1969

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Recommended Citation

Mitchell, Kenneth J., "Simulation of the Growth of Even-Aged Stands of White Spruce" (1969). *Yale School of Forestry & Environmental Studies Bulletin Series*. 62.
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YALE UNIVERSITY : SCHOOL OF FORESTRY

Bulletin No. 75

SIMULATION OF THE GROWTH OF EVEN-AGED STANDS OF WHITE SPRUCE

BY

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New Haven : Yale University
1969

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ACKNOWLEDGMENTS

THE author gratefully acknowledges his indebtedness to the staff of the School of Forestry of Yale University, especially the members of his Dissertation Committee: Professors David M. Smith, George M. Furnival and Garth K. Voigt.

Thanks are also extended to the Department of Fisheries and Forestry of Canada for educational leave to undertake graduate studies, financial assistance while attending university, support of this dissertation and use of departmental facilities. Appreciation is particularly extended to Mr. V. H. Phelps, Section Head, Forest Research Laboratory, Victoria, and Mr. R. H. Meyer for their constructive criticism, and to Mr. W. M. Stiell and Mr. L. G. Brace of the Petawawa Forest Experiment Station for their assistance in the collection of data.

TABLE OF CONTENTS

ABSTRACT

STUDIES of white spruce (*Picea glauca* (Moench) Voss) in central British Columbia led to the following results: (1) Annual longitudinal growth of the main axis of all branches, excluding those below the point of maximum crown spread, is a function of the concurrent height growth of the terminal, regardless of the degree of suppression. Therefore, (2) the horizontal radial growth of any vigorous portion of the crown can be estimated from height growth or a height-age curve, provided that corrections for the crooks, curvature and angle of branches are incorporated into the relationship. (3) The height of a tree is a function of the height (Hd) of dominant trees and the width of its crown (CW) relative to the maximum crown width (CWMAX) it could have attained had it grown without competition from surrounding trees (square of correlation coefficient $r^2 = 0.55$). (4) Trees have a 50 per cent chance of being overtopped when the natural logarithm of CW/CWMAX is ≤ -1.75 and, based on data from Ontario, usually die if it is < -1.85. (5) Crown area, defined by the vertical projection of the crown, and tree height provide an accurate estimate of bole diameter ($r^2 = 0.93$) and bole volume ($r^2 = 0.92$).

A mathematical model was developed which simulates the growth of stands in terms of the crown expansion of individual trees. A particular plot from which growth predictions are to be made is represented in the memory unit of the computer by a matrix which contains one entry for each square foot of growing space. Each entry contains a code denoting the number of the tree if the particular location is occupied. The number of entries occupied by each tree increases as the crowns of individual trees expand into vacant growing space. The spread of the crown, within the limitations imposed by the size and location of competing trees, is predicated on the expected height-age relationship of dominant trees on the particular site. A random variable is generated by Monte Carlo methods to simulate unexplained sources of variation, e.g. heredity. The resulting asymmetrical development of tree crowns is facilitated by a complex scanning program which directs the computer to search out growing space available to each tree. The height of each tree depends on Hd and CW/CWMAX. Diameter and volume of the bole are estimated from crown area and height. *All* simulated parameters are derived directly or indirectly from the height growth of dominant trees and the spatial distribution of individual trees.

A comparison of the actual and simulated growth of permanent sample plots showed close agreement in terms of bole and crown parameters.

The model is designed to replace conventional yield tables and provide a tool for testing silvicultural practices and management plans. It can be applied over large areas with information from low-level aerial photographs, thus expediting the collection of data.

INTRODUCTION

THIS study attempts to develop a means whereby years of tree and stand growth can be simulated in minutes on a computer by compressing the physical dimensions of stands and the time scale on which they grow so that estimates of growth and yield may be obtained quickly, and results of stand treatments tested and demonstrated rapidly. The problem is not unique. It may be solved by constructing miniature forests analogous to model ships or airplanes. Aeronautical engineers, for example, cannot build and fly an aircraft each time they wish to examine the aerodynamic properties of a fuselage or airfoil. Instead, they build a model and simulate flight in a wind tunnel. Similarly foresters cannot wait for decades to evaluate cultural practices. Instead, they should rely on stand models which will likely be mathematical and quite abstract because many aspects of the growth of stands are too complex to be studied with physical models. All models are analogous to reality but are simpler in structure because of the omission of irrelevant detail. They can be organized, manipulated and studied in a way not feasible in real life.

The model forest formulated, assembled and tested in this investigation employs original methods which utilize the close relationship between the growth of the crown and the bole. A programmed computer processes the spatial distribution of trees and simulates the development of the stand, with special emphasis on the competition for growing space. The volume of wood and other parameters of the stand are determined from crown dimensions at the end of the prediction period.

The model represents an initial step in the evolution of a precise analytical tool for use in the development of optimum forest management regimes. Further application as a teaching device and instrument of research is expected.

Gould and O'Regan (1965), and O'Regan *et al.* (1966) recently constructed a very comprehensive stand model for forest planning. Economic considerations and possible losses by fires and storms were incorporated into the model. The model herein constructed is comparable to their "wood generator."

Clutter (1963) developed a mathematical model in which the growth equation was the first derivative of the yield function, thus making the growth and yield predictions compatible. His formulae were later employed in the simulation of a forest enterprise (Clutter and Bamping, 1966). The stand model which Newnham (1964) derived is described later.

The problem of constructing models for mixed stands was studied by Nelson

(1965), who said "the ultimate model . . . would be a system whereby the growth of each individual tree of each species or species group could be characterized in relation to its competitor." The problem of the pure stand is studied in the present investigation.

THE APPROACH

The approach employed to describe the dynamics of forests recognizes, firstly, that the internal forces which mould the development of forests are generated by individual trees. Consequently, the individual tree is the basic unit in the simulation. Secondly, the crowns and root systems react directly to environmental factors, whereas the bole mainly reflects the physiological activities of the crown. Therefore the influence of the environment on the growth of a tree is described in terms of the foliage and root system where possible. Lastly, factors which are not understood or easily quantified are not ignored. Variation in growth habits caused by root grafting and genetic factors are examples.

Emphasis in this study is directed towards an understanding of the general principles governing the dynamics of stands. Therefore, the model's form is patterned after the forest community and is not determined by an arbitrarily chosen mathematical language.

THE VARIABLES

The choice of variables included in the model is based on discussions by Kramer and Kozlowski (1960) and subjective examination of stands to select the factors which contribute most to the dynamic features of forests. Reasons for the selection or omission of variables are summarized below.

Species Only one tree species is considered, in order to simplify the model and reduce data collection. However, a second species with similar growth habits can be easily incorporated.

Age Age is an important variable, especially from a conceptual point of view.

Genetics Variation of uncertain origin, likely due in part to heredity, is simulated even though the sources of the variance cannot be isolated.

Root grafting Evaluation of the extent and importance of root grafting is essential before it can be assumed that trees act as individuals.

Site quality Soil, climate and other factors affecting the productivity of forests are fundamental variables but are awkward to measure directly and synthesize into an expression of site quality. Consequently, it is expedient to use tree parameters as an integrated expression of site factors.

Competition Parameters of the crown are used to assess inter-tree competition

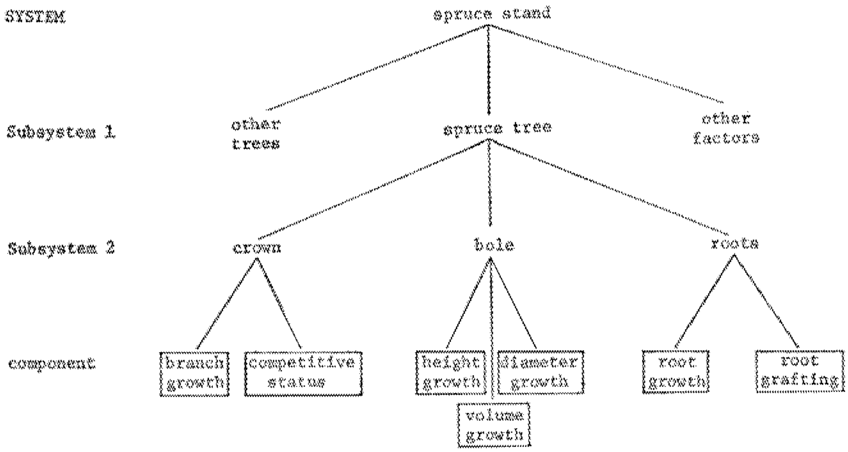


FIGURE 1. An even-aged stand of white spruce, viewed in a system context.

because the carbohydrates needed for tree growth are produced in the foliage. Furthermore, crowns can be measured more readily than root systems, and the size of a root system is likely reflected in the dimensions of the crown.

Cultural practices It is advantageous to simulate the removal of trees in the model because thinnings will likely become an integral part of management plans in the near future. Allowance will not be made for the simulation of other cultural practices, such as fertilization, until the necessity arises.

Damaging agencies The effects of fire, insects, disease and other damaging agencies will not be simulated until the model is used to predict yield over large areas, rather than on small plots as expected at the present time.

THE SYSTEM

A spruce stand, when thought of as a *system*, is an orderly arrangement of interrelated pieces that form a connected unit or system. Systems analysis is used to define these pieces and establish the links between them (Figure 1).

The "components" form the lowest level in the system. They serve as blocks for building a *system model* which incorporates the essential features of the real system and disregards those believed to be of minor importance (Figure 2). The arrows are symbolic of mathematical expressions which must be derived to describe the action and interaction of components and elements of the environment. The quality of the site in conjunction with the age and the species of the tree

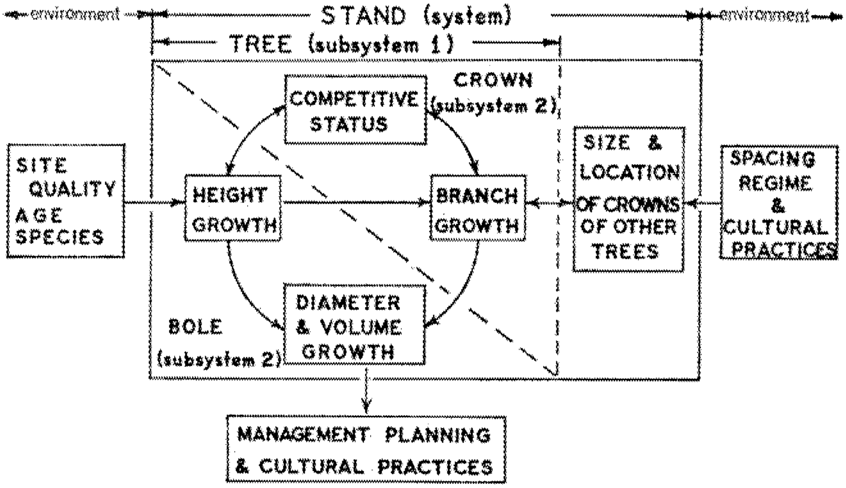


FIGURE 2. The system model.

initially regulates height increment which, in turn, regulates the growth of the branches, possibly through the medium of hormones (Kramer and Kozlowski, 1960). The size of the crown is limited by available growing space and cultural practices. The degree of suppression or competitive status of an individual tree depends on available light as determined by its height and crown size relative to competing trees. In return, height and crown growth are influenced by the competitive position of the tree. The volume and diameter of the bole are, for present purposes, viewed as being solely dependent upon the size of the crown and the height of the tree. Application of this information is anticipated in management planning. Note that root components and other factors have been omitted for simplicity. This description of components is highly simplified but it does provide a realistic foundation on which to build a model for describing the behavior of forests.

Construction of the system model in Figure 2 is hampered because it is not feasible to derive mathematical equations that relate the size, shape and location of the crowns of all competing trees to the growing space available to the crown of a particular tree. This difficulty can be overcome by developing a *system simulation model.* The term "simulation" refers to the operation of a second system, usually an electronic computer, for the purpose of imitating the actual system. Simulation models can be realistically complex because a computer, with the numerical techniques and speed that it affords, permits a degree of detail that would render ordinary mathematical models intractable. The model described later accepts specifications of various system parameters and uncontrollable variables and, with the aid of a computer, simulates the response of the forest to the conditions specified.

The Monte Carlo method (Hammersley and Handscomb, 1964) is a common but possibly unfamiliar technique used in simulation models. It is applied when data are incomplete or relationships are incapable of rigorous solution, and the only information available pertains to the mathematical characteristics of a probability distribution. Random samples are drawn from a population with this probability distribution in order to simulate naturally occurring variation. Sampling from a previously defined population to simulate variation in the rate of tree growth is an example of the use of Monte Carlo methods.

ANALYSIS OF COMPONENTS

THE relationship of the components analyzed in this section, with the exception of root development, is illustrated in Figure 2.

Data used in the analysis are from pure even-aged stands of white spruce (*Picea glauca* (Moench) Voss) sampled in the vicinity of Prince George (latitude 53° 75′ N., longitude 122° 45′ W.) in the central interior of British Columbia. The forests are in the Montane Transition Section (M4) of the Montane Forest Region (Rowe, 1959) on Bednesti Bisequa Gray Wooded soil derived from silty glaciolacustrine deposits.

All statistical relationships are significant at the one per cent level of confidence and are judged to be important. The coefficient of correlation (r) or coefficient of determination (r^2) expressed in per cent, and number of observations (n) are shown with each of these relationships. The standard error of estimate (S.E.) is reported if the variables are not transformed.

Root Development

Superficial excavation of the surface roots of 10 white spruce in the study area showed that the average radial spread of roots is two to four times the width of the crown. Dr. R.I. Grose (personal communication) recently reported that the radial spread of the roots of white spruce is roughly equal to the height of the trees in 30-year-old plantations at the Petawawa Forest Experiment Station in Ontario.

