INDICES OF BRANCH CONTRIBUTION TO BOLE GROWTH IN *PINUS RESINOSA* AIT.

BY

© Philip James Behman

A thesis submitted in partial fulfillment for the
requirements of the degree of
Master of Science in Forestry

Lakehead University
School of Forestry
January 1982

ProQuest LLC.
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106 - 1346

ABSTRACT

The contribution of individual branches to the current annual xylem increment of the main stem of six young red pine (Pinus resinosa Ait.) was investigated. Logical estimates of branch productivity including: branch foliage dry weight, current extension length of the primary branch axis, and the current annual xylem increment measured as ring width at branch base (CAXI-branch base); were related to wood growth on the tree bole. CAXI-branch base was hypothesized to be the best single indicator of a branch's contribution to bolewood growth. This parameter was incorporated into a crown vigor index (CVI) designed to simulate vertically distributed bolewood increment. CVI was also related to other similar bole growth simulation models.

No clear correspondence was found between the vertical distribution of the annual bolewood increment and the branch parameters: foliage dry weight, current extension length of the primary branch axis, and CAXI-branch base. The regularity of these branch parameter measurements throughout the tree crown compared to a well defined bolewood increment pattern suggested, however, that an indirect relationship between the two existed.

The incorporation of CAXI-branch base into the crown vigor index made it possible to statistically relate this branch parameter to actual bolewood increment. CVI bole growth simulations, in general, corresponded closely to bolewood increment values. Notable exceptions occured on trees with anomalous growth patterns and at points of localized bending stress. CVI bole growth simulations proved to be superior to other bole growth models of similar construction.

The technique for measuring CAXI-branch base is a destructive process which is complex and tedious. A practical modification to the CVI model was to estimate CAXI-branch base from readily obtainable branch parameters. The best estimate of CAXI-branch base was the product total branch foliage dry weight and the current extension length of the primary branch axis.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

ACKNOWLEDGEMENTS

DR. K. M. Brown supervised the study and provided enthusiastic support and guidance. I am particularly indebted to Frances Bennett and Erhard Dobesberger without whose assistance, tolerance and friendship this study could not have been completed.

Dr. W. H. Parker and Prof. R. J. Day advised on various aspects of the study. Special thanks are due to Dr. R. E. Farmer for constructive critisism and review of the manuscript. Dr. R. A. Leary from the North Central Forest Research Station, St. Paul, Minnesota also reviewed the manuscript.

I am also indebted to Dr. J. E. Barker for providing useful information in the early planning of the study. Thanks are also due to Mr. B. Spencely for advice and Maida LeBaron for technical assistance in carrying out the detailed branch and stem analysis.

Ms. Angela Pepe and Mrs. Naomi Behman did much of the typing for the final copy of the thesis.

Financial support was provided by a Canadian Forestry Service Grant and by the Natural Science and Engineering Research Council of Canada.

INTRODUCTION

There have been relatively few reports on the relationship between simple crown dimensions and wood growth on tree boles. Pruning studies such as those by Ladefoged (1946), Young and Kramer (1952), Mar:Moller (1960), and Stiell (1969) have proved effective in demonstrating contributions made by foliage from different crown parts, but none of these studies, indicate the contributions made by individual branches to wood growth on tree boles. Labyak and Schumaker (1954), Beckwith and Shackelford (1976), and Barker (1981) quantified individual branch characteristics and related these measures to bolewood growth. They incorporated quantified branch attributes into mathematical growth models designed to simulate the current annual xylem increment on the tree main stem. However, no clear statement was made about the use of individual branch characteristics as measures of branch contribution.

Certain branch attributes, such as foliage dry weight or current extension length of the primary branch axis, may indicate the approximate amount of branch-produced growth substances translocated into the main stem (Hall 1965, Barker 1981). If so, these and other branch attributes may be related, in some way, to wood growth on the tree bole and thus reflect the productivity of individual branches. These measures may be inadequate to precisely reflect variation in the production and distribution of growth promoting materials at a level of resolution of interest to physiologists. Branch attributes, however, may be related to the distribution of radial bole growth at a level of resolution useful to forest managers and silviculturists. If so, such measures could be used, with relative ease, to determine the effects of silvicultural treatment on crown - bolewood increment relationships. Further, measured branch characteristics could be used to better assess and understand the impacts of management activities on forest growth and yield.

There were three main objectives to this study. The first objective was to relate various branch attributes to the radial growth of the tree bole. Of particular interest were the branch parameters foliage dry weight, the current extension length of the primary branch axis, and the current annual xylem increment measured at branch base (CAXI-branch base). The second objective was to test the hypothesis that CAXI-branch base is the best single indicator of a branch's contribution to bole growth in red pine (Pinus resinosa Ait.). The third objective was to determine the correlation of CAXI-branch base with other, more easily measured branch parameters.

The results of this study suggest that the vertical distribution of foliage dry weight, current extension length of the primary branch axis, and CAXI-branch base do not correlate directly with the vertical distribution of the annual xylem increment of the tree bole. However, a simple mathematical model of crown productivity, which uses branch attributes as input, gave good estimates of the vertical pattern of bole growth. On the basis of this analysis, CAXI-branch base appeared to be a useful indicator of individual branch productivity in the trees studied.

LITERATURE REVIEW

The vertical distribution of the annual xylem increment in tree boles and the resultant stem form has been extensively studied. One approach uses mensurational concepts and emphasizes the yield of the tree in terms of a commercial product (Larson 1963). Another approach considers biological concepts and emphasizes the development of the tree in terms of a living system. This review emphasizes the latter approach.

Much of the research on stem development in individual trees has been related to factors influencing the taper of the stem or stem form. Forest biologists are particularly interested in elucidating processes which regulate the formation of the current annual xylem increment along the tree bole for these processes determine stem form. The annual xylem increment has, therefore, become a focal point for various tree growth studies. Several of the most pertinent studies will be emphasized here.

General Observations on the Distribution of Bolewood Growth

Much literature has accumulated on tree ring analysis. Reviews by Farrar (1961), Larson (1963), and Wilson (1970) provide valuable summaries of this work. Ring width has been the most commonly studied parameter of annual xylem increment. It is a measure of cambial activity for it does not take stem cross-sectional area into account (Hall 1967). The following patterns in the vertical distribution of the annual xylem ring have often been reported (Farrar 1961, Larson 1963, Wilson 1970): In dominant polesize trees of medium density, ring widths are comparatively narrow in the apical internode then increase rapidly for a few internodes reaching a first maximum near the whorl of branches bearing the most foliage (see figure 1a). In the lower part of the crown and along most of the bole, ring width decreases. At tree base the ring becomes thicker and reaches a second maximum near ground level.

In suppressed trees, the point of maximum ring width is higher in the stem, with width decreasing down the stem, sometimes to extinction in the lower levels (figure 1c). Butt swell is usually absent.

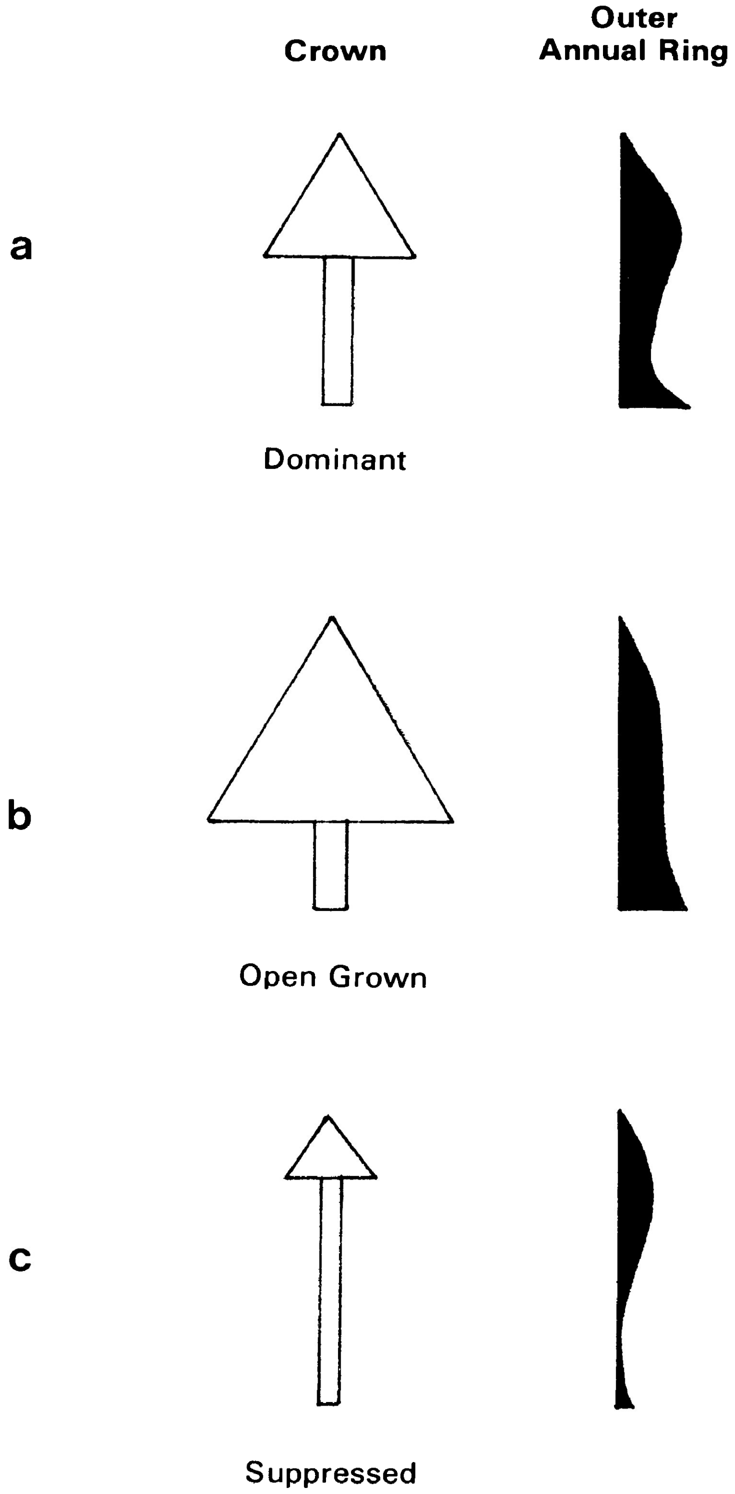


FIGURE 1. The relation of crown size to the distribution of cambial activity in the outermost annual growth ring (adapted from Wilson 1970).

In open grown trees with crowns extending to near tree base, ring width may increase all along the stem as shown in figure 1b.

These basic bole growth patterns in the vertical distribution of the annual ring can be modified through silvicultural treatment. Silvicultural operations that directly or indirectly modify crown development also modify cambial growth distribution. Thinning reduces root and crown competition allowing increased development of the residual trees. The stem growth reponse may occur immediately after thinning or after a period of crown expansion. Usually a year or two after thinning the annual ring in the lower part of the bole becomes thicker while within the crown ring thickness is almost unchanged. Consequently, ring width increases continuously from the apex to stem base. A few years after thinning the vertical distribution of annual ring thickness returns to its 'normal' form with a maximum near the branch whorl bearing the most foliage.

Live crown pruning tends to affect the pattern of xylem deposition below the pruned portion. Here, the thickness of the annual ring is reduced, especially if pruning removes the branch whorls with the most foliage.

