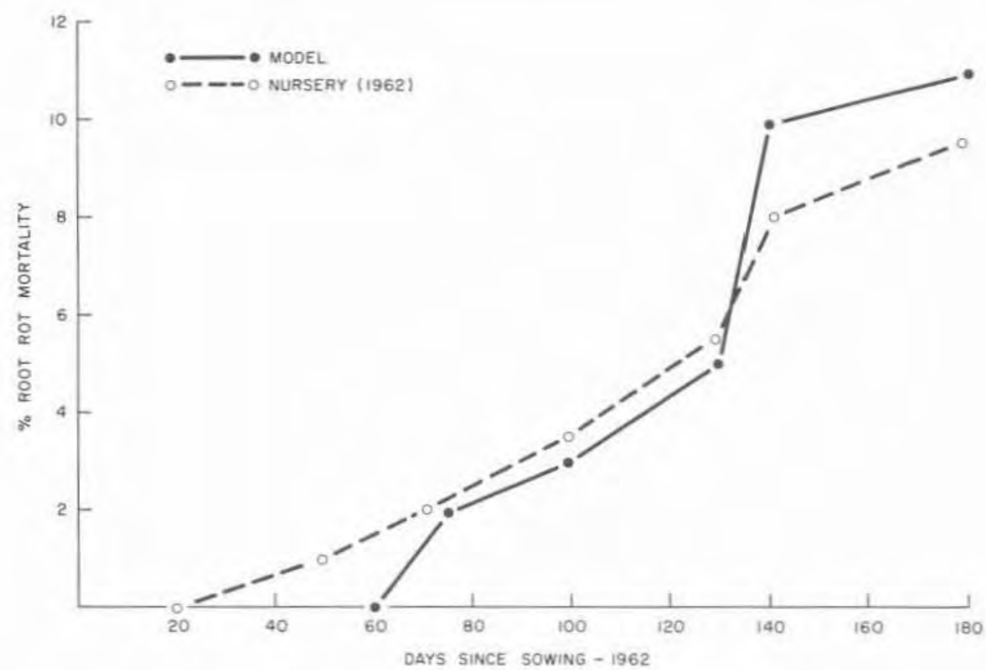



**Figure 24.** Comparison of root-rot mortality in Douglas-fir seedlings in nursery and as predicted by model. Air and soil temperatures were computed from meteorological records. Inoculum concentration and infectivity were estimated from experimental data.

## MODEL APPLICATIONS

Results of systematic tests over a range of temperature, disease and seedling conditions will be reported separately. Some examples are given here to illustrate use of the model. Since the model realistically represents root growth, it can provide guidelines for optimizing seedling growth. For example, choice of time and depth for root pruning should take into account depth and distribution of $1^{o}$ roots, and time at which $2^{o}$ roots are most prolifically produced. These parameters can be predicted by the model under various conditions. Likewise, timing of fertilizer application for maximum uptake by roots can be guided by prediction of where and how many root tips are distributed at a given time.

Since the model simulates interplay of factors, allowing for natural variation, detailed comparisons are possible; e.g. effects of fungicide penetration to different depths in the soil, with differential effects according to depth. Depending on the time of application, roots may or may not have already penetrated to particular depths, thus may or may not have become infected at the time of fungicide application. If roots were already infected, the fungicide might have little effect on the course of disease. On the other hand, if the fungicide has penetrated before the roots to depths of greatest inoculum density, the amount of infection should be greatly reduced. Subsequent destruction of the root system by lesion growth would depend on where in the root system infections occurred, especially on their proximity to the taproot. For example, multiple infections far from the taproot and deep in the soil may have less impact on root destruction than a few infections on or close to the taproot near the root crown. Critical timing and depths for fungicide penetration and activity can, therefore, be predicted.

## SUMMARY

A simulation approach to studying root growth, damping-off and root rot of Douglas-fir seedlings in a B.C. forest nursery was adopted as being more effective than classical-type factorial experiments in dealing with dynamic processes, variation in environmental factors and seedling and pathogen populations, and effects of nursery practices. The determining processes and factors were considered as a system comprising components for pathogen behavior, seedling attributes and environmental factors. The system was defined in space as a plot 40x40x20 cm deep, containing approximately 100 seedlings, and in time from May 1 (seed sowing) to October 31 (end of root-rot damage).

Mathematical relationships describing system processes were derived from published reports, the author's unpublished results, special experiments, field observations and logical relationships. Pathogen relationships were confined to *Fusarium oxysporum,* the major cause of damping-off and root rot in coastal Douglas-fir, and essentially involved inoculum size, spatial distribution and infectivity, and effect of temperature on lesion growth. An infection process algorithm, based on a three-dimensional matrix of inoculum in the soil, was used to calculate the probability of infection based on pathogen parameters and length and depth of root tip.

Root geometry, necessary for prediction of infection, was represented as a series of three-dimensional relationships over time. It was determined by the initiation points, growth rates and direction of radicle, taproot, and first- and higher-order roots. Germination generated the seedling population in space and time and was determined by the heatsum requirements of seedlots for initiation and rates of germination for normal and slow-germinating fractions. Nursery soil moisture was assumed, and found, to be optimal for germination.

Total root growth was mainly affected by temperature. Soil moisture, fertility and structure were not regarded as limiting under nursery conditions. Root elongation

was assumed to follow the law of compound interest and, during any period, was a function of total root length at the beginning of the period and the growth rate during it. Periodic growth rate was calculated as a fraction of the maximum, as determined in two seedlots grown at near-optimal temperature, from Lavender and Overton's (1972) data for seedling growth at different temperatures.

Taproot growth was determined from a well-defined curvilinear relationship with total root over a range of seedlots and nursery conditions. Distribution of 1° root initials along the taproot and their growth were derived as functions of seedling age and depth in soil, based on periodic measurements of three seedlots in one nursery and observations from others. Direction of 1° root growth was periodically determined by root plotter from two seedlots grown in pots fitted with root cages. Vertical growth angle showed a fairly good relationship to length and depth of origin. No effects of horizontal direction were detected. Distribution of 2° roots along 1° roots was determined in three seedlots in a nursery and found to depend on seedling age and depth of 1° root origin. No significant differences were found among seedlots in any root growth parameters. Data from all seedlots were therefore pooled for calculation of relationships.

The system was translated into a computerized model by subdividing the time frame into 5-day periods and the spatial frame into 2-cm soil depth and distance classes from the soil surface and taproot axis, respectively. Relationships were expressed by linear regressions, interpolation in non-linear regressions, tabular values and probabilistic functions. Inputs to operate the model included daily heatsum in the germination zone, and 5-day heatsums in the shoot growth and root growth zones. These were derived by hourly temperature measurement in a nursery with diode sensors at various heights and depths from the soil surface. Inputs for germination and disease parameters were obtained from experiments. Management practice inputs included setting length of growth period and number of seeds sown, and changing temperature regime and growth rates.

Results of the model were compared to actual nursery results, using recorded temperatures over 2 years and temperatures estimated from meteorological reports in another 2 years. Model accuracy exceeded 90% for total root growth, 80% for number of infected seedlings and 70% for diseased root length. Root-rot mortality was 80% accurate. Applications of the model include determining optimum timing and depth for root pruning, and timing of fertilizer application.

## ACKNOWLEDGMENTS

Thanks are extended to Dr. E.D. Ford, Institute of Tree Biology, Edinburgh, who guided the author into simulation techniques; Dr. F.T. Last, Director, for making Institute facilities available; Mr. A.A. Hall for undertaking a considerable load of field work and data processing, and Mr. F.G. Heywood for advice on computer system use.

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