Root grafting appeared to be minimal in spite of the interlocking nature of the root systems. An excavation, in the Prince George study area, of the root systems of three trees which were approximately 4 feet apart and about 65 feet tall, revealed a single graft. One tree had captured a root from a fourth tree situated 15 feet away. Dr. Grose excavated several one-tenth-acre plots and concluded that root grafting was unimportant.

The preceding evidence indicates that the root systems of the trees spread horizontally without any clear interaction with one another. Furthermore, even though the roots of different trees are thoroughly intermingled, root grafts are remarkably few. In the absence of indications of any strong effects of interference or assistance among the root systems of adjacent trees, it is concluded that there is no need to include competition parameters in the model because of any effects in limiting root extension.

ANALYSIS OF COMPONENTS

Site Quality

Site quality, as mentioned earlier, is one component for which a satisfactory description cannot be obtained in terms of environmental factors. For this study, site quality is defined as the height-age curve of dominant trees (tallest 10% in the stand). This relationship is not an integral component of the model. However, it must be available for the particular plots from which growth predictions are made. In practice, a height-age curve would be determined for each site by conventional methods of stem analysis or a set of site index curves. The success of the simulation will rely heavily on the accuracy of these curves.

Height Growth

The height-age curve used to define site quality is more useful for simulating tree heights if the relationship is modified to estimate the maximum rather than the average height of dominant trees. The maximum height that a tree can attain at a particular age can then be reduced to allow for the effects of competition. This height was estimated by comparing the average height of dominant trees in each of 13 plots with the height of the tallest trees in the plot. Only one of the 304 sample trees, ranging in dominant height from 47 to 115 feet, was found to exceed the average height of dominants by more than 10 per cent. Consequently, 10 per cent added to the calculated height of dominant trees is assumed to be the maximum height that any tree can attain.

Growth of the Crown

This component, in fact the entire model, is developed to exploit the results of an earlier study (Mitchell, 1965) in which estimation of bole diameter at breast height (D) of dominant and codominant white spruce was found to be independent of stand density. This relationship applied when the width of the crown (CW) was used as the independent variable in addition to age and site index (SI). Neither plot basal area nor point density (Spurr, 1962) reduced the standard error of Equation 1. This implies that crown width and bole diameter at breast height

$$D = 0.00626\,(CW)\,(Age) + 0.00328\,(CW)\,(SI) \qquad \begin{array}{cc} \text{S.E.} & r^2 \times 100 \\ \underline{\text{(inches)}} & \underline{(n = 400)} \\ \pm 2.07 & 88.0\% \end{array} \qquad (1)$$

respond similarly to differences in stand density so that their relative size remains constant. Such results are expected because density regulates the length and width of the crown which controls the size and development of the bole. Consequently, the relative width or area of the crowns of individual trees in an even-aged stand

FIGURE 3. Definition of crown area.

is a good integrated expression of the amount of competition to which a tree has been subjected.

Estimation of the area of the crown, defined as the area outlined by the vertical projection of the crown (Figure 3), requires an accurate description of the growth of branches and adjustments for branch angle and other factors affecting the radial growth of the crown. Annual growth of branches was measured with a technique developed to detect past browsing damage to the stems of young Douglas-fir trees (Mitchell, 1964). The use of this technique to analyze the branches of white spruce is described below.

Branches are removed at or above the point of maximum crown spread with the aid of an aluminum extension ladder and climbing belt if the trees cannot be felled. Each branch selected should extend to the edge of the vertical profile of the crown and be free of abnormalities other than forks. The vertical displacement of the tip of the branch from the horizontal plane is measured with the aid of an abney level before removing the branch. The length and the horizontal extension of the branch is estimated by reconstructing the angle of the branch after it is cut from the tree. These measurements are to determine the horizontal growth rate of the crown.

The branches must be analyzed by several means to obtain curves depicting the growth in length in relation to the age of each branch. Recognition of bud scars provides an obvious means of locating each node. Unfortunately, bud scars are rarely apparent near the bases of old branches so it is necessary to expose the pith by splitting each branch lengthwise. Changes in the morphology and color of the

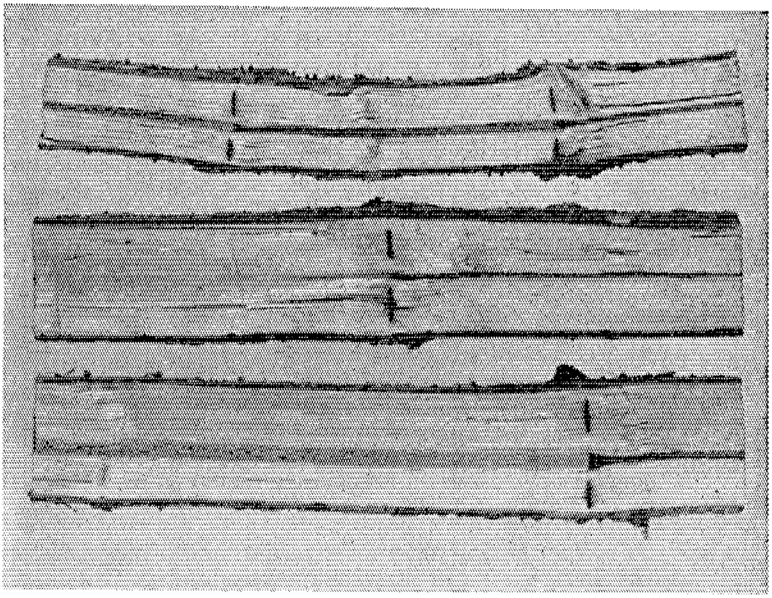


FIGURE 4. Radial sections of nodes (marked at the sides with an indelible pencil) showing changes in the morphology and color of the pith of white spruce.

pith at the nodes of white spruce are portrayed in Figure 4. The pith is dark brown towards the distal end of each annual segment where it also increases in width and forms a cup. The pith formed when growth resumes is light brown and about the same width as the cup. Frequently, the color change is the only evidence of a node, as illustrated by the second branch section in Figure 4.

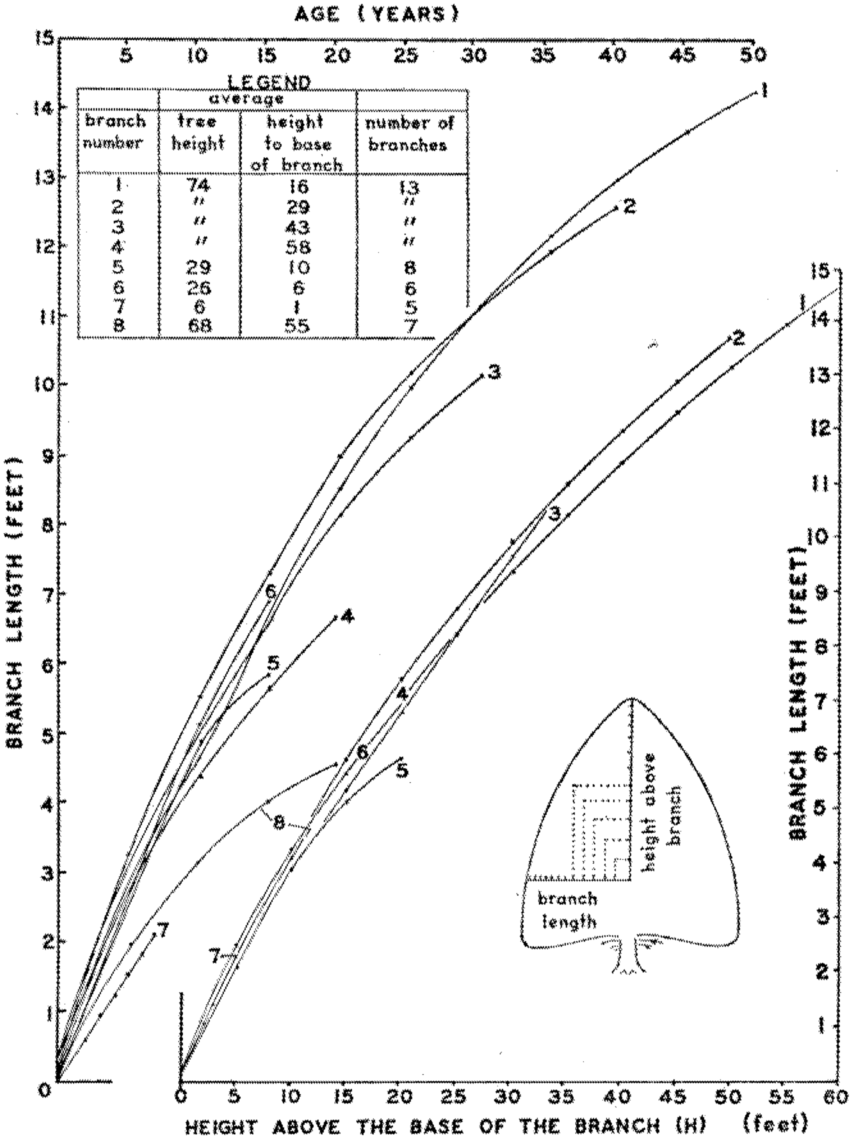
Measurement of the longitudinal growth of each branch is simple if the nodes have been marked distinctly with an indelible pencil. The distance from the base of the branch to the first node plus the radius of the bole is equal to the growth during the first year unless the first branch internode is encased entirely within the bole. This is unusual in immature trees.

The relationship between the length and age of branches in the study area was determined by analyzing four branches at equally spaced intervals up the boles of 13 free-growing trees. These trees were in 80-year-old stands and far enough from competitors to be free of physical contact between crowns. Branches were chosen at the widest part of the crown and above in order to eliminate those which showed the decline in the rate of growth indicative of approaching death. These lowermost branches die slowly even when trees are free of competition. Consequently, free-growing trees from young stands were sampled to obtain information on the juvenile growth of crowns.

Curves 1 to 4 in the uppermost portion of Figure 5 illustrate the average relationship between the length and age of branches removed at four levels from the crowns of trees in the 80-year-old age class. Branch length (BL) refers to measurements made along the axis of branches. The same measurements corrected for angle and curvature give the horizontal radius of the crown (CR). Growth information is also shown for three younger age classes (branches 5, 6 and 7) in which case only one branch, at or slightly above the widest part of the crown, was analyzed from each tree. Figure 5 indicates that the rate of growth of branches is influenced by some variable other than age, possibly the rate of height growth. Branch 8, representing intermediate and suppressed trees from the 80-year-old stands, is added to show that the rate of crown growth is reduced considerably when there is little height increment.

The relationship between branch length and total height growth during the same period should not be affected by the stage of development or the age of the tree if the annual longitudinal growth of the branch is dependent upon, or closely related to, the height increment of the same year. The validity of this reasoning is supported by the relationship illustrated by curves 1 to 8 in the lowermost portion of Figure 5. These curves are not significantly different. The diagram inserted in the lower right-hand corner shows the axes of a hypothetical graph which has been rotated and superimposed over a sketch of a tree to illustrate the variables under consideration. Note that the independent variable is the distance from the base of the branch to the terminal of the tree so that there is a one-to-one correspondence between height and branch increment. Measurement of height growth is based on internodal measurements or interpolated from a height-age curve developed for each tree from the age count of increment cores taken at various heights. The value of this relationship lies in its simplicity. *Estimation of crown growth from this relationship does not depend on the height of the branch above the ground, the age of the tree or the degree of suppression.*

The relationship between branch length (BL) and height above the base of the branch (H) becomes linear when plotted on logarithmic paper (both axis graduated logarithmically). One branch from each of three large isolated trees (100 to 125 years old) was analyzed to show that linearity continues beyond the upper limit (60 feet) of the independent variable shown in Figure 5. The longest branch provided limited evidence that the range of such linearity extends an additional 30



LEGEND

branch number	average tree height	average height to base of branch	number of branches
1	74	16	13
2	"	29	"
3	"	43	"
4	"	58	"
5	29	10	8
6	26	6	6
7	6	1	5
8	68	55	7

Figure 5. Relationship between branch length, age and height.

feet. These branches, plus five shorter ones from the same trees, did not differ significantly from the curves illustrated in Figure 5. Consequently, all data were combined in the derivation of an equation for the estimation of branch length. The slope of the linear relationship on logarithmic axes was ¾ suggesting an equation in the form

$$BL = bH^{3/4} \qquad (2)$$

The weighted regression coefficient, b, is calculated as

$$b = \Sigma l_i / \Sigma h_i^{3/4},\ i = 1, 2, \ldots, 86$$

where

l_i = length in feet of the i^{th} branch, measured from the center of the bole,
h_i = distance in feet from the base of the i^{th} branch to the top of the most recent leader.

The regression coefficient is included in Equation 4:

$$BL = 0.738\ H^{3/4} \qquad (4)$$

This coefficient is an expression of the rate of branch growth in which height rather than age is used as the independent variable. Hence, 0.738 feet of branch growth is expected per unit of height growth (after transformation). A probit diagram (Bliss, 1967) revealed that the variation of the regression coefficients of individual branches can be described by a normal distribution with a mean of 0.738 and a standard deviation of 0.125. This information is required later in the construction of the model.

Equation 4 expresses the cumulative growth of branches and not the horizontal distance from the tip of the branch to the center of the bole because:

(1) branches grow in a "zig zag" manner, especially when extension is slow (Figure 6a),
(2) branches tend to curve downward, especially toward the ends where foliage is concentrated on slender twigs (Figure 6b),
(3) branches rarely grow perpendicular to the bole (Figure 6c).

