CROWN DYNAMICS IN PINUS RESINOSA AIT. :

ANALYSIS AND STOCHASTIC DESCRIPTION OF BRANCH

PRODUCTION, BRANCH EXTENSION GROWTH AND

FOLIAGE DRY WEIGHT - BRANCH LENGTH RELATIONSHIPS

BY

(C)

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ABSTRACT

The development of the crown structure of _Pinus resinosa_ Ait. was analysed in terms of three component processes of tree growth: the number of first order branches per whorl within the crown, the annual extension increments of the main stem and first order branches, and first order branch length - foliage dry weight relationships. Factors regulating these components were analysed and stochastic models to describe them were developed.

Thirty-two trees from five different planted stands located in the Quetico Section (L.11) of the Great Lakes - St. Lawrence Forest Region (Rowe 1972) were examined. These stands represented various site conditions, stand ages, and spacing categories.

The number of branches per whorl was weakly correlated with two attributes of the parent structure: the length of the terminal leader at the time of whorl bud inception, and the length of the terminal leader on which the branches occurred as whorl buds. The number of branches per whorl was not related to the age of the tree at the time of whorl bud inception. The binomial

probability density function was a suitable model to describe the number of branches per whorl.

Extension growth of first order branches varied greatly from year to year. Differences in the extension growth of individual branches were associated with: differences in the annual height increment of the tree, factors governing apical control, and the relative position of a branch within the crown.

There appeared to be a potential length which one-year-old branches could attain that was dependent upon the concurrent height increment of the tree. There also seemed to be a potential extension increment for branches after their first growing season that was dependent upon initial branch length and branch age. The observed extension increments of branches were related in a stochastic manner to the potential for branch extension growth to simulate naturally occurring variation.

Total branch length was a useful estimator of the total foliage dry weight for branches of the same age.

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INTRODUCTION

The tree crown is of central importance to the study of the dynamics of tree and stand growth. Crown structure determines the distribution and orientation of foliage within an individual tree. This is important to the efficiency of the tree in trapping solar energy to produce photosynthate (Horn 1971; Bunting 1976). Larson (1962a,b , 1963, 1969) and others before him (Pressler 1865, quoted by Larson 1963 and Assmann 1970; Onaka 1950a,b) have hypothesized that the vertical distribution of the annual stemwood increment is regulated by the size and the vertical distribution of the crown. The relationship between the crown and growth of the stem is thought to be mediated by the vertical distribution of one or more crown produced metabolites in the stem phloem (Beckwith and Shackelford 1976). Mediators that have been proposed include carbohydrates, auxin, or a combination of carbohydrates and hormonal growth regulators. Regardless of the identity of the crown produced mediator, many tree physiologists believe that environmental factors affect stem growth mainly indirectly through their direct effects upon the crown and its productive capacity (Farrar 1961; Larson 1962a; Kramer and Kozlowski 1979).

Quantification of crown growth and development could provide a useful tool for both the forest manager and the forest scientist. This is of practical importance to the silviculturalist because silvicultural treatments can be implemented to manipulate the live crown directly to increase both wood yield and quality (Smith 1963; Assmann 1970).

In addition, tree crowns affect forest ecosystems in other important ways. The tree crown has a bearing on the water economy of a forest stand. It intercepts a substantial amount of precipitation and, therefore, affects the quantity of precipitation which reaches the forest floor (Ford and Deans 1978). The foliage complement of a tree or of the entire stand is a food source for defoliators and plays an important role in pest dynamics (Kay 1978; White 1979). The quantity of crown fuel is of interest to the fire manager (Brown 1976). Even pathologists interested in the epiphytic population of a forest stand could benefit from quantification of crown growth and development (Pike et al. 1977).

The efficient crown has specific space requirements within the stand. Crown size, usually measured by crown width or length, will determine the upper limit of tree stocking per unit land area (Curtin 1970; Curtis and

Reukema 1970). The interactions between the size and shape of individual trees and their crowns will be important in any attempt to reconcile the growth behaviour of both trees and entire stands.

Recently, there has been a proliferation of computer simulation models to predict various aspects of growth and yield of individual trees or stands (Goulding 1979). Computer simulation models are useful because with them foresters can evaluate alternative forest management regimes in a relatively short time. A program of research designed to yield quantitative knowledge about tree growth must include a systematic study of crown dynamics.

The objective of the present study is to construct and analyse a mathematical model of crown growth and development for _Pinus resinosa_ Ait. Crown structure was analysed in terms of three component processes of tree growth: the number of first order branches per whorl within the crown, the annual extension increments of the main stem and first order branches, and first order branch length - foliage dry weight relationships. Factors regulating these components were analysed and stochastic models to describe them are presented. The uninodal growth habit of _P. resinosa_ makes it a particularly suitable study species.

The results of this thesis revealed that the number of first order branches within the crown and their extension growth varied greatly from year to year. Nonetheless, definite trends were found in the pattern of first order branch development and resulting crown form. Branch production was only weakly related to the length of the parent structure. Differences in first order branch extension growth were associated with differences in the annual height increment of the tree, with factors governing apical control, and with the relative position of the first order branch within the crown. The stochastic model developed in this thesis is an attempt to represent simultaneously the underlying biological pattern and the random variability observed in first order branch production and extension growth for P. resinosa.

The vertical distribution of foliage within the crown was also examined. The length of the first order branch was a useful estimator of the total foliage dry weight for first order branches of the same age.

LITERATURE REVIEW

Crown organization and the mathematical modelling of crown growth and development are the subjects of this review. Although complex models have been developed which relate tree growth to rather basic biochemical (Promnitz 1975; Ledig 1976; Chung and Barnes 1980a,b), biophysical (Borchert 1973; Paltridge 1973), and environmental processes (Reed 1980) within individual trees, the emphasis here is on physically measurable exterior tree dimensions. Forest biomass studies have provided valuable information on techniques for estimating biomass components of an individual tree (Ogawa and Kira 1977). Few studies, however, have adopted a 'systems approach' (Goulding 1979) to the problem of modelling crown dynamics.

Crown Structure in _Pinus resinosa_ Ait.

The crown structure of a tree can be viewed as an organized heirarchy of vegetative shoot axes. Two morphologically distinct types of vegetative shoots commonly referred to as long-shoots and dwarf-shoots occur

in the genus <u>Pinus</u>. The manner in which long-shoots and dwarf-shoots develop defines the branching network, and resulting crown structure. In <u>P. resinosa</u> Ait., the annual developmental pattern of long-shoots and dwarf-shoots is almost always the same and is characterized by fixed growth. Fixed growth refers to the elongation of predetermined stem units[1] after a period of rest, typified by the elongation of a winter bud. Thus, past annual branching patterns and crown dimensions are easily reconstructed for this species. Only the first year of seedling growth and development are characterized by free growth. Free growth refers to the formation of a shoot as a result of the simultaneous initiation and elongation of new stem units. Thompson (1976) describes the morphology of pine seedling growth and development.

The branching pattern is fundamental to understanding the organization and structure of the crown in <u>P. resinosa</u>. Trees of this species have a single trunk which supports a series of lateral long-branches that are arranged as false-whorls along the trunk axis. Such long-branch false-whorls are commonly, but incorrectly referred to as branch whorls in the forestry literature (Madgwick 1975). The traditional term 'whorl', however, is adopted throughout this thesis.

[1] A stem unit is the internode portion of a shoot, together with a cataphyll and its axillary structure, if any (after Lanner 1976).

Each lateral long-branch bears spirally arranged dwarf-branches. Each dwarf-branch supports a single fascicle of usually two needles at its stem tip. The needle-bearing dwarf-branches usually persist from 2 to 8 years. Since dwarf-branches have a limited life span they only occur on the youngest few annual stem internodes of their supporting stem axis. The youngest few annual stem internodes of the mainstem or trunk also bear spirally arranged dwarf-branches.

Lateral long-branches may also bear higher order whorls of lateral long-branches that develop in a similar manner to those of their parent branch axis. This pattern is repeated as a tree grows, but generally lateral long-branches of higher order than five are rare in Pinus (Flower-Ellis et al. 1976). Although dwarf-branches generally do not give rise to new branches, all dwarf-branches have the latent capacity to develop into ordinary long-branches. This ability diminishes as the dwarf-branch ages.

Both ordinary long-branches and dwarf-branches originate in the apical bud as a primordium in the axil of a cataphyll. The formation of an ordinary long-branch takes two years before it is actually visible as a long-branch on the supporting stem axis. In contrast, the

formation of a dwarf-branch only takes a single growing season. The formation of an apical or terminal bud in P. resinosa, and subsequent extension growth comprise a distinct sequence of developmental stages (Duff and Nolan 1958; Sucoff 1971; Lanner 1976). The over-wintering terminal bud contains all the primordia required for the following season's growth.

The most proximal organs in the terminal bud are a series of spirally arranged cataphylls (Figure 1A) that do not subtend axillary budlets and enclose the terminal bud. These are followed by a long series of cataphylls which bear the dwarf-branch budlets without needle primordia (Figure 1B), and then by a few cataphylls which bear the lateral long-branch budlets (Figure 1C). Reproductive primordia are not shown in Figure 1. Ovulate cone primordia, however, are thought to differentiate in the axils of the more distal cataphylls, as is the case with the long-branch budlets. In contrast, male cone primordia arise in the axils of the cataphylls near the terminal bud base (Figure 1A). The lateral long-branch budlets are the last axillary structures to be formed. Finally a series of sterile cataphylls is produced which will develop the following year into the terminal bud scales that enclose the successor terminal bud (Figure 1D) (Larson 1969).

APICAL BUDLET
FORMS SUCCESSOR BUD ($i+1$)

LONG-BRANCH BUDLET
FORMED AUGUST (i)

DWARF-BRANCH BUDLET
FORMED JUNE - AUGUST (i)

STERILE STEM UNITS
FORMED MAY (i)

TERMINAL BUD SCALES
FORMED SEPTEMBER ($i-1$)
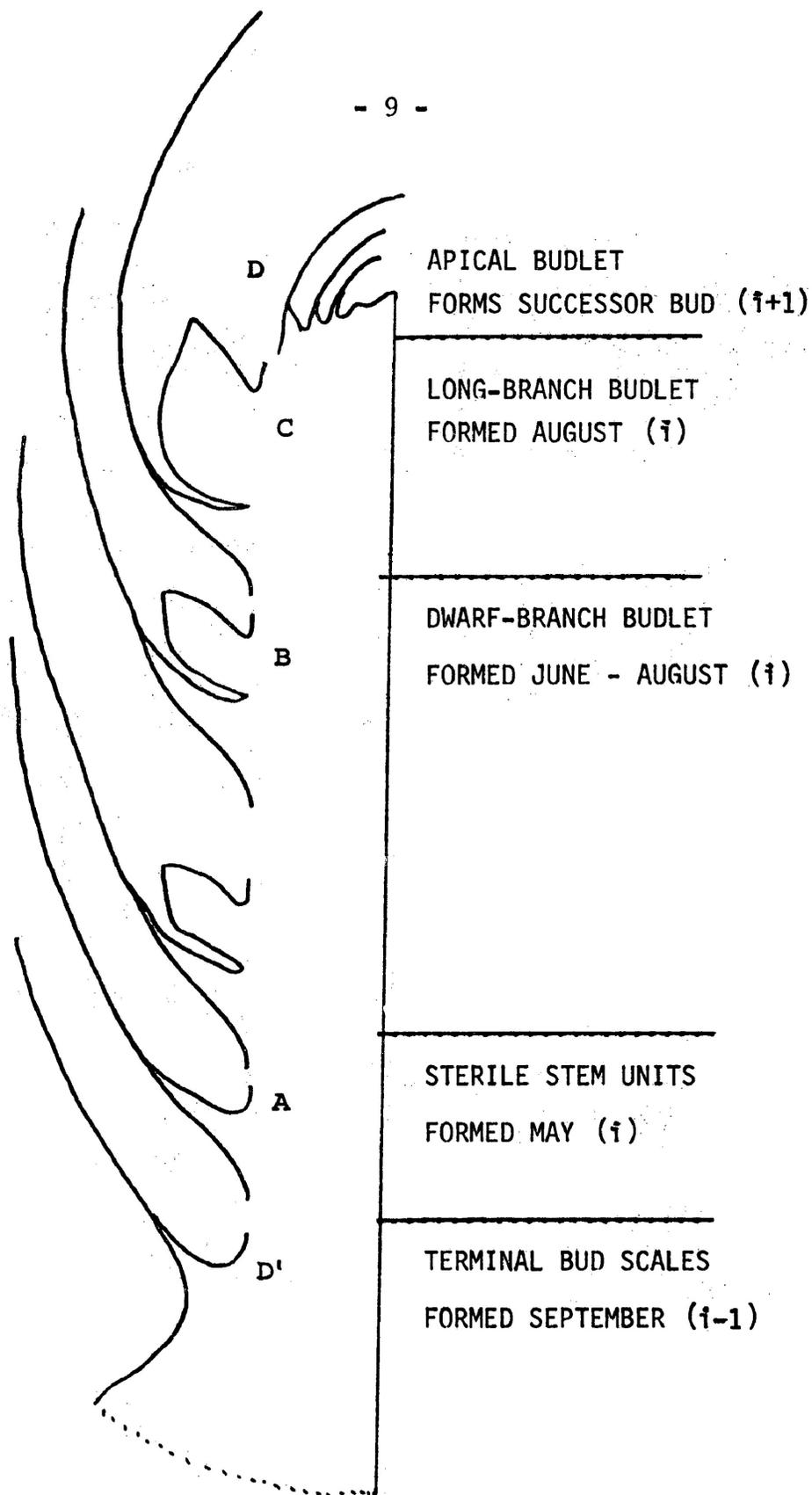
Figure   1.   The winter bud of Pinus resinosa Ait. contains all the
structures required in the ($i+1$) th growing season. The
sequence of primordia formation is described in the text.
(After Farrar 1974, unpublished manuscript)

During the following growing season, bud expansion proceeds by extension growth of the internodal region between each cataphyll (stem unit), with the exception of the terminal bud scales. The dwarf-branch budlets develop into dwarf-branches which bear the needle fascicles at their tip. The dwarf-branch only reaches a length of about 2-3 mm, and is enveloped by a sheath of cataphylls (fascicle-sheath). Its apical meristem eventually becomes vacuolated, dehisced, and reduced in size (Sacher 1954; Hanawa 1967). Occassionally, however, the dwarf-branch apex remains meristematic and forms an interfoliar bud which develops into an ordinary long-branch (Thomson 1914; Little 1970; Curtis and Popham 1972).

The dwarf-branch possesses an intercalary meristem at its base just where it joins the cambium of the parent stem. As the cambium of the parent stem lays down new cells to increase in girth, the centrally positioned meristem of the dwarf-branch extends by a similar amount. Thus, the dwarf-branch is not buried by stem diameter growth as is an ordinary long-branch. Occassionally, however, stem diameter growth is so vigorous that the dwarf-branches are sloughed off prematurely. This usually occurs in young, vigorous, fertilized stands, for example (Farrar 1974, unpublished manuscript).

At the same time that the dwarf-shoots are developing, the lateral long-branch budlets also extend and only increase in size slightly to form a whorl (false-whorl) of lateral buds. They do not extend to form long-branches. The formation of the subtending lateral buds approximately coincides with the development of the successor terminal bud which occurs when the extension growth of the current season terminal bud is almost complete. Thus, a whorl of lateral buds is formed which subtends each new terminal bud. These lateral buds are

similar in structure to the parent terminal bud. Extension growth of the terminal and subtending whorl of lateral buds occurs concurrently during the following growing season. Thus, the formation of new branch whorls begins two growing seasons prior to their appearance as ordinary long-branches. Unless otherwise stated, the term branch will refer henceforth to ordinary long-branches.

As a tree grows in height, new branches are formed annually at the crown top and older branches in the lower crown die. The rates at which these processes occur determine whether live crown length decreases, increases, or remains static. New branch whorls are produced at a constant rate of one per year. The rate of branch mortality, however, is more complex and varies with tree age, crown classification, and the degree to which

available growing space is utilized.

The mechanisms of branch mortality are largely unknown. Larson (1969), however, has speculated that each branch in _P_. _resinosa_ is an autonomous source of essential photosynthates and hormonal growth regulators. Branches in lower crown positions produce little of these metabolites because their reduced light environment severely limits photosynthesis. Under these conditions branch growth is impeded which further limits the supply of water and nutrients to the lateral branch. Eventually the branch dies.

Crown size, measured by length and width, varies with the competitive status of the tree. Both live crown ratio (percent of total tree height occupied by functional branches), and crown radius decrease when trees are grown at closer spacings (Curtis and Reukema 1970). For a particular stand spacing these dimensions are fairly stable. They may change, however, in response to cultural treatments such as thinning and fertilization (Reukema 1964; Barker 1978).

Regulation of Crown Structure in <u>Pinus</u> <u>resinosa</u> Ait.

The dwarf-branch habit and the excurrent branching pattern of <u>P</u>. <u>resinosa</u> may be explained in terms of strong apical control (Brown et al. 1967). Strong apical control usually refers to the inhibition of growth of axillary buds by the shoot apex (Phillips 1975). With reference to the leading terminal shoot in <u>P</u>. <u>resinosa</u>, apparent correlative inhibition exists between the long-branch forming lateral buds and the needle-bearing dwarf-branches below. The latter appear to be inhibited because they are able to develop interfoliar buds or ordinary long-branches when both the terminal and lateral buds above are removed.

Further growth correlations occur between the terminal bud and the subtending whorl of lateral buds during their concurrent extension growth. Normally, the terminal leader is longer than any of the newly formed lateral long-branches. Loss of the leader results in increased extension growth of the laterals while the removal of the laterals has little effect upon leader extension growth. This phenomenon is usually referred to as compensatory growth in the forestry literature (Little 1970; Brown 1971; Jankiewicz and Stecki 1976).

The leading terminal bud of the mainstem axis is usually the largest, develops the most preformed dwarf-branches, becomes the longest shoot, and tends to support the most lateral long-branches (Jankiewicz and Stecki 1976). With few exceptions, there is a regular decrease in these parameters for branch whorls in progressively lower positions of the crown (Forward and Nolan 1964; Rehfeldt and Lester 1966; Little 1970; Kozlowski and Ward 1961; Jankiewicz and Stecki 1976; Riding 1978). The overall mechanism of apical control, however, is complex and appears to involve both hormonal and nutritional factors (Little 1970; Brown 1971; Phillips 1975; Pharis 1976; Jankiewicz and Stecki 1976; Kramer and Kozlowski 1979).

Modelling Branch Growth and Development

Several studies have revealed some interesting relationships about branching networks of botanical living structures. Cohen (1967) briefly defines some theoretical rules which govern two-dimensional branching patterns. The model incorporates variables such as branch length, branch angle in relation to the parent axis, and branching probability. These variables are largely determined by the density of the branching network, and the previous angle of the free end of the branch. By specifying the maximum and minimum values of the parameters, a wide range of branching patterns can be simulated.

More recently, Bell et al. (1979) have developed a two-dimensional data structure analogue for modelling plant architecture. The structural unit of a plant is defined to be the apical meristem, and its product, which is referred to as a shoot-unit. Both quantitative and qualitative parameters of each shoot-unit such as meristem fate, potential, location, duration and length comprise the data base.

The system is operated in either an empirical or purely subjective manner. In the former case, the details of simulation are based on measurements of plants in the field and lead to a graphical representation of the architecture possible for a given species. In the latter case, the data on which the simulation is based is entirely subjective. Details of the simulation are adjusted until the graphic model appears accurate when compared with actual plants. Subjective simulation may be confirmed subsequently by field observation.

The model can be expanded to simulate the three-dimensional aspect of plant architecture. Modelling plant architecture in three dimensions, however, involves compilation of a data base organized in 'rooted-tree' form. A rooted-tree data base is a special kind of linked data structure that allows for the full integration and control over the selection of parameters required during simulation. Smith and Scoullar (1975) have previously suggested the use of a rooted-tree data structure analogue for modelling the crowns of young conifers.

A link is the length of the branching path between any two branching nodes or forks. Branching patterns in trees have also been quantitatively analysed by assigning a heirarchy of integers to the various links which

comprise a branching network. Originally this technique of ordering links or branch segments was developed by Horton(1945, quoted by Leopold 1971) and later modified by Strahler(1957, quoted by Barker et al. 1973) to study river networks. Leopold (1971) used Horton's method to describe the branching patterns of _Abies_ _concolor_ Lindl. Gord. and _Pinus_ _taeda_ L., and found that they obeyed the same laws as river networks. Strahler's method has been used to describe the branching network of various deciduous tree species in a similar manner (Barker et al. 1973; McMahon 1975; McMahon and Kronauer 1976). By this method, the end branches are order one, and two of these meet to form an order two branch, and so on up to the main stem. This is a new meaning for branch order in contrast to the older meaning where branches are ranked from the main axis on up to the end branches. These studies reveal a strong, negative, linear correlation between the number of branch segments per order and order serial number. In contrast, the logarithm of the mean basal diameter, mean length, and the mean number of buds for each branch segment per order show strong, positive, linear correlations with order serial number.

McMahon and Kronauer (1976) show that the decreasing diameter of branch ramifications is related to the 3/2 power of the total length of the branching path from its

tip to the point where the diameter measurement is made. Elastically similar columns which uniformly resist bending stress prove to be proportional to the 3/2 power of their length (McMahon 1975). Thus, trees appear to preserve elastic similarity in their branching structure.

The total number of current season long-branches of young P. resinosa is easily estimated from such variables as current season tree height, previous season's tree height, and stem diameter at breast height. By adding the number of mainstem internodes as an interaction term with any of the above independent variables more precise estimates are obtained (Miller 1965). In a comprehensive study of provenance differences in Pinus contorta Dougl. and Picea sitchensis (Bong.) Carr., Cannell (1974) reports a strong, positive, linear correlation between the mean number of lateral branches and the mean length of the parent shoot on which the laterals were predetermined as buds prior to extension growth. The number of dwarf-branch budlets within the leading terminal bud of the mainstem axis in P. resinosa is highly correlated with parent bud length and total tree height (Marion et al. 1968). The length of the terminal leader and the number of dwarf-shoot branches that it bears is also positively and linearly correlated with the length of the parent terminal bud (Clements 1970).