These general remarks on bole growth pattern suggest that the distribution of the xylem increment is related to the development of the crown. This idea is not new. As early as 1864, Pressler (Larson 1963) realized the importance of the crown as a controlling factor determining growth ring patterns. He proposed three basic growth concepts: (1) ring area growth at any point in the stem is proportional to the quantity of foliage above it, thus (2) ring area is constant in the branch free bole, but (3) decreases with height in the crown in a manner dependant upon the distribution of foliage. Pressler summarized these general stem growth laws by suggesting that ultimately the form of the stem is a function of the crown.

Pressler's work, although not completely accepted by his colleagues, stimulated research into growth ring variation. From these investigations it was realized that stem form is indirectly governed by crown development and that direct regulation of xylem increment must finally be explained in terms of physiological mechanisms (Larson 1963).

Early Theories of the Regulation of Cambial Growth Distribution

Early forest botanists advanced three theories concerning the control of bole growth distribution. They are: the nutritonal theory, the mechanistic theory, and the water conduction theory (Larson 1963).

About 100 years ago, Theodor Hartig, proposed the theory that longitudinal gradients of crown produced growth substances (photosynthates) in tree boles determined longitudinal variations in ring width (Farrar 1961). Hartig's nutritional theory holds that vertical gradients in the supply of photosynthates result from the fact that growth materials are synthesized in the leaves and move mainly basipetally. As these materials pass downward through the phloem, some move laterally to nourish the cambium. Each branch is assumed to contribute growth materials in relation to its quantity of foliage with some reduction to compensate for shading and use of growth materials by the branch itself. It follows that the growth substances supplied to the cambium will increase from the apex downward as long as the quantity of foliage per unit stem length increases. Lengthening branches and shading of the lower foliage tends to raise the point of the maximum supply of growth materials above the live crown base. As the bole circumference increases, the supply of growth materials per unit of circumference decreases. Further, the use of growth materials at one level leaves less material for the lower levels. Hence, below the widest part of the crown an increasing reduction in growth substances available to the cambium would be expected.

Schwendener first proposed the mechanistic theory in 1874. This theory, later developed by Metzger(see Busgen and Munch 1929), envisages a tree stem as a beam of uniform resistance to the bending action of wind loads. Wind action was assumed to be concentrated at the centre of gravity of the crown, and, ignoring the stem within the crown and the region of butt-swell, the stem was thought to approximate a cubic paraboloid i.e. $d^3 = c \times l$ where: d = diameter measured at some point on the tree bole, c = a constant, and l = distance from center of gravity of the crown. In other words, the diameter at any point on the tree bole increases with increasing distance from the central point of application of the wind force i.e. the center of gravity of the crown. Metzger considered lateral wind forces to be the only important stimulus diverting metabolites from the crown to that part of the stem which was weakest and needed reinforcement.

Jaccard developed the water conduction theory during the second decade of the twentieth century (Larson 1963). Jaccard viewed the stem as a structure of uniform water conduction supplying water to the transpiring leaves of an expanding crown. The form of the tree's bole was therefore determined by the requirements placed upon it by growth of the tree's aerial parts. It was hypothesized that the cross-sectional area of water conducting tissue was constant within the branch free bole so to provide for uniformly free movement of water. The outermost three to five growth rings were assumed to be primarily responsible for the translocation of water. Since stem diameter decreases up the stem, it follows that the width of the annual ring must increase up the stem to maintain a constant cross-sectional area. Within the crown, ring width decreases with increasing height as the number of water conducting branches decreases.

Assmann (1970) cites many studies which support or refute the three early theories on the regulation of cambial growth. He concluded that none of the stem form theories discussed can sufficiently explain all variations of stem form. During the past two decades a considerable body of evidence has accumulated supporting a hormonal control of growth ring formation (Larson 1962,1969; Shepherd and Rowan 1967, Brown 1971, Beckwith and

Shackelford 1976, Barker 1981).

The Hormonal Theory of Xylem Growth Control

The hormonal hypothesis of the regulation of xylem growth distribution results from studies of the plant growth hormone auxin, carried out over the past 35 years (Thimann 1974). A series of disbudding, pruning, and girdling experiments, supplemented by measurement of growth hormone in the stem, led Onaka (1950a,b) to conclude that the vertical distribution of radial increment is governed by the production of growth hormone and the flow of nutritive substances. He also concluded that the growth hormone is produced by growing buds, cones, new and even old needles, and that nutritive substances are manufactured chiefly by old needles in the early part of the season and by new needles later in the season. Larson (1962), an important proponent of the hormonal hypothesis, expanded upon Onaka's studies and concurred with the idea that nutitional gradients could not possibly serve as the solitary regulatory mechanism in secondary xylem growth. It has been repeatedly demonstrated that cambial activation on the stem fails regardless of the availability of nutrients in the adjoining tissues unless initiated by a stimulus (auxin) emanating from the crown (Wareing 1958, Wilcox 1962, Larson 1962, Hall 1965, Whitmore and Zahner 1966). Larson's concepts about a hormonal control of xylem growth supplemented earlier stem form theories. The hormonal theory is believed to provide a physiological basis to describe certain facts influential in the construction of earlier stem form theories.

Larson's (1962,1969) ideas on the regulation of xylem growth in conifers are summarized as follows: A growth hormone, auxin, capable of stimulating cambial activity in approximate proportions to its concentration, is produced primarily in the buds and elongating shoots and secondarily in developing and mature foliage. The rate of auxin production varies both vertically and laterally in the crown. Terminal buds and shoots on the primary branches decrease in auxin productivity with increasing whorl rank below the stem apex. A similar pattern is repeated on an increasingly diminished scale in the primary, secondary, tertiary, etc. branches. Due to these differences in auxin synthesis, the lateral branches nearest the stem apex are the most vigorous and contribute the greatest quantity of auxin to the main stem. Proceeding downward, bud vigor and auxin synthesis not only decrease but the branch distance over which the auxin must be translocated to the main stem increases so that the lower branches contribute less and less auxin to the supply of the main stem.

The regulation of xylem growth is considered by Larson to be regulated by vertical gradients in auxin concentration. In general, trees with long, vigorous, crowns have both a high potential for auxin synthesis and an advantageous distribution of auxin producing branches on the bole. Trees with small, high, crowns have a reduced capacity for auxin synthesis and a greater distance over which the limited auxin supply must be translocated to reach stem base.

Larson (1963) claimed that his hypothesis shows promise in clarifying the physiology of stem form development but noted that it required extensive refinement before it could meet with general acceptance. Larson pointed to correlations between shoot growth, auxin levels, and the type of wood produced as direct evidence for hormonal control of growth ring formation (Brown and Zimmerman 1971). Since Larson proposed his original hypothesis much evidence has accrued to support this concept. Two areas of research are of immediate importance. These areas relate to studies concerning the control of shoot growth and to studies determining the control of cambial activity.

Apical Control Of Shoot Growth

Apical dominance is "the correlative inhibition of growth of lateral buds or shoots by the apical shoot" (Pharis and Kuo 1977). In red pine, both bud size and the length of the shoots produced from them decreases progressively from upper to lower whorls (Kramer and Kozlowski 1979). The terminal leaders, with large buds, often expand faster and for a longer time than do leading shoots of lateral branches. This difference in branch extension rate causes a corresponding decrease in shoot growth from the top of the tree downward producing typical excurrent growth. Excurrent growth is a result of weak apical dominance causing the incomplete inhibition of the lateral buds (Brown and Zimmermann 1971). Because the terminal leader always maintains complete control over the partially suppressed branches below, the tree is considered to exert strong apical control. Decurrent forms of crown growth are a result of strong apical dominance and weak apical control. This results in the complete inhibition of the lateral buds on the current year's shoot. The release and rapid growth of two or more of the uppermost lateral buds the following spring tends to suppress the terminal leader so that apical control is lost and repeated forking occurs in the crown. Brown and Zimmermann (1971) consider the term 'apical control' to be better suited for describing the physiological condition governing the excurrent or decurrent pattern of growth.

The mechanism of inhibition of lateral shoots by terminal meristems has been widely investigated. The overall control of apical dominance is complex and appears to involve both hormonal and nutritional factors that influence differences in bud opening, and rate and duration of shoot expansion (Kozlowski 1971a).

Most investigations stress the importance of an inhibitory signal originating in the apical part of the shoot. For example, removal of the growing apical bud is followed by outgrowth of previously inhibited lateral buds (Kramer and Kozlowski 1979). Phillips (1975) reasoned that lateral buds are inhibited by a downward movement of apically produced hormones rather than by a lack of nutrients or water. Auxins, gibberellins and cytokinins have been implicated in apical control of lateral shoot growth. Early investigations (Thimann and Skoog 1933,1934 cited by Phillips 1975) suggested that auxin alone controlled apical dominance but this was refuted when

Camus (1949) showed that apical buds checked growth of lateral buds even though the auxin content of apical and lateral buds were not significantly different. Thimann (1965) suggested that the mechanism involved interactions between auxin and cytokinin. Exogenous auxin inhibited growth, but the inhibition could be cancelled by kinetin (Wickson and Thimann 1958). It was suggested that lateral buds could not synthesize the cytokinins necessary for their growth, and that release from auxin inhibition permitted cytokinin synthesis.

Studies by Pharis et al. (1965), Phillips (1969), Tomaszewski (1970) and McGraw (1973) have implicated gibberellins as playing a role in apical dominance although this role is not at present clear.

In addition to hormones, the nutritional status of a plant plays an important role in apical dominance. Evidence comes from Wareing et al. (1964) who observed that some trees exhibit much stronger apical dominance under conditions of low soil fertility and low light intensity than under more favourable conditions. Work by Gregory and Veale (1957) support this observation.

It is tempting to suggest nutritional control of apical dominance but this has long been refuted. Stem girdling experiments have shown that interruption of the continuum of living cells along the stem usually results in outgrowth of lateral buds situated below the girdle and yet at the same time the upper portion of the shoot continues to grow and consume nutrients and water (Kramer and Kozlowski 1979). This suggests that lack of growth by lateral buds is attributable to the downward movement through living tissues of an influence originating in the apical part of the shoot, and not to their starvation of nutrients or water (Phillips 1975). Other studies which support this are Goodwin and Cansfield (1967), Phillips (1968), Wardlow and Mortimer (1970).

It has been demonstrated that metabolites such as sugars, phosphates and cytokinins are translocated to and accumulate in growing buds and other sites of metabolite demand (Milthorp and Moorby 1969, Morris and Winfield 1972). Metabolites and cytokinins are also mobilized by localized applications of certain growth hormones, particularly auxins which can induce long-distance metabolite transport. The term hormone directed transport (HDT) has been applied to this phenomenon (Phillips 1975). The mechanism by which HDT occurs remains obscure, however, it has been assumed to be related to either; (a) a direct effect of the hormone on phloem transport or (b) an indirect effect on long distance transport through activation or maintenance of local sink activity in the hormone centered tissue (Mullins 1970, Bowen and Wareing 1974, Patrick and Woolley 1973, Wareing and Patrick 1973).

The implications of hormone directed transport of metabolites are many. Little (1969) suggested that the amount of nutrients mobilized by a shoot, and its subsequent growth depended on the capacity of the shoot to produce hormone growth regulators. He emphasized that the degree of dominance of various whorls of *Pinus strobus* L. depends upon the supply of nutrients available at the time bud primordia are produced in the developing winter bud. The size of the buds borne in the current whorl of the shoot arising from the winter bud depends on the amount of nutrients available during the period of current shoot development. When these buds elongate during the following year, differences in shoot size depend on the minimum level of nutrition during shoot elongation. The level of nutrition available for shoot elongation in a branch is determined by its ability to produce and mobilize photosynthate.