The correction for the first two considerations is derived by relating the sum of the internodal lengths of branches to the straight line distance between points A and B in Figure 6b. The adjustment is very small, especially when branches are less than 10 feet long. The following equations, developed from freehand curves, are designed to show that the correction (c) is a function of branch length. Other factors such as the weight of foliage and diameter of the branch have been ignored. The corrected length of the branch (BLc) is always less than the original length (BL),

$$c = 0.00150\ BL^{7/3} \qquad (5)$$

$$BLc = BL - c \qquad (6)$$

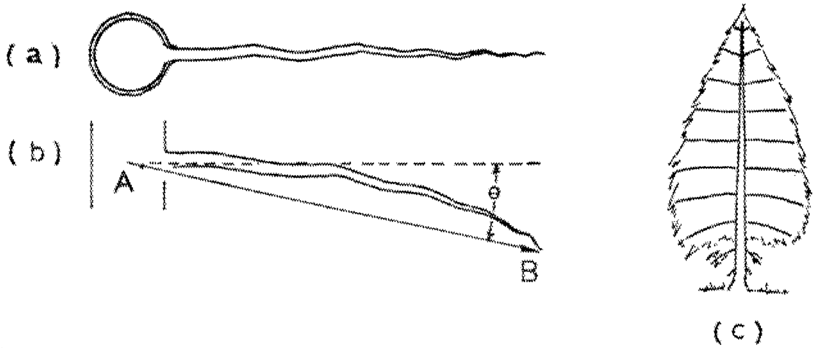


FIGURE 6. Typical branching habit of white spruce.

Note that BL*c* is equal to the slope distance from the tip to the origin of the branch. Eighty-six branches were used in the analysis.

Derivation of an equation to correct for branch angle (θ) (Figures 6b and c) is facilitated by a linear relationship between cosine θ and branch length which applies if branches are less than 15 feet long. The cosine can be estimated by the equation

$$\text{cosine}\ \theta = 1 - |0.170 - 0.0135\ \text{BL}| \qquad (7)$$

The radius of the crown (CR) is calculated as

$$\text{CR} = (\text{BL}c)\ (\text{cosine}\ \theta) \qquad (8)$$

The equations for estimating the length of branches and the radius of the crown are illustrated in Figure 7. Height above the base of the branch is the independent variable. The size of the correction for converting branch length to crown radius is shown in the lower part of Figure 7. Equations 4 to 8 may be combined and simplified algebraically into the form

$$\text{CR} = 0.738\ \text{H}^{3/4}\ (1 - 0.00100\ \text{H})\ (1 - |0.170 - 0.0100\ \text{H}^{3/4}|) \qquad (9)$$

where

CR = radius of the crown (feet)

H = height of the tree above the base of the branch (feet).

The relationship expressed in Equation 4 can be reversed to obtain a crude estimate of the length of the crown above the point of maximum crown spread. Since

$$\text{BL} = 0.738\ \text{H}^{3/4} \qquad (4)$$

therefore

$$\text{H} = 1.50\ (\text{BL})^{4/3}$$

$$\text{CL} \cong 1.50\ (\text{CR})^{4/3} \qquad (10)$$

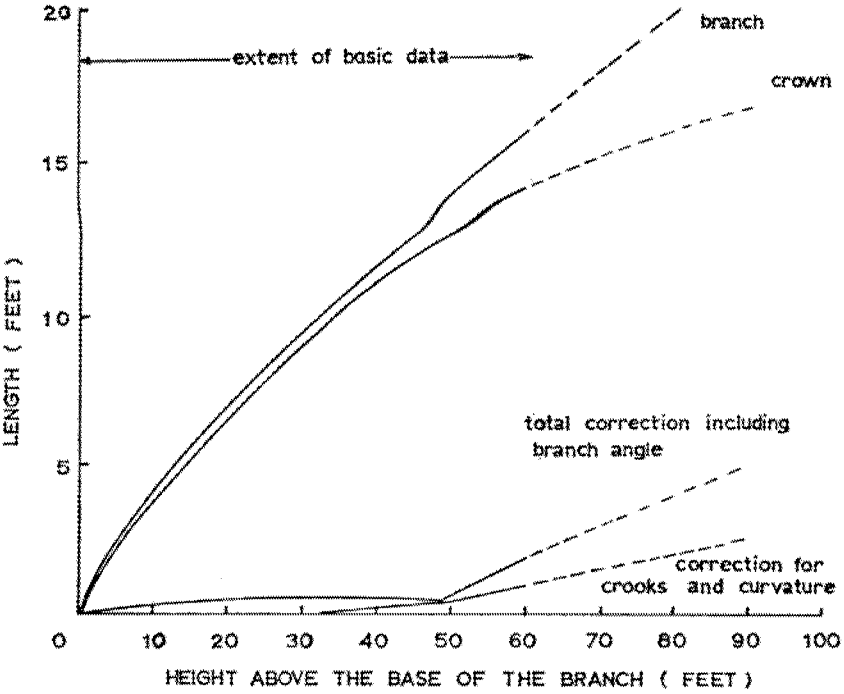


FIGURE 7. Cumulative branch and crown growth.

where

CR = crown radius at the point of maximum crown spread (feet),
CL = crown length above the point of maximum crown spread (feet).

The length of the crown (CL) is equal to the height (H) above the base of the branch when CL is measured above the point of maximum crown spread. Substitution of crown radius (CR) for branch length (BL) omits, for simplicity, the corrections derived in Equations 5 to 7. However, in the model subsequently presented the value of CL is adjusted by approximating the corrections shown in Figure 7.

Preliminary investigation of the development of crowns of dominant and codominant trees in moderately dense stands was initiated after the study of crown growth of free-growing trees to provide information on:

(1) the effect of competition in two or three quadrants of the crown on the growth of branches around the remaining perimeter,

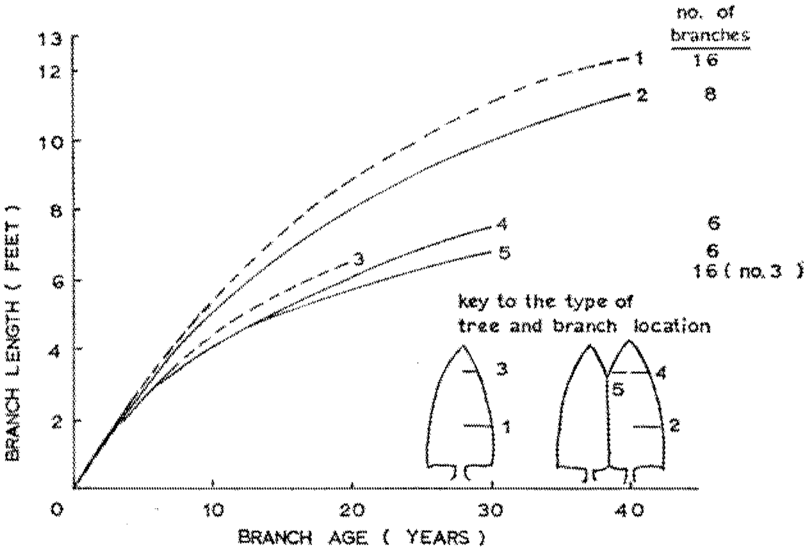


FIGURE 8. Effect of inter-tree competition on branch length.

(2) the rate of branch growth before and after contact with crowns of neighboring trees,

(3) the response of the crown to the death or removal of a competitor.

Branches on the free-growing side of a tree grow at approximately the same rate as branches of completely free-growing trees, judging by statistical tests and a comparison of average growth curves for branches 1 and 2 from the middle of the crown, and branches 3 and 4 from the upper crown (Figure 8).

Branches facing potential competitors show a slight decline in the rate of growth immediately before the crowns make contact. For example, the growth of branches directly above the point of crown contact is slightly but significantly less than for those not facing other trees, as is illustrated by branches 4 and 5 in Figure 8. Note that growth is almost identical until age 15. This minor reduction in the rate of growth before contact is ignored in the development of the model. Small amounts of growth added by branches in the zone of crown contact are usually lost as a result of whipping damage. This damage is not common in very young stands, thus allowing crowns to interlock.

The third objective of the preliminary study was to investigate differences in the growth of released and comparable free-growing branches of the crown. Analysis of released trees in the Prince George study area and in 40-year-old plantations at the Petawawa Forest Experiment Station, indicates that vigorous branches in the zone of crown contact respond to release. However, the rate of growth is usually much less than that of branches immediately above the zone of crown contact and the released branches are therefore much shorter.

CRITERIA OF SUPPRESSION AND DEATH

Criteria of suppression and death are critical components in models of stand growth if trees die during the life of the stand either from inadequate growing space or, more directly, because they cannot tolerate certain combinations or levels of environmental factors. Light is often the main variable that limits survival even though other factors may occasionally affect growth. Trees receiving insufficient light must eventually be eliminated from the stand during the simulation to permit competing trees to increase in size. Omission of these criteria would result in apparent stagnation of the stand.

The aerial growing space occupied by a tree, measured by the area or equivalent width of its crown, is used in the model to estimate the amount of light received by the tree and thus its competitive status. However, the area or width of the crown alone is not an adequate expression of competition because it is also a function of the age of the tree and the quality of the site. The width of the crown (CW) of an individual tree relative to the width of the crown of the same tree had it grown without appreciable competition is a satisfactory measure of suppression. For analytical simplicity, the crown width of each tree is expressed relative to the *maximum* crown width (CWMAX) that could be attained by open-grown trees had they been growing on the same plot at the time of measurement.

Equation 4 can be modified to calculate the maximum crown width (CWMAX) of open-grown trees. The variable H, in the case of open-grown trees, is equal to the distance from the leader to the widest part of the crown. Variable H was estimated to be approximately 85 per cent of the total height (HT) based on a sample of 64 free-growing trees. A second allowance is made for variation in the rate of branch growth (b). The maximum rate of growth can be estimated from the probability distribution of regression coefficients (b) described earlier. Ninety-nine per cent of the trees are expected to have a value of b less than 1.029 which is 2.33 standard deviations above the mean of 0.738. This coefficient is arbitrarily assumed to represent the maximum rate of crown growth. No value of b equal to

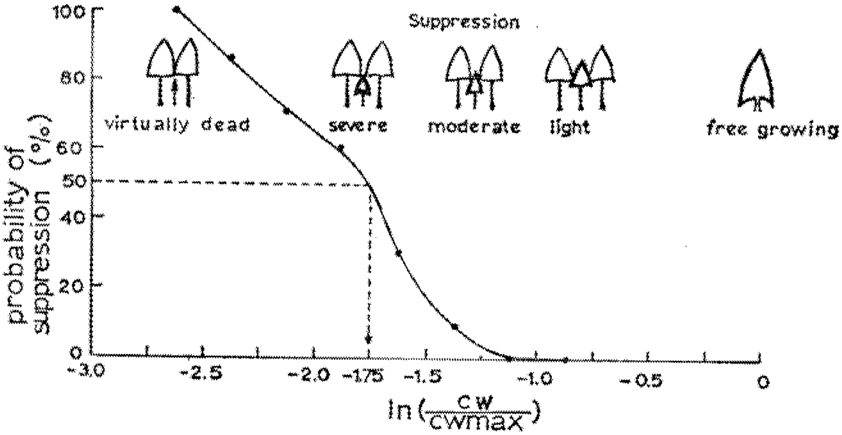


FIGURE 9. Relationship between relative crown width and probability of suppression.

or greater than 1.029 will be generated by the model, therefore simulated crown widths never exceed CWMAX. Thus

$$BL = 0.738\ H^{3/4} \tag{4}$$

is converted into

$$BL = 1.029\ (0.85\ HT)^{3/4} \tag{11}$$

and the equation for estimating the maximum radius of the crown (CRMAX) is derived in the same manner as Equation 9 to obtain

$$CRMAX = 0.911\ HT^{3/4}\ (1 - 0.00132\ HT)\ (1 - |0.170 - 0.0123\ HT^{3/4}|) \tag{12}$$

and

$$CWMAX = 2\ (CRMAX). \tag{13}$$

Equations 12 and 13 incorporate corrections for branch angle and curvature.

For the purpose of the model, a tree is arbitrarily considered to be suppressed when there is a 50 per cent possibility that the tree will be completely overtopped by competitors. The severely suppressed tree in the series of diagrams in Figure 9, for example, has just been overtopped. The probability of this event occurring is related to (CW/CWMAX), expressed as a natural logarithm to facilitate later analysis.

The data collected to establish a criterion of suppression consist of the crown width, the height to the widest part of the crown and the total height of 303 trees

TABLE 1. CRITERION OF SUPPRESSION

Hd		54			76			109				
H2CW		31			52			76				
No. trees-plots[1]		93–3			45–2			57–4			Total	
							tree count					
ln(CW/CWMAX)	below (b)	above (a)	% below	b	a	% b	b	a	% b	b	a	% b
−0.750 to −0.999	0	3	0	0	1	0	0	3	0	0	7	0
−1.000 −1.249	0	10	0	0	2	0	0	5	0	0	17	0
−1.250 −1.499	1	14	7	1	13	7	2	16	11	4	43	9
−1.500 −1.749	5	12	29	3	9	25	5	9	36	13	30	30
−1.750 −1.999	7	6	54	5	2	71	6	3	67	18	11	62
−2.000 −2.249	11	5	69	5	2	71	4	1	80	20	8	71
−2.250 −2.499	12	3	80	2	0	100	3	0	100	17	3	85
−2.500 −2.749	4	0	100							4	0	100

---

[1] Four of the 13 plots were omitted because of insufficient data for this type of analysis.

in 13 plots in which the average height (Hd) of the tallest 10 per cent of the trees ranged from 47 to 115 feet. Plots were located subjectively in dense stands to ensure an adequate sample of all crown classes.