Length of the terminal bud can be used as an index of height growth in different genetic materials, as in provenances of P. resinosa (Rehfeldt and Lester 1966). Terminal bud diameter and bud length of both the mainstem and first-order branch axes of P. resinosa are also useful indicies of extension growth potential in young P. resinosa. A strong, linear relationship exists between final shoot length and either parent bud length or diameter (Kozlowski et al. 1973). In young Pinus strobus L., however, Little (1970) reports a strong, allometric relationship between these same variables. The length of the current season terminal leader of the mainstem axis is also linearly correlated with the length of the previous season's terminal leader. The final length of a terminal mainstem axis shoot is linearly related to the final length of the longest lateral shoot inserted into the same whorl (Little 1970).

In all of the aforementioned studies there is no attempt to simulate the three-dimensional orientation of each branch unit nor the geometry of the tree crown. The first completely geometrical simulation of theoretical tree-like bodies was presented by Honda (1971). Honda demonstrated that a wide variety of crown forms may result by allowing parameter values to vary for a few simple rules of branching angle and extension growth. He varied

only four parameters: the two angles which daughter branches made with the mother and their lengths relative to the mother and, once fixed, these remained constant within each individual tree simulation. Honda assumed that (1) branches are straight, (2) branching occurs in concurrent generations, and (3) a mother branch forks into two daughters in the plane whose steepest gradient coincides with the direction of the mother branch.

More recently, Honda's model has been refined and calibrated to simulate the branching pattern and geometry of _Terminalia_ sp. (_Combretaceae_), a tropical tree (Fisher and Honda 1977). Two vigour classes of sympodial branching units are recognized in this genus (Fisher 1977). The trunk and the branch axes are assumed to be straight and to extend at an empirically determined constant rate relative to the length of the mother axis. The bifurcation angle is expressed as a linear function of the vertical position of a branch from the mainstem apex. The bifurcation angle is relatively stable below the fourth branch whorl and is assumed to remain constant. The state of a branch is measured by the order (i.e. rank) of bifurcation, the direction of the daughter unit which is indicated by the sign of the branching angles, and the vigour class of the mother branching unit. A detailed quantitative study of _Terminalia_ sp. is

presented by Fisher (1977).

Height growth is related to crown form through the mechanism(s) of apical control. Mitchell (1975) presents an individual tree growth model for Pseudotsuga menziesii (Mirb.) Franco. that establishes quantitative relationships between various parameters of the crown and the bole. The annual extension rate of a first order branch is defined to be inversely proportional to the vertical position of the branch from the mainstem apex. Empirically determined constants specify the initial rate of branch extension. Integration of the resulting extension rate function defines the cumulative length of a branch. Factors are introduced which compensate for crooks and irregularities which shorten branches slightly. Past crown profiles are easily reconstructed by specifying the annual change in the vertical distance of a branch from its mainstem axis apex. Mitchell's model, however, assumes that branches extend in length at a constant decreasing rate from the mainstem apex to the base of the crown.

Crown volume is estimated by treating the cumulative branch length function as a volume of revolution about the mainstem axis. An annual shell of crown volume which is an index of foliage volume is calculated from this

information. Foliage volume is limited to the outer five shells of the tree crown, since the life span of Pseudotsuga menziesii foliage is about five years. Weighting factors for foliar volume are introduced to account for reductions in photosynthetic efficiency and retention as foliage ages. In the model, foliar volume is linearly related to bolewood increment (volume) for open-grown trees. The model operates by allowing the components to interact and vary with time.

In nature the pattern of crown growth and development is not the same for each tree within a stand because of genetic and environmental factors. For a population of trees, the parameters of the component functions of Mitchell's individual tree growth model are characterized by the normal distribution (Mitchell 1969, 1975). This relationship allowed Mitchell to stochastically simulate naturally occurring variation of crown growth and development for trees within an entire stand. The growth of even-aged white spruce (Picea glauca (Moench) Voss.) has been simulated in a similar manner (Mitchell 1969).

Cochrane and Ford (1978) outline a comprehensive stochastic model to describe the development of the branching structure of young, P. sitchensis. Their model defines the rules for specifying the number of branches

that occur per mainstem whorl, branch orientation, as measured by the azimuth around the circumference of the tree in a single plane, and the mean angle of insertion into the mainstem. Branch extension increment in the first season is treated entirely as a stochastic process and is simulated by the gamma probability density function. Subsequent branch extension increments are based on the relative extension rate of a branch (G) defined as:

$$(1) \qquad G(I) = \frac{\text{Branch extension increment in the I th season}}{\text{Length of branch in (I-1) th season}}$$

The branch extension increment in any season (I) then has the gamma distribution with parameters:

$$(2) \qquad \left(\frac{\rho}{G(I) \prod\limits_{J=2}^{I-1} (I + G(J))} \right), \alpha$$

Forest Biomass Studies

Forest biomass studies have contributed substantially to the understanding of the distribution of crown foliage. The total dry weight of living foliage supported by the crown of a coniferous tree is allometrically related to various parameters of the bole such as diameter at breast height (Kittredge 1944; Shinozaki et al. 1964a,b; Loomis et al. 1966; Honer 1971; Kinerson et al. 1974), diameter at the base of the live crown (Shinozaki et al. 1964a,b; Loomis et al. 1966; Madgwick 1970; Brown 1976), and to the length of the live crown (Loomis et al. 1966). A similar rationale has been extended to estimate the total foliage dry weight supported by individual branches that compose the crown. The most useful estimator of total branch foliage dry weight is basal branch diameter at a position about 5 - 10 cm from the point of insertion into the bole (Loomis et al. 1966; Riedacker 1971; van Laar 1973; Madgwick and Jackson 1974; Gary 1976; Ek 1979). The inclusion of some measure of branch position within the crown significantly increases the precision of the estimation of total branch foliage dry weight from basal branch diameter (Ek 1979).

Madgwick (1968) has modelled the vertical distribution of foliage within P. resinosa and Pinus sylvestris L. His model is based on the allometric relationship between total foliage dry weight of the topmost mainstem whorl of branches (one-year-old) and the length of the terminal leader. The annual dry weight foliage increment of a branch whorl within the upper crown increases exponentially at an empirically determined constant rate of 160 percent. The foliage increment of the lower branch whorls is reduced by empirically determined constants to account for competition (Madgwick 1974).

The pipe model theory of tree growth simply states that the quantity of foliage existing above a certain horizontal level within a plant community is always proportional to the sum of the cross-sectional area of the stems and branches found at that level (Shinozaki et al. 1964a). This theory has formed the basis for modelling foliage dynamics in P. taeda L. (Kinerson et al. 1974). The normalized cumulative foliage dry weight at each branch whorl in P. taeda L. is related to its normalized vertical position within the live crown. In order to generate the foliage distribution within the forest canopy, the above relationship is re-scaled from empirical data in terms of live crown length, and total foliage

biomass for each tree within the stand. Stem diameter at breast height is used to estimate total crown foliage dry weight per tree. The canopy foliage distribution for any part of the stand is calculated by summing the re-scaled model crowns for respective trees.

Kinerson et al. (1974) express new foliage production and foliage loss as a simple function of time elapsed during a specific growing season. The normalized total crown foliage dry weight increment, and normalized foliage dry weight litterfall are related in a sigmoid manner to normalized time (days) elapsed in a specific growing season. Normalized terminal leader elongation of the mainstem axis is linearly correlated with normalized time (days) elapsed during a specific growing season. By combining this information, the distribution of foliage biomass by age class and position within the crown or canopy is simulated. The model has been further extended to estimate the vertical distribution of branch-wood biomass within the crown of P. taeda (Kinerson and Higginbotham 1973).

In a similar manner, Kinerson and Fritschen (1971) have modelled the foliage area distribution within crowns of P. menziesii. By treating the canopy as a composite of trees of average height and crown length, Stephens

(1969) concluded that the vertical distribution of foliage in even-aged _P._ _resinosa_ canopies can be characterized by the normal distribution.

Satoo and Imoto (1979) recently introduced a new concept to model the distribution of foliage within the stand canopy of _Cryptomeria_ _japonica_ (L.f.) D. Don. The canopy is treated as a composite of crowns of average shape. Crown shape is approximated to be a cone from the relationship between cumulative foliage biomass from the tree top, crown length, and crown radius. Foliar biomass at a specific horizontal level is estimated from a single surface of revolution for this cone. By specifying the height and location of trees, and the average cone inclination for the stand, the vertical distribution of foliage within the crown, crown length, and crown width are reconstructed.

MATERIALS AND METHODS

Crown Terminology, Mathematical Notation and Crown Relationships

The branching network of the crown in P. resinosa may be analysed in terms of the annual extension increments of the various long-branch axes including the main stem or trunk of the tree. The past record of the annual extension increments of any order long-branch axis and the mainstem axis is easily reconstructed because a new whorl of lateral long-branches is produced annually along the parent axis. Each new long-branch whorl identifies an annual node of the branching network and each node is separated by a stem internode. Each stem internode represents an annual extension increment of the parent long-branch axis. Each node of the mainstem axis and any order long-branch axis is referred to as an annual node and the subtending stem internode is referred to as an annual internode.

The main axis of the crown is the main stem of the tree itself. Annual internodes of the main stem are numbered consecutively from the mainstem base (Figure 2).
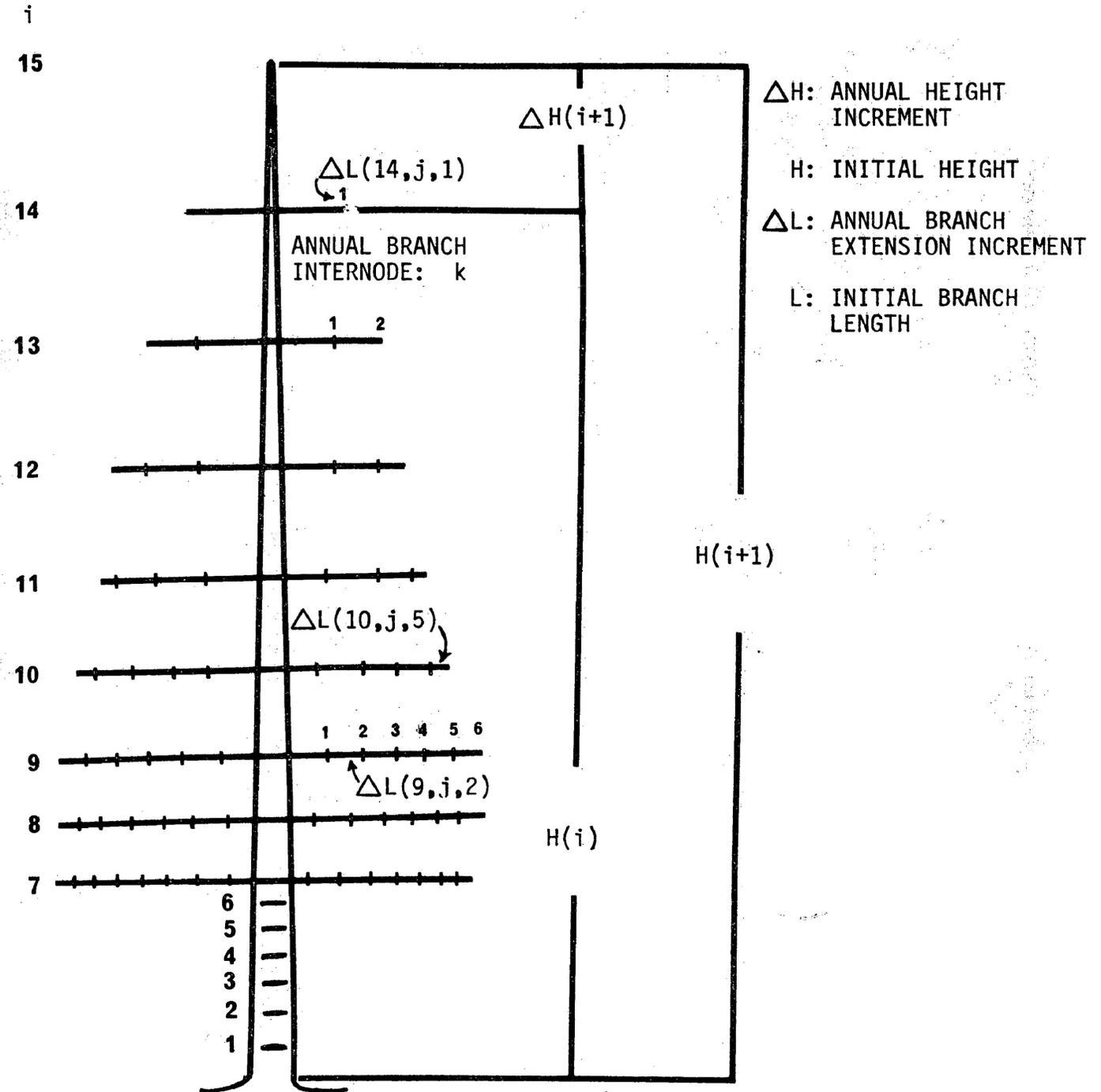
Figure 2. Schematic representation of the annual internodes of the main stem and first order branches of a 15-year-old Pinus resinosa Ait. tree. Branches older than 8 years are dead and are not shown.

The length of the i th mainstem internode from the tree base will be denoted, $\triangle H(i)$. It represents the annual height increment of the tree, $\triangle H$, at the end of the i th growing season. Since stem internodes are formed annually, the address number, i, also represents the age of the tree at the end of the i th growing season. The total length of the mainstem or total tree height, H, at the end of the i th growing season is simply:

$$H(n) = \sum_{i=1}^{n} \triangle H(i).$$

A long-branch whose parent axis is the main stem of the tree is referred to as a first order long-branch. Long-branches of higher order than one are not concidered in the present study. The architecture of each first order long-branch parallels that of the main stem. Several long-branches occur per whorl and new first order long-branch whorls are formed annually along the mainstem axis. Thus, it is necessary to distinguish first order long-branches within the crown of P. resinosa.

Annual internodes of every first order long-branch are numbered consecutively from the long-branch base. The length of the k th stem internode from the base of the j th first order long-branch inserted in the i th whorl along the mainstem axis will be denoted, $\triangle L(i,j,k)$. $\triangle L(i,j,k)$ represents the annual extension increment of

the specified long-branch at the end of its k th growing season. The long-branch address number, k, also represents the age of the first order long-branch at the end of its k th growing season. The total length of any first order long-branch or total branch length, L, at the end of its m th growing season is simply:

$$L(i,j,m) = \sum_{k=1}^{m} \triangle L(i,j,k).$$

It is sometimes necessary to locate a first order long-branch stem internode that extended concurrently with a particular mainstem internode. The first order long-branch stem internodes which extend concurrently with the mainstem internode, $\triangle H(i)$, i = ,3,4,5...,[2] belong to the set of first order long-branch internodes $\{\triangle L(i-1,j,1),\quad \triangle L(i-2,j,2),...,\quad \triangle L(i-k,j,k),...,\quad \triangle L(2,j,1)\}$. The values of j run through the appropriate integers, 0,1,2,... up to the number of long-branches in the particular mainstem whorl.

Conversely, given a first order long-branch stem internode, $\triangle L(i,j,k)$, the concurrent height increment of the tree is $\triangle H(i+k)$.

[2] This series begins with the integer 3 because P. resinosa seedlings do not normally produce first order long-branches at whorl address (1,j,k). P. resinosa seedlings, however, do produce first order long-branches at whorl address (0,j,k), but these are ignored because they are usually very small and soon die.

Study Site Location and Sampling Method

Thirty-two P. resinosa trees were selected from five different planted stands located in the Quetico Section (L.11) of the Great Lakes-St. Lawrence Forest Region (Rowe 1972). Trees with straight boles and healthy symmetrical crowns were chosen. The scarcity of P. resinosa stands in northwestern Ontario made it impossible to select the sample trees from one uniform site.

Two stands (Stands A and B) were planted at regular spacing on similar sites at the Ontario Ministry of Natural Resources, Thunder Bay, Forest Tree Nursery. Stand A was classified as open-grown at 6.6 -by- 6.6 m spacing and was approximately 29-years-old at the time of sampling. Two trees were felled in this stand in early May 1978. The trees ranged between 10.47 to 12.03 m in height. The trees from stand B were grown at 2.3 -by- 2.3 m spacing and ranged in apparent age from 29 to 30 years. Three trees were felled from this stand in early May 1978 and another three were felled in early May 1979. These six trees ranged in height from 14.18 to 17.59 m (Table 1).

Table 1.   Location and description of sample trees.

Stand	Sample Size	Location	Total Tree Height (m)	Age (years)	Spacing (m)
A	2	Thunder Bay Forest Tree Nursery	10.47-12.03	29	6.6 x 6.6
B	6	Thunder Bay Forest Tree Nursery	14.18-17.59	27-32	2.3 x 2.3
C	8	Sapawe,Ontario	8.24-9.73	19-20	Irregular
D	8	Kawene,Ontario	3.48-4.89	10-12	Irregular
E	8	Nym Lake,Ontario	4.96-6.04	12-14	Irregular

The remaining stands were planted at irregular spacing at three locations in the vicinity of Atikokan, Ontario (Figure 3). Stand C was located near Sapawe, Ontario approximately 22 km east of Atikokan. The trees were approximately 20-years-old and ranged between 8.24 to 9.73 m in height. Stand D was located near Kawene, Ontario approximately 30 km east of Atikokan. The trees were 10 to 12-years-old and ranged between 3.48 to 4.89 m in height. Stand E was located near Nym Lake, Ontario approximately 15 km east of Atikokan. The trees were 12 to 14-years-old and ranged between 4.96 to 6.04 m in height (Table 1).

Stand Characteristics and Site Evaluation

An indication of site index was provided by calculating the growth intercept at breast height (GI_{BH}) for each tree (Alban 1979). Growth intercept values were pooled by site (Table 2). Analysis of variance indicated no significant differences of growth intercept values between sites (P = 0.05).

A,B   Thunder Bay Forest Tree Nursery study site - 30-year-old red pine
C   Sapawe study site - 19-year-old red pine
D   Kawene study site - 11-year-old red pine
E   Nym Lake study site - 13-year-old red pine
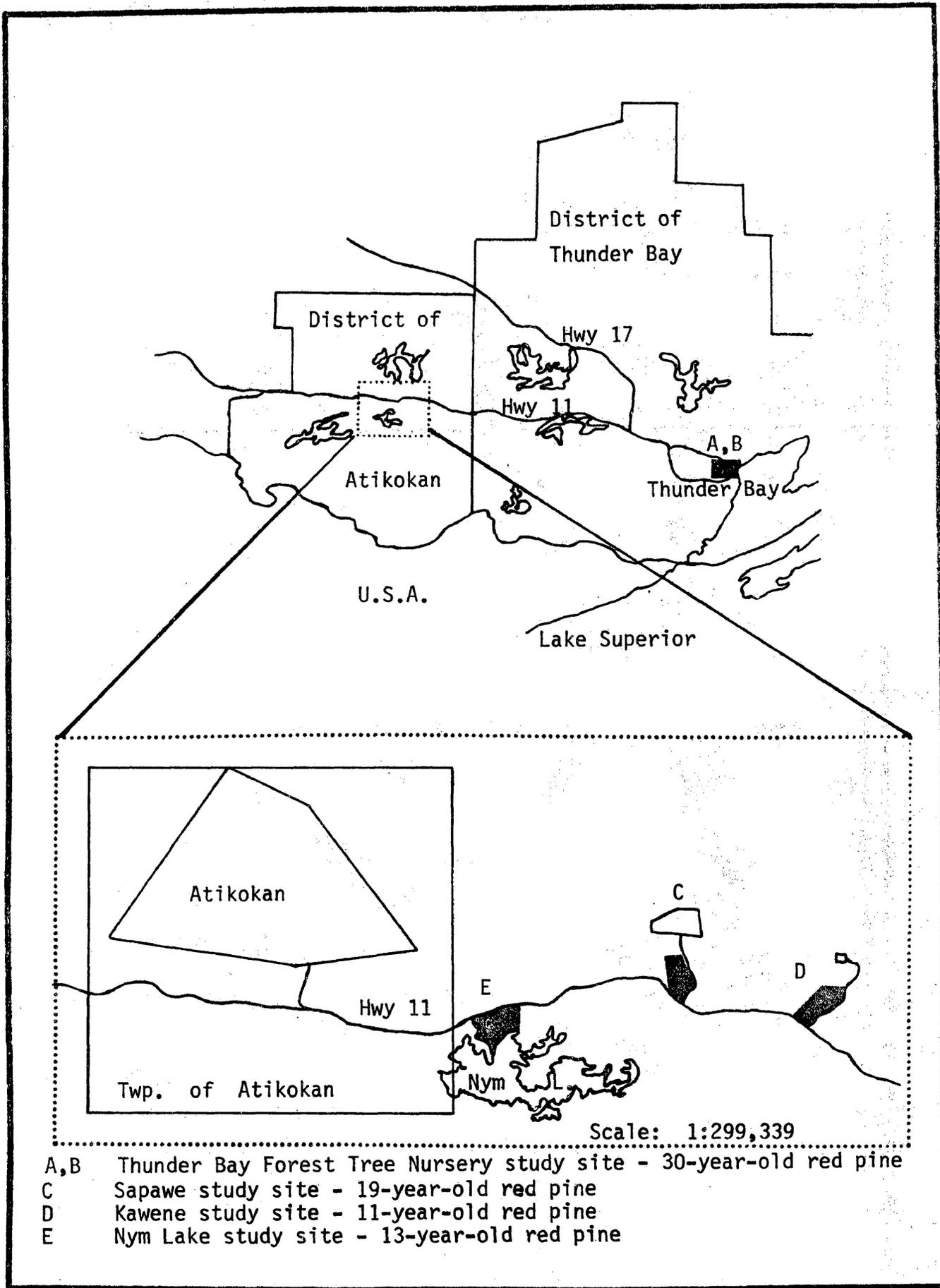
Figure 3. Location of study sites.

Table 2 . Growth intercept for all trees grouped by similar sites.