Growth Regulators and Cambial Activity

Cambial activity is a general term that covers cell division, enlargement and maturation (Wilson, Wodzicki and Zahner 1966). Auxin control of cambial activity seems to be a very important element in the mechanism regulating xylem production in the branch and stem (Westing 1965,1968; Roberts 1969, Kozlowski 1971b, Wodzicki and Wodzicki 1973, Zajaczkowski 1973, Little 1975, Zajaczkowski and Wodzicki 1975, Denne and Wilson 1977), however, the interaction between several hormones is likely to control cambial activity (Wareing et al. 1964, Hejnowicz and Tomaszewski 1969, Wodzicki and Wodzicki 1973). Wodzicki and Wodzicki (1973) observed that chromatographic extract of pine auxin contained substances which altered growth stimulation as compared with synthetic auxin (indole-3-acetic acid;IAA). Hejnowicz and Tomaszewski (1969) found synergistic interactions between IAA and some phenolic compounds. Such interactions may depend on the relative amounts of both auxin and other extractable substances. Experiments by Zajaczkowski and Wodzicki (1975) and Denne and Wilson (1977) support this view.

Gibberellins (Wareing et al. 1964, Farrar and Fan 1970, Pharis 1976), cytokinins (Westing 1965,1968; Hejnowicz and Tomaszewski 1969), abscissic acid (Little and Eidt 1968,1970; Little and Bonga 1974, Little 1975), ethylene (Leopold et al. 1972, Brown and Leopold 1973) and other, non-hormonal, substances (Wodzicki and Zajaczkoski 1974) in addition to auxin, have been implicated as native growth regulators of cambial activity in conifers.

The effects of the different interactions of growth hormones are varied. They control most aspects of cambial growth including cell initiation, division, differentiation, expansion, thickening, earlywood - latewood relations and reaction wood formation.

Dual Mechanism of Xylem Growth Control

Several studies have shown that restraining a tree against wind sway results in decreased growth below the portion of the stem under restraint (Jacobs 1954, Larson 1965, Burton and Smith 1972). Other studies have demonstrated a positive growth response of plants to mechanically induced bending or swaying (Venning 1949, Walker 1960, Reich and Ching 1970, Quirk et al. 1975, Fayle 1976).

Larson (1965) extended his original hormonal hypothesis to account for stress induced wood growth. He proposed a dual, active - passive, system of xylem growth control. The tendency for growth to be distributed to areas of physical bending stress was termed 'active' or 'stimulatory' growth. Stress areas were thought to create metabolic sinks to which assimilates actively flowed. The tendency for growth to concentrate on the upper portion of the stem, particularly just beneath the branch whorl contributing most to stem growth, was termed 'passive' growth. Excess photosynthates were hypothesized to gravitate passively downward in the stem but were used preferentially for growth on the basis of availability.

The physiological response of the tree to the mechanical effects of wind is not clearly understood. There is evidence to suggest that auxin may stimulate cambial growth during the formation of compression wood by increasing ethylene production. Imposition of stress on branches of _Pinus strobus_ and _Prunus persica_ (L.) Batsch, by bending and tying them in a U, increased ethylene levels (Leopold et al. 1972). When a paste of ethaphon was applied to _Pinus strobus_ branches, ethylene production increased and cambial growth was stimulated (Brown and

Leopold 1973). Abeles (1973) postulated that some auxin effects may be mediated through ethylene regulation because increases in auxin generally enhance ethylene production. Doerner (1966) calculated stress distribution patterns in branches and noted a similarity of these to Thimann's (1934) curves for the distribution of growth substances and growth rate. Doerner did not suggest a causal relationship but instead an interrelationship of these growth parameters. It was proposed that the cambium sensitized to a degree proportional to the amount and frequency of stress. Boyd (1977) noted that the distribution of stress, arising from bending forces in branches, is similar to that produced by the development of reaction wood. Asher (1968) studying mechanically induced electrical charges in red pine leaves suggested that mechanically induced stress initiates a chain of physical and biochemical stimuli that promote the reactivity of growth hormones.

The idea that photosynthates gravitate passively downward in a completely 'passive' system of xylem growth control has been brought into question with the advent of the competetive-sink hypothesis (Little 1969, Wilson 1981) and elucidation of a hormone directed metabolite transort phenomenon (Patrick 1976).

The Competetive Sink Hypothesis

The competetive-sink hypothesis has been currently proposed to further describe the nature of growth control in plants. Active growing sites in plants appear to compete for a common pool of metabolites by influencing their transport. The hormone directed transport of metabolites phenomenon (HDT) may be involved (Patrick 1976). Evidence suggests that food materials, primarily carbohydrates, move from where they are synthesized or stored (the 'source') to where they are being used (the 'sink') under the influence of HDT (Kozlowski and Keller 1966; Kozlowski 1971a,b; Ursino 1973). Reserve carbohydrate and currently produced photosynthates move in response to the strength of the demand for them and the proximity of growing tissue to source of supply (Kramer and Kozlowski 1979). Little (1969) and Wilson (1981) have suggested that branches and stems of trees, particularly the stem internode just below a branch, compete for branch produced photosynthate.

The strength of growth sinks vary seasonally. In young temperate gymnosperms the roots typically are the major carbohydrate sinks before buds open (Nelson 1964). After buds open a reversal of translocation takes place, with larger amounts of carbohydrate moving into expanding shoots. At this time cambial growth forms secondary carbohydrate sinks. When seasonal shoot growth is completed, cambial growth and renewed root growth comprise the major carbohydrate sinks. This generalized seasonal pattern may be greatly altered during a year of heavy fruiting when reproductive tissues mobilize the bulk of available carbohydrate (Kozlowski and Keller 1966, Kozlowski 1971a,b). When both roots and shoots are growing, the proportion of photosynthate retained by the shoots and translocated to the roots depends upon the relative strength (growth rate) of each of these sinks and the proximity of carbohydrate sources (Ursino 1973). Also, Kozlowski and Winget (1964) and Ursino et al. (1968) found that carbohydrates exported early in the growing season from the leaves of seedlings may move upward to strong sinks in rapidly expanding shoots.

MATERIALS AND METHODS

Twenty-four young red pine were selected for study from three stands in northwestern Ontario. Red pine is a particularly suitable study species because of its uninodal growth habit and well defined growth rings. Six of the twenty-four study trees were randomly selected for detailed analysis. The following Materials and Methods describes: 1. the characteristics of the study sites (or stands), 2. the procedures of branch and stem measurement, and 3. a model of the current radial increment of the tree bole. The model is used as a tool to test the hypothesis that the current annual xylem increment measured at branch base (CAXI-branch base) is an indicator of branch contribution to bole growth.

Study Areas

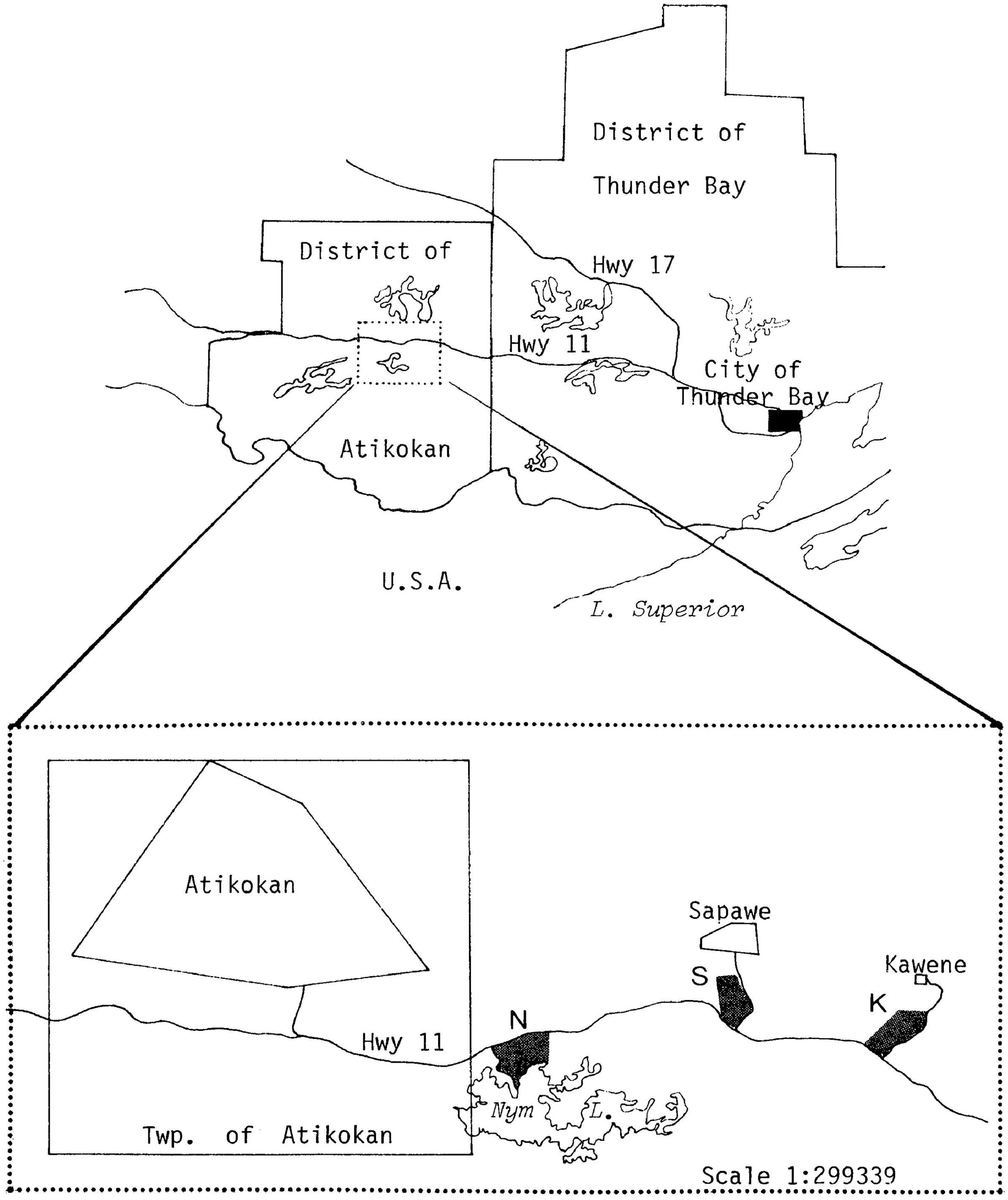
Location

Study trees were selected from three different aged, readily accessible stands on similar sites at Atikokan, Ontario, 190 km west of the city of Thunder Bay. Three areas of about 40 hectares each, containing stands of 13, 16, and 21 years were chosen. They were located at latitude 48°44' N and longitude 91°21' W. This region falls within the Quetico Section (L.11) of the Great Lakes-St. Lawrence Forest Region (Rowe 1972). Figure 2 illustrates the location of these areas.

The 13-year-old red pine stand was located 4 km south of the village of Kawene; Universal Transverse Mercator grid reference 15 6308 53984. The 16-year-old red pine stand was located on the north shore of Nym Lake; Universal Transverse Mercator grid reference 15 6129 53972. The 21-year-old red pine stand was located 2 km south of the village of Sapawe; Universal Transverse Mercator grid reference 15 6235 53998.