The analysis of the data is presented in Table 1. The height to the widest part of the crown (H2CW) of dominant trees (of total height Hd) exposed to heavy competition is estimated by calculating the average H2CW of the 10 per cent of the trees in the plot with the highest crowns. Heights (HT) of individual trees are divided into two groups:

(1) HT $\leqq$ mean H2CW (overtopped trees)

(2) HT $>$ mean H2CW

and then separated into classes of ln(CW/CWMAX). In other words, a tree is assumed to be overtopped when its total height (HT) is equal to or less than the height, above ground, of the widest parts of the crowns of dominant trees in the same even-aged stand. Column two of Table 1 shows that the average height to the point of maximum crown spread is 31 feet in dense stands. Of the 93 trees in the three quite similar plots, only three have values of ln(CW/CWMAX) between −0.750 and −0.999. All heights exceed 31 feet. However, in the range −1.500 to −1.749, for example, the heights of 12 trees are greater than 31 feet. The remaining five trees, constituting 29 per cent, are overtopped. The likelihood of suppression, expressed in per cent, is summarized for all plots in the last column of Table 1 and illustrated by a free hand curve in Figure 9. The results show that the heights of approximately 50 per cent of the trees, with values of ln(CW/CWMAX) less than or equal to −1.75, are entirely below the crowns of dominant trees. Consequently, suppression or overtopping is assumed to take place when the value of ln(CW/CWMAX) is less than or equal to −1.75.

The effect of competition can be incorporated into estimates of tree height by relating CW/CWMAX to a function which combines tree height (HT) and the height (Hd) of dominants, where Hd is equal to the average height of the tallest 10 per cent of trees in the plot. The relationship between relative height (HT/Hd) and crown width (CW/CWMAX) is sigmoid in form and can be transformed into a straight line by applying a log logistic transformation (Bliss, 1967). Specifically, the natural logarithm of HT/(1.1 Hd − HT) is related to the natural logarithm of CW/CWMAX, where 1.1 Hd is the maximum height a tree can attain. This height can be estimated by increasing the average height (Hd) of dominant trees by 10 per cent, as explained earlier. The one tree out of 304 that exceeded the maximum height was omitted in the derivation of the following equations.

$$\begin{array}{lcc} & n & r^2 \text{ x } 100 \\ \ln(HT/(1.1Hd - HT)) = 3.107 + 1.390 \ln(CW/CWMAX): & 303 & 54.5\% \end{array} \tag{14}$$

where

ln = natural logarithm
HT = height of a particular tree (feet)
Hd = height of a dominant tree of the same age (feet)
CW = crown width of the tree in question (feet)
CWMAX = maximum crown width in feet of a free-growing tree of height Hd

Equation 14 can be solved algebraically for HT to estimate total height from the width of the crown:

$$HT = (1.1Hd)/(1.0 + 0.0447\,(CW/CWMAX)^{-1.39}) \tag{15}$$

Estimation of Bole Parameters

Estimation of the future size of tree crowns is of limited practical value unless bole dimensions can be estimated from the width or area of the crown.

Diameter at breast height

Equation 1 is inadequate for estimating bole diameter in a model of stand growth because the relationship does not apply to intermediate and suppressed trees. Moreover, age is an unsuitable variable because it has no causal effect on biological processes and frequently must be used in conjunction with an estimate of site quality. The introduction of height to replace age as a variable is expedient. The correlation between the width of the crown (CW) and diameter (D) of the bole of dominant Messmate (*Eucalyptus obliqua* (L.) Herit), for example, was improved by the inclusion of the mean height of dominant trees as a third variable (Curtin, 1964).

The form of an equation for estimating the diameter of the bole (D) in inches is based on four assumptions:

(1) bole diameter at breast height (outside bark) is a function of average crown width (CW) in feet and total tree height (HT) in feet, each raised to an unknown exponent,
(2) CW and HT are interdependent variables,
(3) $D = 0$ if $CW = 0$,
(4) $D = 0$ if $HT \leqq 4.5$.

The following relationship is applicable to all crown classes because the basic data used in its derivation include 131 intermediate and suppressed trees and 51 open-grown trees, in addition to the 400 trees used in the derivation of Equation 1. The revised equation,

$$\begin{array}{lrr} & n & r^2 \text{ x } 100 \\ \ln D = -1.739 + 0.660 \ln CW + 0.585 \ln (HT - 4.5): & 582 & 93.0\% \end{array} \quad (16)$$

or

$$D = 0.1757\, CW^{0.66} (HT - 4.5)^{0.585}, \quad (17)$$

is a considerable improvement over Equation 1 because the coefficient of determination (r^2) is increased by 5 per cent and an index of site quality is no longer required.

Volume

The volume of the bole can be estimated directly from the area of the crown and height of the tree based on considerations similar to those underlying Equations 16 and 17.

Eighty-eight trees, representative of a range of heights (17 to 112 feet) and live crown ratios (27 to 93%), were measured for total height, crown area and diameter of the bole at various heights. The area of the crown was determined by mapping the vertical projection of the crown. Each tree was climbed to obtain four or five measurements of diameter and bark thickness of the upper bole. Breast height and upper bole diameters were plotted on Reineke tree volume graphs to determine the inside bark volume of each tree.

The equation derived to estimate the volume of the bole (V) from measurements of crown area (CA) and height (HT) is

$$\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad n \quad r^2 \times 100$$

$$\ln V = -9.673 + 0.591 \ln CA + 2.300 \ln HT{:}\ 88 \quad 92.3\% \qquad (18)$$

$$V = 0.0000629\,(CA)^{0.59}\,HT^{2.3} \qquad (19)$$

Review

The results summarized below form the basis of the mathematical model developed in the next section

(1) The cumulative height growth (H) of trees in all crown classes describes the radial growth (CR) of the crown within the growing space limitations imposed by competing trees.

$$CR = 0.738\,H^{3/4}\,(1 - 0.00100\,H)\,(1 - |0.170 - 0.0100\,H^{3/4}|) \qquad (9)$$

(2) The height (HT) of a tree is a function of the height (Hd) of dominant trees and the width of its crown (CW) relative to the maximum crown width (CWMAX) it could have attained had it grown without competition from surrounding trees.

$$HT = (1.1\,Hd)/(1.0 + 0.0447(CW/CWMAX)^{-1.39}) \qquad (15)$$

(3) There is a 50 per cent possibility that a tree will be overtopped if its value of $\ln(CW/CWMAX)$ is less than or equal to -1.75.

(4) Tree height (HT) and the width (CW) or area (CA) of the crown provide accurate estimates of diameter (D) and volume (V) of the bole.

$$D = 0.1757\,CW^{0.66}\,(HT - 4.5)^{0.583} \qquad (17)$$

$$V = 0.0000629\,(CA)^{0.59}\,HT^{2.3} \qquad (19)$$

THE MODEL

A COMPUTER model, developed by Newnham (1964) was designed to simulate the growth of individual trees in stands of Douglas fir. His model estimated mean diameter growth, basal area growth and number of trees per acre, at intervals of five years from age 10 to 100 years. Trees were assumed to be spaced in a square pattern and free of competition until age 10. Diameter increment of each tree from age 10 to 15 years was based on the growth of open-grown trees but was reduced in relation to the proportion of the circumference of the crown that was occupied or overlapped by the crowns of surrounding competitors. The diameter of the crown was derived from the relationship between the width of the crown and the bole diameter at breast height of open-grown trees. Trees were assumed to die if the reduction in diameter increment was sufficiently great. The procedure was repeated for all trees before considering the succeeding intervals of growth.

The model presented in the current study differs from Newnham's model in that it simulates the actual mechanism of competition. The crown of each tree expands and competes with the crowns of neighboring trees for growing space in a simulated forest and thus takes on an irregular shape to utilize unoccupied space. Those trees that cannot find adequate space eventually die. Furthermore, the size of the bole of each tree is estimated from parameters of the crown, and the assumption of square spacing is not required.

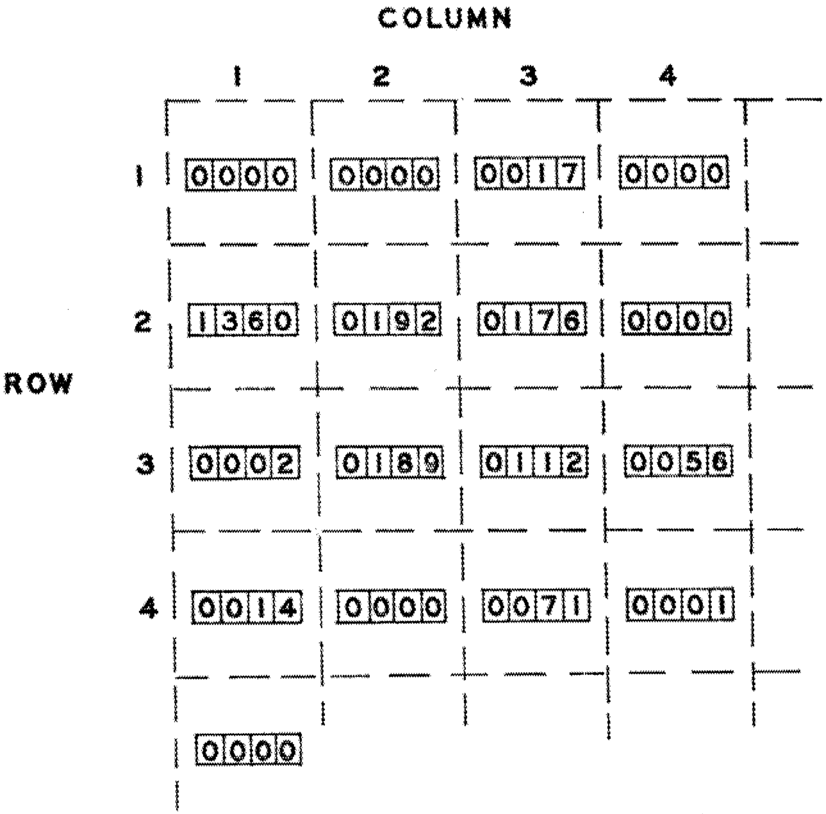
COMPUTER SIMULATION

The storage unit of a computer may be visualized as a two-dimensional matrix of registers, each of which can retain a 10-digit number although only four digits are shown in Figure 10. The matrix can contain thousands of registers, if necessary. Numbers may be entered into the matrix or recalled by specifying the register's location or address, which is given by the number of the row and column. The contents of the location containing the number 189 in Figure 10, for example, can be expressed as

$$\text{Location } (3,2) = 189.$$

The programming language employed is FORTRAN IV. The matrix is regarded as an area of land divided into units of one square foot.

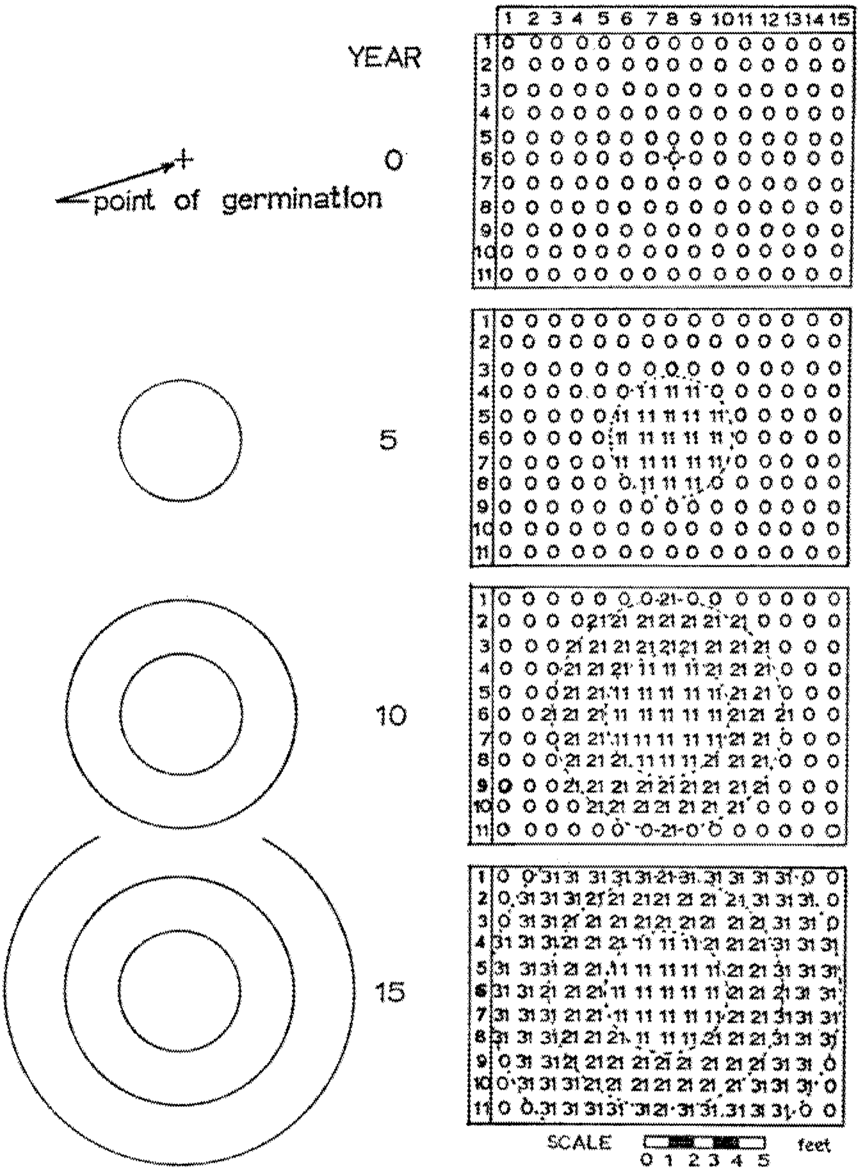
The hypothetical growth of the crown of a single tree, viewed from above, is outlined in Figure 11a. The time interval chosen in this example is five years, during which time the radius of the crown increases 2.5 feet. Figure 11b illustrates



	1	2	3	4
1	0000	0000	0017	0000
2	1360	0192	0176	0000
3	0002	0189	0112	0056
4	0014	0000	0071	0001
	0000			

FIGURE 10. Storage locations in the form of a two-dimensional matrix.

the method which uses the storage locations of the computer to simulate the growth of the crown. Initially, all locations or registers in the matrix are set equal to zero (year 0). Germination occurs at location (6,8), which is the origin of the tree. Growth of the crown during the first five years is sufficient to occupy all locations into which the number 11 has been entered. The digit in the units position denotes the number of the tree while the number in the "tens" position indicates the time interval during which the location was occupied. The growth from age 0 to 15 years of only one tree is shown in Figure 11. The shapes of crowns may become very irregular when trees grow in close proximity because locations containing numbers greater than zero have been claimed and cannot be occupied by any other tree.