Tree Number	Stand A&B GI^1_{BH}	Tree Number	Stand C GI_{BH}	Tree Number	Stand D GI_{BH}	Tree Number	Stand E GI_{BH}
1	2.24	9	2.70	17	2.30	25	2.62
2	2.99	10	2.67	18	2.55	26	2.79
3	1.89	11	2.45	19	2.57	27	2.74
4	2.89	12	2.73	20	2.71	28	3.07
5	2.75	13	2.27	21	3.03	29	2.59
6	2.74	14	2.43	22	2.51	30	2.58
7	2.51	15	2.26	23	2.62	31	3.01
8	2.91	16	2.54	24	3.00	32	2.74

GI^1_{BH} = total length of 5 internodes beginning at the first whorl above breast height (BH)

Units = m

Crown Analysis and Measurement

Sample trees were felled and the first order branches were ranked according to their age. Small branches were severed from the bole with clippers. Large branches, however, were cut with a chainsaw which removed a saw kerf of 0.75 cm. First order branch annual internode lengths were measured to the nearest half centimetre. Both live and dead branches were measured. Anomalous features including forked or partially defoliated but living branches, branches adjacent to a damaged mainstem leader, browsed branches, and interfoliar branches were noted. The foliated portions of living branches were clipped and collected in kraft paper bags.

Mainstem internode lengths were measured with a steel-reinforced cloth tape to the nearest half centimetre. The diameter of the bole at each whorl was measured with a steel diameter tape to the nearest tenth of a centimetre, after all branches were severed from the bole.

Laboratory Procedure

Foliage was air-dried and the needle fascicles were then removed from the supporting shoots. The foliage was replaced into the bag, and both foliage and bag were oven-dried at 105° C for 24 hours. Bag plus foliage dry weights were determined to the nearest tenth of a gram. Net foliage dry weight was obtained by subtracting the mean oven-dry weight of a random sub-sample of bags from the total dry weight. The mean oven-dry bag weight, based on a sub-sample of 423 bags was 23.6 g. The standard error of the estimate was 0.5 g.

Initial Data Preparation

The length of the first internode of each first order branch, $\triangle L(i,j,l)$, has three components: the internode segment buried in the bole, the kerf lost if the branch was severed from the bole with the chainsaw, and the internode segment measured in the field. Field measurements of $\triangle L(i,j,l)$ were corrected by adding one-half the bole diameter at the appropriate whorl plus the kerf where necessary. In the case of branches removed with clippers, the kerf is negligible and it was ignored. In the case of branches removed by chainsaw, a kerf of 0.75 cm was included in the corrected internode length.

The number of branches in the i th mainstem whorl was determined by examination of the live whorls only. Dead branches and mainstem internodes with obvious signs of past leader damage, and branches which were coded as having other various anomalous growth features were excluded from analysis.

THE MODEL

The system in Figure 4 and the following biological and mathematical relations describe the hypothesized development of the crown in P. resinosa. Crown dynamics are controlled by a combination of genetic and environmental factors. The excurrent branching pattern of P. resinosa may be explained in terms of strong apical control (Brown et al. 1967). Annual height increment is largely determined by site quality, age, and the genetic constitution of the individual tree (Carmean 1975, Mitchell 1975).

Modelling height growth was not the primary objective of this study. Height growth based on measurements of the mainstem internode lengths and age in P. resinosa has been successfully modelled by Hahn and Carmean (1980). Their model is based on generalizations of the Richards' function (Richards 1959; Monserud 1975) and reflects the changes that occur in the cumulative height increment of a tree as it ages (Assmann 1970). Site index is included as an independent variable and accounts for the rate and pattern of height growth that is directly related to site quality (Carmean 1975).
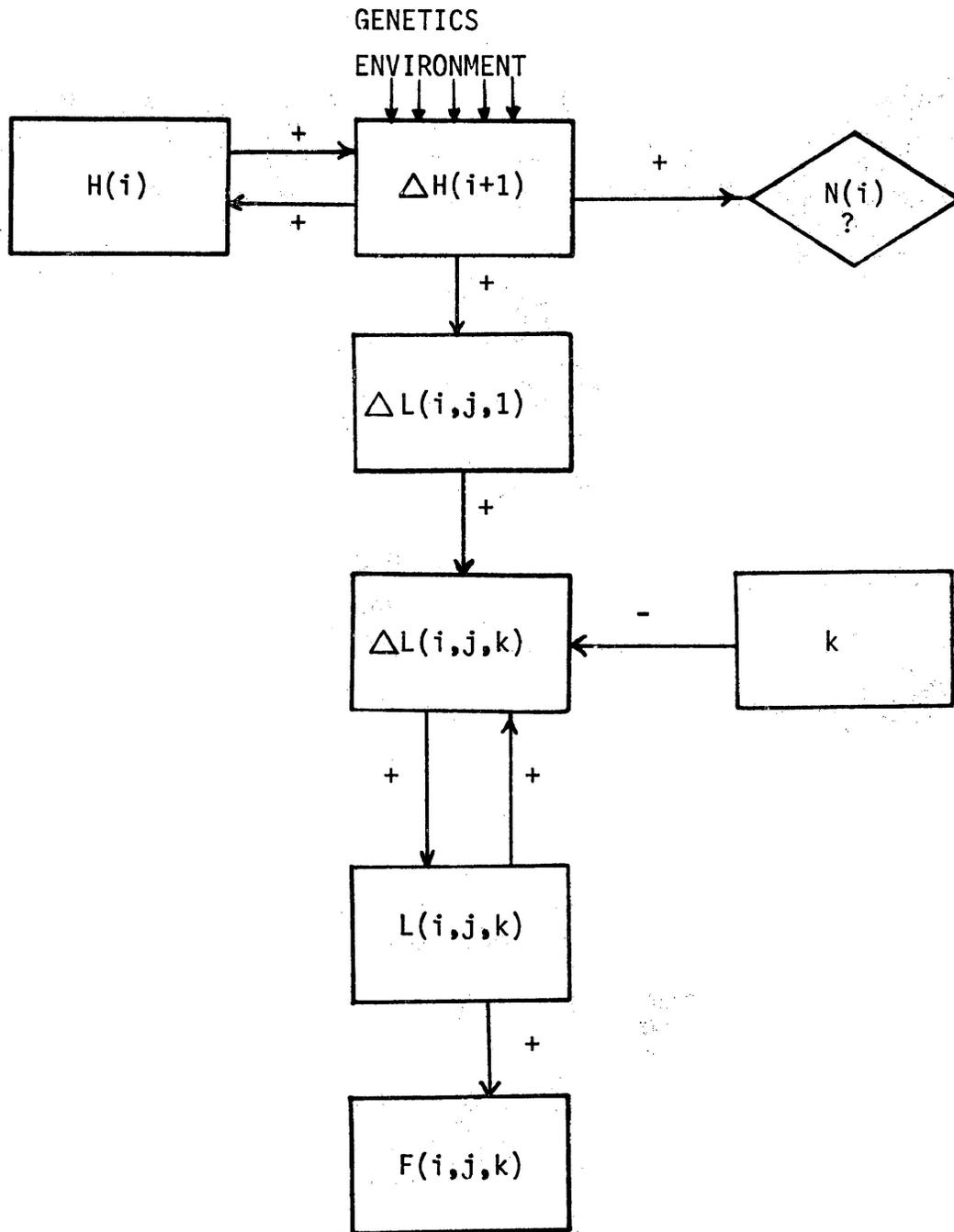
Figure 4. Material components and communicating processes of the crown dynamics system of Pinus resinosa Ait. Arrows indicate either a positive, +, or negative, -, feedback mechanism. For interpretation of symbols see text.

Cannell (1974) has suggested a positive, linear relationship between the number of lateral branches, and the length of the parent shoot on which the laterals were predetermined as buds prior to extension growth. Thus, the number of branches in the i th mainstem whorl, $N(i)$, may be expressed as a function of the length of the terminal leader on which they occurred as lateral buds in the season prior to their extension growth. This past terminal leader length corresponds to the mainstem internode length which subtends each branch whorl, $\triangle H(i)$. Symbolically,

(3) $N(i) = f_1(\triangle H(i))$, i = 2,3,4...

In the genus <u>Pinus</u>, however, the inception of the branch-forming buds occurs two years prior to their extension growth. Thus, the number of branches in the i th mainstem whorl as a function of the length of the terminal leader at the time of lateral bud inception should also be investigated. This past leader length corresponds to the second mainstem internode below each appropriate branch whorl, $\triangle H(i-1)$. The general mathematical relationship is

(4) $N(i) = f_2(\triangle H(i-1))$, i = 2,3,4...

The extension increment of branches in their first growing season, $\triangle L(i,j,1)$, is assumed to be unobstructed and influenced by the concurrent height increment, $\triangle H(i+1)$. Evidence of strong apical control supports this hypothesis (Kramer and Kozlowski 1979). In mathematical terms,

$$(5) \qquad \triangle L(i,j,1) = f_3(\triangle H(i+1)), \quad i = 2,3,4\ldots$$

where $\triangle L(i,j,1)$ represents the extension increment of the j th branch in the i th mainstem whorl during its first growing season, and $\triangle H(i+1)$ represents the concurrent height increment.

Subsequent extension increments of a lateral branch, $\triangle L(i,j,k)$, depend upon its age, k, total branch length at the beginning of the growing season, $L(i,j,k-1)$, tree vigour, and environmental conditions (Cochrane and Ford 1978). The relative annual extension increment of the j th branch in the i th mainstem whorl at the end of its k th growing season, $G(i,j,k)$, may be defined as:

$$(6) \qquad G(i,j,k) = \frac{\triangle L(i,j,k)}{L(i,j,k-1)}, \qquad k = 2,3,4\ldots$$

Cursory inspection of the current season extension increment of the first order branch axes of a coniferous tree reveals a gradual decrease in length from the top of the crown to its base (Kozlowski and Ward 1961; Forward and Nolan 1964; Mitchell 1969, 1975). This is one reason why the crown resembles a paraboloid more closely than a cone. Since the age of a branch reflects its position within the crown, the relative annual branch extension increment (Equation 1) may be expressed as a function of branch age, k. In mathematical terms,

(7) $G(i,j,k) = f_4(k)$, $k = 2,3,4\ldots$

The dry weight of foliage supported by a branch can be related to various exterior branch dimensions (Riedacker 1971; Ledig 1974; Ek 1979). Riedacker (1971), however, points out that branch age is an important parameter to consider in such regressions.

The original quantity of foliage, however, does not stay constant as it ages (Kinerson et al. 1974; Reed 1980). Some foliage biomass is lost through either abiotic or biotic factors. Thus, branch age must be incorporated into regressions that estimate the total foliage dry weight supported by a branch from some

exterior branch dimension. Branch age is useful because it reflects the relative position of a branch within the crown. In this study, the total dry weight of foliage supported by a first order branch is estimated from the current season length of its axis at the time of sampling. The effect of branch age on the relationship between total foliage dry weight and branch length is unknown. Thus, it is useful to develop a family of equations which relates the total foliage dry weight of the j th branch inserted into the i th mainstem whorl, $F(i,j,k)$, to its length. For a tree at the end of its n th growing season, the general relationship is:

(8) $\qquad F(n-k,j,k) = f_5(L(n-k,j,k))$, $k = 1,2,3...,n-2$.

RESULTS

Branch Production

The sample trees were stratified by stand location
and randomly divided into two independent data sets which
are referred to as the calibration data set and the
validation data set, respectively.

A regression analysis of the calibration data plotted
in Figure 5 revealed no relationship between the number of
branches per whorl, $N(i)$, and total tree age at the time
of whorl bud inception, $i-1$. The regression was not
significant ($P = 0.05$; Equation 1, Table 3). Simple
linear regression of the number of branches per whorl as a
function of the length of the terminal leader at the time
of whorl bud inception, $\triangle H(i-1)$, (Figure 6) revealed a
weak, but significant relationship ($P = 0.05$; Equation 3,
Table 3). A better linear relationship, however, was
found between the number of branches per whorl and the
length of the terminal leader on which they occurred as
whorl buds in the season prior to their extension growth,
$\triangle H(i)$, (Figure 7 and Equation 2, Table 3). Since even
the best of these correlations was weak, the number of
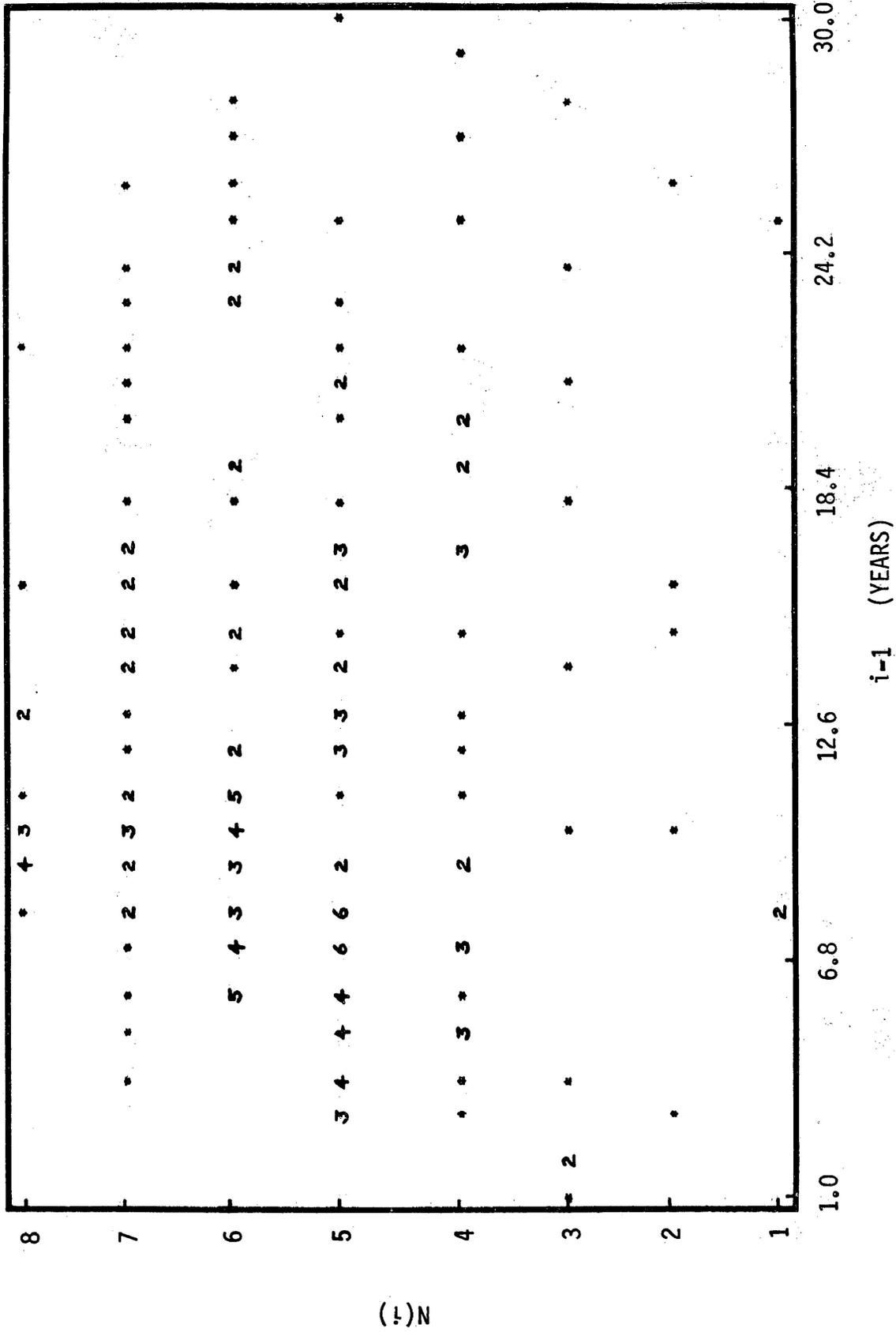
Figure 5.   The number of branches per whorl, $N(i)$, as a function of total tree age at the time of whorl bud inception, $i-1$. (Source: Calibration Data Set).

Table 3. Estimation of the number of branches per whorl as functions of total tree age at the time of whorl bud inception, terminal leader length on which the whorl branches occurred as whorl buds prior to extension growth, and terminal leader length at the time of whorl bud inception, respectively (Source: Calibration Data Set).

Relationship[1]	Equation	r^2	$S_{y.x}$	n	Equation number
N(i) : i-1	$N(i) = [6.30 \times 10^{-5}][i-1] + 5.37$	0.00 ns *	0.02	180	1
N(i) : $\Delta H(i)$	$N(i) = 4.64[\Delta H(i)] + 2.91$	0.23	1.34	180	2
N(i) : $\Delta H(i-1)$	$N(i) = 3.14[\Delta H(i-1)] + 3.78$	0.12	1.43	180	3

[1] N(i) = number of branches inserted into the i th whorl

i-1 = tree age at the time of whorl bud inception (years)

$\Delta H(i)$ = length of terminal leader on which the whorl branches occurred as whorl buds (m)

$\Delta H(i-1)$ = length of terminal leader at the time of whorl bud inception (m)

ns * not significant at the 0.05 level

Figure 6. The number of branches per whorl, N(i), as a function of the length of the terminal leader at the time of whorl bud inception, ΔH(i-1), (Source: Calibration Data Set.

Figure 7. The number of branches per whorl, N(i), as a function of the length of the terminal leader on which the whorl branches occurred as whorl buds prior to extension growth, ΔH(i). (Source: Calibration Data Set).

branches per whorl was treated as a purely stochastic phenomenon.

The Monte Carlo method is a common technique used to simulate stochastic processes (Kleijnen 1974). Each stochastic variable is represented by an appropriate probability density function (p.d.f.). The values of stochastic variables are then simply drawn at random from their respective simulated distributions.

Figure 8a shows the frequency distribution of whorls sorted by the number of branches per whorl from the calibration data set. The number of branches per whorl can be simulated by specifying an appropriate discrete probability density function and the numerical values of its parameters. The Poisson distribution is biologically meaningful because it allows the generation of discrete, random variables between zero and infinity. Parameters to calculate the Poisson probabilities were estimated from the sample whorl population data from the calibration data set (Table 4). The methodology outlined by Kossack and Henschke (1975) was used to fit the Poisson probability density function to discrete, empirical data. Goodness-of-fit was tested by the chi-square statistic:
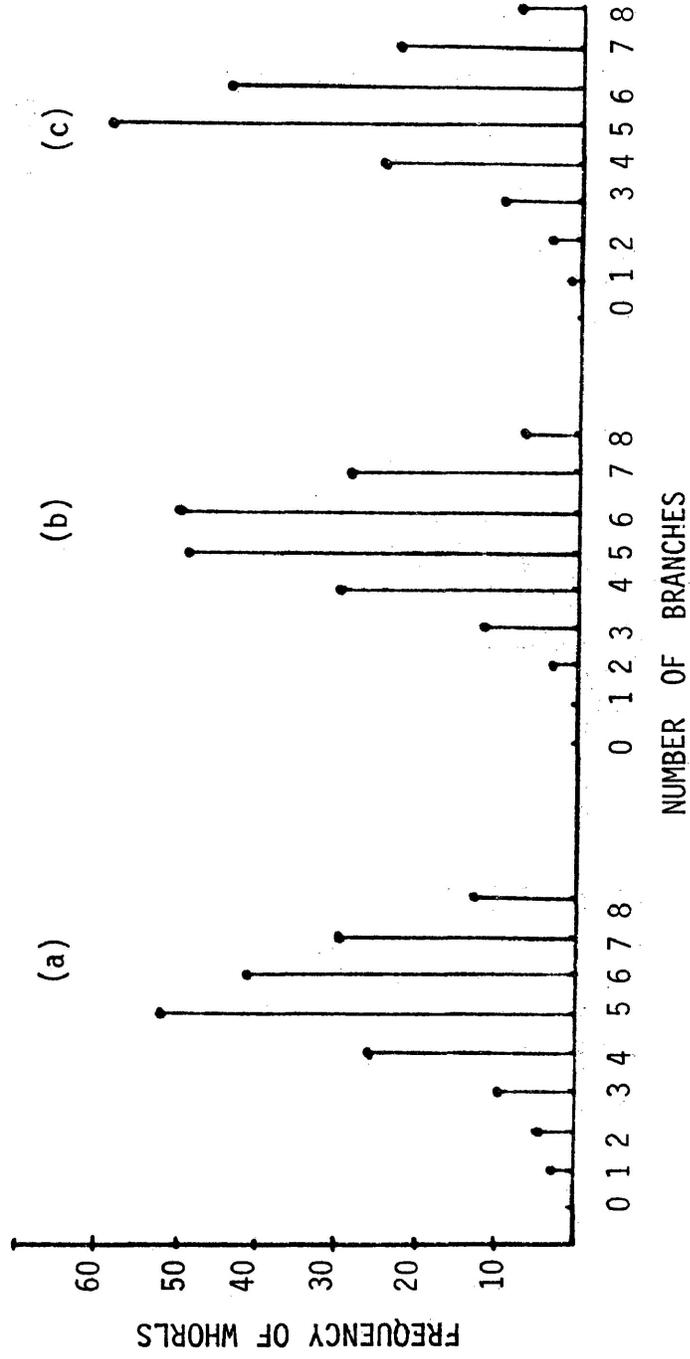
Figure 8 . The frequency distribution of the number of whorls sorted by the number of branches per whorl (a) from the calibration data set (b) from that estimated by the binomial model (c) from the validation data set .

Table 4 . Frequency distribution of whorls sorted by the number of branches per whorl from the calibration data set.

Number of Branches per Whorl	Frequency of Whorls	Total Number of Branches
0	0	0
1	3	3
2	5	10
3	10	30
4	26	104
5	52	260
6	41	246
7	30	210
8	13	104
Total	180	967

Mean number of branches per whorl for the sample population = 967/180 = 5.372

$$(9) \qquad X^2 = \sum_{i=1}^{n} (O_i - E_i)^2 / E_i$$

where O_i represents the observed frequency of values in the i th class, and E_i represents the expected frequency of values in the i th class (Kossack and Henschke 1975).