Site Description

Soils. The dominant geological surface feature in the area was ground moraine (Zoltai 1965). The soil was coarse textured, composed of rocky, sandy, glacial till. Bedrock outcroppings were evident, especially at the Nym Lake site. Soil depth ranged from 15 cm to 1 m. Clayton et al. (1977) employed the FAO/UNESCO system of soil classification in listing the soil type in and around the study areas as Orthic Humo Ferric Podzol. This soil



N Nym L. study area 16-year old red pine

S Sapawe study area 21-year old red pine

K Kawene study area 13-year old red pine

FIGURE 2. The location of study areas.

subgroup is widely distributed in Canada and forms primarily under moist, well-drained, course-textured soils. The soil moisture regime is listed in Clayton et al. (1977) as boreal: moderately cool, subhumid. This is the FAO/UNESCO classification for soil moisture status and implies a moist, unsaturated soil that shows water deficits for short periods during the growing season. Such water deficits may inhibit tree growth. The growing season generally begins in late April and extends into early November, a time period of about 200 days.

Stand Origin. The Sapawe, Nym Lake, and Kawene study areas were handplanted with 3+0 red pine nursery stock in the spring of 1960, 1965, and 1968 respectively. Generally the areas were planted at 8 x 8 foot (2.43 x 2.43 m) spacing but excessive stoniness and rock outcroppings forced large sections of land to be spot planted.

Site Productivity. Site index is the most frequently used indicator of site productivity in the United States and Canada (Carmean 1975). When stands are too young to measure site index by the conventional height/age approach, terminal height growth can be a useful estimator of site index (Alban 1979). Alban measured the growth of stem internodes above specific heights in young red pine and found average internode length above these points to be reasonable estimators of site index. Appendix A contains the vital information and calculations, using this method, for site index estimates at the Sapawe, Nym Lake, and Kawene study areas. The findings are summarized in Table 1.

Site index estimates showed that site quality differed slightly between sites. However, interpolation from Plonski's (1974) Normal Yield Tables placed all areas into site class 1.

Field Procedure

Field work was carried out from May 15 to May 18, 1979 just prior to bud flush. Eight red pine were selected from each of the three study areas. Only healthy trees with robust, symmetrical crowns were chosen. Trees were harvested as close to ground level as possible and transported to Lakehead University in Thunder Bay for processing.

Table 1. Site index and site class estimates for the Sapawe, Nym Lake and Kawene study areas.

Study Site Location	Site (ft)	Index† (m)	Site†† Class
Sapawe (21-years-old)	65.6	19.9	-
Nym Lake (16-years-old)	69.0	20.8	
Kawene (13-years-old)	72.2	22.1	1

†. Predicted tree height at age 50, averaged values from Table A1.
††. From Plonski, 1974.

Laboratory Methods

Data Collection

Branch. The branches of all twenty-four trees were processed first, due to their quickly drying foliage. As foliage dries it becomes brittle and eventually drops off. This condition is accentuated with increased foliar age. Thus to further minimize needle loss the branches were processed systematically from oldest to youngest. Branches were removed flush with the bole. The length of each branch internode was measured along the primary branch axis to the nearest half centimetre. Three branches from whorl four and whorl eight, and one branch from each of the other live whorls were selected randomly and set aside. The foliage from these branches was removed and bagged according to its year of origin. An assessment of the age structure of the branch foliage could be made from these data. Only total foliage weight was determined for all other branches. All foliage was air dried for three weeks prior to oven drying at 105 °C. for 24 hours. The foliage was then weighed to the nearest tenth of a gram. A 50 cm butt section from each denuded branch was saved and stored.

Six trees were randomly selected from the twenty-four, two from each of the 13, 16, and 21-year-old stands. A 2 cm thick cross section was cut 5 cm from the base of their branches and the current annual growth ring width was measured from these sections (see Branch and Stem Analysis).

Bole. A thin bole cross- section approximately 4 cm thick was removed 5 cm above and below each whorl of branches. The distance from the tree apex to the top of each bole section and to the centre of each whorl node was measured. Foliage was stripped from the main stem and processed with the branch foliage.

Polyethylene Glycol 1000 Treatment

Wood shrinks in different planes and directions as it dries (Mitchell 1972). This may cause bole sections to warp or check, causing serious error when they are measured. To minimize this problem bole sections were impregnated with a 30 percent solution of polyethylene glycol 1000 (PEG). PEG is chemically related to antifreeze and stabilizes wood by filling and solidifying in spaces usually occupied by water.

The change in dimension of fifteen PEG treated wood samples was determined. A five centimeter distance measured on the wood samples before and after treatment showed that the dimensions of the wood changed less than two per cent.

One difficulty encountered during the course of PEG impregnation was the growth of fungi (Ceratocystis spp.) on the bole sections and on the surface of the PEG solution. This was combatted by rinsing sections in a 1 percent solution of sodium hypochloride (NaOCl) when fresh cut.

Branch and Stem Analysis

The classic works of Duff and Nolan (1953,1961) contain branch and stem analysis methodology which have become standard for tree growth studies that look at annual growth rings (Myers 1963, Hall 1965, 1967, Larson 1965, Shea and Armson 1972, Barker 1981). Modifications of this methodology may be necessary due to: the purpose of the individual study, the accuracy and precision of measurement required, and the time and funds available for the completion of these measurements. This study required that the measurements be precise and accurate. Duff and

Nolan and others measured annual growth ring widths directly from branch or stem cross-section samples. A number of ring width measurements were taken around the same ring and averaged to obtain a mean ring width. The accuracy and precision of this technique is acceptable except when measuring very narrow growth rings.

The accuracy of a measurement depends on the technique used to do the measurement and on the systematic error inherent in the technique: an accurate or exact measurement is one which (i) measures just what it purports to measure and (ii) is practically free from systematic error (Bunge 1967). The two conditions are mutually independent: the first depends on technique design, the second on the method of measurement execution. The precision of a measurement, free from systematic error, depends both on the technique used and on the associated random error: the smaller the random error the greater the precision of measurement. The methodology used in this study to measure ring widths is an attempt to increase both the accuracy and precision of branch and stem annual ring width measurements while also increasing the efficiency of the measurement process.

Disc preparation. The sample trees were measured for current growth ring width in branch and bole. All sections were prepared to show a clearly visible, well defined outer ring. The stem sections were sanded to reduce surface roughness. Branch sections were comparatively smooth and did not need this treatment. A sharp scalpel was used on both branch and stem sections to smooth any remaining surface irregularities and to further improve ring definition.

Photography. All stem and branch sections from the six sample trees were then photographed. A millimeter ruler was placed beside each section to provide scale. Figure 3 shows the camera setup and a contact print of some photographed branch sections. The camera is a Pentax 135 mm Spotmatic II. A Vivitar 90 mm macrolens with attached screwmount extention tubes was used to photograph all small sections, i.e., those sections less than 4 cm in diameter. The smallest section photographed was 0.4 cm in diameter. The macrolens was employed alone for larger branch sections, i.e., those sections less than 10 cm in diameter. A Tacumar 55 mm normal lens was used to photograph those sections greater than 10 cm in diameter. The largest stem section photographed was 20 cm in diameter. The different camera lens attachments made it possible to photograph each section at a magnification

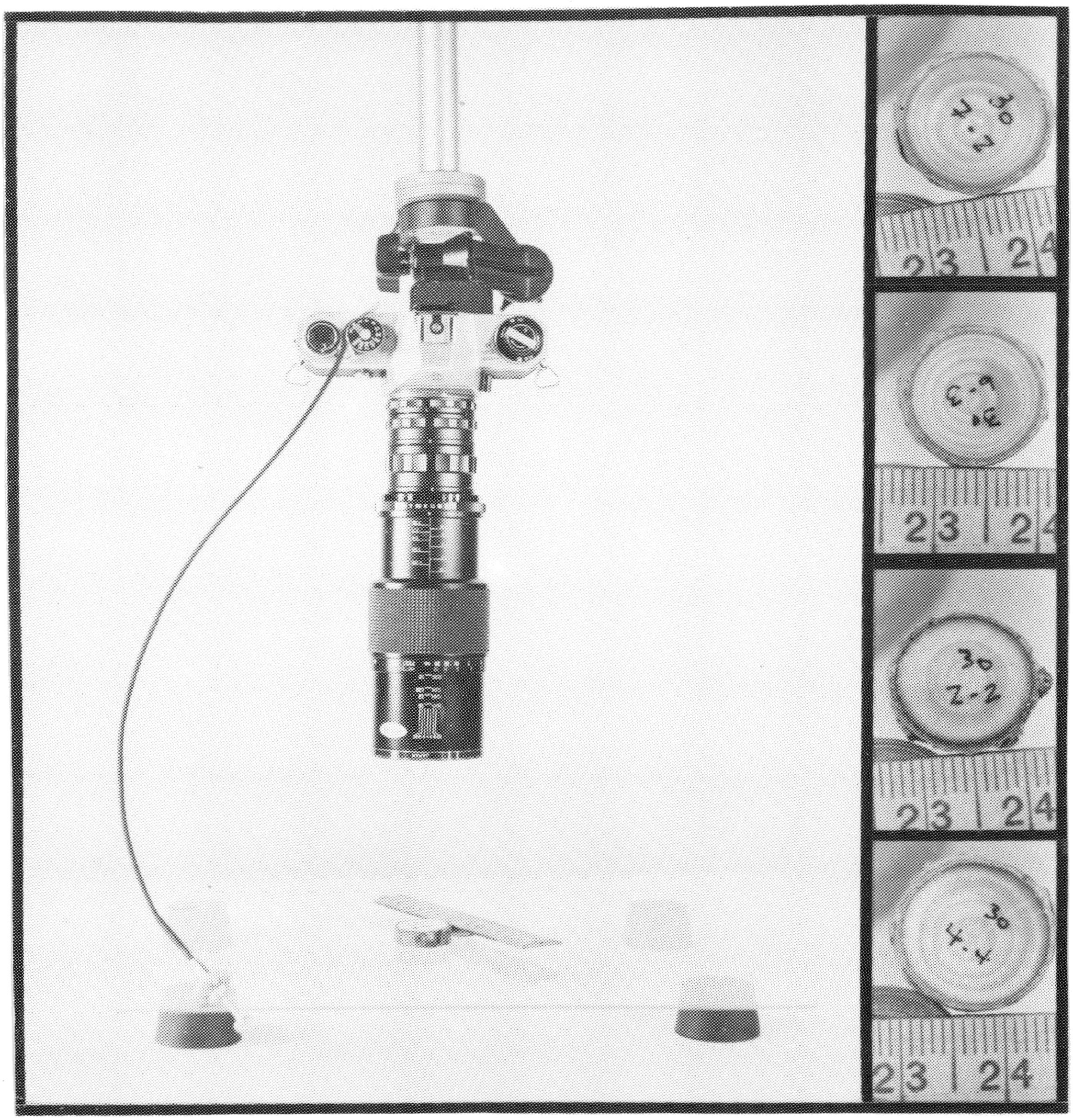


FIGURE 3. Camera set-up and a contact print of some photographed branch sections.

high or low enough to produce detailed, quality negatives.

Shadows created problems in the branch section photography because they decreased negative contrast and definition. To alleviate this problem, each branch section was placed on a raised, clear glass plate when photographed. Three 150 watt flood lamps directed at a 45 angle onto the disc surface forced shadows away and out of the camera field of view.

Kodak, Plus-x, a black and white 35 mm film, was used for all photographs. It was exposed and developed following techniques and recommendations found in Adams(1970).