	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	11	11	11	0	0	0	0	0	0
5	0	0	0	0	0	11	11	11	11	11	0	0	0	0	0
6	0	0	0	0	0	11	11	11	11	11	0	0	0	0	0
7	0	0	0	0	0	11	11	11	11	11	0	0	0	0	0
8	0	0	0	0	0	0	11	11	11	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

1	0	0	0	0	0	0	0	21	0	0	0	0	0	0	0
2	0	0	0	0	21	21	21	21	21	21	21	0	0	0	0
3	0	0	0	21	21	21	21	21	21	21	21	21	0	0	0
4	0	0	0	21	21	21	11	11	11	21	21	21	0	0	0
5	0	0	0	21	21	11	11	11	11	11	21	21	0	0	0
6	0	0	21	21	21	11	11	11	11	11	21	21	21	0	0
7	0	0	0	21	21	11	11	11	11	11	21	21	0	0	0
8	0	0	0	21	21	21	11	11	11	21	21	21	0	0	0
9	0	0	0	21	21	21	21	21	21	21	21	21	0	0	0
10	0	0	0	0	21	21	21	21	21	21	21	0	0	0	0
11	0	0	0	0	0	0	0	21	0	0	0	0	0	0	0

1	0	0	31	31	31	31	31	21	31	31	31	31	31	0	0
2	0	31	31	31	21	21	21	21	21	21	21	31	31	31	0
3	0	31	31	21	21	21	21	21	21	21	21	21	31	31	0
4	31	31	31	21	21	21	11	11	11	21	21	21	31	31	31
5	31	31	31	21	21	11	11	11	11	11	21	21	31	31	31
6	31	31	21	21	21	11	11	11	11	11	21	21	21	31	31
7	31	31	31	21	21	11	11	11	11	11	21	21	31	31	31
8	31	31	31	21	21	21	11	11	11	21	21	21	31	31	31
9	0	31	31	21	21	21	21	21	21	21	21	21	31	31	0
10	0	31	31	31	21	21	21	21	21	21	21	31	31	31	0
11	0	0	31	31	31	31	31	21	31	31	31	31	31	0	0

Figure 11. Hypothetical and simulated growth of the crown of one tree.

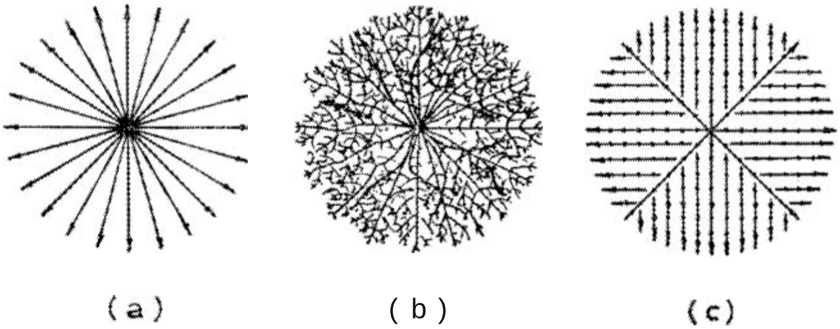


FIGURE 12. Pattern of branching.

The system whereby the crown is incremented represents a compromise between the actual growth pattern of tree crowns and the limitations imposed by a square matrix. The growth pattern of the crown is basically radial about the bole if viewed from above (Figure 12a). Figure 12b is a more realistic representation of the actual pattern of branching. This is simulated in the model by the network shown in Figure 12c. This system can be readily fitted to a square matrix.

The program that instructs the computer to perform the simulation is too complex to describe in detail. The highly simplified flow-chart in Figure 13 depicts the steps and decisions included in the program. Instructions are given to increment the radius of the crown, test for and occupy available growing space and remove overtopped and dead trees from the main canopy.

Growing space, made available by the suppression, death or removal of a tree, is reoccupied by neighboring trees according to the scheme in Figure 14. All locations occupied by tree 2 (Figure 14a) are set equal to 10,000,000 (shown as —1 in Figure 14b) when the tree is suppressed or dead. The locations containing the number 31 in Figure 14c are occupied during the next interval of growth. Note that the indentation left in the crown of tree 1 is not completely filled. The procedure that accomplishes the asymmetrical increment can be understood by tracing the steps required to occupy location (7,10), abbreviated L(7,10), in Figure 14b. Locations L(7,8) and L(7,9) are occupied so that control passes to L(7,10). The number —1 signals the computer to calculate the amount of crown growth lost because of the presence of tree 2. This radial distance is equal to a — b = c (Figure 14d). Therefore, the maximum distance that the crown can grow during this particular interval of growth is CR — c = I). Location (7,10) and subsequent locations in row 7 of Figure 14' are occupied by tree 1 only if their distance from

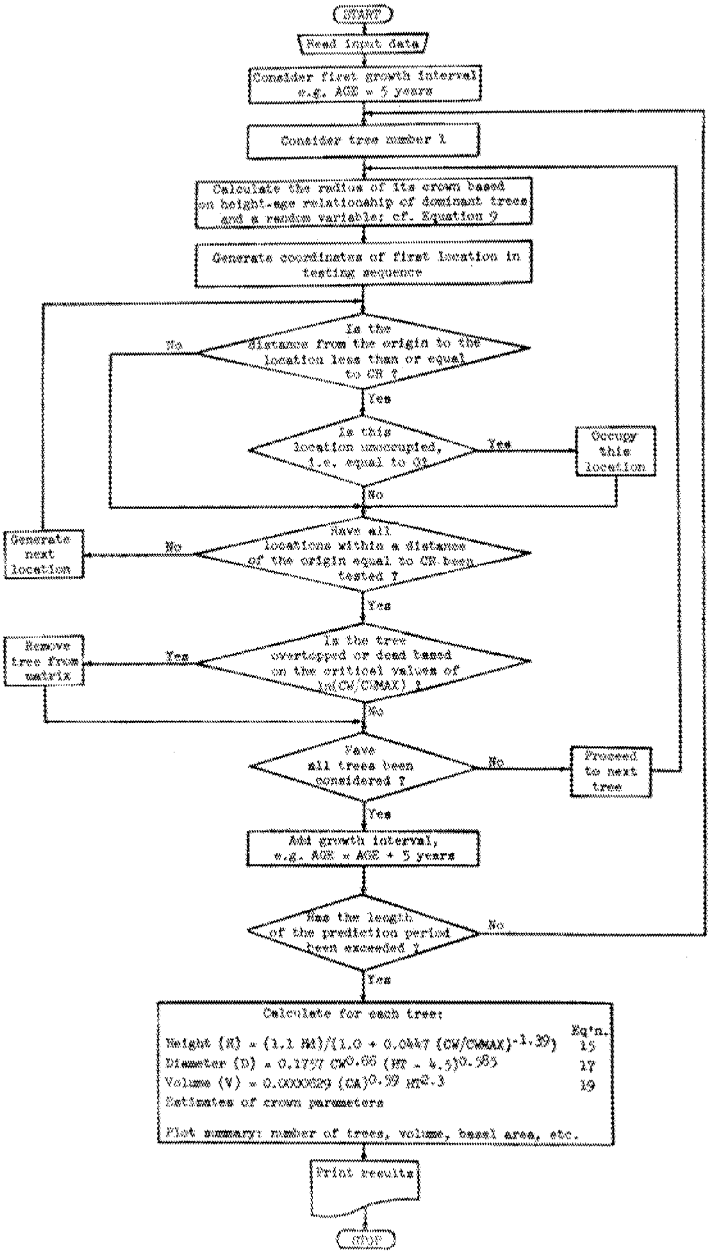
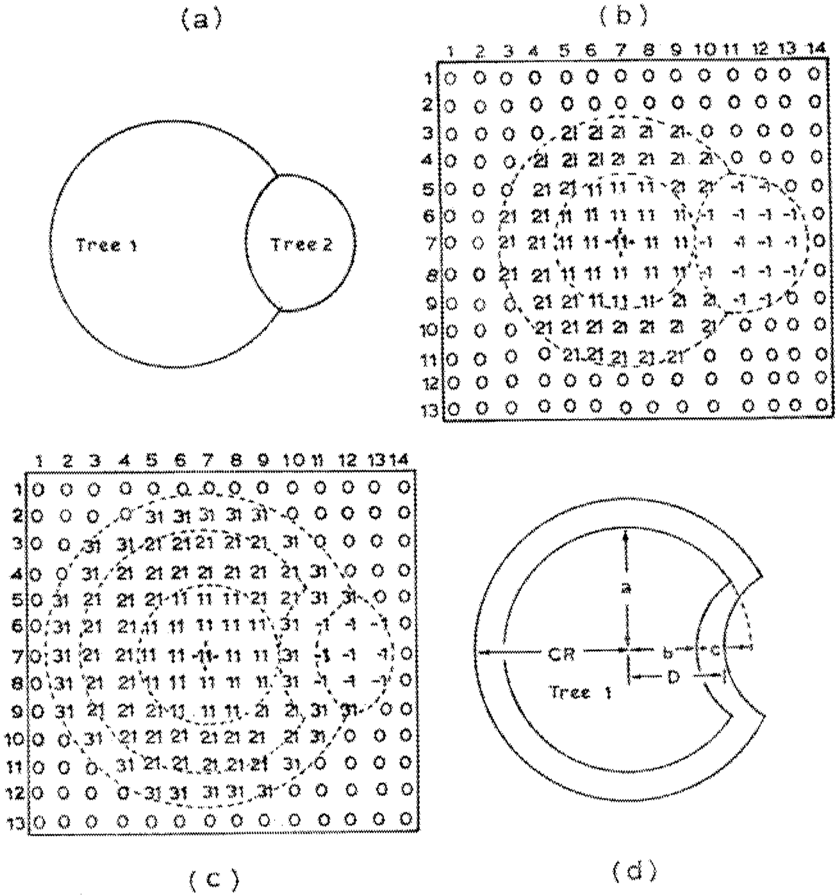


FIGURE 13. Simplified flow-chart of the model.



	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	21	21	21	21	21	0	0	0	0	0
4	0	0	0	21	21	21	21	21	21	21	0	0	0	0
5	0	0	0	21	21	11	11	11	21	21	-1	-1	0	0
6	0	0	21	21	11	11	11	11	11	-1	-1	-1	-1	0
7	0	0	21	21	11	11	11	11	11	-1	-1	-1	-1	0
8	0	0	21	21	11	11	11	11	11	-1	-1	-1	-1	0
9	0	0	0	21	21	11	11	11	21	21	-1	-1	0	0
10	0	0	0	21	21	21	21	21	21	21	0	0	0	0
11	0	0	0	0	21	21	21	21	21	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	31	31	31	31	31	0	0	0	0	0
3	0	0	31	31	21	21	21	21	21	31	0	0	0	0
4	0	0	31	21	21	21	21	21	21	21	31	0	0	0
5	0	31	21	21	21	11	11	11	21	21	31	31	0	0
6	0	31	21	21	11	11	11	11	11	31	-1	-1	-1	0
7	0	31	21	21	11	11	11	11	11	31	-1	-1	-1	0
8	0	31	21	21	11	11	11	11	11	31	-1	-1	-1	0
9	0	31	21	21	21	11	11	11	21	21	31	31	0	0
10	0	0	31	21	21	21	21	21	21	21	31	0	0	0
11	0	0	0	31	21	21	21	21	21	31	0	0	0	0
12	0	0	0	0	31	31	31	31	31	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0

FIGURE 14. Reoccupation of vacated growing space.

the origin (L(7,7)) is less than or equal to D. The distance c is retained because it is needed each time the area of the crown is incremented. The same principle of reoccupation applies along each vector shown in Figure 12c although the method of calculating and storing c increases in complexity.

Extra instructions are included in the program to allow the crown of one tree to grow a short distance through the crown of a second tree into an opening in the stand.

Feedback from crown area to height growth that could partially dictate the subsequent crown expansion has not been built into the model. This refinement would be necessary if many intermediate or suppressed trees were released by a selection cut of dominant trees.

Some trees invariably grow beyond the boundaries of the plot during the simulation. No data were recorded on the competition from trees outside the plot because this problem can be overcome by assuming that trees which grow out of the plot on one side grow into the opposite side. This method gives good results, especially in homogeneous stands. Measurement of trees around the periphery of the plot is more exact but very wasteful of data.

In nature the rate of growth of the crown is obviously not the same for every tree in the stand because of genetic variation and other factors. These sources of variation in the growth are simulated by Monte Carlo methods and a random number generator which allow the regression coefficient (b) in Equation 2 to vary in accordance with a normal distribution having a mean of 0.738 (Equations 4 and 9) and a standard deviation of 0.125.