The results of the chi-square test are presented in Table 5. Since the calculated chi-square value of 47.02 is greater than the tabulated chi-square value of 12.59 ($X^2_{0.05,6}$) the Poisson model was rejected at the 95 percent confidence level.

The binomial p.d.f. was considered as an alternative to the Poisson distribution. The binomial distribution, however, limits the generation of discrete, random variables between zero and a specified range (Chatfield 1975). Examination of both the calibration and validation data sets revealed that the maximum number of branches observed in any whorl was eight. Parameters of the binomial distribution were also estimated from the sample whorl population data from the calibration data set according to the methodology outlined by Kossack and Henschke (1975) (Table 4). Results of the chi-square test are presented in Table 6. The calculated chi-square value of 8.01 is less than the tabulated chi-square value of

Table 5. Comparison of the observed frequency distribution of whorls from the calibration data set with that simulated by the Poisson probability density function.

Number of branches per whorl	Observed frequency of whorls	Poisson probability $x = 5.372$	Poisson frequency of whorls	Chi-square statistic (df = n-2)
0	0	0.005	1	
1	3	0.025	4	4.76
2	5	0.067	12	
3	10	0.120	22	6.55
4	26	0.161	29	0.31
5	52	0.173	31	14.22
6	41	0.155	28	6.04
7	30	0.119	21	3.86
8	13	0.080	14	
9	0	0.048	9	
10	0	0.026	5	11.28
11	0	0.013	2	
12	0	0.006	1	
13	0	0.002	1	
Total	180	1.000	180	47.02 *

Class values ≤ 5 were summed to the next highest class

* significant at the 0.05 level

Table 6. Comparison of the observed frequency distribution
          of whorls from the calibration data set with that
          simulated by the binomial probability density
          function.

Number of branches per whorl	Observed frequency of whorls	Binomial probability $p = 0.672$ $n = 8$	Binomial frequency of whorls	Chi-square statistic $(df = n-2)$
0	0	0.000	0	
1	3	0.002	3	0.50
2	5	0.016	5	
3	10	0.065	12	
4	26	0.166	30	0.53
5	52	0.271	49	0.18
6	41	0.277	50	1.62
7	30	0.162	29	0.03
8	13	0.041	7	5.14
Total	180	1.000	180	8.01 ns *

Class values ≤5 were summed to the next highest class

ns * = not significant at the 0.05 level

9.49 ($X^2_{0.05,4}$). Thus, the binomial model was accepted at the 95 percent confidence level.

In the model, the number of branches per whorl is generated from the binomial distribution with parameters:

$$(10) \quad Pr(N(i) = r) = \binom{8}{r} 0.672^r (1-0.672)^{8-r}; \quad r = 0,1,2...8.$$

where r represents the number of branches per whorl, 8 is the maximum observed number of branches per whorl, and 0.672 is the calculated mean number of branches per whorl for the sample whorl population divided by eight (Table 4).

Simulation of the number of branches per whorl proceeds in Monte Carlo-fashion by drawing a random number, X, from the continuous, uniform distribution on the interval [0,1]. The number of branches per whorl, N(i), is then assigned according to the following probability statements which are derived from the binomial model (Equation 10; Table 6):

$$\begin{array}{llll}
& \text{if} & [0.000 \le X \le 0.002], & N(i) = 1 \\
& \text{if} & [0.002 < X \le 0.018], & N(i) = 2 \\
& \text{if} & [0.018 < X \le 0.083], & N(i) = 3 \\
(11) & \text{if} & [0.083 < X \le 0.249], & N(i) = 4 \\
& \text{if} & [0.249 < X \le 0.520], & N(i) = 5 \\
& \text{if} & [0.520 < X \le 0.797], & N(i) = 6 \\
& \text{if} & [0.797 < X \le 0.959], & N(i) = 7 \\
& \text{if} & [0.959 < X \le 1.000], & N(i) = 8
\end{array}$$

The binomial probability that $N(i) = 0$ is so small (1.4×10^{-4}) that I assumed it to be equal to zero (Table 6).

Comparison of the observed number of branches per whorl (Figure 8c) with that simulated by the binomial model (Figure 8b) from the validation data set indicated no significant differences $(P = 0.05)$ between the two distributions ($X^2_{0.05,4} < 9.49$). Table 7 presents the results of the chi-square test.

Table 7.   Comparison of the observed frequency distribution
of whorls from the validation data set with that
simulated by the binomial probability density
function.

Number of branches per whorl	Observed frequency of whorls	Binomial frequency of whorls	Chi-square statistic (df = n-2)
0	0	0	
1	1	1	0.06
2	4	0	
3	10	15	
4	25	26	0.04
5	59	48	2.52
6	44	44	0.00
7	23	34	3.56
8	8	6	0.67
Total	174	174	6.85 ns *

Class intervals ≤ 5 were summed to the next highest class

ns * = not significant at the 0.05 level

Branch Extension Increment: Year One

Figure 9 shows a plot of the extension increment of branches in their first growing season, $\triangle L(i,j,1)$, against their concurrent height increments, $\triangle H(i+1)$, from the calibration data set. Examination of the plotted data suggested that for any given height increment there exists an upper bound on the concurrent extension increment of branches in their first growing season.   To test this hypothesis, the maximum extension increment of one-year-old branches observed in each whorl was identified and plotted against its concurrent height increment (Figure 10). The relationship appeared linear and so simple linear regression was performed assuming the model:

(12) $\triangle L(i,j,1)_{Maximum} = a + b[\triangle H(i+1)]$

where $\triangle L(i,j,1)_{Maximum}$ denotes the maximum extension increment (cm) of a branch in its first growing season (k=1) inserted into the i th whorl, and $\triangle H(i+1)$ denotes its concurrent height increment. The resulting equation,

(13) $\triangle L(i,j,1)_{Maximum} = 1.1 + 69.0[\triangle H(i+1)]$
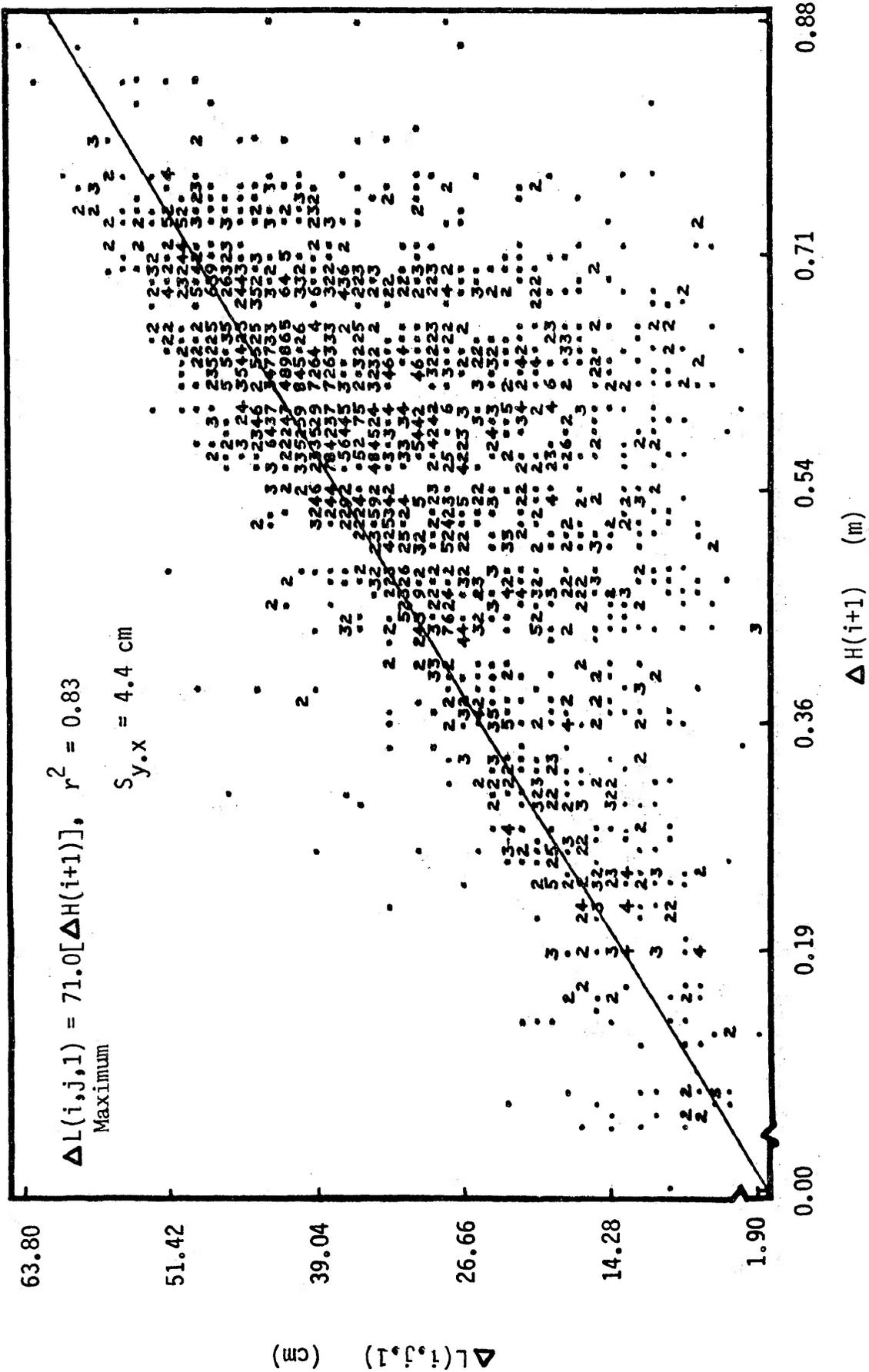
Figure 9. The extension increment of branches in their first growing season, $\Delta L(i,j,1)$, as a function of their concurrent height increments, $\Delta H(i+1)$. (Source: Calibration Data Set).
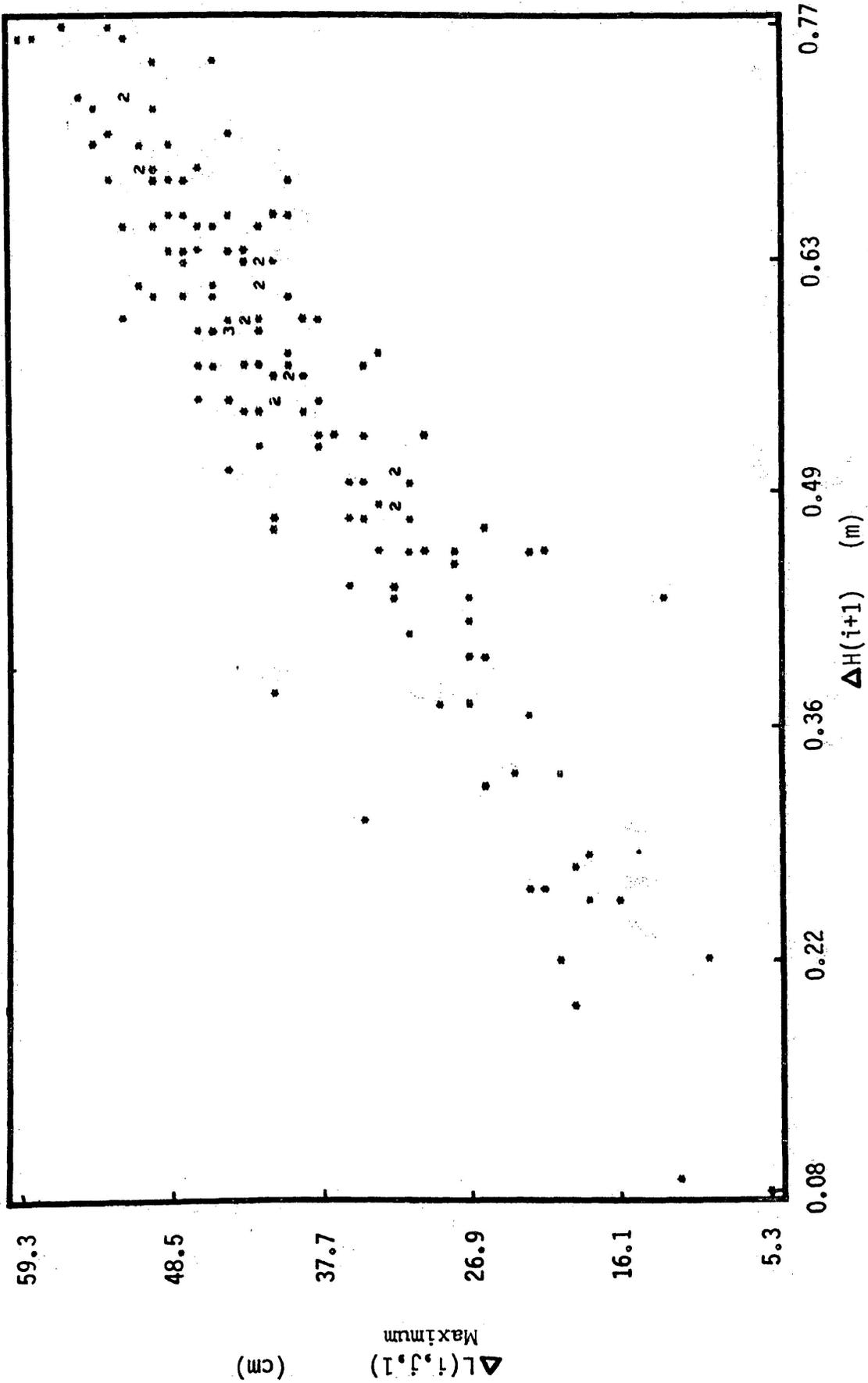
Figure 10. The maximum extension increments of branches in their first growing season, $\Delta L(i,j,1)_{Maximum}$, as a function of their concurrent height increments, $\Delta H(i+1)$. (Source: Calibration Data Set).

has a coefficient of determination (r^2) of 0.83, and a standard error of the estimate of 4.4 cm. The regression was significant at the 95 percent confidence level.

Biological considerations suggest that the regression should pass through the origin. Since the intercept in Equation 13 was not significantly different (P = 0.05) from zero, the model $\Delta L(i,j,1) = b[\Delta H(i+1)]$ was adopted and its coefficient estimated (Steel and Torrie 1960; Freese 1964). The result was

(14) $\Delta L(i,j,1)_{\text{Maximum}} = 71.0[\Delta H(i+1)]$

Equation 14 is superimposed on the total data set in Figure 9.

Equation 14 can be viewed as the biological potential for extension increment of branches in their first growing season. As Figure 9 clearly shows, most branches do not achieve this potential; only relatively few branches exceed it. The observed extension increment of branches in their first growing season was treated as a stochastic process which is bounded somewhat loosely about Equation 14. In order to develop a stochastic model of this process, each observed extension increment of branches in their first growing season was expressed as a

proportion of the hypothesized biological potential defined by Equation 14. Mathematically this is equivalent to a ratio:

(15) $R1 = \triangle L(i,j,1)/\triangle L(i,j,1)_{Maximum}$

Table 8 and Figure 11 show the frequency distribution of R1 values from the calibration data set by 10 percent class intervals.

R1 was hypothesized to be a stochastic variable that can be simulated by specifying an appropriate p.d.f. and the numerical values of its parameters. A continuous probability density function that can assume a variety of shapes is the 2-parameter Weibull p.d.f. (Bailey and Dell 1973).

(16) $F(x) = \frac{\psi}{\beta}[\ x\ ]^{\psi} \cdot e^{-x^{(\psi/\beta)}}$; $x > 0,\ \beta > 0,\ \psi > 0$

From the observed frequency distribution of R1 values (Table 8), the scale, β, and shape, ψ, parameters were estimated to be 0.895 and 3.633, respectively. The parameters of the Weibull p.d.f. were estimated according to the methodology outlined by Bailey and Dell (1973) and Bailey (1974). Goodness-of fit was tested by the chi-square statistic (Table 9). The test suggests that

Table 8. Frequency distribution of $R1^1$ values from the calibration data set.

Class code	Class interval of R1 values	Absolute frequency	Relative frequency	Cumulative relative frequency
1	0.00 - 0.10	2	0.002	0.002
2	0.10 - 0.20	15	0.017	0.019
3	0.20 - 0.30	27	0.031	0.050
4	0.30 - 0.40	40	0.046	0.098
5	0.40 - 0.50	54	0.063	0.159
6	0.50 - 0.60	56	0.065	0.224
7	0.60 - 0.70	103	0.120	0.344
8	0.70 - 0.80	100	0.116	0.460
9	0.80 - 0.90	140	0.163	0.623
10	0.90 - 1.00	180	0.209	0.832
11	1.00 - 1.10	104	0.121	0.953
12	1.10 - 1.20	29	0.034	0.987
13	1.20 - 1.30	6	0.007	0.994
14	1.30 $^+$	5	0.006	1.000
Total		861	1.000	

[1]R1 is defined in Equation 15 as the ratio of the observed extension increments of branches in their first growing season to the hypothesized biological potential defined by Equation 14.
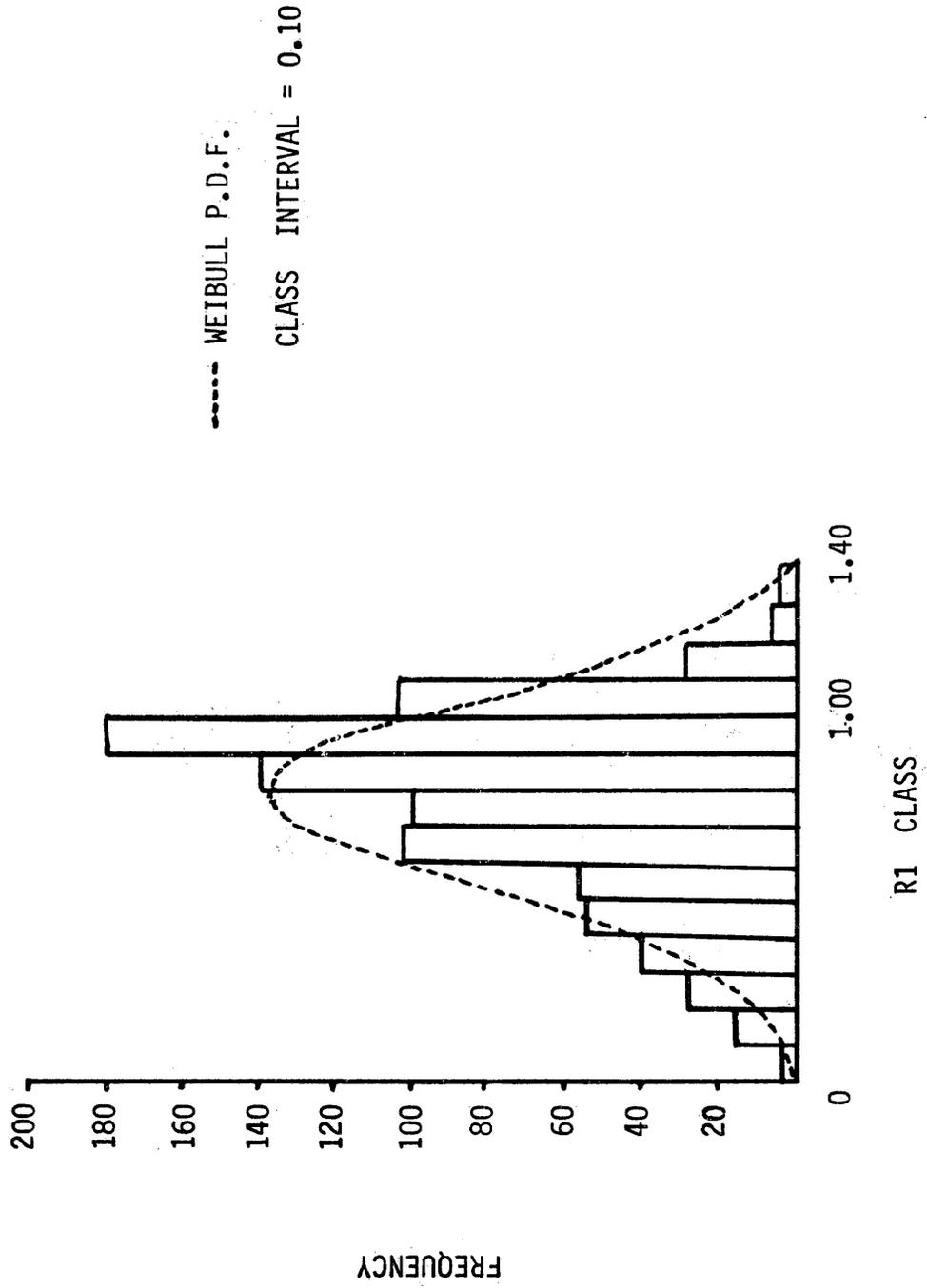
Figure 11. The observed frequency distribution of R1 values and those simulated by the Weibull probability density function (Source: Calibration Data Set).

Table 9. Comparison of the observed frequency distribution of Rl[1] values from the calibration data set with that simulated by the Weibull probability density function.

Class code	Class mid-point of Rl value	Frequency of Rl value	Weibull probability B = 0.895 C = 3.633	Weibull frequency of Rl value	Chi-square statistic (df = n-3)
1	0.05	2	0.001	1	
2	0.15	15	0.005	4	32.89
3	0.25	27	0.017	14	
4	0.35	40	0.039	34	1.06
5	0.45	54	0.071	61	0.80
6	0.55	56	0.107	92	14.09
7	0.65	103	0.141	121	2.68
8	0.75	100	0.160	138	10.46
9	0.85	140	0.156	134	0.27
10	0.95	180	0.130	113	39.72
11	1.05	104	0.090	78	8.67
12	1.15	29	0.051	44	5.11
13	1.25	6	0.024	20	9.80
14	1.35	5	0.008	7	0.57
Total		861	1.000	861	126.12 *

Class values ≤ 5 were summed to the next highest class

* significant at the 0.05 level

[1] Same footnote as Table 8.

the observed frequency distribution of Rl values is significantly different (P = 0.05) from that simulated by the Weibull model. Therefore, the model was rejected.