Measurement of negatives. The negatives of each stem and branch section photograph were projected through a Simon Omega B8 enlarger onto a flat surface. A Numonics 237 Graphic calculator was used to measure the enlarged image. Figure 4 shows the calculator components and its position in relation to the enlarger. The graphic calculator functions as a free standing electronic planimeter and will measure simple lengths to plus or minus 0.5 mm or areas of any shape to plus or minus 0.5 mm^2.

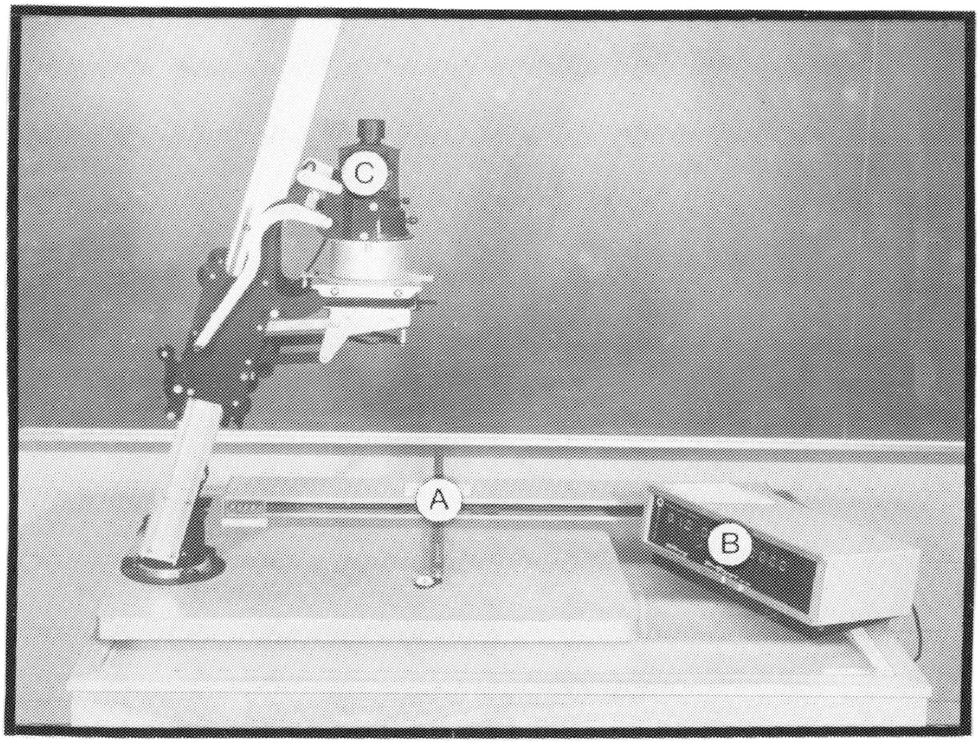


FIGURE 4. Numonics 237 graphic calculator with traverse reading arm (A), and digital display (B), set-up in relation to a Simon Omega B8 enlarger (C).

Figure 5 is a photograph of an enlarged, projected branch section negative. The length at 'C' is a measure of scale and was used to determine the magnification of the projected image. Circumferences indicated at 'A' and 'B' represent the outer and inner extent of the last formed growth ring. These circumferences were tracked with the traverse arm of the grapic calculator which automatically converted the linear distance to inside circumference area. The area inside the circumference marked at 'A' is equal to the total area of all rings. The area inside the circumference marked at 'B' is equal to the total area of all growth rings less the area of the last formed growth ring.

Mean ring width calculations. It is assumed that growth rings are laid down in concentric circles. Knowing that the area of a circle is π times its radius squared, area measurements were converted to linear measurements by $R = (A/\pi)^{\frac{1}{2}}$. R and A equal the radius and area of a circle respectively. The radius from the pith to the inner margin of the last formed growth ring, pith to position B in Figure 5, was subtracted from the radius from the pith to the outer margin of the last formed growth ring; pith to position A in Figure 5. The result was divided by the image magnification factor to give an average ring width value for the last formed growth ring.

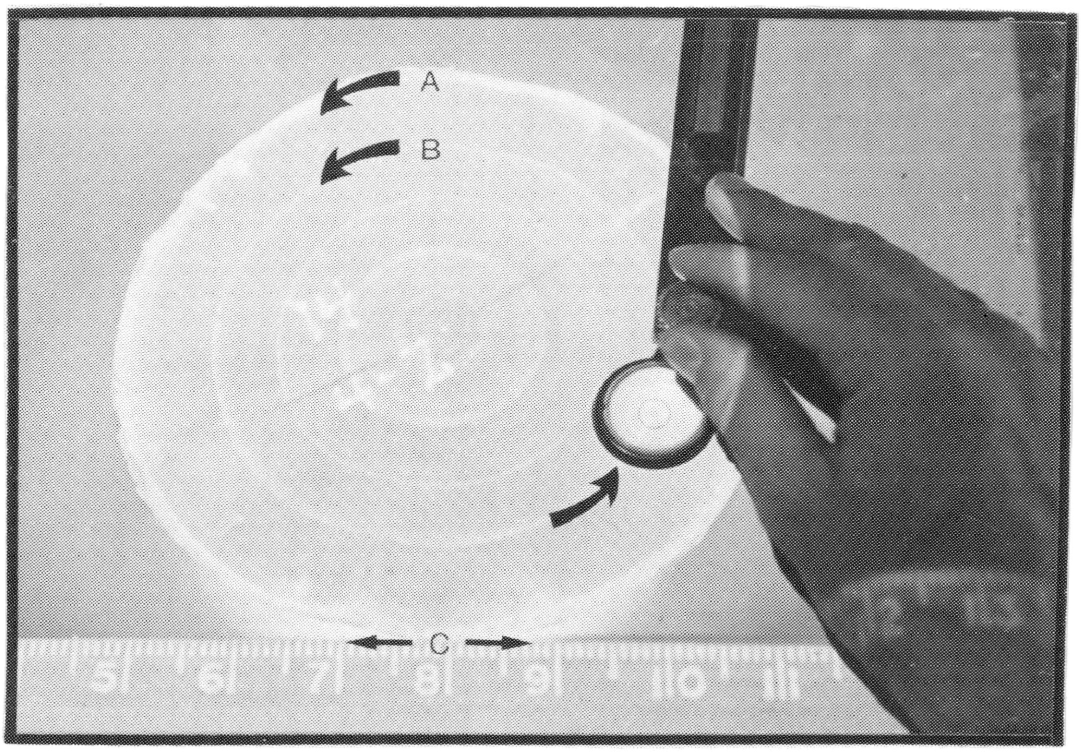


FIGURE 5. Enlarged branch section negative showing path followed by the traverse reading arm to measure outside circumference (A) and inside circumference (B) of the outer annual growth ring. Scale (C) is in centimeters.

Error analysis. An error analysis was conducted to determine the precision of the growth ring measurements. Three branch section sample negatives were selected for repeated measurement. The diameters of these sections were 1.04 cm, 1.73 cm, and 2.51 cm. They were chosen to represent a small, medium and large size branch disc. Each section negative was enlarged to 5x, 10x, and 15x its original size. The diameter of the resultant image was recorded, then measured according to previously described procedures (see Measurement of negatives pg. 38). The image created by enlarging the 2.51 cm section 15x, was too large to be measured by the numonics calculator so this treatment combination was dropped.

Thirty sample estimates of mean ring width were determined for each combination of disc size and enlargement factor. The mean and variance of each sample was calculated.

Appendix B summarizes the error analysis for growth ring measurements. Results indicate that two factors were largely responsible for determining the precision of growth ring measurements. They were: the size of the section images, and the size of the actual photographed sections. The larger the projected image the smaller was the standard error of measurement. Assuming a constant absolute error for machine and operator, a larger measuring surface will yield greater precision. This is similar to decreasing the field of view on a microscope to improve resolution.

The smaller the photographed section was the smaller was the standard error of measurement. This occurs because small sections were magnified more times than larger sections. Therefore section surfaces were more accurately represented and measurement was conducted with greater precision. Using conventional measuring techniques the reverse is found to be true.

The technique compared. Few investigators present error calculations with growth ring measurement data. Svenonius and Olausson (1975) did, however, calculate the measurement error associated with repeated ring width measurements on pine, spruce, and oak core samples. Their techniques are comparible to others in the field. Svenonius used a Zeiss measuring microscope, magnifying power 10x to 20x, and obtained a mean absolute error of approximately 0.03 mm. For wide rings this value corresponds to about 1 percent and for narrow rings 20 percent. In this study repeated measurements were conducted only on sections with narrow rings (1.88 mm to 2.39 mm). The standard errors ranged from 0.0051 mm to

0.0137 mm corresponding to a 0.49 to 1.17 percent error in measurement. The major limitation of past growth ring width measurement procedure has been the inability to increase instrument precision as ring widths get smaller.

Assumptions and Procedures used in the Construction of a Bole Growth Simulation Model

The proposed model is an attempt to simulate the contribution of individual branches to the current annual xylem increment in the main stem (CAXI-main stem) of red pine. It was not the purpose of this study to produce an exact analogue of this highly complex physiological system. Only details thought to be of major importance to the dynamics of the phenomenon under study have been included.

Biological Basis

Larson(1965) hypothesized that two distinct systems are instrumental in the control of ring growth in tree boles: a passive system which depends upon nutritional and hormonal gradients arising as a result of physiological processes in the crown; and an active system which involves a physiological response to a gradient of physical bending stress generated by tree sway. A detailed explaination of Larson's hypothesis is contained in the Literature Review (pg. 21).

The tree growth model proposed here considers only the hypothesized passive system of secondary xylem growth control. A number of assumptions are implicit in this hypothesis. The input of growth regulator and photosynthate from a branch is assumed to be distributed and utilized over the tree bole as follows:

-crown-produced growth regulators are transported basipetally. The effects of each branch are thus felt downstream but not upstream.

-the effect of each branch on the total solute load in the phloem is greatest at branch base and diminishes as the surface area over which the solute load is distributed increases.

-the additive effect of all branches is realized in the bole as xylem increment: the effect of an individual branch upon a particular point on the bole depends upon its contribution of excess photosynthates and growth regulators to the bole and its distance from the point in question. The richer the supply of these materials collected at a given bole location from all contributing branches, the greater will be the annual increment.

Previous Models

The structure of the model proposed here is based upon previous attempts by Beckwith and Shackelford (1976) and Barker (1981) to simulate the contribution of individual branches to bole growth in 12-year-old loblolly pine (*Pinus taeda* L.) and 19-year-old Monterey pine (*Pinus radiata* D.Don), respectively. They hypothesized that the effect of an individual branch on a particular point in the bole could be expressed as a quotient: the numerator represented the input of growth regulators from branch to bole; the denominator was a measure of the distribution and utilization of these regulators down the bole.

Measurable branch parameters have been used to represent the numerator in previous models. Beckwith and Shackelford used rate of extension of the primary branch axis and Barker used primary branch extention length as a measure of the branch's contribution of growth regulators to the bole. The denominator for both models was represented by the distance from branch base to a particular point on the tree bole. The numeric value of these models, when evaluated for a particular point on the main stem, is calculated as the sum of the individual quotients for all branches above the point in question. The value is hypothesized to represent the combined 'crown effect' at that point. The value of the model obviously varies continuously along the stem.