Suppressed trees ($\ln(CW/CWMAX) \leqq 1.75$) are assumed to live under the main canopy of the stand. All locations, with the exception of the origin, that are occupied by a suppressed tree are set equal to 10,000,000 thus allowing the tree to be overtopped by competitors. The location at the origin of each suppressed tree retains a number representing the area of the crown. This area does not change and is kept available because estimates based on the area of the crowns of suppressed trees are required for the plot summary. The location at the origin is not set equal to 10,000,000 until the tree dies.

Special steps must be incorporated into the model to remove trees for any reason other than death. Thinnings, for example, are readily simulated if the criterion for cutting can be defined mathematically.

The preceding method of simulating growth is applicable to even-aged stands of species that are sufficiently intolerant of shade to preclude the possibility of trees thriving under the main canopy. Interlocking of tree crowns, common in young stands, is not a serious limitation. The model assumes that the area shared by crowns is divided between the trees. The greater wind movement of trees as they increase in height and crown size results in the loss of new growth of shoots in the zone of crown contact and thereby prevents appreciable interlocking of crowns.

The following example illustrates the use of the model to simulate the growth of an even-aged plantation of white spruce. These plot data must be supplied with the model before the simulation can proceed:

Specifications:	
plot dimensions (feet)	40 x 32
length of simulation (years)	45
number of trees	45
site index (height at age 30)	33.9
Age sequence in simulation (years)	8, 10, 15, 20, 25, 30, 37, 42, 45
Plot summaries (years)	10, 15, 20, 25, 30, 37, 42, 45
Map summaries (years)	10, 15, 20, 25, 30, 37, 42, 45
Location of every tree (feet)	(2,4), (2,10) . . . , (2,27) (7,2), (7,7) . . . , (7, 29) etc.

The age sequence is chosen so that the growth of the crown during the first interval is greater than one foot, otherwise no locations will be occupied, thus wasting at least one pass. The interval during the remainder of the simulation can be of any length and may be varied. An interval of 5 years, for example, is suitable for simulating growth over a period of 50 years.

Plot summaries can be requested at the end of any interval. Individual tree data and means of the following variables are printed: crown area, crown width, crown length, diameter of the bole at breast height, basal area, height, volume and degree of suppression (ln(CW/CWMAX)). Basal area and total volume per acre are also given. Diameter of the bole, height, and volume of individual trees are tallied by classes to show distribution of values. Even though individual tree data may be requested, it should be remembered that the model is not meant to describe the growth of any particular tree but rather the growth and development of the plot as a whole.

A coded map showing the growing space occupied by each tree and the age at which any particular location was occupied will be printed on request. An incomplete sequence of coded crown maps corresponding to the preceding specifications is illustrated in Figures 15 to 18 to show the development of a typical stand. The crowns of individual trees have been outlined schematically to emphasize the code, which in this case includes only the number of the tree. Variation in the rate of crown growth is very obvious at age 10 (Figure 15). The canopy closes within the next 10 years (Figure 16). Suppression and mortality are evident by age 30 (Figure 17) and increase rapidly until age 45 (Figure 18).

Testing of the Model

Building models and simulating "ad absurdum" can lead to very erroneous conclusions if tests of validity are not applied at various stages in the development of a model. The model under construction in the current study is now ready for

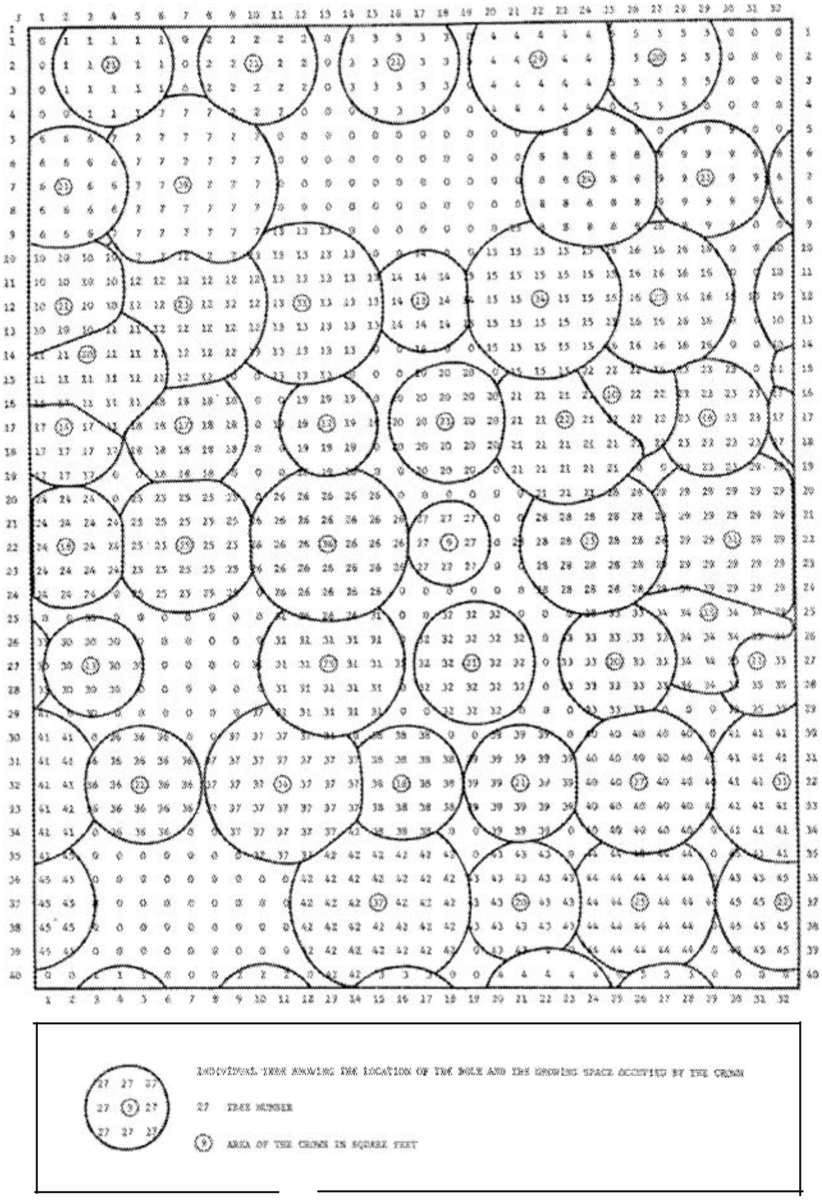


FIGURE 15. Crown map of simulated stand at age 10.

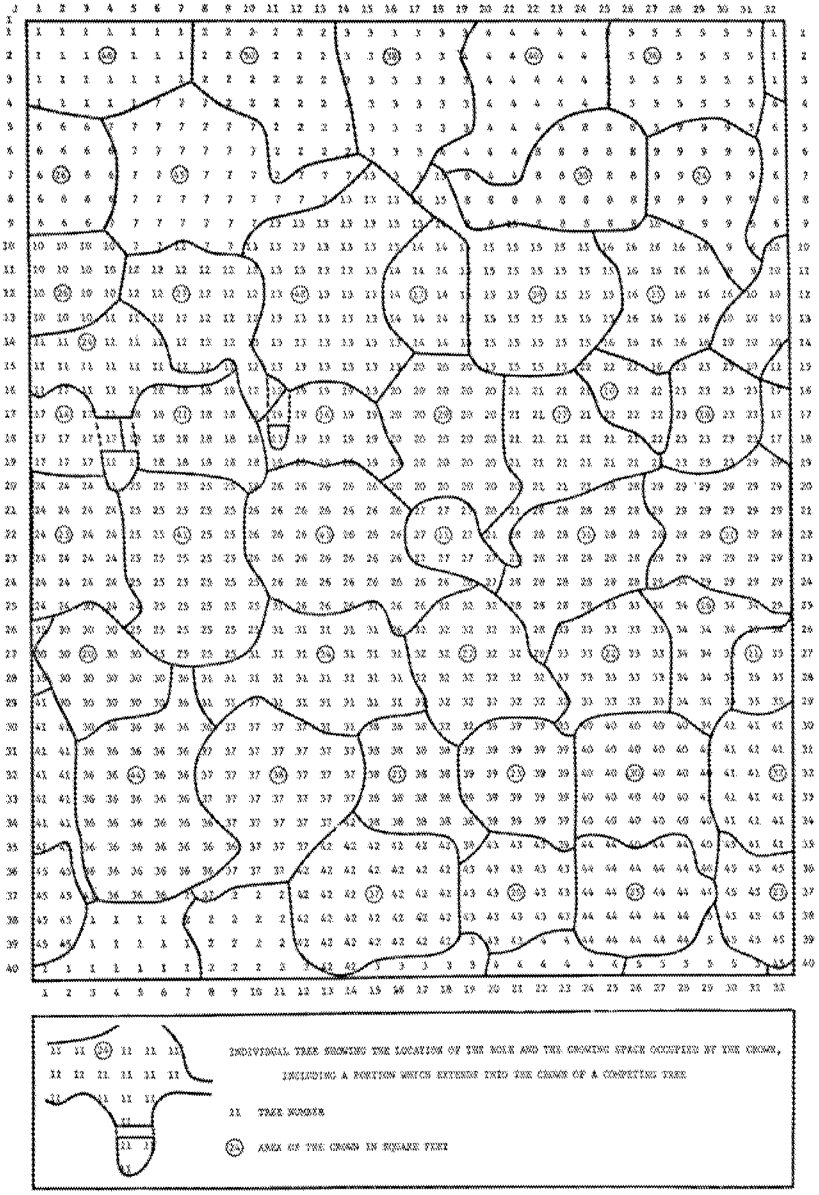


FIGURE 16. Crown map of simulated stand at age 20.

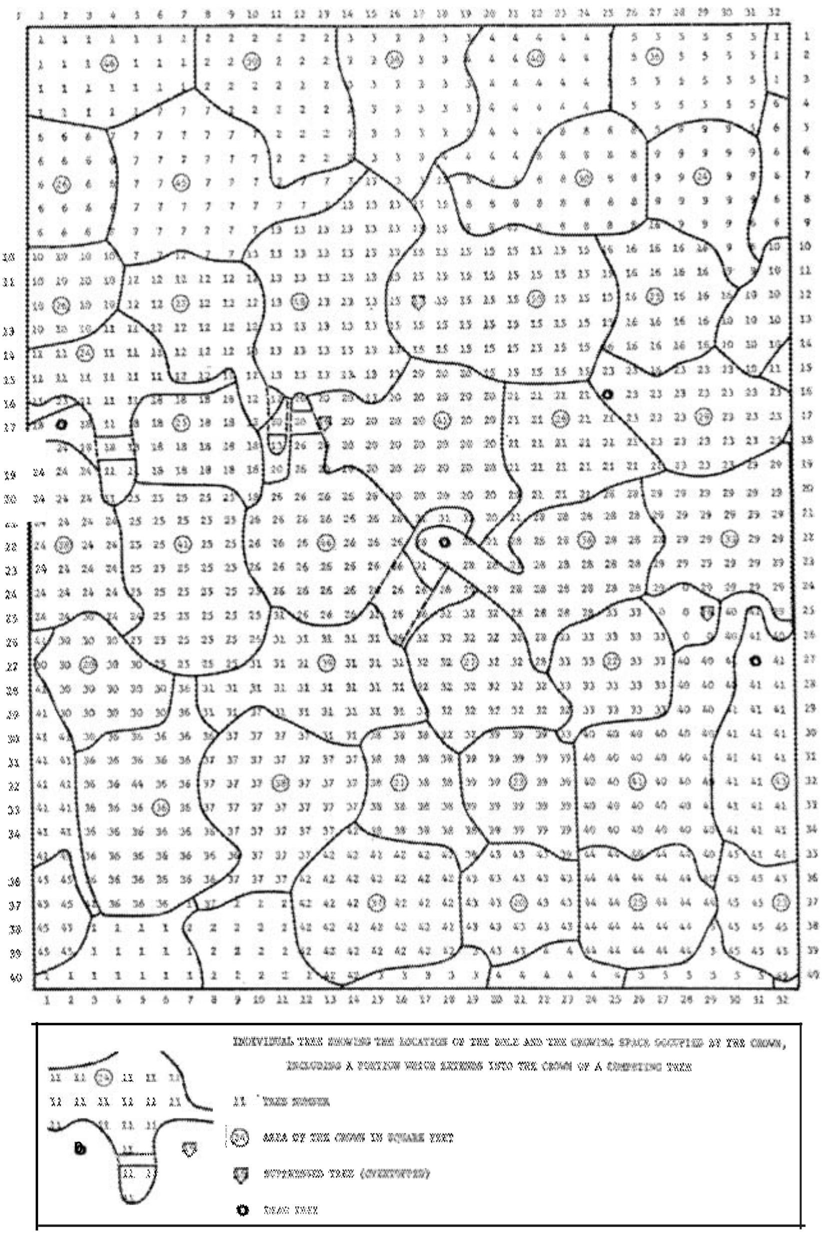


FIGURE 17. Crown map of simulated stand at age 30.