It is possible that another standard p.d.f. could be used to represent the observed frequency distribution of Rl values, but none were tried. Instead a method of randomly generating Rl values was derived directly from the observed frequency distribution of Rl values. To assign Rl in such a way that the desired probabilities are in effect, a random number, X, is drawn from the continuous, uniform distribution on the interval [0,1]. Rl is then assigned according to probability statements derived from the cumulative frequency of Rl values (Table 8) as follows:

$$
\begin{array}{lll}
\text{if} & [\ 0.000 \le X \le 0.002\ ], & R1 = 0.05 \\
\text{if} & [\ 0.002 < X \le 0.020\ ], & R1 = 0.15 \\
\text{if} & [\ 0.020 < X \le 0.051\ ], & R1 = 0.25 \\
\text{if} & [\ 0.051 < X \le 0.098\ ], & R1 = 0.35 \\
(17) \quad \text{if} & [\ 0.098 < X \le 0.160\ ], & R1 = 0.45 \\
\text{if} & [\ 0.160 < X \le 0.225\ ], & R1 = 0.55 \\
\text{if} & [\ 0.225 < X \le 0.345\ ], & R1 = 0.65 \\
\text{if} & [\ 0.345 < X \le 0.461\ ], & R1 = 0.75 \\
\text{if} & [\ 0.461 < X \le 0.624\ ], & R1 = 0.85
\end{array}
$$

if   [0.624 < X ≤ 0.833],   R1 = 0.95

if   [0.833 < X ≤ 0.954],   R1 = 1.05

if   [0.954 < X ≤ 0.987],   R1 = 1.15

(17)   if   [0.987 < X ≤ 0.994],   R1 = 1.25

if   [0.994 < X ≤ 0.995],   R1 = 1.35

if   [0.995 < X ≤ 0.998],   R1 = 1.45

if   [0.998 < X ≤ 1.000],   R1 = 1.70

The extension increment of branches in their first growing season is then calculated as the product of $\triangle L(i,j,1)_{Maximum}$, and R1:

(18) $\triangle L(i,j,1) = R1[\triangle L(i,j,1)_{Maximum}]$

where $\triangle L(i,j,1)_{Maximum}$ is calculated from Equation 14 and R1 is calculated from Equations 17.

Equation 18 was developed with data from the calibration data set. Comparison of the observed and simulated frequency distributions of the extension increments of branches in their first growing season from the validation data set indicated no significant differences at the 95 percent confidence level ($X^2_{0.05, 11}$ < 19.68). Table 10 presents the results of the chi-square test.

Table 10. Frequency distribution of observed and simulated extension increments of branches in their first season (Source: Validation Data Set).

Class Code	Class Interval of Extension Growth (cm)	Observed Frequency	Simulated Frequency	Chi-square Statistic (df=n-1)
1	0.0 - 5.0	8	8	0.00
2	5.0 - 10.0	29	29	0.00
3	10.0 - 15.0	65	61	0.26
4	15.0 - 20.0	93	91	0.04
5	20.0 - 25.0	82	94	1.53
6	25.0 - 30.0	109	122	1.38
7	30.0 - 35.0	115	98	2.95
8	35.0 - 40.0	128	131	0.07
9	40.0 - 45.0	120	111	0.73
10	45.0 - 50.0	67	68	0.01
11	50.0 - 55.0	24	21	0.43
12	55.0 - 60.0	8	14	2.57
Total		848	848	9.97 ns *

ns *   not significant at the 0.05 level

Branch Extension Increment: 2-Years-Old and Older

A model of the extension increment of branches 2-years-old and older was based on the relative annual branch extension increment, $G(i,j,k)$, (Equation 1). In order to ensure equal representation of branches by age in the sample data, both the calibration and validation data sets were pooled. Branch data were then stratified by branch age and randomly reallocated to form two new calibration and validation data sets of equal size. Relative annual branch extension increment from the calibration data set is plotted against branch age in Figure 12. Examination of Figure 12 suggested that for any given age of a branch there exists an upper bound on the associated relative annual branch extension increment. To test this hypothesis, the maximum relative annual branch extension increment for branches of each age was identified and plotted against the corresponding branch age. The relationship between the maximum relative annual branch extension increment, $G(i,j,k)_{Maximum}$, and branch age, k, appeared non-linear (Figure 13). An acceptable fit was obtained with the following allometric model:

(19) $G(i,j,k)_{Maximum} = ak^b$, $k = 2,3,4...$
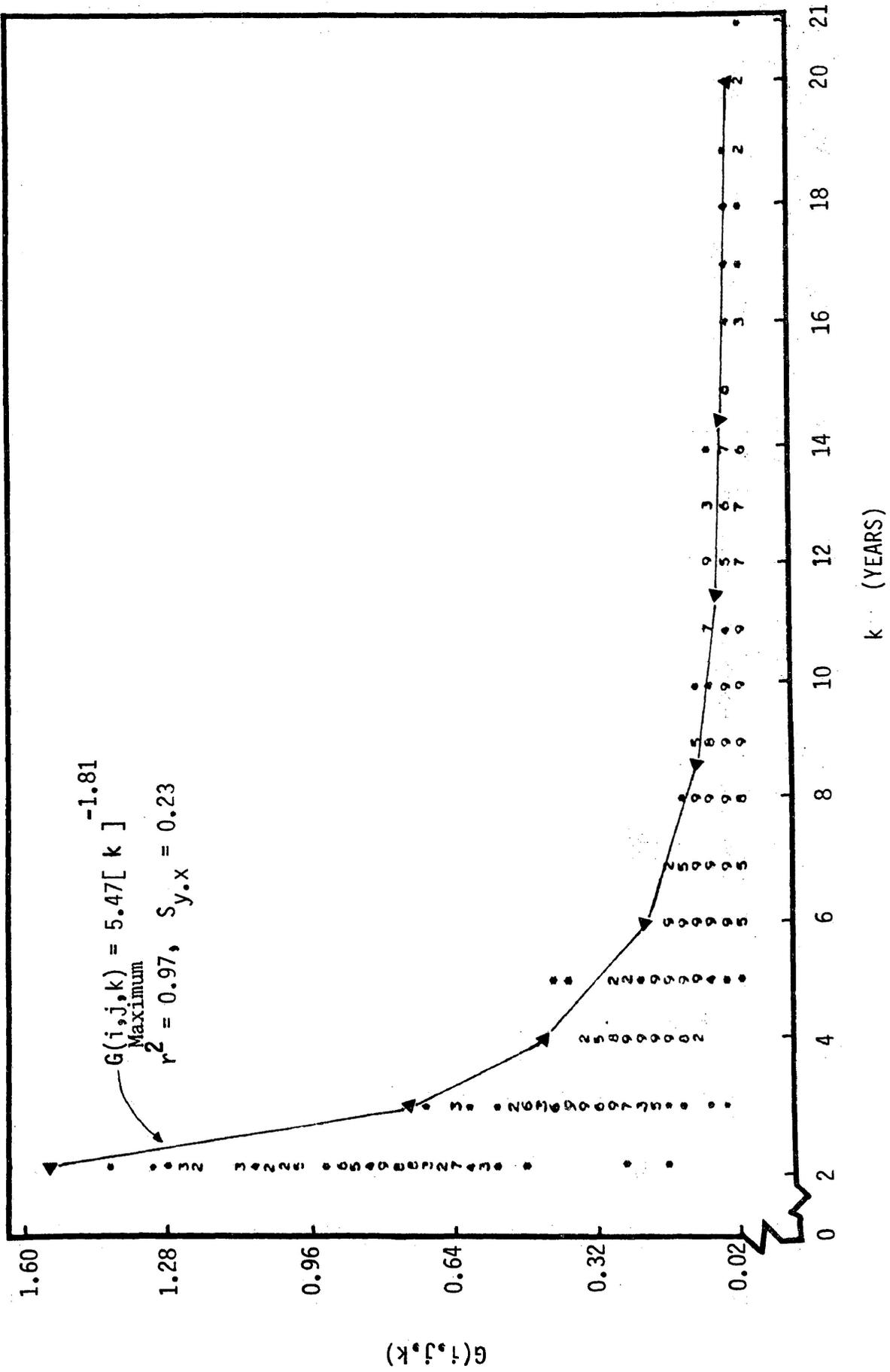
Figure 12. The relative annual branch extension increment, G(i,j,k), as a function of branch age, k, (Source: Calibration Data Set).

$$G(i,j,k)_{Maximum} = 5.47[\ k\ ]^{-1.81}$$

$$r^2 = 0.97, \quad S_{y.x} = 0.23$$
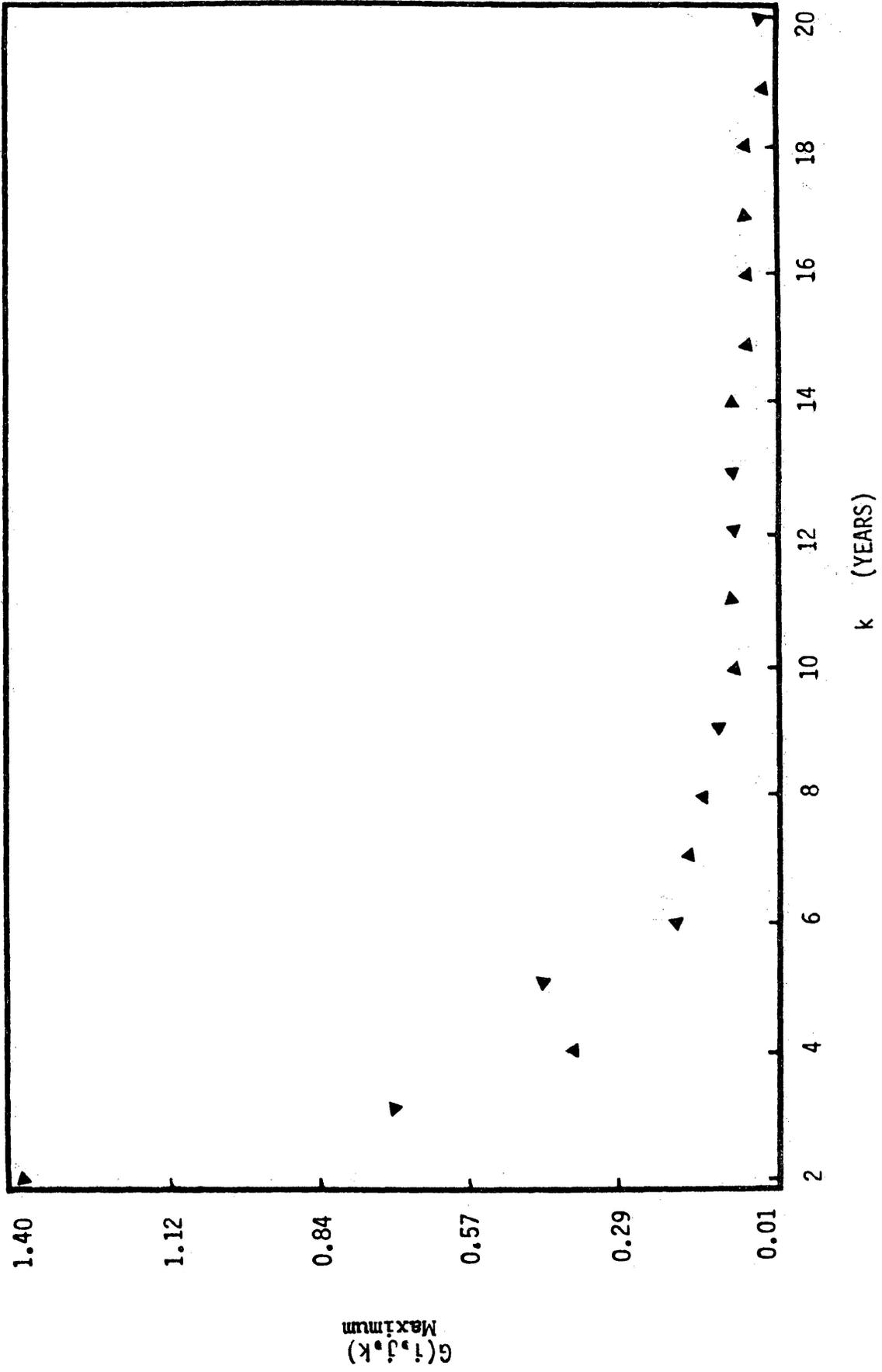
Figure 13. The maximum relative annual branch extension increment, G(i,j,k), as a function of branch age, k, (Source: Calibration Data Set).

The coefficients a and b were estimated by linear least-squares methods on the logarithmic transformation of Equation 19 (Freese 1964; Zar 1968). The retransformed values were corrected for bias by the method outlined by Baskerville (1972). The resulting equation,

$$(20) \qquad G(i,j,k) = 5.47[\ k \ ]_{\text{Maximum}}^{-1.81}$$

has a coefficient of determination (r^2) of 0.97, and a standard error of the estimate of 0.23. The regression was significant at the 95 percent confidence level. Equation 20 is superimposed on the total data set in Figure 12.

Equation 20 can be viewed as the biological potential relative annual extension increment that a branch of given age may attain after its first growing season. As Figure 12 clearly shows most of the calculated relative annual branch extension increments of any given branch age do not achieve this potential; only very few exceed it. The extension increment of branches after their first growing season was treated as a stochastic process which is bounded somewhat loosely about Equation 20. In order to develop a stochastic model of this process, each observed relative annual extension increment of branches was expressed as a proportion of the hypothesized

biological potential defined by Equation 20. Mathematically, this is equivalent to a ratio:

(21)   R2 = G(i,j,k)/G(i,j,k), k = 2,3,4...
                            Maximum

Table 11 and Figure 14 show the frequency distribution of R2 values from the calibration data set by 10 percent class intervals.

R2 was hypothesized to be a stochastic variable that can be simulated by specifying an appropriate p.d.f. and the numerical values of its parameters. An attempt was made to fit the 2-parameter Weibull p.d.f. to the observed frequency distribution of R2 (Table 11). From these data, the scale, β, and shape, ψ, parameters were estimated to be 0.513 and 1.846, respectively. Goodness-of fit was tested by the chi-square statistic and the results of the test are presented in Table 12. The test suggests that the observed frequency distribution of R2 is significantly different (P = 0.05) from that simulated by the Weibull model. Therefore, this model was rejected.

Again it is possible that another standard p.d.f. could be used to represent the observed frequency distribution of R2, but none were tried. Instead, the

Table 11. Frequency distribution of $R2$[1] values from the calibration
data set.

Class code	Class interval of R2 values	Absolute frequency	Relative frequency	Cumulative relative frequency
1	0.00 - 0.10	44	0.064	0.064
2	0.10 - 0.20	70	0.101	0.165
3	0.20 - 0.30	63	0.091	0.256
4	0.30 - 0.40	103	0.149	0.405
5	0.40 - 0.50	128	0.185	0.590
6	0.50 - 0.60	102	0.147	0.737
7	0.60 - 0.70	76	0.110	0.847
8	0.70 - 0.80	35	0.051	0.897
9	0.80 - 0.90	28	0.040	0.938
10	0.90 - 1.00	25	0.036	0.974
11	1.00 - 1.10	11	0.016	0.990
12	1.10 - 1.20	4	0.006	0.996
13	1.20 - 1.30	2	0.003	0.999
14	1.30 - 1.40	0	0.000	0.999
15	1.40 $^+$	1	0.001	1.000
Total		692	1.000	

[1] $R2$ is defined in Equation 21 as the ratio of the observed relative
annual branch extension increment to the hypothesized biological
potential defined by Equation 20.
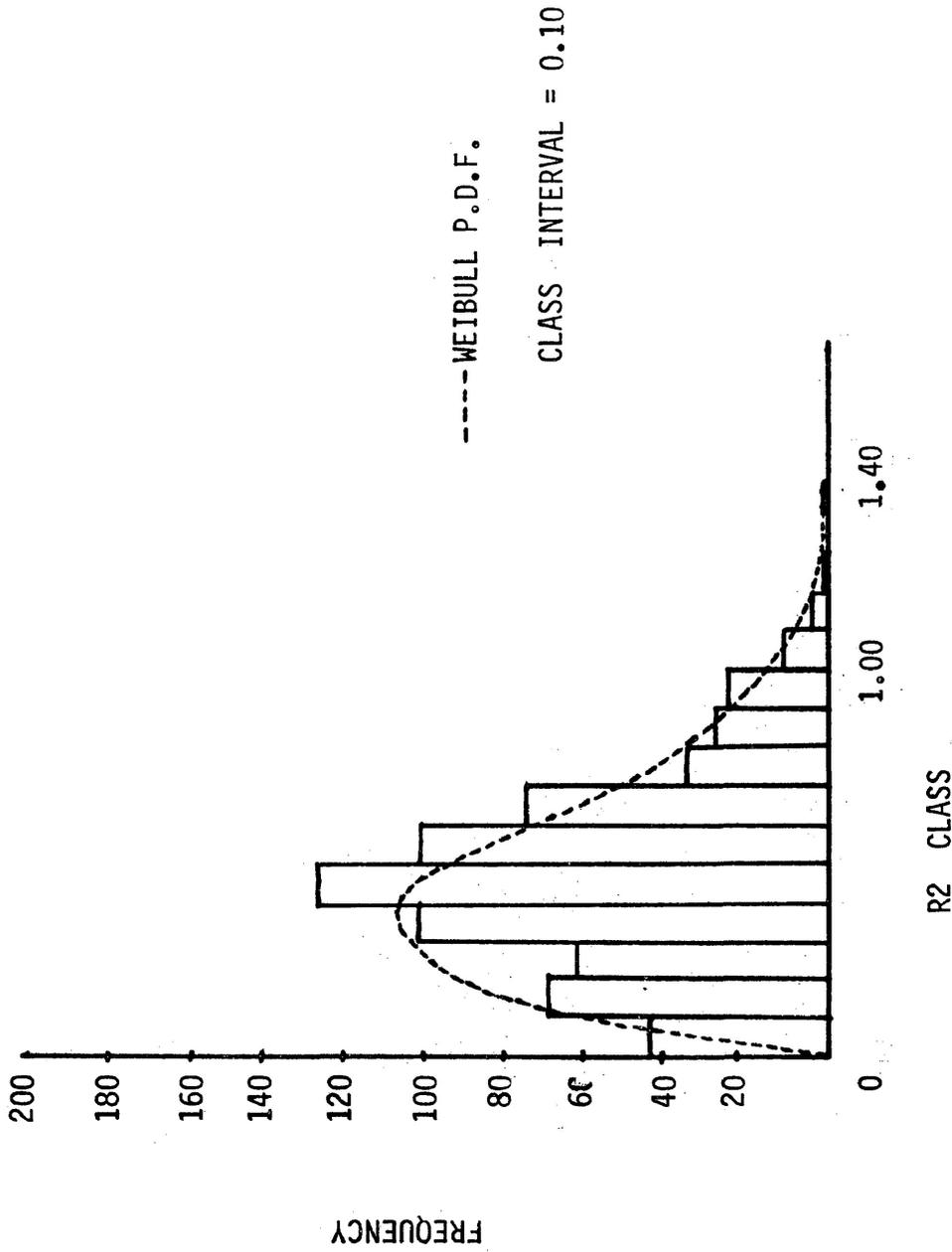
Figure 14. The observed frequency distribution of R2 values and those simulated by the Weibull probability density function (Source: Calibration Data Set).

Table 12. Comparison of the observed frequency distribution of R2 values from the calibration data set with that simulated with the Weibull probability density function.

Class code	Class mid-point of R2 value	Frequency of R2 value	Weibull probability B = 0.513 C = 1.846	Weibull frequency of R2 value	Chi-square statistic (df = n-3)
1	0.05	44	0.048	33	3.67
2	0.15	70	0.113	78	0.08
3	0.25	63	0.149	103	15.53
4	0.35	103	0.158	109	0.33
5	0.45	128	0.147	102	6.63
6	0.55	102	0.122	85	3.40
7	0.65	76	0.094	65	1.86
8	0.75	35	0.066	46	2.63
9	0.85	28	0.044	30	0.13
10	0.95	25	0.027	19	1.89
11	1.05	11	0.016	11	
12	1.15	4	0.009	6	
13	1.25	2	0.004	3	0.73
14	1.35	0	0.002	1	
15	1.45	1	0.001	1	
Total		692	1.000	692	36.88 *

Class values ≤ 5 were summed to the next highest class

* significant at the 0.05 level

observed frequency distribution of R2 was used in Monte Carlo-fashion to randomly generate simulated R2 values. To assign R2 in such a way that the desired probabilities are in effect, a random number, X, is drawn from the continuous, uniform distribution on the interval [0,1]. R2 is then assigned according to the following probability statements as specified by the cumulative relative frequency of R2 values (Table 11):

$$
\begin{array}{lll}
& \text{if} \quad [\ 0.000 \le X \le 0.064\ ], & R2 = 0.05 \\
& \text{if} \quad [\ 0.064 < X \le 0.165\ ], & R2 = 0.15 \\
& \text{if} \quad [\ 0.165 < X \le 0.256\ ], & R2 = 0.25 \\
& \text{if} \quad [\ 0.256 < X \le 0.405\ ], & R2 = 0.35 \\
& \text{if} \quad [\ 0.405 < X \le 0.590\ ], & R2 = 0.45 \\
(22) \quad & \text{if} \quad [\ 0.590 < X \le 0.737\ ], & R2 = 0.55 \\
& \text{if} \quad [\ 0.737 < X \le 0.847\ ], & R2 = 0.65 \\
& \text{if} \quad [\ 0.847 < X \le 0.897\ ], & R2 = 0.75 \\
& \text{if} \quad [\ 0.897 < X \le 0.938\ ], & R2 = 0.85 \\
& \text{if} \quad [\ 0.938 < X \le 0.974\ ], & R2 = 0.95 \\
& \text{if} \quad [\ 0.974 < X \le 0.990\ ], & R2 = 1.05 \\
& \text{if} \quad [\ 0.990 < X \le 1.000\ ], & R2 = 1.20
\end{array}
$$

The relative annual branch extension increment, $G(i,j,k)$, is then calculated as the product of $G(i,j,k)_{Maximum}$ and R2:

(23) $G(i,j,k) = R2[G(i,j,k)_{Maximum}]$, k = 2,3,4...