Components of the Proposed Model

In compliance with the Beckwith and Shackelford, and Barker models, the proposed model is in the form of a quotient. The numerator, or input parameter, is represented by the width of the last ring formed at the base of a branch (CAXI-branch base). This is a specific growth parameter that measures cambial activity (Duff and Nolan 1957). The activity of the cambium is thought to be regulated by the concentration of growth substances translocated in the phloem. Therefore, CAXI-branch base is hypothesized to be a measure of the concentration of growth materials flowing past the branch base into the stem. If this hypothesis is true, CAXI-branch base is a measure of a branch's contribution to the supply of growth solutes in the stem.

The denominator, or distribution parameter, of the model is represented by the bole surface area calculated from branch base to the specific point on the tree bole at which the model is to be evaluated. The concentration gradients of basipetally translocated solutes are simulated by dividing the input parameter, CAXI-branch base, by estimates of the phloem surface area, i.e., inside bark bole surface area, between the branch in question and the bole locations of interest. A crown vigor index is calculated by summing the individual quotients for all branches above the bole location of interest. This sum is an index value hypothesized to represent the concentration of growth regulating solutes flowing down the bole but measured at a specific point. The crown vigor index values represents the collective contribution of all branches affecting bole growth at a specific point over one growing season.

Model Computation

Bole surface area calculations were based upon the assumption that a tree stem can be viewed as a series of segments, each segment being represented by the frustrum of a right circular cone. The formula for calculating the lateral surface area of such a frustrum is presented in Figure 6a. An additional surface area was computed for each branch. The surface area of a 5 cm long stub section was added to the bole surface area measurements to account for the region between the CAXI-branch base measurement and branch insertion into the bole. The formula for the calculation of the lateral surface area of a cylinder was used to determine this measure. The formula is presented in Figure 6b. Although small, a measure of the surface area at branch base was influential when index values were calculated immediately below branch whorls.

A crown vigor index (CVI) was calculated for a number of points along the bole as:

$$\mathrm{CVI}(x) = \sum_{j=1}^{N} \sum_{k=1}^{n_j} \frac{\text{CAXI-bb}(j,k)}{[A(h_j,x) + B(j,k)]^{\frac{1}{2}}}$$

where: x = height above ground of a point on the bole.

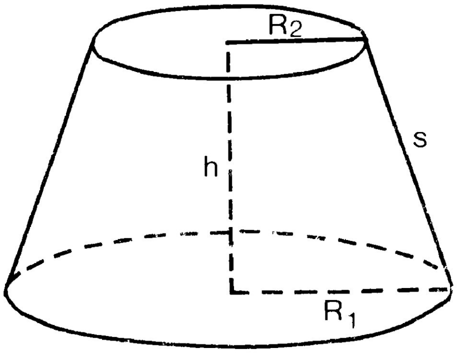
N = total number of branch whorls above x.

n_j = number of branches in the j^{th} whorl.

h_j = the vertical height from ground to the j^{th} whorl.

Symbol Definition

R_1 = radius lower base
R_2 = radius upper base
h = height
s = slant height
S = lateral surface area



Formulae

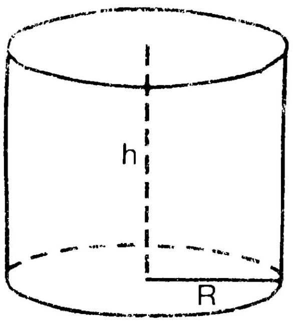
$$s = \sqrt{(R_1 - R_2)^2 + h^2}$$

$$S = \pi (R_1 + R_2)s$$
$$= \pi (R_1 + R_2)\sqrt{(R_1 - R_2)^2 + h^2}$$

FIGURE 6a. Formulae for the calculation of the lateral surface area of the frustrum of a right circular cone.

Symbol Definition

R = radius at base
h = height
S = lateral surface area



Formula

$$S = 2\pi Rh$$

FIGURE 6b. Formula for the calculation of the lateral surface area of a right circular cylinder.

CAXI-bb(j,k) = last formed ring width 5 cm. from the bole of the kth branch in the jth whorl.

$A(h_j,x)$ = the lateral surface area of the bole between the jth whorl and x.

B(j,k) = the lateral surface area of the 5 cm. branch base section of the kth branch in the jth whorl.

The formula for $A(h_j,x)$ and B(j,k) are:

$$A(hj,x) = \pi(r_j + r_x)[(r_j - r_x)^2 + (h_j - h_x)^2]^{\frac{1}{2}}$$

where: r_j = radius of the bole at the jth whorl.

r_x = radius of the bole at point x.

h_j = vertical height from ground to jth whorl.

h_x = vertical height from ground to a point on the bole at x.

$$B(j,k) = 2\pi r_{j,k} \cdot 5$$

where: r_{jk} = radius of branch 5 cm from insertion into the stem.

The distribution parameter and denominator of the crown vigor index is raised to the power 1/2 similar to Barker's crown activity index. Bole growth simulations were attempted with exponents ranging from 1/4 to 1. The exponent 1/2 produced the best results.

Only branches from the top eight whorls were considered as input sources. In the analysis of the six study trees the CAXI-branch base values of lower branch whorls were either non-existent or too narrow to measure. Thus, their contribution to bole growth could not be simulated by the CVI model.

Model Validation

Validation is an attempt to increase confidence in a model's ability to provide useful and correct inferences (Goulding 1979). Two approaches were used to validate the crown vigor index model. The first approach compared simulated bole growth values to real stem ring width measurements. If hypotheses used to construct the index are correct, little deviation should occur between the simulated and real values. The second approach compared the crown vigor index to other similar models. Different bole growth models are usually based upon different sets of assumptions. The fact that one model does a better job than another at predicting real world events may provide insight into the correctness of these assumptions.

The crown vigor index was used to simulate the bole growth patterns of six sample red pine; two from each of the 13, 16, and 21-year-old samples. Index values were calculated for points above and below each branch whorl and compared to corresponding stem ring width measurements. The pattern of measured stem ring widths down the bole was compared to the pattern of plotted index values. If unexplainable deviations between the two occur then this is considered as evidence against the hypotheses used in forming the index.

Crown vigor index values and main stem ring width measurements (CAXI-main stem) do not correspond directly. Therefore, the two parameters within each tree were expressed relative to their respective maximums. The largest main stem ring width and highest index value were designated as 100 percent. All other parameter values were expressed in relation to these maxima on a percentage basis. The percentages were then plotted against relative tree height and compared. These data transformations appear in Appendix C.

Student's t-test applied to paired comparisons was used to evaluate the crown vigor index statistically. This test is used when the difference between pairs of measurements is of interest (Chatfield 1975). The null hypothesis tested is that the population of differences is zero. The test criterion is distributed as t when the assumption that differences are normally distributed is correct and the null hypothesis is true. Assumptions used in forming both the crown vigor index and Barker's crown activity index are based upon a strictly passive system of xylem growth control. These models ignore bole growth factors related to physical bending stress. Specific stress induced growth points within a tree bole would therefore be expected to be poorly related to corresponding index values calculated from either model. Thus, it was thought logical to exclude points from the t-test which in past have been hypothesized to be under a prime influence of localized bending stress. These points occur in the upper crown at the base of stem internodes above branch whorls (Brown 1971), and in the region of butt swell (Fayle 1976). For sample trees, points considered to be under the influence of bending stress are indicated in Appendix C. All tests were performed at the 0.01 percent level of significance.

The crown vigor index is closely related to other growth indices designed to simulate bole growth from branch parameters. The index developed by Barker(1981) was calculated and plotted in relation to the crown vigor index for comparison. Barker's crown activity index is based upon the assumption that primary branch extension growth is a good representaion of the amount of growth regulator produced by that branch. It also assumes that the effect of these regulators on bole growth is determined by their translocation length down the bole. The specific calculations for Barker's activity index appear in Appendix D.

Model Modification

A primary assumption in constucting the crown vigor index was that CAXI-branch base, the width of the last growth ring formed at branch base, is a reliable representation of the flow of growth regulators from branch to bole. For index calculation, CAXI-branch base must be measured for all tree branches. The technique for measuring CAXI-branch base is a process that is complex and tedious. A practical modification to the index would be to estimate CAXI-branch base from readily obtainable branch parameters such as foliage dry weight or branch length. Four branch parameters and three combinations of these parameters were selected as potential indicators of CAXI-branch base. These are summarized in Table 2.

Simple linear regression was used to determine the relationship between branch parameters (independant variables) and CAXI-branch base (dependant variable). Branch data from all trees, excluding the six used in the bole growth simulation, were separated by whorl and lumped. Eight regression equations, one per whorl, were calculated for each branch parameter. The set of eight regression equations that best explained the variation in CAXI-branch base was used to estimate CAXI-branch base.

CAXI-branch base was estimated for the branches of the six simulated trees. These estimates were substituted into the original crown vigor index and main stem ring width patterns of the six sample trees were simulated. The effect of using estimated CAXI-branch base values was determined by comparing the modified main stem ring width simulations to the unmodified simulations.

Table 2. A summary of branch parameters used to estimate the width of the current annual growth ring measured at branch base (CAXI-branch base).

Branch parameters used to estimate (CAXI-branch base)	Symbol
1. Total branch foliage dry weight	F
2. Total branch length	L
3. Current year branch extension length	ΔL
4. Dry weight, 1-year-old foliage	ΔF
5. Quotient: 3 / 2	ΔL/L
6. Product: 1 x 3	F•ΔL
7. Product: 3 x 4	ΔF•ΔL

RESULTS

A summary of sample tree bolewood increment patterns, and the vertical distribution throughout the crown of important branch parameters, are presented in Figures 7, 8, and 9. The branch parameters branch foliage dry weight, current primary branch extension length, and basal branch ring width (CAXI-branch base) are considered important for they have in past and are at present considered to be logical estimates of branch to stem input sources. The distribution patterns of these branch parameters are presented in the figures both summed by whorl and as average branch values per whorl.

Distribution of Bolewood Increment

Thirteen year-old trees K2 and K4 (Figure 7), 16-year-old trees N1 and N6 (Figure 8), and 21-year-old trees S3 and S6 (Figure 9) showed similar general trends in the vertical distribution of the current annual xylem increment of the main stem (CAXI-main stem) measured as stem ring width. CAXI-main stem was relatively narrow near tree top, increased to a maximum at about the fourth