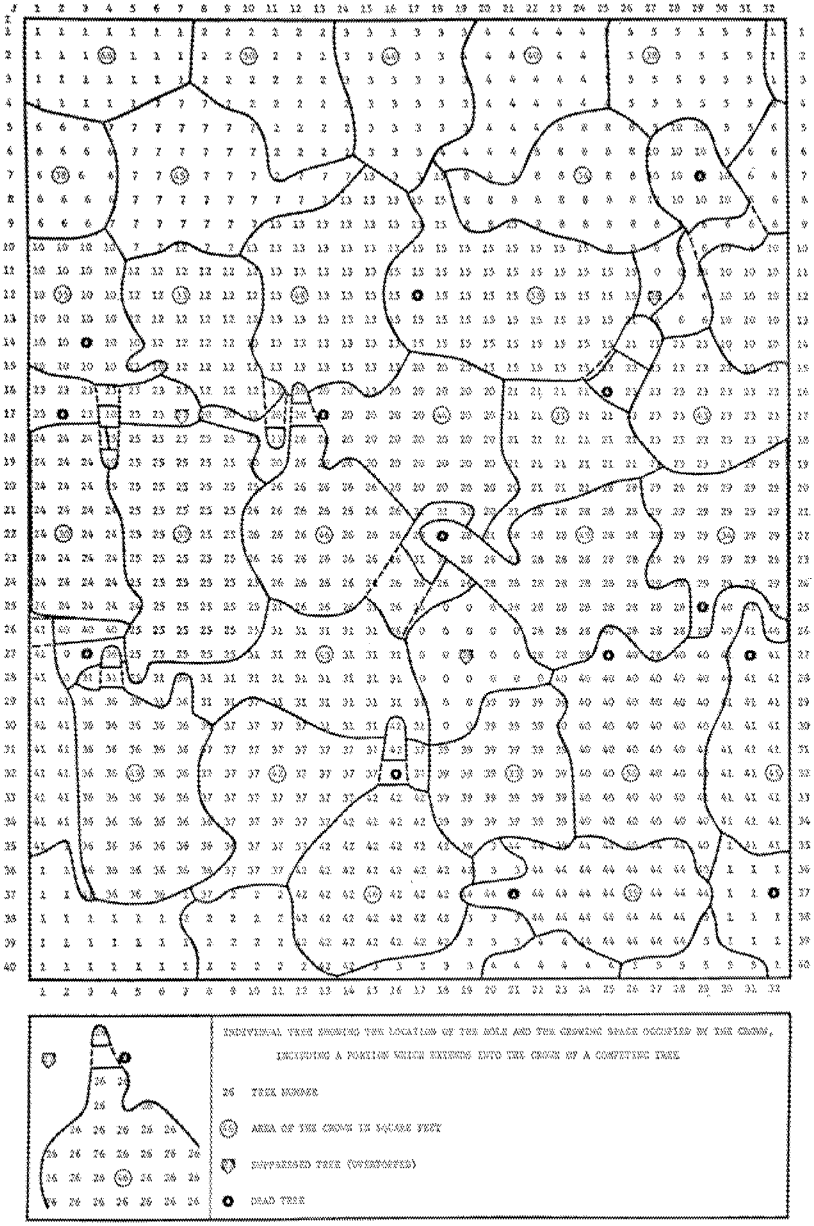


FIGURE 18. Crown map of simulated stand at age 45.

testing against experience before proceeding further. Extension or refinement at this time could be superfluous if tests expose the need for major revisions. However, the tests need not be exhaustive until the model is fully developed and ready for application.

The model is best tested against permanent sample plot data. This, however, introduces certain limitations with respect to age and growth habits because the oldest white spruce plantations with permanent sample plots are only 45 years of age and they are on the Petawawa Forest Experiment Station near Chalk River, Ontario, which is 2,000 miles from the study area. A description of the plots is presented in Table 2. Testing of the model is limited to a subplot within each permanent sample plot to reduce the data requirements and simulation costs.

Plots 324, 325 and 326 are suitable test plots because the height and the planting

TABLE 2. DESCRIPTION OF PLOTS

Number of PSP	310	324[1]	325[2]	326
Year of establishment	1951	1951	1951	1951
Year of planting	May 1926	May 1924	May 1926	May 1925
Planting stock	—	2–0	2–2	3–0
Spacing (feet)	5 x 4.5	5 x 5	5 x 5	5 x 5
Site index (feet)[3]	33.2	31.4	29.5	33.9
Subplot data				
Dimensions (feet)	32 x 32	40 x 30	30 x 30	40 x 32
Measurement dates[4] and age of plantation		1929 (8)	1929 (8)	1929 (8)
	1951 (30)	1951 (30)	1951 (30)	1951 (30)
	1956 (35)	1956 (35)	1956 (35)	1956 (35)
		1958 (37)	1958 (37)	1958 (37)
	1961 (40)	1961 (40)		
			1963 (42)	1963 (42)
	1966 (45)	1966 (45)	1966 (45)	1966 (45)

---

[1] Plots 324, 325 and 326 are in plantations which were established to test three types of planting stock.

[2] Subplots 325 and 326 were thinned from below to 167 and 143 square feet of basal area per acre respectively in November 1958.

[3] Site index is based on the average height of the tallest 10 per cent of the trees in the plot at age 30 (Stiell, 1957).

[4] Tree records:

1929	height (HT)
1951	HT, bole diameter (D), length of live crown, crown class (CC)
1956–61	D, heights of six trees in each one-inch diameter class
1963	D
1966	HT, D, CC, crown width, length of the crown above the point of maximum crown width.

location of every tree are available from measurements of survival in 1929. Such data are not available for other plots. Plot 310 is also included because inspection of living and dead trees indicated that survival was very high between the time of planting and crown closure.

The height-age relationship of white spruce in the permanent sample plots at the Petawawa Forest Experiment Station was developed by Stiell (1955).

Use of permanent sample plot records from southern Ontario (latitude 46°N., longitude 77°W.) to test a model based on data collected in central British Columbia (latitude 54°N., longitude 123°W.) is extremely rigorous. It presupposes that tree growth and growing conditions are similar in both places. This assumption has to be verified, or adjustments must be made in the model to compensate for differences.

Analyses of nine branches from four trees on the Petawawa Forest Experiment Station indicate that branch growth, relative to height growth, is greater there than at Prince George. Two branches came from the plantation that contained subplots 324, 325 and 326. Others were from mature stands about 5 miles away. The regression coefficient of Equation 4 must be modified to allow for the difference in the relationship between height growth and branch extension:

$$BL = 0.738\ H^{3/4} \qquad \text{(Prince George)} \qquad (4)$$

is changed to

$$BL = 0.886\ H^{3/4} \qquad \text{(Petawawa)} \qquad (20)$$

Equations 11 and 12 were modified accordingly.

Unfortunately, circumstances made it necessary to rely on data from subplots 310, 324, 325 and 326 to adapt the model to conditions at Petawawa. The information was used to derive values discussed below, which incorporate differences between Prince George and Petawawa into the model and establish a criterion of death. The resulting modifications in the model are minor, and are not expected to jeopardize the validity of the test.

The standard deviation of the regression coefficient in Equation 20 was estimated to be 0.160 from the variation in the relationship of the radius and length of the crown. Both measurements were taken at the point of maximum crown spread.

Investigation of the crown width–bole diameter relationship revealed a difference between white spruce at Prince George and Petawawa. Trees in the latter area produce 25 per cent more diameter growth at breast height per unit of crown width. Hence, estimates of diameter and volume of individual trees, from Equations 17 and 19, must be increased by factors of 1.25 and $(1.25)^2$, respectively.

Trees die in the simulation when the value of $\ln(CW/CWMAX)$ falls below

—1.85. Insufficient information on crown size in relation to tree death made it necessary to establish this criterion through an iterative procedure. The value of ln(CW/CWMAX) at which trees die was varied until the total number of simulated trees living in all plots in 1951 agreed with the actual number of living trees. Fortunately, the critical value of ln(CW/CWMAX) has only a minor effect on the results of the simulation because the few suppressed trees which remain alive do not contribute appreciably to the parameters of the stand.

Plots 325 and 326 were subjectively thinned from below in 1958. These thinnings were simulated by removing trees with the smallest diameters until the remaining basal area agreed with the actual basal area in the subplot after thinning.

The results of the simulation are compared in Tables 3 to 6 with permanent sample plot data for subplots 310, 324, 325 and 326. Values derived from field measurements of the subplots are in italics. An other figures were simulated by the model. The figures in parentheses show the growth trend which would be expected had the stands not been thinned. The variables tested are discussed below:

Number of trees The actual and the simulated number of trees per subplot never differ by more than three trees except after thinnings. The low estimate of basal area in subplot 325 before thinning (194 vs. *217*ft^2/acre) meant that comparatively few trees (290 vs. *726* trees/acre) had to be eliminated to achieve the same basal area as on the actual subplot.

Crown width Measurements of crown width are not included in permanent sample plots records. Consequently, they could only be obtained for 1966 as part of this study. The simulated and actual values agree within 3 per cent in subplots 325 and 326, but the difference is greater in the unthinned plots. The discrepancy probably lies in the field measurements as there is a tendency to underestimate the width of crowns in dense stands.

Crown length Estimates of crown length are consistently low, suggesting that Equation 10 for calculating the length of the crown should be revised.

Bole diameter Little difference is apparent between the actual and the simulated average of bole diameter although the model does not show the slight decline in the rate of growth after age 35 evident in the field data. Note that diameter growth continues between ages 15 and 20 years following crown closure even though the average size of crowns cannot change until suppression begins (Tables 4 to 6). This demonstrates the influence on diameter increment of additions to crown surface through height growth.

Height The height of every tree in the subplots had not been determined since 1951, until necessitated by this study in 1966. The estimated average heights are

TABLE 3. ACTUAL AND SIMULATED CHARACTERISTICS OF SUBPLOT 310

Subplot								
Age (years)	10	15	20	25	30	35	40	45
Year	1931	1936	1941	1946	1951	1956	1961	1966
Number of trees	46[1]				41	36	33	30
	46[2]				*38*	*33*	*33*	*28*
Per tree (averages)	no summary requested (1931–1946)							
Crown width (feet)					5.8	6.1	6.6	6.9
								5.9
length (feet)					6.8	7.4	8.2	8.9
								9.7
Bole diameter (inches)					4.2	4.9	5.7	6.5
					4.4	*5.2*	*5.6*	*6.1*
basal area (square feet)					0.10	0.13	0.18	0.24
					0.12	*0.16*	*0.18*	*0.22*
height (feet)					25.9	30.8	36.0	41.3
					25.2			*45.4*
volume (cubic feet)					1.2	2.0	3.1	4.5
					1.5	*2.6*	*3.6*	*5.0*
Per acre								
Number of trees					1744	1531	1404	1276
					1616	*1404*	*1404*	*1191*
Basal area (square feet)					174	191	251	306
					187	*219*	*258*	*266*
Volume (cubic feet)					2134	2991	4340	5736
					2499	*3626*	*5122*	*5945*

[1] Simulated values.

[2] Actual figures in italics.

generally high at age 30 and low at age 45, implying that Equation 15 is inadequate or that the height-age relationship used in the model does not accurately describe height growth in the subplots.

Basal area The simulated *rate* of basal area growth per acre is consistently greater than the actual rate (Figure 19). One possible explanation lies in the "blanket" correction of 25 per cent in the diameter of the bole to allow for differences between Prince George and Petawawa. The adjustment was derived from 1966 data only and may have to be varied in relation to age or height of each tree. It would, however, be better to revise Equation 17 with data from southeastern Ontario. Note that the rate of growth in subplots 325 and 326 did not respond to the thinnings as expected in the simulation. Further information is needed to assess the effects of thinning.

Volume Actual and simulated volume per acre figures are in reasonable agreement (Figure 19) although the preceding comments about basal area are applicable.

TABLE 4. ACTUAL AND SIMULATED CHARACTERISTICS OF SUBPLOT 324

Subplot								
Age	10	15	20	25	30	35	40	45
Year	1931	1936	1941	1946	1951	1956	1961	1966
Number of trees	49[1]	49	49	48	43	40	38	36
	49[2]				*44*	*41*	*38*	*34*
Per tree (averages)								
Crown width	4.9	5.5	5.5	5.6	6.0	6.2	6.4	6.7
								5.1
length	5.5	6.4	6.4	6.7	7.2	7.6	8.0	8.5
								9.8
Bole diameter	0.6	2.1	2.8	3.5	4.2	4.8	5.5	6.1
					4.1	*4.6*	*5.2*	*5.6*
basal area	0.00	0.02	0.04	0.07	0.10	0.13	0.16	0.21
					0.10	*0.13*	*0.16*	*0.17*
height	5.4	11.2	16.1	20.4	25.1	29.6	34.3	39.0
					22.3			*37.0*
volume	0.0	0.1	0.3	0.7	1.2	1.8	2.7	3.8
					1.3	*2.0*	*3.3*	*3.5*
Per acre								
Number of trees	1788	1788	1788	1752	1570	1460	1387	1314
					1606	*1496*	*1387*	*1214*
Basal area	3	42	80	117	152	186	226	271
					167	*194*	*217*	*226*
Volume	48	302	698	1218	1866	2626	3681	4952
					2024	*3038*	*3688*	*4327*

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[1] Simulated values.

[2] Actual figures in italics.

The true and the simulated frequency distributions of bole diameters, representing subplots 310 and 324, are compared in Figure 20. The simulated diameters show less spread than the actual values. This means that the standard deviation of the regression coefficient in Equation 20 should be increased to introduce greater variation in the growth rates of the crown and bole. The pronounced shortage of simulated diameters in the lower diameter classes is partly due to the criterion of death, which always eliminates the smallest tree. A criterion of death incorporating a random variable may overcome this problem. Some severely suppressed trees would remain alive even though more vigorous trees had died, thus creating a flatter frequency distribution. It is not known whether such modifications would duplicate the bimodal nature of the actual distributions.