The extension increment of branches after their first growing season, $\triangle L(i,j,k)$, is simulated as follows:

(24) $\triangle L(i,j,k) = R2[G(i,j,k)_{Maximum}][L(i,j,k-1)]$, k = 2,3,4,...

where $L(i,j,k-1)$ denotes initial branch length, $G(i,j,k)_{Maximum}$ is calculated from Equation 20, and R2 is calculated from Equations 22. Equation 24 was developed with data from the calibration data set. To evaluate Equation 24, the validation data set was used to compare the observed frequency distributions of the current season branch extension increments and those simulated by the model (Table 13). Since the calculated chi-square value of 91.92 was greater than the tabulated chi-square value of 15.51 ($X^2_{0.05,8}$) the model was rejected at the 95 percent confidence level. Figure 15 shows the frequency distributions of the observed and simulated current season

Table 13.   Frequency distribution of the observed and simulated
             extension increments of branches after their first
             growing season (Source: Validation Data Set).

Class Code	Class Interval of Extension Growth (cm)	Observed Frequency	Simulated Frequency	Chi-square Statistic (df=n-1)
1	0.0 - 5.0	170	153	1.89
2	5.0 - 10.0	95	152	21.34
3	10.0 - 15.0	83	112	7.51
4	15.0 - 20.0	112	75	18.25
5	20.0 - 25.0	103	70	15.56
6	25.0 - 30.0	67	50	5.78
7	30.0 - 35.0	36	28	2.28
8	35.0 - 40.0	17	17	0.00
9	40.0 - 45.0	8	14	
10	45.0 - 50.0	0	6	
11	50.0 - 55.0	1	6	19.31
12	55.0 - 60.0	0	1	
13	60.0^{+}	0	8	
Total		692	692	91.92^{*}

Class values $\leqq 5$ were summed to the next highest class

*   significant at the 0.05 level
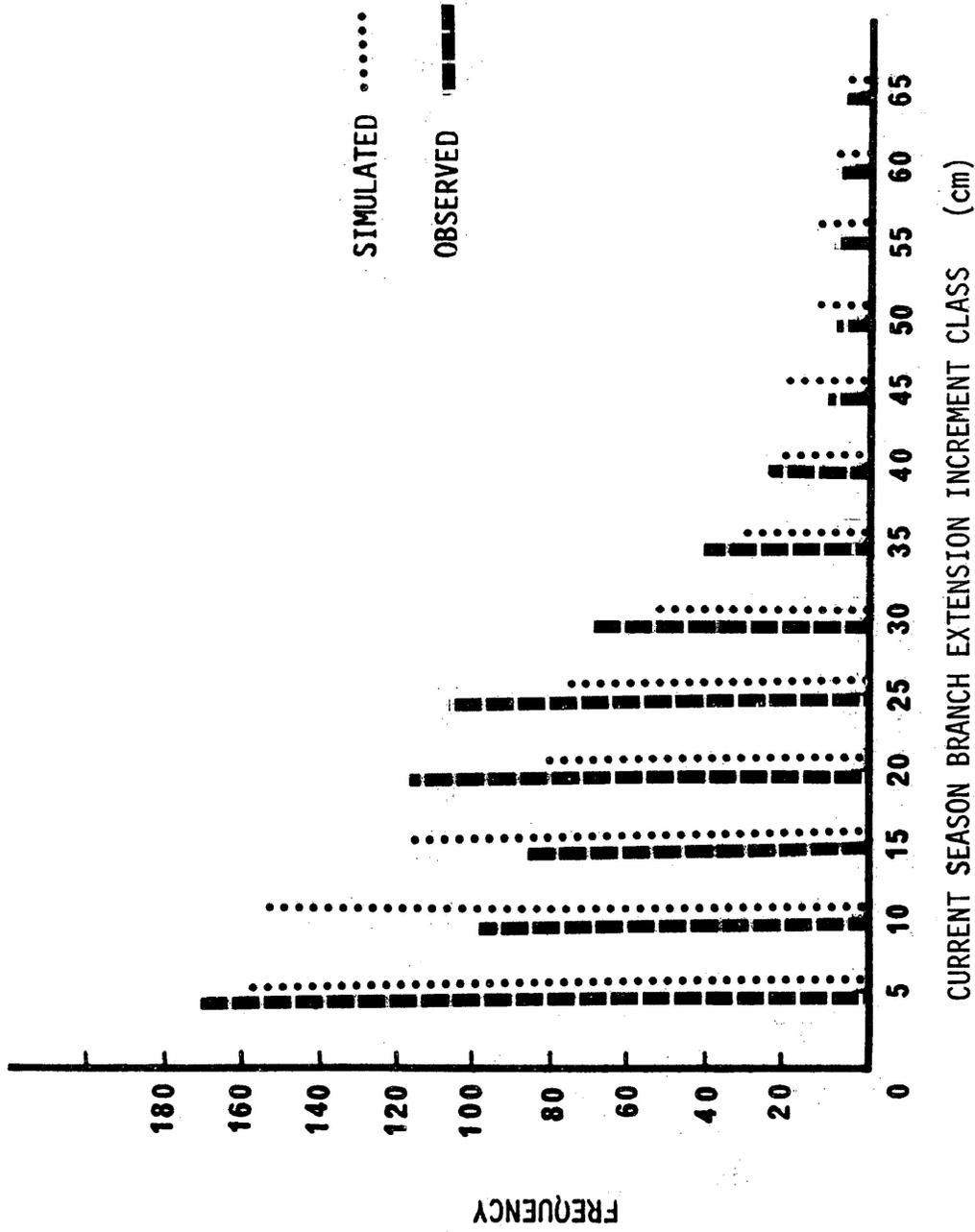
Figure 15. Frequency distribution of the observed and simulated branch extension increments by 5.0 cm classes (From Table 13, Validation Data Set).

branch extension increments by 5.0 cm classes (From Table 13).

Table 14 shows the mean and the variance of the observed and simulated current season branch extension increments stratified by age. The variances were tested for homogeneity by the Students-t-test (Steel and Torrie 1960). The results of this test are shown in Table 14. The means of the observed and simulated current season branch extension increments for each age class were not significantly different (P = 0.05).

Individually the branch extension growth models (Equations 18 and 24) may reliably represent the data. Simulating the cumulative annual branch extension increment over time, however, may be in error owing to the interaction between errors in the separate models and compounding of errors over time (Goulding 1979). To test the behaviour of the branch extension growth models, the observed and simulated mean total branch lengths were compared for the live whorls of an open-grown tree from

the validation data set. Figure 16 shows a flow chart of the simulation procedure. Simulation of the extension increment of a branch in its first growing season was based on the observed concurrent height increment of the sample validation tree and Equation 18. Subsequent branch

Table 14. Mean and variance of the observed and simulated extension increments of branches after their first growing season for branches of the same age (Source: Validation Data Set).

Branch age	n	Observed current branch extension increment (cm)		Simulated current branch extension increment (cm)	
		Mean	Variance	Mean	Variance
* 2	88	28.8	99.5	26.0	283.3
* 3	82	22.7	105.0	25.3	230.5
* 4	81	19.2	45.9	19.4	146.9
* 5	77	15.3	43.0	16.8	105.7
6	71	12.6	60.1	13.6	76.8
* 7	60	12.1	68.3	11.4	38.1
* 8	55	9.7	59.0	8.8	29.7
9	41	8.2	50.4	10.0	48.2
* 10	29	8.2	57.6	6.2	13.8
11	27	5.8	38.9	5.9	19.0
12	21	6.0	32.0	7.4	23.1
13	16	5.0	22.8	5.6	17.2
14	15	8.1	24.2	5.2	11.3
15	6	10.8	7.7	4.2	13.8
16	6	6.8	8.5	4.6	10.0
17	6	8.0	10.8	4.2	6.8
18	4	4.4	1.9	3.6	7.8
19	4	6.6	13.7	2.0	3.9
20	2	2.0	2.0	1.8	2.2

* Variances are not homogeneous at the 0.05 level
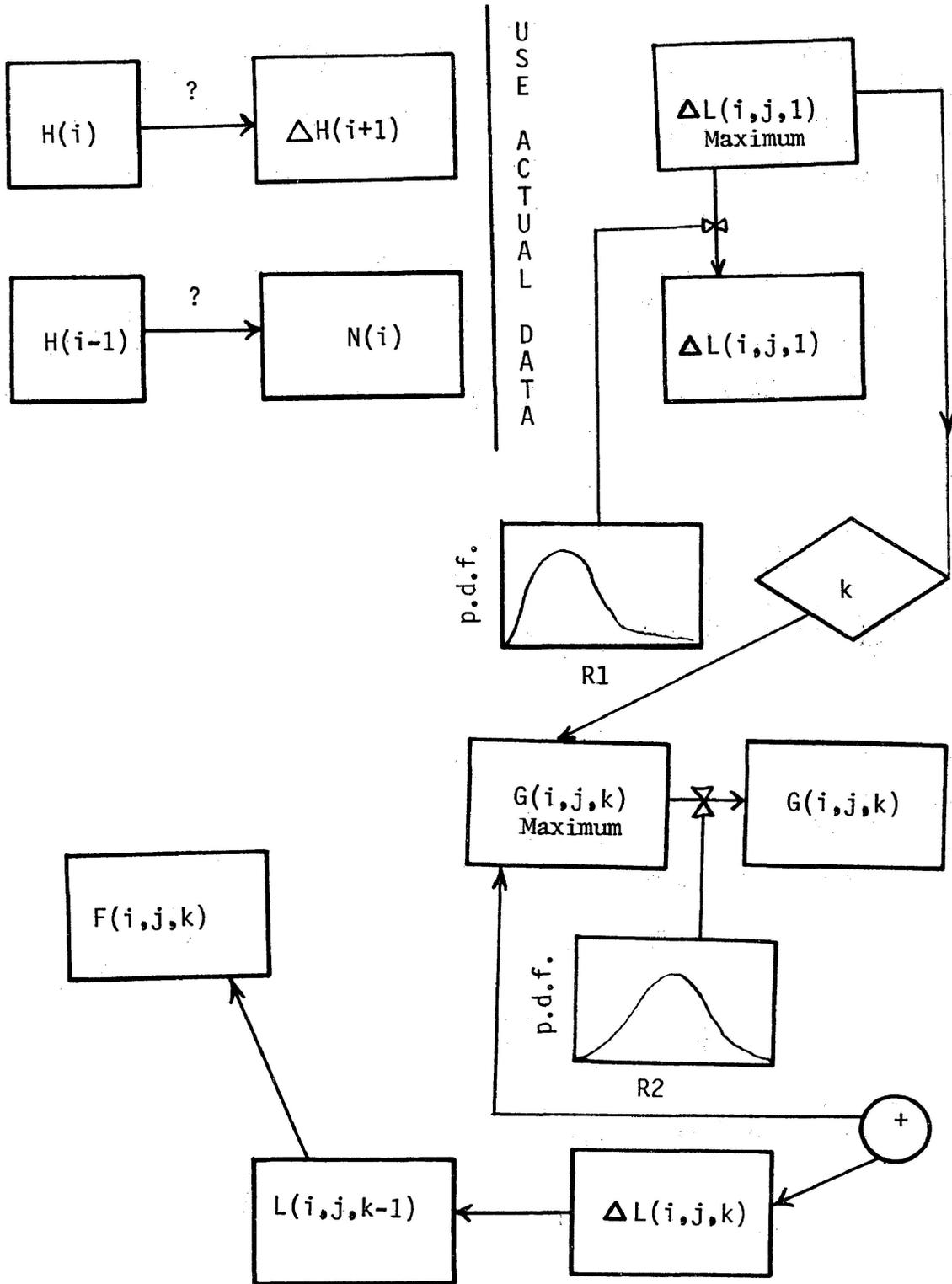
Figure 16.   Flow chart outling procedure to simulate the mean total branch lengths per whorl in P. resinosa Ait.

extension increments were simulated by Equation 24. The number of branches per whorl in the simulated tree was set equal to the observed number of branches per whorl in the real tree. If this were not done, differences in the observed and simulated number of branches per whorl would affect the calculation of the observed and simulated mean total branch lengths per whorl. Table 15 and Figure 17 summarize the results of the comparison between the observed and simulated mean total branch lengths per whorl of the sample validation tree. No significant differences ($P = 0.05$) were found between the observed and simulated mean total branch lengths per live whorl less than 8-years-old.

Table 15. The observed and simulated mean total branch lengths per whorl of an open-grown tree Source: Validation Data Set.

BRANCH AGE (years)	ANNUAL HEIGHT INCREMENT (cm)	NUMBER OF BRANCHES PER WHORL	OBSERVED TOTAL BRANCH LENGTH (cm)		SIMULATED TOTAL BRANCH LENGTH (cm)	
			MEAN	VARIANCE	MEAN	VARIANCE
1	41	5	16.4	40.2	23.0	32.6
2	36	8	39.2	82.1	41.5	407.5
3	44	5	68.2	131.8	60.6	649.5
4	61	7	85.4	1654.1	125.1	3268.9
5	52	7	109.1	2174.4	85.7	861.0
6	50	5	149.2	1728.2	103.6	1245.3
7	39	4	125.2	5057.7	115.0	3816.6
8	27	4	178.6 *	3095.8	51.3	744.9
9	25	4	154.3 *	6251.4 +	48.9	826.9
10	23	3	220.0 *	199.0	34.6	282.4
11	28	5	222.1 *	386.7 +	92.3	2038.7
12	34	6	170.1	10010.0 +	94.6	896.2
13	47	7	196.7	4564.3	169.3	3780.2
14	60	7	243.8 *	561.7	142.9	1358.3
15	61	5	256.6	1486.7 +	166.9	10790.5
16	56	3	200.6 *	3336.3 +	187.3	37915.1
17	19	4	227.6 *	2953.9	51.0	839.1
18	49	6	216.4 *	839.0	112.6	1232.2

* mean observed value is significantly different from the mean simulated value (P=0.05)

+ variance about the observed mean is significantly different from the variance about the simulated mean (P=0.05)
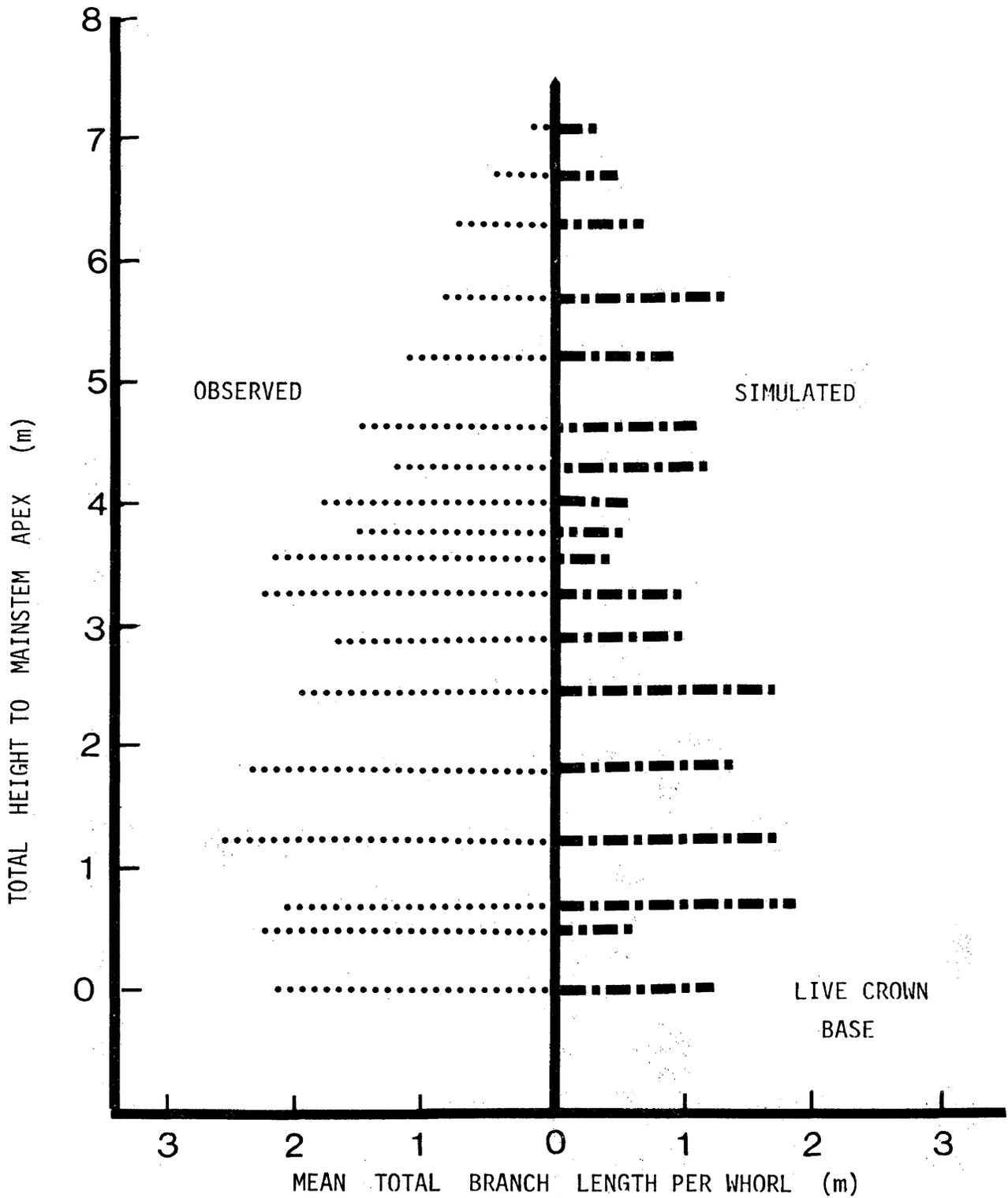
Figure 17. The observed and simulated mean total branch lengths per live whorl of an open-grown tree (Source: Validation Data Set).

Total Branch Foliage Dry Weight as a Function of Total

Current Season Branch Length

A family of regression equations stratified by branch age was developed to estimate total foliage dry weight from current season branch length. For branches of all ages, an acceptable fit to the foliage dry weight data was obtained with the following allometric model:

(25) $F(i,j,k) = a[L(i,j,k)]^b$,$k = 1,2,3,...$

where $F(i,j,k)$ denotes the total foliage dry weight, g, of the j th branch inserted into the i th mainstem whorl at age k, $L(i,j,k)$ denotes current branch length at age k, and a,b are constants. The coefficients a and b were estimated by linear-least squares methods on the logarithmic transformation of Equation 25 (Freese 1964; Zar 1968). The retransformed values were corrected for bias by the method outlined by Baskerville (1972). Table 16 summarizes the statistics for these equations.

Table 17 lists the results of simple linear regression of the observed total foliage dry weight as a function of the simulated total foliage dry weight for

Table 16 . The relationship between total branch foliage dry weight and current season branch length for branches of the same age fitted by the allometric model: $F(i,j,k) = a\left[L(i,j,k)\right]^b$.

Branch age	a	b	r^2	$S_{y \cdot x}$	Correction[1] factor	n	Equation number
1	0.4×10^{-1}	1.56	0.81	0.43	1.10	54	1
2	2.3×10^{-1}	1.23	0.89	0.20 ·	1.02	86	2
3	6.3×10^{-2}	1.57	0.90	0.27	1.04	80	3
4	6.7×10^{-3}	2.06	0.91	0.22	1.02	74	4
5	1.4×10^{-2}	1.90	0.90	0.25	1.03	74	5
6	1.9×10^{-3}	2.28	0.93	0.25	1.03	65	6
7	6.4×10^{-3}	2.02	0.91	0.30	1.04	56	7
8	2.3×10^{-3}	2.18	0.91	0.35	1.06	55	8
9	2.1×10^{-3}	2.16	0.70	0.43	1.10	40	9
10	2.7×10^{-5}	2.93	0.80	0.44	1.10	27	10
11	2.5×10^{-5}	2.89	0.75	0.77	1.34	28	11
12	2.0×10^{-7}	3.79	0.57	0.91	1.51	20	12
13	2.4×10^{-9}	4.56	0.82	0.60	1.20	16	13
14	5.1×10^{-9}	4.42	0.77	0.70	1.28	16	14
15	6.1×10^{-9}	4.44	0.97	0.13	1.01	5	15
16[+]	3.2×10^{-10}	4.85	0.72	0.44	1.10	26	16

[1] after Baskerville (1972)

$F(i,j,k)$ = total branch foliage dry weight (g) of the j th branch inserted into the i th mainstem whorl at age k.

$L(i,j,k)$ = current total branch length (cm) of the j th branch inserted into the i th mainstem whorl at age k.

Note: k represents the age of the branch at the time of sampling.

Source: Calibration Data Set

Table 17 . Simple linear regression of the observed total branch foliage dry weight on that simulated by the allometric model: $F(i,j,k) = a\left[L(i,j,k)\right]^b$ (Source: Validation Data Set).

Branch age	Intercept a	Slope b	r^2	$S_{y.x}$	n	Equation number
1	3.5	0.71 *	0.53	8.1	54	1
2	-3.4	1.14 *	0.79	10.0	91	2
3	-9.6	1.18 *	0.79	21.1	84	3
4	-5.1	1.10	0.81	30.7	89	4
5	-36.8	1.30 *	0.84	36.1	79	5
6	-24.1	1.26 *	0.91	53.6	77	6
7	-25.3'	1.21 *	0.82	57.4	61	7
8	-13.0	1.10 *	0.91	38.2	55	8
9	-54.3	1.48 *	0.93	72.8	42	9
10	-2.5	1.13	0.92	76.5	32	10
11	-20.8	1.10	0.93	88.3	25	11
12	27.4	0.58 *	0.93	94.8	23	12
13	85.8	0.47 *	0.66	27.6	16	13
14	222.8	0.13 *	0.12 +	127.1	13	14
15	275.8	0.18 *	0.50	156.4	7	15
16+	182.9	0.19 *	0.32	134.7	20	16

* significantly different from 1 at the 0.05 level

+ not significant at the 0.05 level

each branch age class from the validation data set. All regressions except Equation 14, Table 17 were significant and the intercept of each equation was not significantly different (P = 0.05) from zero. The slope of each equation was significantly different (P = 0.05) from one, except for Equations 4, 10, and 11, Table 17, respectively.