TREE K2

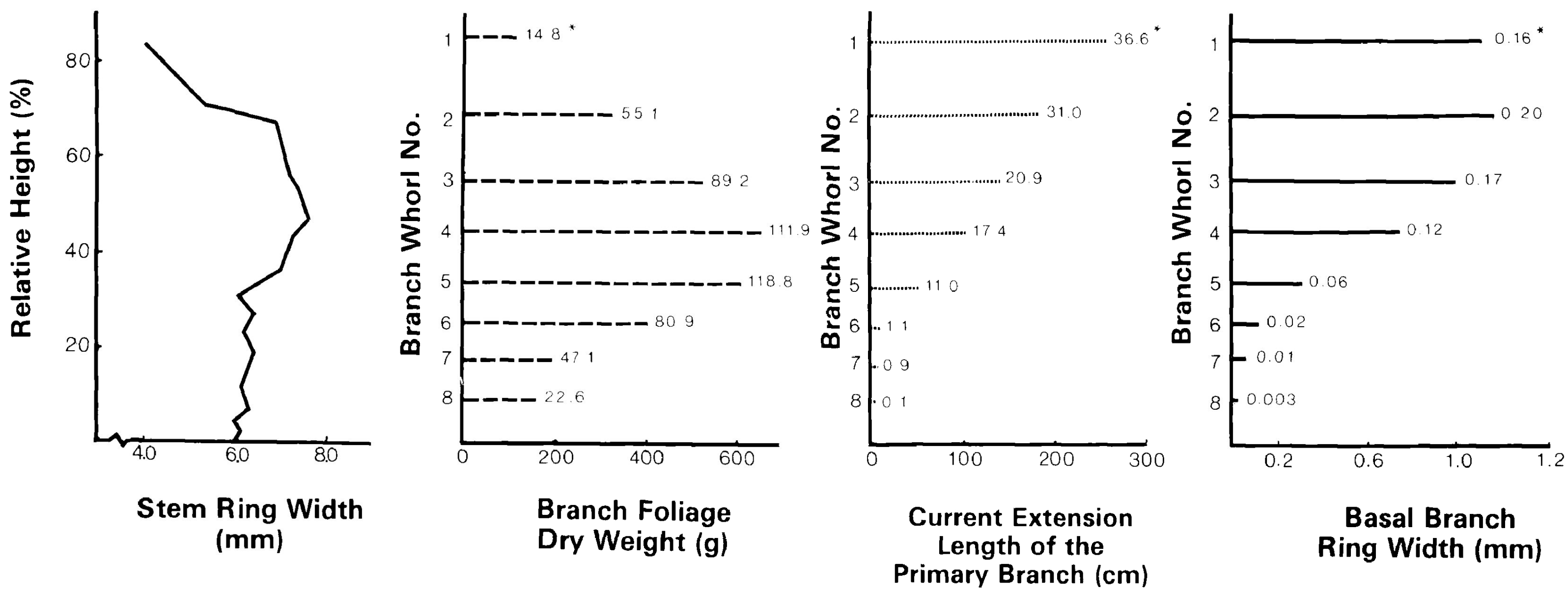


FIGURE 7a. Branch foliage dry weight, current extension length of the primary branch, and current basal branch ring width summed by whorl and as average branch per whorl (*) distributed throughout the crown of 13-year-old tree K2 plotted in relation to vertically distributed bolewood increment.

TREE K4

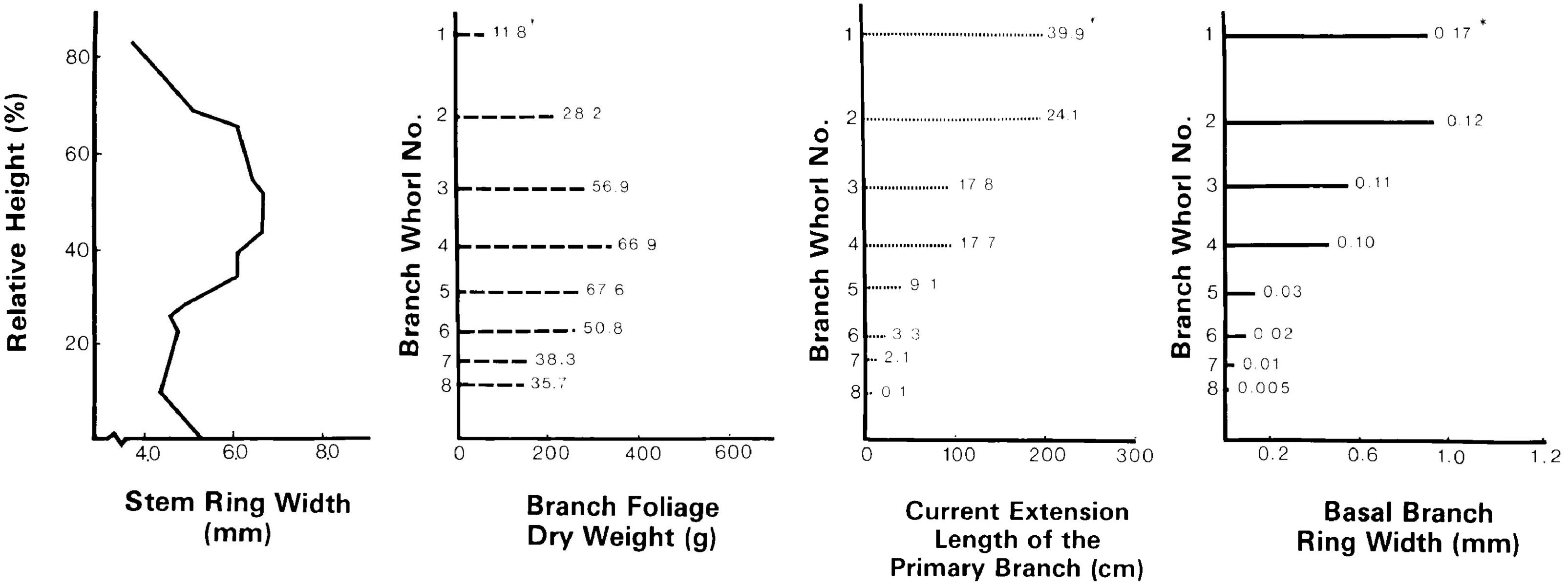


FIGURE 7b. Branch foliage dry weight, current extension length of the primary branch, and current basal branch ring width summed by whorl and as average branch per whorl (*) distributed throughout the crown of 13-year-old tree K4 plotted in relation to vertically distributed bolewood increment.

TREE N1

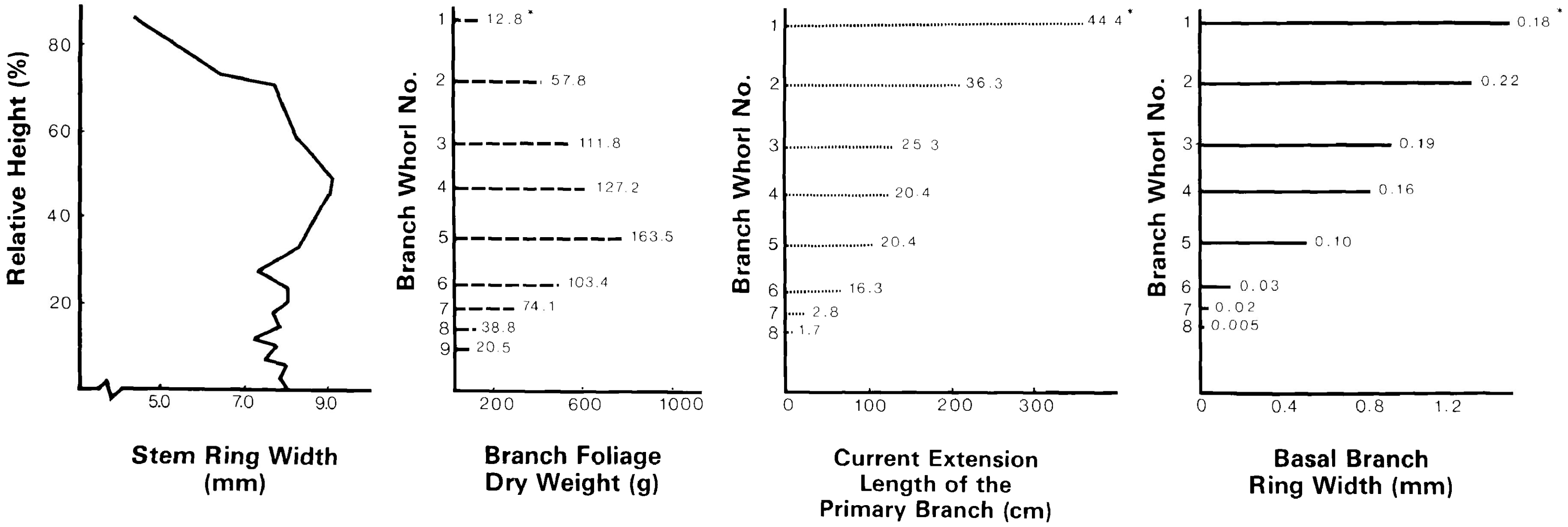


FIGURE 8a. Branch foliage dry weight, current extension length of the primary branch, and current basal branch ring width summed by whorl and as average branch per whorl (*) distributed throughout the crown of 16-year-old tree N1 plotted in relation to vertically distributed bolewood increment.

TREE S3

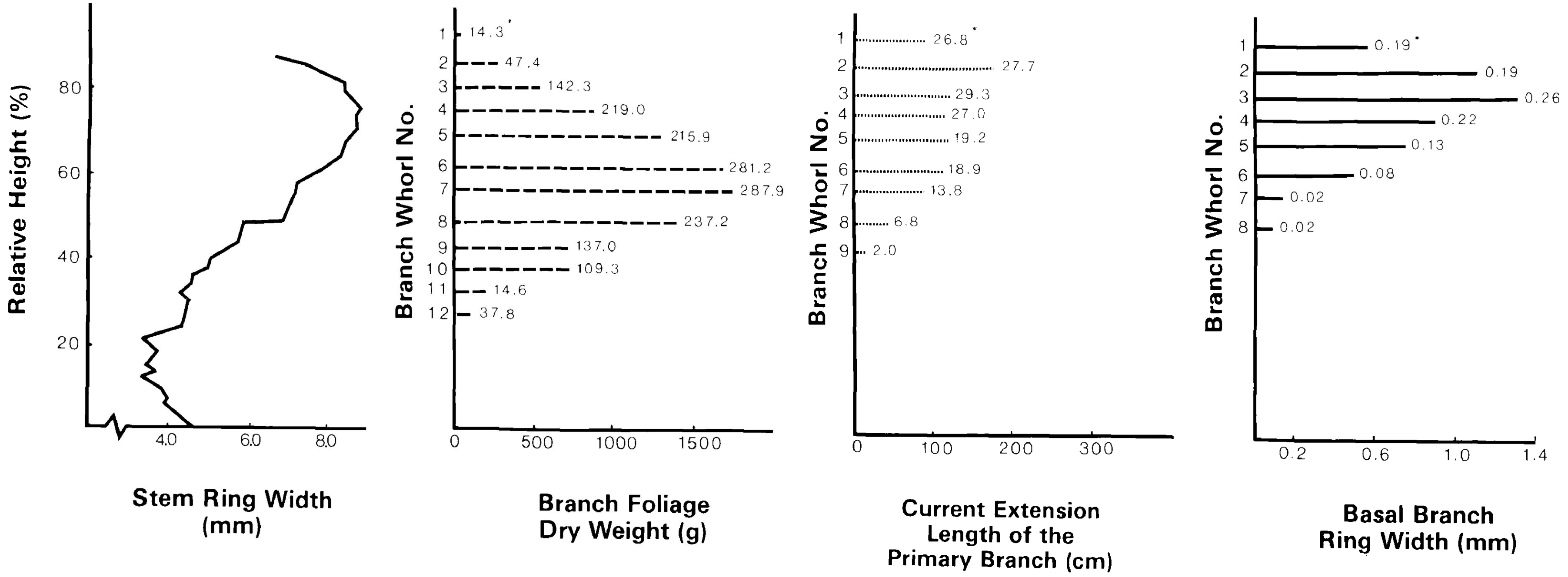


FIGURE 9a. Branch foliage dry weight, current extension length of the primary branch, and current basal branch ring width summed by whorl and as average branch per whorl (*) distributed throughout the crown of 21-year-old tree S3 plotted in relation to vertically distributed bolewood increment.