Further testing of the model is anticipated if permanent sample plot records can be obtained for older stands (60–100 years) covering a range of sites. Data from European stands may be available. There is also the possibility of using species

TABLE 5. ACTUAL AND SIMULATED CHARACTERISTICS OF SUBPLOT 325

Subplot										
Age	10	15	20	25	30	35	37	after	42	45
Year	1931	1936	1941	1946	1951	1956	1958	thinning	1963	1966
Number of trees	38[1]	38	38	37	34	30	30			(25)[2]
								24		24
	38[3]				*37*	*33*	*32*	*17*	*17*	*17*
Per tree (averages)										
Crown width	4.7	5.4	5.4	5.5	5.8	6.1	6.2			(6.8)
								6.5	not simulated	6.9
										6.7
length	5.3	6.3	6.3	6.4	7.0	7.6	7.7			(8.8)
								8.2		9.0
										12.8
Bole dbh[4]	0.4	1.9	2.7	3.3	4.0	4.6	4.9			(6.0)
								5.1		6.0
					3.8	*4.5*	*4.8*	*5.9*	*6.5*	*6.7*
basal area	0.00	0.02	0.04	0.06	0.09	0.12	0.13			(0.20)
								0.15		0.20
					0.09	*0.13*	*0.14*	0.20	*0.24*	*0.26*
height	5.0	10.6	15.3	19.4	23.7	28.0	29.1			(37.1)
								29.6		37.2
					21.8					*42.5*
volume	0.0	0.1	0.3	0.6	1.0	1.6	1.9			(3.5)
								2.0		3.5
					1.2	*2.0*	*2.3*	*3.5*	*4.6*	*5.2*
Per acre										
Number of trees	1839	1839	1839	1791	1646	1452	1452			(1210)
								1162		1162
					1791	*1597*	*1549*	*823*	*823*	*823*
Basal area	2	38	74	108	145	169	194			(242)
								169		237
					168	*202*	*217*	*167*	*199*	*214*
Volume	41	272	628	1089	1684	2314	2706			(4182)
								2362		4090
					2106	*3136*	*3596*	*2897*	*3756*	*4262*

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[1] Simulated values.

[2] Simulated values of unthinned subplot.

[3] Actual figures in italics.

[4] Diameter at breast height.

TABLE 6. ACTUAL AND SIMULATED CHARACTERISTICS OF SUBPLOT 326

Subplot										
Age	10	15	20	25	30	35	37	after	42	45
Year	1931	1936	1941	1946	1951	1956	1958	thinning	1963	1966
Number of trees	45[1]	45	45	42	41	38	36		(35)[2]	(31)
								20	20	20
	45[3]				*41*	*36*	*35*	*16*	*16*	*16*
Per tree (averages)										
Crown width	5.3	5.9	5.9	6.2	6.3	6.5	6.7		(7.0)	(7.3)
								7.4	8.2	8.4
										8.4
length	6.0	7.1	7.1	7.5	7.8	8.3	8.6		(9.2)	(9.7)
								9.7	11.8	12.1
										13.8
Bole dbh[4]	0.8	2.3	3.2	3.9	4.6	5.3	5.7		(6.3)	(6.9)
								6.2	7.4	7.8
					4.4	*5.2*	*5.4*	6.9	*7.5*	*7.7*
basal area	0.00	0.03	0.06	0.09	0.12	0.16	0.18		(0.22)	(0.26)
								0.21	0.30	0.33
					0.12	*0.16*	*0.17*	*0.26*	*0.31*	*0.34*
height	5.8	12.1	17.4	22.4	27.2	32.2	34.4		(39.5)	(43.0)
								35.8	42.0	45.3
					25.1					*49.1*
volume	0.0	0.2	0.5	1.0	1.5	2.4	2.8		(4.1)	(5.2)
								3.6	5.6	6.8
					1.6	*2.8*	*3.1*	*5.0*	*6.3*	*7.6*
Per acre										
Number of trees	1531	1531	1531	1429	1395	1293	1225		(1191)	(1055)
								681	681	681
					1395	*1225*	*1191*	*544*	*544*	*544*
Basal area	5	46	86	126	164	200	215		(264)	(275)
								141	201	228
					165	*197*	*207*	*143*	*170*	*184*
Volume	53	340	787	1361	2154	3056	3481		(4886)	(5476)
								2441	3839	4658
					2233	*3364*	*3674*	*2704*	*3425*	*4123*

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[1] Simulated values.

[2] Simulated values of unthinned subplot.

[3] Actual figures in italics.

[4] Diameter at breast height.

other than white spruce, provided that allowances can be made for differences in growth habits.

LIMITATIONS

At present, simulations must begin before the crowns close. However, the model can be easily modified to accept data obtained from crown maps or low-level aerial photographs taken before or after the closure of crowns.

Death caused by natural factors other than suppression cannot be simulated but may be incorporated into the model if the mortality can be resolved mathematically (Smith *et al.*, 1965).

Plots must be square or rectangular if trees along the edge of the plot are to compete with trees on the opposite border. Otherwise plots of any shape may be used, with minor changes in the computer program.

The model does not simulate the growth of all trees simultaneously during each interval of growth as in nature. Radial increment of the crown progresses tree by tree down one row and up the next until all trees have been updated. Thus each tree has a slight advantage over the following tree in the sequence. The advantage tends to be compensating. Problems caused by the sequencing can be overcome by decreasing the growth interval, e.g. from five to two years.

The cost of projecting the growth of stands by this model may be prohibitive unless very fast computers are used. Subplot 310 (approximately 0.025 acres), for example, took 3 minutes and 15 seconds for a total cost of $21.67 (at $400.00 per hour) to compile the program and simulate 45 years of growth on an IBM 7094 computer. The cost will increase rapidly as the period of growth is extended. Larger plots will increase the cost in direct proportion to their areas.

APPLICATION

The model is designed to provide estimates of growth and yield of spruce for any acreage from a woodlot to a large management unit. Low-level aerial photographs, taken any time after trees become discernible, can be used to locate sample plots and determine the area occupied by the crowns of individual trees. Either airplanes (Kippen and Sayn-Wittgenstein, 1964) or helicopters (Lyon 1961) can be employed. Eventually, methods will be invented to interpret information from photographs automatically (Langley 1966). Complete photocoverage is not necessary. Each photograph can represent a plot if taken according to a statistically valid sampling design.

Computer simulation of the growth of stands can provide estimates of the time of crown closure, mortality, diameter distribution of the boles and total cubic-foot-

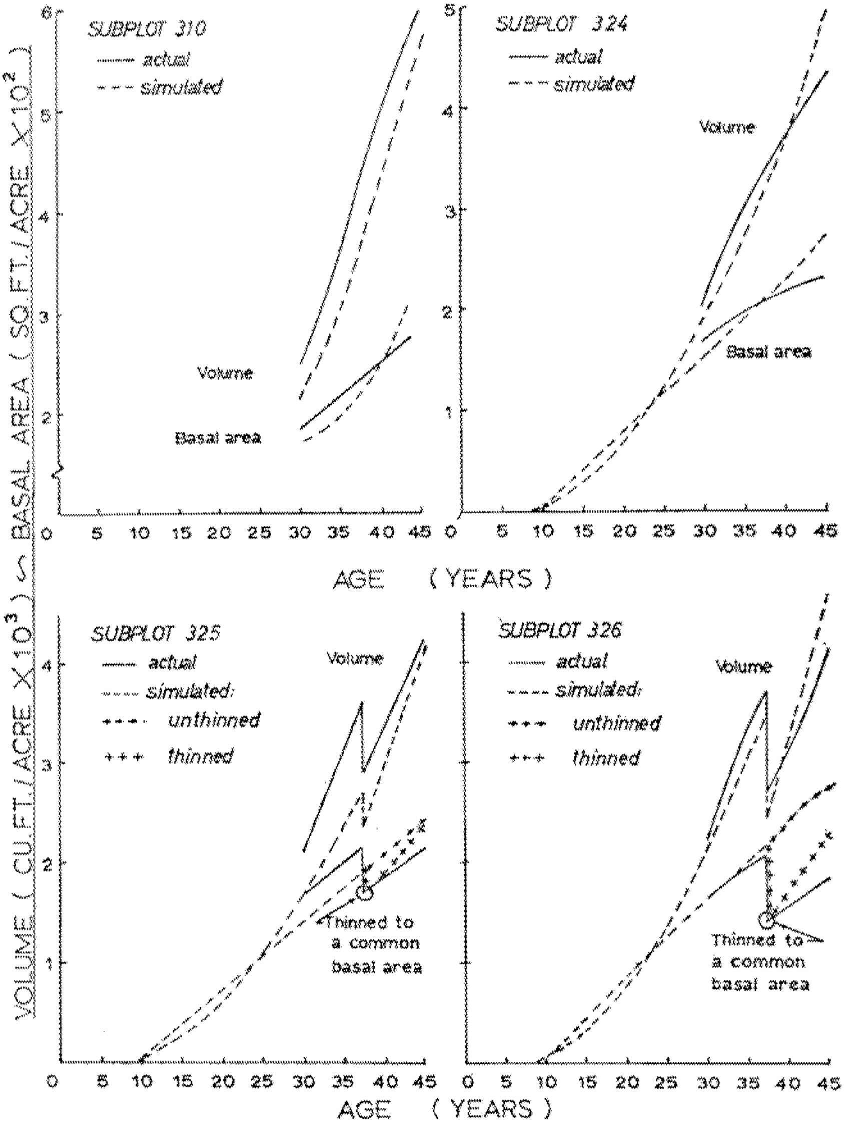

Figure 19. Comparison of volume and basal area growth.

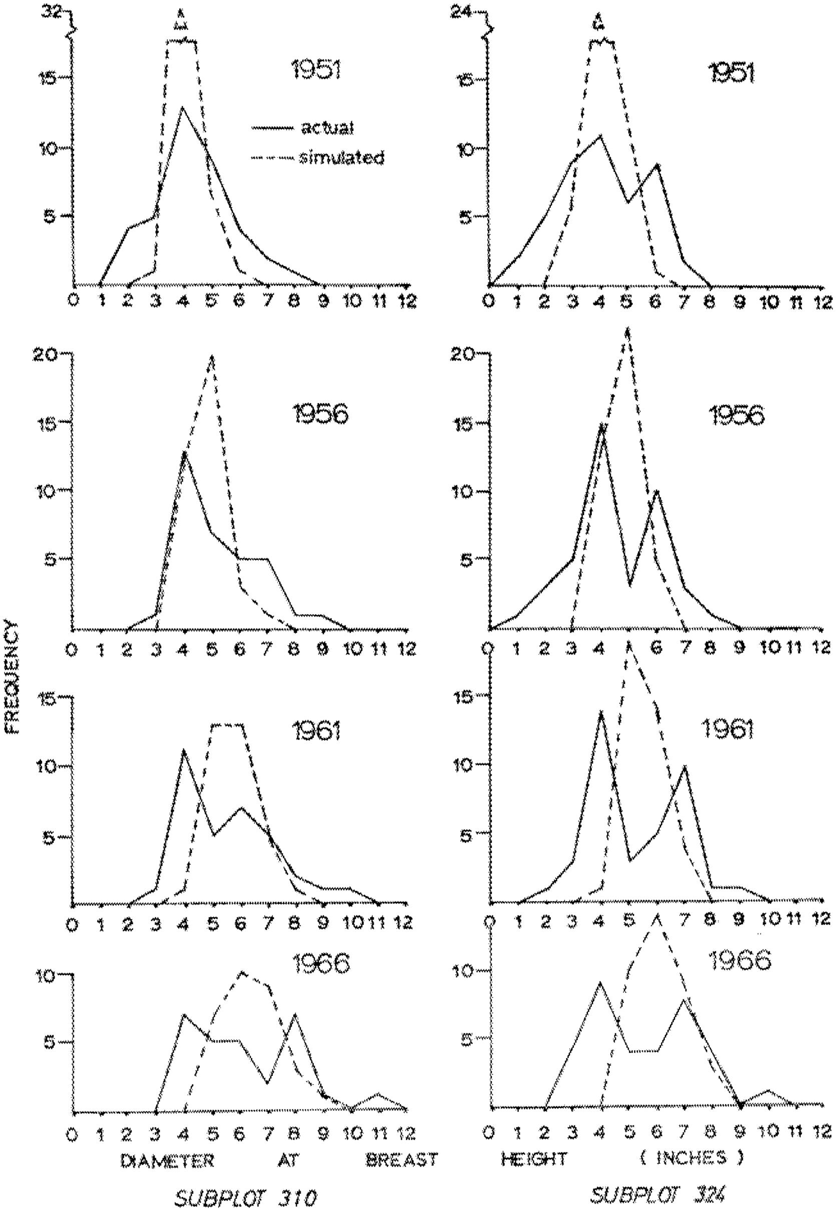

Figure 20. Frequency distribution of bole diameters.

volume by diameter classes. This information is required by foresters who must anticipate stand treatments, and managers who must develop management plans based on expected yield figures. The model may also enable comparisons of the results of initial spacing regimes before seedlings are planted provided the amount and distribution of early mortality are known. It may not be necessary to observe field trials for 10 to 20 years to determine the time of crown closure because reliable results can be obtained in a matter of weeks by determining the rates of crown growth and simulating the development of the plantations. Knowledge of the time of crown closure may prevent an uneconomic cleaning or improvement cut but ensure a profitable thinning at an early age. Various thinning regimes or methods of cutting can be simulated to eliminate approaches that are unlikely to give the desired results.

CONCLUSIONS

THE model developed in this study is a prototype system designed to provide a realistic solution to the urgent problem of projecting the growth of stands into the future to obtain estimates of yield. The results of preliminary tests are promising. However, the full potential of the model will not be realized until the system is expanded, improved and thoroughly tested.

Simulation techniques will equip foresters of the near future with a powerful tool for promoting efficient use and development of forest land. Furthermore, models will expand the experience of foresters by enabling them to test the validity of their proposals mathematically before embarking upon expensive and time-consuming trials.

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