Figure 18 and Figure 19 show plots of the a and b coefficients from the foliage dry weight - branch length regression equations against branch age, respectively.
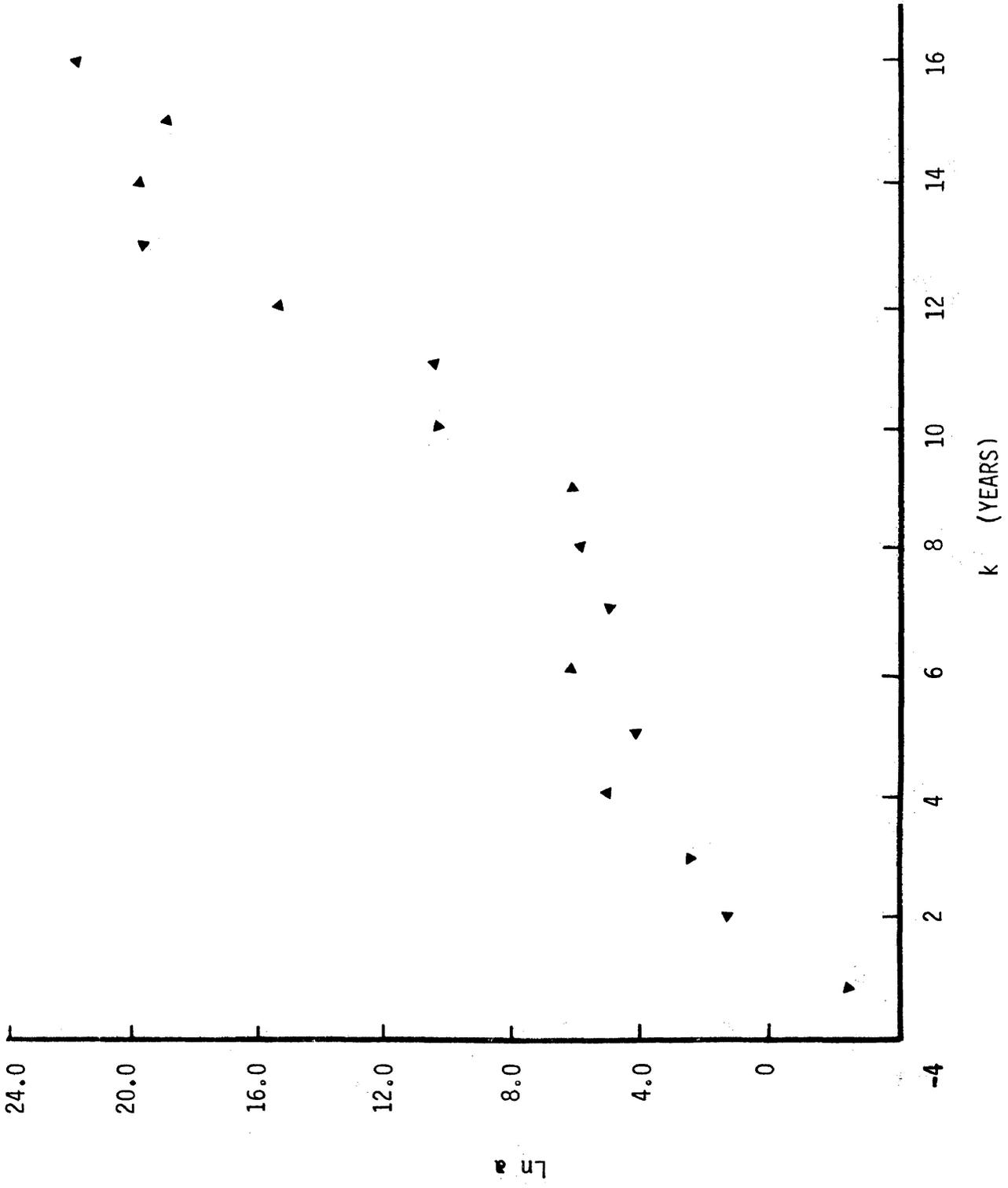
Figure 18. Plot of the natural logarithm of the a coefficients, Ln a, from the foliage dry – weight branch length regressions against branch age, k, (Source: Table 16).
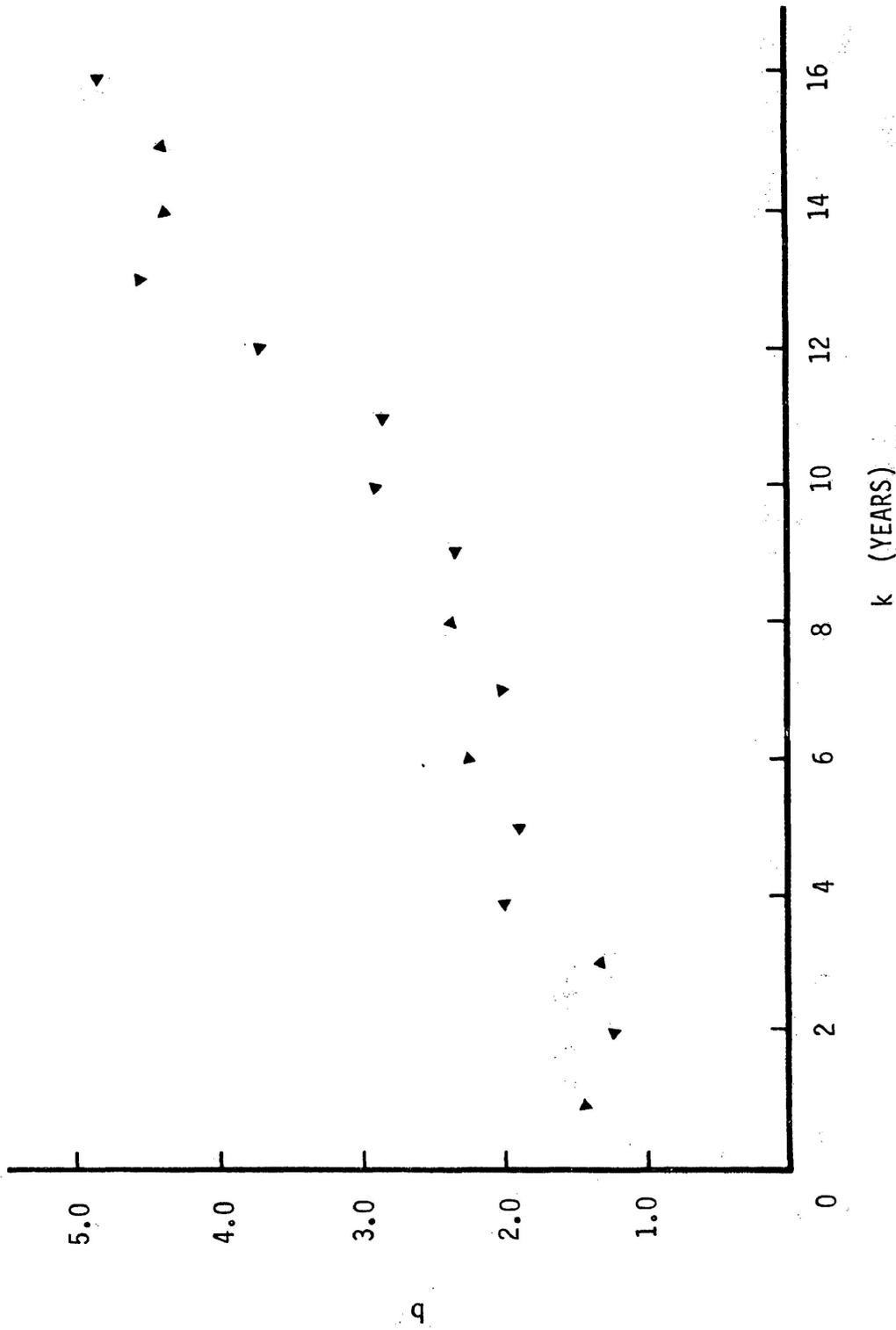
Figure 19. Plot of the b coefficients from the foliage dry weight - branch length regressions against branch age, k, (Source: Table 16).

DISCUSSION

This study revealed definite trends in the pattern of branch development, and resulting crown form. The regularity of these trends suggests that differences in branch extension growth are associated with: differences in the annual height increment of the tree, factors governing apical control, and the relative position of the branch within the crown. The data also showed that the extension growth of branches of P. resinosa is highly variable. This conclusion corroborates the finding of others (Forward and Nolan 1964; Rehfeldt and Lester 1966). Such variation is most likely associated with: the seasonal variation in environmental factors such as light intensity and duration, temperature, soil moisture and fertility, etc. (Reed 1980; Denne 1979); differences in the seasonal development of new shoot growing points, both vegetative and reproductive, of a branch; differences in apical control; differences in the size, structure, and duration of the photosynthetic crown (Farmer 1976);and differences in the genetic constitution of the tree (Nienstadt 1964; Fowler 1965; Holst 1975). The stochastic model developed in this thesis (Figure 16) is an attempt to represent

simultaneously the underlying biological pattern and the random variability of the production and extension growth of first order branches in P. resinosa.

Branch Production

Factors that control whorl bud formation in $\underline{P}$. resinosa can only be indirectly related to the length of the parent structure. This study revealed a weak, linear relationship between the number of branches per whorl and two attributes of the parent structure: length of the terminal leader on which the branches occurred as whorl buds, $\triangle H(i)$, and the length of the terminal leader at the time of whorl bud inception, $\triangle H(i-1)$. Several authors have reported a non-random increase in branch numbers with total tree height (Miller 1965); with the basal diameter or length of the parent structure (Barker et al. 1973; Cannell 1974) and before crown closure (Cochrane and Ford 1978).

The development of strobili may account for some of the variation in the number of branches per mainstem whorl in $\underline{P}$. resinosa. Both female strobili and lateral, long-branch buds are thought to originate from identical primordial tissue (Duff and Nolan 1958). Strobili production decreased the number of long-branch budlets in Pinus contorta (Cannell 1974).

The length of the terminal leader on which branches occurred as whorl buds (Equation 2, Table 3) provided a better estimate of the number of branches per whorl than the length of the terminal leader at the time of whorl bud inception (Equation 3, Table 3). It is possible that the

length of the former terminal leader is affected by some of the same factors which control the survival of whorl buds which develop into branches. Lateral bud primordia or lateral branches may abort at any time during the course of the first growing season of their development in response to various abiotic and biotic factors. Cannell (1974), however, noted that very few lateral, long-branch budlets aborted or remained dormant in Pinus contorta during the second growing season of their development. Although age might reflect the vigour and sexual maturity of a tree, and therefore influence lateral branch numbers, no significant (P = 0.05) relationship existed between the number of branches per whorl and tree age at the time of whorl bud inception, (i-1), (Equation 1, Table 3). Lateral bud production is also an inherently variable character (Cannell et al. 1976). The physiological mechanism(s) that control the formation and number of long-branch budlets in Pinus is still unknown. Future work in this area would be warranted.

It is, therefore, reasonable to treat the number of branches per whorl as a stochastic phenomenon. The binomial p.d.f. is a suitable distribution to describe the number of branches that occur at a given whorl position within $\underline{P}$. $\underline{resinosa}$. Although the binomial model developed in this study (Equation 10) limits the maximum number of branches per whorl to eight, there appears to be a maximum number of branches that a given whorl can support simply because space is a limiting factor (Cannell and Bowler 1978). Even if more than eight branches per whorl do occur in reality, the probability of such an observation occurring seems to be low (Table 6).

Branch Extension Increment: Year One

Both the terminal leader and its subtending whorl of
lateral, one-year-old branches can be treated as a single
growth unit. During each growing season there appears to
be a potential length that a one-year-old branch can
attain. This potential length is regulated by factors
that govern leader extension growth.   Although apical
control is certainly a factor that influences   the
potential length of a one-year-old branch in a specific
growing season, it is clear that seasonal differences in
this   potential   reflect seasonal changes in leader
extension growth.   The strong, positive, and linear
correlation between the length of the longest branch of an
annual whorl of one-year-old laterals and the length of
the   concurrent   leader   seems to substantiate this
conclusion (Equation 14).

Cannell (1974) defined a measure of the degree of
apical control as the mean length of an annual whorl of
one-year-old laterals as a percentage of the length of
their concurrent terminal leader. A high ratio indicates
weak apical control because relatively long laterals are
associated with their terminal leader.   Equation 14
indicates that the potential length of a one-year-old

branch during any growing season is always about 71 percent of the length of its concurrent terminal leader. Thus, the degree of apical control expressed by a mainstem terminal leader over the potential length of its one-year-old laterals during any growing season is highly regular and uniform. This suggests that the seasonal variation in the potential length of a one-year-old lateral branch is not associated with differences in the degree of apical control, but rather with factors regulating leader extension growth.

The actual lengths of one-year-old branches inserted into the same whorl vary greatly. The majority of these laterals are shorter than the potential length that can be attained during any growing season (Figure 9). The most likely cause is the occurrence of further growth correlations between the laterals. Within a whorl of lateral, one-year-old branches, there is competition between branches for available growth resources from the supporting terminal leader which tends to keep them all short to the advantage of the terminal leader (Little 1970). Thus, branch numbers may have a bearing on the extension growth potential within a one-year-old branch whorl because of the division of the supply of growth resources to new shoot growing points.

Under normal circumstances, few branches exceed the estimated potential length of a one-year-old branch during any growing season (Figure 9). Compensatory growth by the laterals may occur, however, if the expression of apical control is suppressed by such factors as damage to the leading terminal shoot (Little 1970), or various environmental factors which affect branch vigour. In general, the degree of apical control exerted by a terminal leader over lateral branches decreases as the tree ages, and the micro-environment of the branch is altered (Moorby and Wareing 1963; Jankiewicz and Stecki 1976). The influence of the aforementioned factors upon extension growth of one-year-old branches is difficult to measure. These factors were therefore treated in a stochastic manner (R1 values, Table 8). The same factors may also account for much of the unexplained variation in the relationship between the length of the longest

one-year-old branch and the concurrent height increment. Both tree age at the time of the initiation of a one-year-old branch whorl 'growth unit' and branch numbers per whorl may also be important variables to consider in the relationship between the length of the longest one-year-old lateral branch and its concurrent height increment. In spite of all the possible confounding sources of variation which may influence the extension

growth of one-year-old lateral branches, Equation 18 provides a method for reliably simulating the extension growth of a one-year-old first order branch in P. resinosa.

Branch Extension Increment: 2-Years-Old and Older

No simple rule was found to explain the extension increment of branches after their first growing season. The relative annual branch extension increment, $G(i,j,k)$, defines the rate of extension during any growing season in relation to the length of the branch prior to extension growth. Figure 12 revealed that branches of equal age vary greatly in their relative extension rates. This variation in relative branch extension rates is greatest for the youngest branches, but decreases as branches age and get longer (Figure 12). The large variation in the relative extension rates of branches located in the uppermost crown positions indicates that differences in initial branch length do not account for differences in branch extension increment during the following growing season. As branches get older and longer, however, it does appear that initial branch length becomes a determining factor for extension growth during the following growing season (Figure 12).

I hypothesized that there exists a potential relative rate of extension for branches that decreases exponentially with branch age (Figure 13). The strong relationship between the maximum relative annual branch

extension increment and branch age seems to substantiate this conclusion (Equation 20)

Branch age reflects the position of a branch within the crown. The potential length increment of a branch declines as it moves into progressively lower positions within the crown. This decline in the potential length increment of a branch is quite rapid between the first and about the eighth whorl position (Figure 13). The decline in the potential length increment of branches as they move into progressively lower crown positions is in general agreement with the findings of others (Forward and Nolan 1964; Mitchell 1969, 1975). The causes of the observed decrease in the relative extension increment of branches as they age are still unknown. There is, however, speculation that the decrease in branch extension growth within lower crown positions is associated with the effects of mutual shading by branches (Reed 1980). The net assimilation rate, NAR, of branches generally decreases in progressively lower crown positions as a result of a decrease in light intensity (Woodman 1971; Kramer and Kozlowski 1979).

Branches do not attain their potential length increment for several reasons. The variation in the observed relative branch extension increments is most

likely attributable to seasonal variation in the field environment, tree vigour, branch vigour, (Cochrane and Ford 1978) or even genetic variation between trees (Holst 1975; Cannell et al. 1976). Competition between neighbouring trees also reduces the potential extension growth of branches in the middle and lower crown positions in P. resinosa. The branches in the upper three whorls, however, are generally unaffected by competition with neighbouring trees (Forward and Nolan 1964). Flowering may reduce the potential extension increment of a branch, but appears to be dependent upon the vigour of the branch (Powell 1977). NAR is also generally greater for branches which have southern exposure (Woodman 1971; Kramer and Kozlowski 1979). Thus, the extension growth pattern of a branch may be sensitive to its orientation about the stem. Overall it appears that branch extension growth is sensitive to the general micro-environment of the branch. Wilson (1970) suggests that the decrease in branch extension growth is related to the angle of insertion of the branch into the main stem. The more nearly horizontal a branch is the greater would be the reduction in elongation; a phenomenon referred to as geotonous growth response in plants. Factors regulating branch angle involve compression wood formation which is linked to apical control, but is still unknown (Wilson 1970; Kramer

and Kozlowski 1979). The effects of these sources of variation are represented in the model by means of a stochastic variable - R2.

Comparison of the frequency distributions of the observed and simulated branch extension increments from the validation data set by the chi-square statistic, however, revealed that the two distributions were significantly (P = 0.05) different (Table 13). Figure 15 shows that the model for extension growth of branches after their first growing season (Equation 24) overestimates the frequency of branch extension increments less than 15 cm and underestimates the frequency of branch extension increments between 15 - 35 cm. These differences possibly reflect bias in the model (Equation 24) associated with differences in branch age. The chi-square test, however, was based upon the frequency distribution of extension increments for branches of all ages. Stratification of the extension increment data by branch age would provide a method for evaluating any possible bias in the branch extension growth model (Equation 24) associated with branch age.

Comparison of the frequency distributions of extension increments stratified by branch age would reduce the size of the sample data. The chi-square

goodness-of-fit test is very sensitive and comparisons of frequency distributions based on a small sample size may not be appropriate. It is generally suggested that data be divided into 10 to 20 classes and that there be at least five observations per class when constructing frequency distributions to be tested by the chi-square statistic (Chatfield 1975). In this study, the sizes of the sample branch populations when stratified by branch age are marginal or do not meet the general requirements for the chi-square 'goodness-of-fit' test. By increasing the sample size it may be possible to characterize the distribution of R2 values (Equation 21) by an appropriate p.d.f. for each age class of branches. Further work in refining the technique of simulating branch extension growth after the first growing season in a stochastic manner is warranted.

Figure 15 , however, reveals a general similarity between the frequency distributions of both the observed and simulated current season branch extension increments from the validation data set. Exact solutions for the frequency distribution of the current season branch extension increments stratified by branch age could not be reliably determined. No significant differences $(P = 0.05)$ were found between the observed and simulated mean current season branch extension increments stratified

by branch age from the validation data set (Table 14).
Therefore, it was concluded that the model (Equation 24)
does simulate the mean annual extension increment of
branches after their first growing season.

In the model, simulation of the cumulative annual
extension increment of a branch (Equations 18 and 24) is
largely dependent upon the magnitude of the concurrent
height increment of the tree when the branch was one year
old. Figure 17 suggests that short concurrent height
increments consistently yielded correspondingly short mean
total branch lengths. Thus, simulation of the cumulative
branch extension growth in **P. resinosa** reflects
differences associated with the annual changes in the
height increment of the tree. Significant differences
(P = 0.05) were found, however, between the observed and
simulated mean total branch lengths per live whorl of an
open-grown tree for several branch whorls greater than
8-years-old (Figure 17, Table 15). Table 15 showed that
the observed mean total branch lengths of these whorls was
always greater than the corresponding simulated mean total
branch lengths, and that these differences were associated
with comparably short concurrent height increments. This
finding suggests that branch extension growth in real
trees is not entirely related to factors regulating the
height increment of the tree.

Compensatory extension growth of branches is known to occur when leader extension growth is impeded for various reasons (Little 1970). Compensatory extension growth by branches of the real tree is the most probable explanation for the differences between the observed and simulated mean total branch lengths for the several whorls within the live crown of the sample validation tree (Figure 17). The stochastic nature of the branch extension growth models (Equations 18 and 24) might allow for compensatory extension growth by branches of the simulated tree, but the probability of such an occurrence is low. It would be more appropriate to compare model behaviour as a whole to a population of several validation trees. An alternative method with which to evaluate crown dynamics in P. resinosa would be to use previously published height growth functions for this species (Hahn and Carmean 1980; Payandeh 1977) instead of using observed height increments from real trees to drive the branch extension growth model developed in this thesis.

Total Branch Foliage Dry Weight

and

Branch Length Relationships

Total current season branch length was a useful estimator of the total foliage dry weight supported by branches of the same age. Higher coefficients of determination were recorded for the regression equations developed for younger branches within the upper crown than for the older branches in lower crown positions (Table 16). These differences in the coefficients of determination are probably associated with differences in needle-fascicle retention between the upper and lower crown branches. Needle-fascicle retention is affected by mutual shading and mechanical abrasion between neighbouring trees (Reed 1980). In general, needle-fascicles persist for up to eight years in P. resinosa. This may account for the strong correlation between total branch foliage dry weight and branch length relationships for 8-year-old or younger branch whorls. Although needle-fascicles are lost for various reasons in branches of the upper crown, the rate of needle-fascicle abscission in lower crown positions is enhanced because of

mutual shading, mechanical abrassion, and senescence of the needle-bearing dwarf-branches. Much of the unexplained variation in the total branch foliage dry weight and branch length regressions may be associated with differences between branches from trees of different age, spacing, or site quality. Potassium nutrition is an important determinant of needle fascicle retention in P. resinosa (Madgwick 1975). Factors regulating dwarf-branch abscission are unknown, but would warrant future investigation if the foliage dynamics in P. resinosa are to be fully understood.

Branch length underestimated the total foliage dry weights of branches in the upper crown (10-year-old or younger branch whorls) and overestimated total foliage dry weights of branches in lower crown positions (Table 17). In the upper crown, first order branches probably bear different numbers and lengths of foliated branches of higher order. Thus, branches within the upper crown which have similar first order axis lengths may have entirely different foliage carrying capacities because of differences in the number and lengths of higher order foliated branches that they support. Validation of the branch length - foliage dry weight regressions with an independent population of branches from different trees may not account for differences in the foliage carrying

capacity of first order branches. Underestimation of foliage dry weights of branches within lower crown positions is most likely associated with factors governing needle-fascicle retention. Similar results were reported by Madgwick and Jackson (1974).

The estimated parameters (a and b coefficients) of the family of regression equations that relate total branch foliage dry weight to branch length for branches of the same age (Table 16) appear to be dependent upon branch age. Figure 18 and Figure 19 show that the natural logarithm of the a coefficients and, that the b coefficients, of the total branch foliage dry weight and branch length regressions, increase with increasing branch age, respectively. Both figures also exhibit parallel cyclic patterns of the two coefficients. This is interesting but as yet an unexplained phenomenon. It is clear that the a and b coefficients could be estimated as simple functions of branch age.

Modelling crown dynamics in P. resinosa is incomplete. The ideal model would simulate height growth, branch production, branch extension growth, and foliage dynamics as affected by site quality and spacing or stand

density. Since the growth of the stem is hypothesized to be regulated by the crown, crown models may provide quantitative information with which to achieve stem growth objectives through silvicultural manipulation of the crown. Deterministic models of crown growth and development, such as those developed by Mitchell (1969, 1975) for _Pseudotsuga menziesii_ and _Picea glauca_, and Fisher and Honda (1977) for _Terminalia_, are site specific and do not account for the observed seasonal variation in the pattern of first order branch extension growth. Although stochastic models of branch production and branch extension growth have been developed for _Picea sitchensis_ on uniform sites (Cochrane and Ford 1978), these authors fail to preserve the excurrent branching pattern of the crown structure of north temperate coniferous trees. The model developed in this thesis is an attempt to elucidate the pattern of crown growth and development in _P. resinosa_. The model is silviculturally meaningful because it provides a quantitative basis upon which to study the biological structure and function of crown dynamics in a structurally simple tree species, and eventually the forest ecosystem as a whole. Serious efforts to make quantitative, theoretical contributions to forest science should continue. Only then will foresters be able to devise alternative silvicultural regimes which will

elicite optimum response from the forest to meet desired management objectives.

LITERATURE CITED

1. Alban, D.A. 1979. Estimating site potential from the early height growth of red pine in the Lake States. U.S.D.A. For. Serv. Res. Pap. NC-166 North Central For. Exp. Stn., St. Paul, Minnesota.

2. Assmann, E. 1970. The Principles of Forest Yield Study. Pergamon Press, New York.

3. Bailey, R.L. 1974. Computer programs for quantifying diameter distributions with the Weibull function. For. Sci. 20:229.

4. Bailey, R.L. and T.R. Dell 1973. Quantifying diameter distributions with the Weibull function. For. Sci. 19:97-104.

5. Barker, J.E. 1978. Some silvicultural effects of fertilisation. N.Z.J. For. Sci. 8:160-177.

6. Barker, S.B., G. Cumming and K. Horsfield 1973. Quantitative morphology of the branching structure of trees. J. Theor. Biol. 40:33-43.

7. Baskerville, G.L. 1972. Use of logarithmic regression in the estimation of biomass. Can. J. For. Res. 2:49-53.

8. Beckwith, J.R. and L.S. Shackelford 1976. Relationship between crown growth and annual xylem sheath development in loblolly pine saplings. For. Sci. 22:247-260.

9. Bell, A.D., D. Roberts and A. Smith 1979. Branching patterns: the simulation of plant architecture. J. Theor. Biol. 81:351-375.

10. Borchert, R. 1973. Simulation of rhythmic tree growth under constant conditions. Physiol. Plant. 29:173-180.

11. Brown, C.L., R.G. McAlpine and P.P. Kormanik 1967. Apical dominance and form in woody plants: a reappraisal. Am. J. Bot. 54:153-162.

12. Brown, C.L. 1971. Growth and Form. In " Trees: Structure and Function ', (M.H. Zimmermann and C.L. Brown, eds.), pp. 125-167. Springer-Verlag, New York.

13. Brown, J.K. 1976. Predicting crown weights for 11 Rocky Mountain conifers. In ' Oslo Biomass Studies', (Young, H.E. ed.), pp.103-115, Orono: Univ. of Maine Press.

14. Bunting, A.H. 1976. Inaugural lecture: Maximizing the product, or how to have it both ways. In 'Tree Physiology and Yield Improvement', (M.G.R. Cannell and F. T. Last, eds.), pp. 1-20, Academic Press, New York.

15. Cannell, M.G.R. 1974. Production of branches and foliage by young trees of _Pinus_ _contorta_ and _Picea_ _sitchensis_: Provenance differences and their simulation. J. Appl. Ecol. 11:1091-1115.

16. Cannell, M.G.R. and K.C. Bowler 1978. Spacial arrangement of lateral buds at the time they form on leaders of _Picea_ and _Larix_. Can. J. For. Res. 8:129-137.

17. Cannell, M.G.R., S. Thompson and R. Lines 1976. An analysis of inherent differences in shoot growth within some north temperate conifers. In 'Tree Physiology and Yield Improvement', (M.G.R. Cannell and F.T. Last, eds.), pp. 173-205, Academic Press, New York.

18. Carmean, W.H. 1975. Forest site quality evaluation in the United States. Adv. Agron. 27:209-269.

19. Chatfield, C. 1975. Statistics for Technology. John Wiley and Sons, Inc., New York.

20. Chung, H.-H. and R.L. Barnes 1980a. Photosynthate allocation in Pinus taeda. II. Seasonal aspects of photosynthate allocation to different biochemical fractions in shoots. Can. J. For. Res. 10:338-347.

21. Chung, H.-H. and R.L. Barnes 1980b. Photosynthate allocation in Pinus taeda. III. Photosynthate economy: its production, consumption and balance in shoots during the growing season. Can. J. For. Res. 10:348-357.

22. Clements, J.R. 1970. Shoot responses of young red pine to watering applied over two seasons. Can. J. Bot. 48:75-80.

23. Cochrane, L. and E.D. Ford 1978. Growth of a sitka spruce plantation: Analysis and stochastic description of the development of the branching structure. J. Appl. Ecol. 15:227-244.

24. Cohen, D. 1967. Computer simulation of biological pattern generation processes. Nature 216:246-248.

25. Curtin, R.A. 1970. Dynamics of tree and crown structure in Eucalyptus obliqua. For. Sci. 16:321-328.

26. Curtis, J.D. and R.A. Popham 1972. The developmental anatomy of long branch terminal buds of Pinus banksiana Lamb. Am. J. Bot. 59:194-202.

27. Curtis, O.R. and D.L. Reukema 1970. Crown development and site estimates in a Douglas-fir plantation spacing test. For. Sci. 16:287-301.

28. Denne, M.P. 1979. Wood structure and production within the trunk and branches of _Picea sitchensis_ in relation to canopy formation. Can. J. For. Res. 9:406-427.

29. Duff, G.H. and N.J. Nolan 1958. Growth and morphogenesis in the Canadian forest species. III. The time scale morphogenesis at the stem apex of _Pinus resinosa_ Ait. Can. J. Bot. 36:687-710.

30. Ek, A.R. 1979. A model for estimating branch weight and branch leaf weight in biomass studies. For. Sci. 25:303-306.

31. Farmer, R.E. 1976. Relationships between genetic differences in yield of deciduous tree species and variation in canopy size, structure, and duration. In 'Tree Physiology and Yield Improvement ', (M.G.R. Cannell and F.T. Last, eds.), pp. 119-137, Academic Press, New York.

32. Farrar, J.L. 1961. Longitudinal variation in the thickness of the annual ring. For. Chron. 37: 323-331.

33. Farrar, J.L. 1974. Fascicle shoot of pine. Unpublished manuscript, University of Toronto.

34. Fisher, J.B. and H. Honda 1977. Computer simulation of branching pattern and geometry in _Terminalia_ (_Combretaceae_), a tropical tree. Bot. Gaz. 138:377-384.

35. Fisher, J.B. 1977. A quantitative study of _Terminalia_ branching. In 'Tropical trees as Living Systems', (P.B. Tomlinson and M.H. Zimmermann, eds.), pp. 285-320, Cambridge University Press, New York.

36. Flower-Ellis, J., A. Albrektsson and L. Olsson 1976. Structure and growth of some scots pine stands: (1) Dimensional and numerical relationships. Swedish Coniferous Forest Project, Tech. Report 3, Uppsula, Sweden.

37. Ford, E.D. and J.D. Deans 1978. The effects of canopy structure on stem flow, throughfall and interception loss in a young sitka spruce plantation. J. Appl. Ecol. 15:905-917.

38. Forward, D.F. and N.J. Nolan 1964. Growth and morphogenesis in the Canadian forest species. VII. Progress and control of longitudinal growth of branches in Pinus resinosa Ait. Can. J. Bot. 42:932-950.

39. Fowler, D.P. 1965. Effects of inbreeding in red pine, Pinus resinosa Ait. III. Factors affecting natural selfing. Silvae Genet. 14:37-46.

40. Freese, F. 1964. Linear regression methods for forest research. U.S. For. Prod. Lab., U.S. For. Serv. Res. Pap. FPL-17, Madison, Wisconsin.

41. Gary, H.L. 1976. Crown development and distribution of biomass in a lodgepole pine stand. U.S.D.A., For. Serv. Res. Pap. RM-165, Rock. Mt. For. and Range Expt. Stn., Fort Collins, Colorado.

42. Goulding, C.J. 1979. Validation of growth models used in forest management. N.Z. Jl. For. 24:108-124.

43. Hahn, J.T. and W.H. Carmean 1980. Lake States site index curves formulated. U.S.D.A., For. Serv., North Central For. Expt. Stn. Res. Pap. NC-,___ (in press).

44. Hanawa, J. 1967. Growth and development in the shoot apex of Pinus densiflora. I. Growth periodicity and structure of the vegetative shoot apex. Bot. Mag. Tokyo 79:736-746.

45. Holst, M.J. 1975. Plus-tree selection:
     Review and out-look. Can. Dept. Environ.
     Pub. No. 1347.

46. Honda, H. 1971. Description of the form of
     trees by the parameters of the tree-like
     body: Effects of branching angle and the
     branch length on the shape of the tree-
     like body. J. Theor. Biol. 31:331-338.

47. Honer, T.G. 1971. Weight relationships in
     open-grown balsam fir trees. In 'Forest
     Biomass Studies', (Young,H.E., ed.),
     pp. 65-78, Orono:Univ. of Maine Press.

48. Horn, H.S. 1971. The Adaptive Geometry of Trees.
     Princeton University Press, Princeton.

49. Jankiewicz, L.S. and Z.J. Stecki 1976. Some
     mechanisms responsible for differences in
     tree form. In 'Tree Physiology and Yield
     Improvement', (M.G.R. Cannell and F.T. Last,
     eds.). pp. 157-172, Academic Press, New York.

50. Kay, M. 1978. Foliage biomass of Douglas-fir
     in a 53-year-old plantation. N.Z.J. For.
     Sci. 8:315-326.

51. Kinerson, R. and L.J. Fritschen 1971. Modeling
     a coniferous forest canopy. Agr. Meteorol.
     8:439-445.

52. Kinerson, R.S. and K.O. Higginbotham 1973. A
     quantitative description and simulation of
     branchwood production relationships in the
     forest canopy. In' IUFRO Biomass Studies ',
     (Young, H.E., ed.), pp. 65-76, Orono:Univ.
     of Maine Press.

53. Kinerson, R.S., K.O. Higginbotham and R.C.
     Chapman 1974. The dynamics of foliage
     distribution within a forest canopy.
     J. Appl. Ecol. 11:347-353.

54. Kittredge, J. 1944. Estimation of the amount of foliage of trees and stands. J. For. 42:905-912.

55. Kleijnen, J.P.C. 1974. Statistical Techniques in Simulation. M. Dekker, New York.

56. Kossack, C.F. and C.I. Henschke 1975. Introduction to Statistics and Computer Programming. Holden-Day, San Francisco.

57. Kozlowski,T.T., J.H. Torrie and P.E. Marshall 1973. Predictability of shoot length from bud size in *Pinus* *resinosa* Ait. Can. J. For. Res. 3:34-38.

58. Kozlowski, T.T. and R.C. Ward 1961. Shoot elongation characteristics of forest trees. For. Sci. 7:357-368.

59. Kramer, P.J. and T.T. Kozlowski 1979. Physiology of Woody Plants, Academic Press, New York.

60. Lanner, R.M. 1976. Patterns of shoot development in *Pinus* and their relationship to growth potential. In 'Tree Physiology and Yield Improvement', (M.G.R. Cannell and F.T. Last, eds.). pp. 223-243, Academic Press, New York.

61. Larson, P.R. 1962a. A biological approach to wood quality. Tappi 45:443-448.

62. Larson, P.R. 1962b. Auxin gradients and the regulation of cambial activity. In 'Tree Growth', (T.T. Kozlowski, ed.), pp. 97-117, Ronald Press, New York.

63. Larson, P.R. 1963. Stem form development in forest trees. For. Sci. Monogr. 5.

64. Larson, P.R. 1969. Wood Formation and the Concept of Wood Quality. Yale Univ. Sch. For. Bull. 74.

65. Ledig, F.T. 1974. Concepts of growth analysis In 'Proc. of 3 rd N.A. Forest Biol. Work.', (C.P.P. Reid and G.H. Fechner, eds.), Colorado State University, Fort Collins.

66. Ledig, F.T. 1976. Physiological genetics, photosynthesis and growth models. In 'Tree Physiology and Yield Improvement', (M.G.R. Cannell and F.T. Last, eds.), pp. 21-54, Academic Press, New York.

67. Leopold, L.B. 1971. Trees and streams: The efficiency of branching patterns. J. Theor. Biol. 31:339-354.

68. Little, C.H.A. 1970. Apical dominance in long shoots of white pine (Pinus strobus). Can. J. Bot. 48:239-253.

69. Loomis, R.M., R.E. Pharis and J.S. Crosby 1966. Estimating foliage and branchwood quantities in shortleaf pine. For. Sci. 12:30-39.

70. McMahon, T.A. 1975. The mechanical design of trees. Scientific American 233:93-102.

71. McMahon, T.A. and R.E. Kronauer 1976. Tree structures: Deducing the principle of mechanical design. J. Theor. Biol. 59:443-446.

72. Madgwick, H.A.I. 1968. Some factors affecting the vertical distribution of foliage in pine canopies. In 'Symposium on Primary Productivity and Mineral Cycling in Natural Ecosystems, (Young, H.E., ed.), pp. 233-245, Orono: Univ. of Maine Press.

73. Madgwick, H.A.I. 1970. Biomass and
     productivity models of forest canopies.
     In 'Analysis of Temperate Forest
     Ecosystems', (D.E. Reichele, ed.), pp. 47-54,
     Springer-Verlag, New York.

74. Madgwick, H.A.I. 1974. Modelling canopy
     development in pines. In 'Growth Models
     for Tree and Stand Simulation', (J. Fries,
     ed.), pp. 253-255, Dept. of For. Yield
     Res., Royal College Forestry, Stockholm,
     Sweden, Res. Notes:30.

75. Madgwick, H.A.I. 1975. Branch growth of Pinus
     resinosa Ait. with particular reference to
     potassium nutrition. Can. J. For. Res.
     5:509-514.

76. Madgwick, H.A.I. and D.S. Jackson 1974.
     Estimating crown weights of Pinus radiata
     from branch variables. N.Z.J. For. Sci.
     4:520-528.

77. Marion, G.M., J.V. Berglund and A.L. Leaf
     1968. Morphological and chemical analyses
     of red pine (Pinus resinosa Ait.) buds -
     their relationships to tree growth on a
     K-deficient to non-deficient site
     continuum. Plant and Soil 28:313-324.

78. Miller, W.E. 1965. Number of branchlets on
     red pine in young plantations. For.
     Sci. 11:42-49.

79. Mitchell, K.J. 1969. Simulation of the
     growth of even-aged stands of white
     spruce. Yale Sch. For. Bull. 75.

80. Mitchell, K.J. 1975. Dynamics and Simulated
     Yield of Douglas-fir. For. Sci. Monogr. 17.

81. Monserud, R.A. 1975. Methodology for
    simulating Wisconsin northern hardwood
    stand dynamics. Ph. D. Univ. of
    Wisconsin, Madison.

82. Moorby, J. and P.F. Wareing 1963. Ageing
    in woody plants. Ann. Bot. 27:291-308.

83. Nienstaedt, H. 1964. Red pine progeny test,
    1931 and 1933 Minnesota plantings. In '
    Proc. 9 th Meet. Comm. Forest Tree Breed.
    Can., Part 2', pp. 151-156.

84. Ogawa, H. and T. Kira 1977. Methods of
    estimating forest biomass. In 'Primary
    Productivity of Japanese Forests -
    Productivity of Terrestrial Communities,
    (T. Shidei and T. Kira, eds.), pp. 15-37,
    (JIBP), University of Tokyo Press, Tokyo.

85. Onaka, F. 1950a. The longitudinal distribution
    of radial increments in trees. Kyoto. Univ.
    For. Bull. 18:1-53 (Japanese--English
    summary).

86. Onaka, F. 1950b. The effects of defoliation,
    disbudding, girdling, and other treatments
    upon growth, especially radial growth of
    evergreen conifers. Kyoto. Univ. For.
    Bull. 18:55-95 (Japanese--English summary).

87. Paltridge, G.W. 1973. On the shape of trees.
    J. Theor. Biol. 38:111-137.

88. Payandeh, B. 1977. Metric site index formulae
    for major Canadian timber species. Can. For.
    Serv., Bi-monthly Res. Notes 33:37-39.

89. Pharis, R.P. 1976. Probable roles of plant
     hormones in regulating shoot elongation,
     diameter growth, and crown form of
     coniferous trees. In 'Tree Physiology
     and Yield Improvement', (M.G.R.
     Cannell and F.T. Last, eds.), pp. 291-306,
     Academic Press, New York.

90. Phillips, I.D.J. 1975. Apical dominance.
     Ann. Rev. Plant Physiol. 26:341-367.

91. Pike, L.H., R.A. Rydell and W.C. Denison 1977.
     A 400-year-old Douglas-fir tree and its
     epiphytes: biomass, surface area, and their
     distributions. Can. J. For. Res. 7:680-699.

92. Powell, G.R. 1977. Patterns of development in
     Abies balsamea crowns and effects of mega-
     strobilus production on shoots and buds.
     Can. J. For. Res. 7:498-509.

93. Promnitz, L.C. 1975. A photosynthate allocation
     model for tree growth. Photosynthetica 9:1-15.

94. Reed, K.L. 1980. An ecological approach to modeling
     growth of forest trees. For. Sci. 26:33-50.

95. Rehfeldt, G.E. and D.T. Lester 1966. Variation in
     shoot length of Pinus resinosa Ait. Can. J. Bot.
     44:1457-1469.

96. Reukema, D.L. 1964. Crown expansion and stem radial
     growth increment of Douglas-fir as influenced by
     release. For. Sci. 10:192-199.

97. Richards, F.J. 1959. A flexible function for
     empirical use. J. Exp. Bot. 10:290-300.

98. Riding, R.T. 1978. Within-crown variation in
     dormant long-shoot apices of mature trees of
     Pinus resinosa. Can. J. Bot. 56:141-147.

99. Riedacker, A. 1971. Measurements of different components of trees for physiological investigations. In 'Forest Biomass Studies', (Young, H.E., ed.), pp. 223-240, Orono: Univ. of Maine Press.

100. Rowe, J.S. 1972. Forest Regions of Canada. Can. Dept. Environ. Pub. No. 1300.

101. Sacher, J.A. 1954. Structure and seasonal activity of the shoot apices of Pinus ponderosa and Pinus lambertiana. Am. J. Bot. 41:749-759.

102. Satoo, T. and H. Imoto 1979. Modelling crown canopy of an even-aged stand of Cryptomeria japonica from measurement of leaf mass - A new approach to the morphology of forest crown. J. Jap. For. Soc. 61:127-134.

103. Shinozaki, K., K. Yoda, K. Hozumi and T. Kira 1964a. A quantitative analysis of plant form - The pipe model theory. I. Basic analyses. Jap. J. Ecol. 14:97-105.

104. Shinozaki, K., K. Yoda, K. Hozumi and T. Kira 1964b. A quantitative analysis of plant form - the pipe model theory. II. Further evidence of the theory and its application in forest ecology. Jap. J. Ecol. 14:133-139.

105. Smith, J.G.H. 1963. Analysis of crown development can establish biological and economic limits to growth of trees and stands. Comm. Forest. Rev. 42:27-33.

106. Smith, S. and K. Scoullar 1975. A data structure analogue for modelling tree crowns. Can. J. For. Res. 5:574-579.

107. Steel, R.G.D. and J.H. Torrie 1960. Principles and Procedures of Statistics. McGraw-Hill Book Co., Inc., New York.

108. Stephens, G.R. 1969. Productivity of red pine. I. Foliage distribution in tree crown and stand canopy. Agr. Meteorol. 6:275-282.

109. Sucoff, E. 1971. Timing and rate of bud formation in Pinus resinosa. Can. J. Bot. 49:1821-1832.

110. Thompson, S. 1976. Some observations on the shoot growth of pine seedlings. Can. J. For. Res. 6: 341-347.

111. Thomson, R.B. 1914. The spur shoots of the pines. Bot. Gaz. 57:362-385.

112. van Laar, A. 1973. Relationship between needle-biomass and growth of Pinus radiata. In 'IUFRO Biomass Studies', (Young, H.E., ed.), pp. 183-193, Orono: Univ. of Maine Press.

113. White, J. 1979. The plant as a metapopulation. Ann. Rev. Ecol. Syst. 10:109-145.

114. Wilson, B.F. 1970. The Growing Tree. The University of Massachussetts Press, Amherst.

115. Woodman, J.N. 1971. Variation of net photosynthesis within the crown of a large forest grown conifer. Photosynthetica 5:50-54.

116. Zar, J.H. 1968. Calculation and miscalculation of the allometric equation as a model in biological data. Bio. Sciences 18:1118-1120.