TREE S6

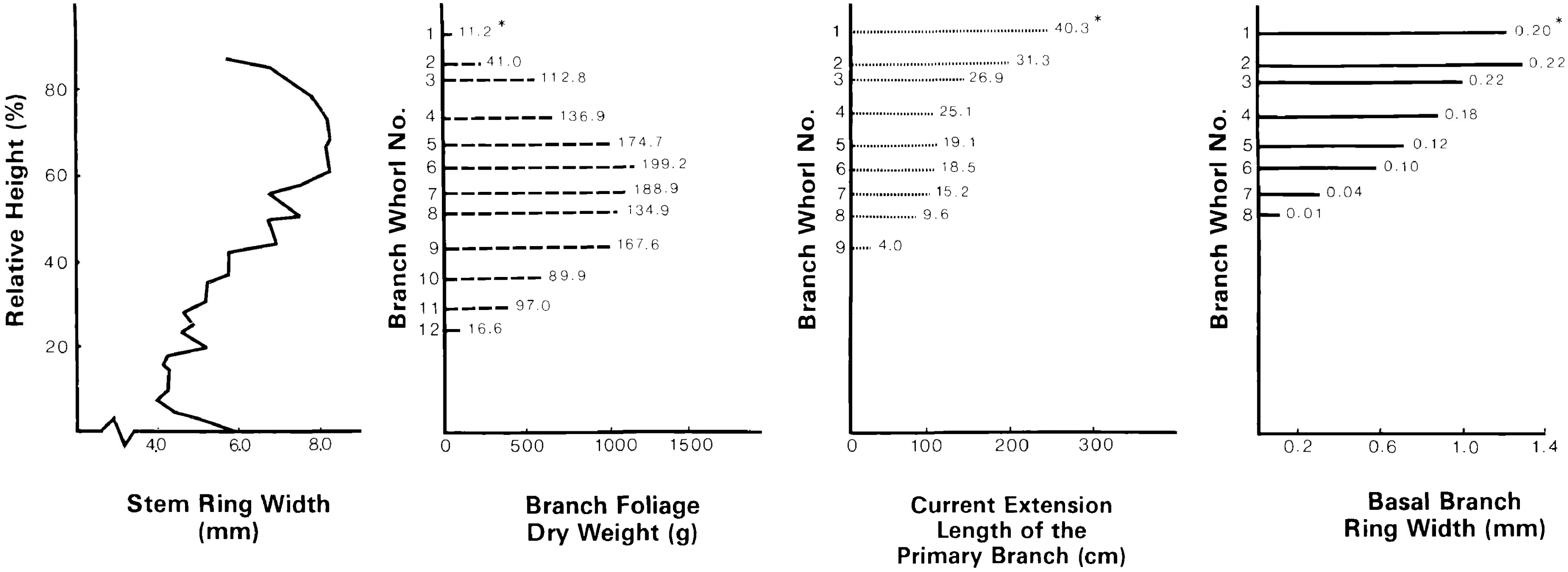


FIGURE 9b. Branch foliage dry weight, current extension length of the primary branch, and current basal branch ring width summed by whorl and as average branch per whorl (*) distributed throughout the crown of 21-year-old tree S6 plotted in relation to vertically distributed bolewood increment.

branch whorl, then deceased to near ground level. At approximately 10 percent tree height CAXI-main stem increased to ground level in the region of butt swell. The exception is tree K2 which showed no increase in CAXI-main stem in the butt swell region.

Specific differences in CAXI-main stem patterns occured within and among trees of different ages. The 21-year-old trees S3 and S6 (Figure 9) reached maximum ring width values high in the tree bole. Maximum CAXI-main stem is less distinct in tree S6. Decreases in ring width from maximum in both trees was erratic but continuous to the region of butt swell. The 13 and 16-year-old trees (Figures 7 and 8) reached maximum CAXI-main stem values near mid bole. Decrease from a maximum CAXI-main stem value in 13-year-old trees K2, K4 and 16-year-old tree N1 was sharp. Between the fifth and sixth branch whorls CAXI-main stem patterns in these trees became more regular. Decrease from this point down the bole was gradual. No clear maximum CAXI-main stem value could be detected in 16-year-old tree N6. Ring widths reached near maximum values high in the tree bole. These values varied only slightly and decreased gradually in the mid to lower bole region to butt swell.

Crown Distributed Branch Measurement Patterns

Foliage Dry Weight

The location of maximum whorl and branch foliage dry weight differed among trees of different ages. Maximum whorl foliage dry weight in the 13-year-old trees K2 and K4 (Figure 7) occured at the fourth branch whorl. This was approximately where maximum stem ring width was located. The largest mean branch foliage dry weight occured lower in the crown in these trees at the fifth branch whorl. In 16-year-old trees N1 and N6 (Figure 8) maximum branch and whorl foliage dry weights occured at the fifth branch whorl and in the 21-year-old trees S3 and S6 (Figure 9) maximum branch and whorl foliage dry weight occured in the sixth and seventh branch whorl, respectively. In the 16 and 21-year-old trees, maximum CAXI-main stem values did not correspond to areas of maximum foliage development. A maximum CAXI-main stem value occured at about the fourth branch whorl.

Branch, whorl, and crown foliage dry weights became progressively heavier with increasing tree age. Foliage weights also varied markedly between trees of the same age. Trees K2, N6, and S3 all showed crown foliage weights considerably higher than the corresponding three trees of the same respective age.

Current Extension Length of the Primary Branch

The mean current extension length of the primary branch in sample trees was greatest in the upper crown (Figure 7, 8, and 9). Extension lengths decreased progressively downward from whorl to whorl. The relative decrease in extension length from whorl to whorl was less, however, in the mid-crown region. This corresponded to the area in the crown where whorl foliage dry weights approached maximum values. Below the point of maximum whorl foliage development, extension lengths deceased rapidly to extinction in the lower crown.

When primary branch extension lengths were summed by whorl and plotted against tree height, a sigmoid distribution pattern resulted (Figure 7, 8, and 9). This pattern may be significant. Summed extension lengths were high in the upper crown, reached near constant values through mid-crown, then decreased rapidly again in the lower crown. This pattern was evident in the 21-year-old trees and less obvious in the 13 and 16 year-old trees.

Growth Ring Width Formed In Current Growing Season And Measured At Branch Base

Xylem formed in the current growing season and measured as ring width at branch base (CAXI-branch base) was relatively wide in the upper crowns of all sample trees (Figures 7, 8, and 9). These ring widths progressively narrowed from whorl to whorl downward throughout the crown. There was a large relative difference in CAXI-branch base between whorls at maximum foliage development and whorls below maximum foliage development. CAXI-branch base values decreased gradually up to whorls of maximum foliage dry weight. In the whorl immediately below this point CAXI-branch base values became relatively very small or were not produced. Tree S3 (Figure 9) deviated slightly from this pattern with maximum foliage dry weight occuring at the seventh whorl. CAXI-branch base values at this point were already relatively small compared to the branches in the sixth branch whorl.

Bole Growth Simulation

The distribution of main stem bole growth increment was simulated using both the newly developed Crown Vigor Index (CVI) and Barker's Crown Activity Index (BCAI). CVI, BCAI, and actual stem ring width distribution patterns for the 13, 16, and 21-year-old sample trees appear in Figures 10, 11, and 12, respectively.

Bole Growth Simulation with the Crown Vigor Index

The relationship between crown vigor index values and main stem ring width measurements, expressed as per cent maximum, was consistent along the boles in the upper crowns of all sample trees. In the mid to lower bole regions within the lower crown and branch free section of the tree, these relationships varied.

As CAXI-main stem increased to a maximum in the upper portion of the bole CVI values followed closely but only at points immediately below branch whorls. At bole locations just above branch whorls CVI underpredicted CAXI-main stem. The resultant zigzagging pattern continued down the bole to about the location of maximum

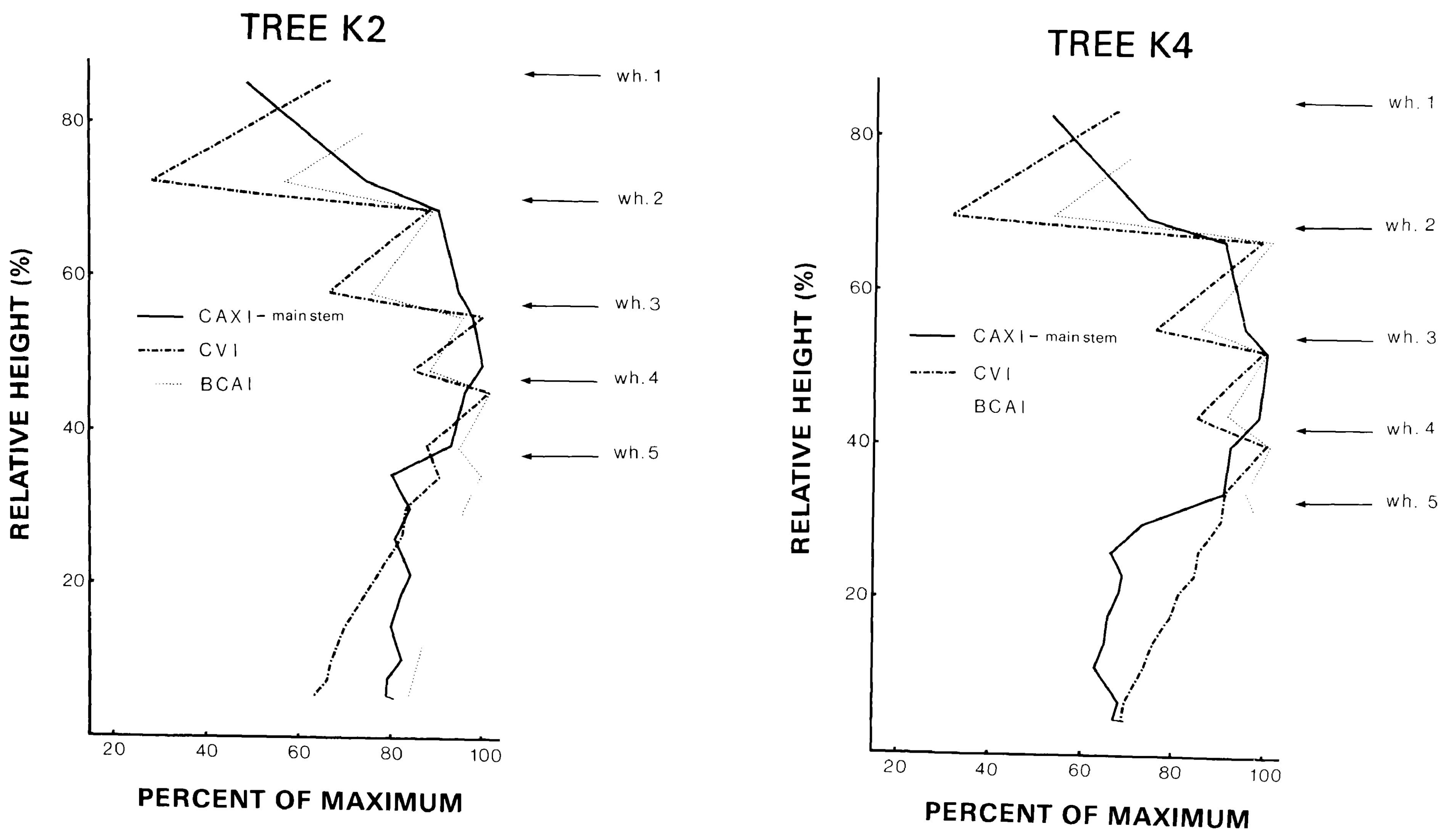


FIGURE 10. Variation of the current annual radial increment of the main stem (CAXI - main stem), crown vigor index (CVI), and Barker's crown activity index (BCAI) with relative tree height and in relation to branch whorls in 13-year-old trees K2 and K4.

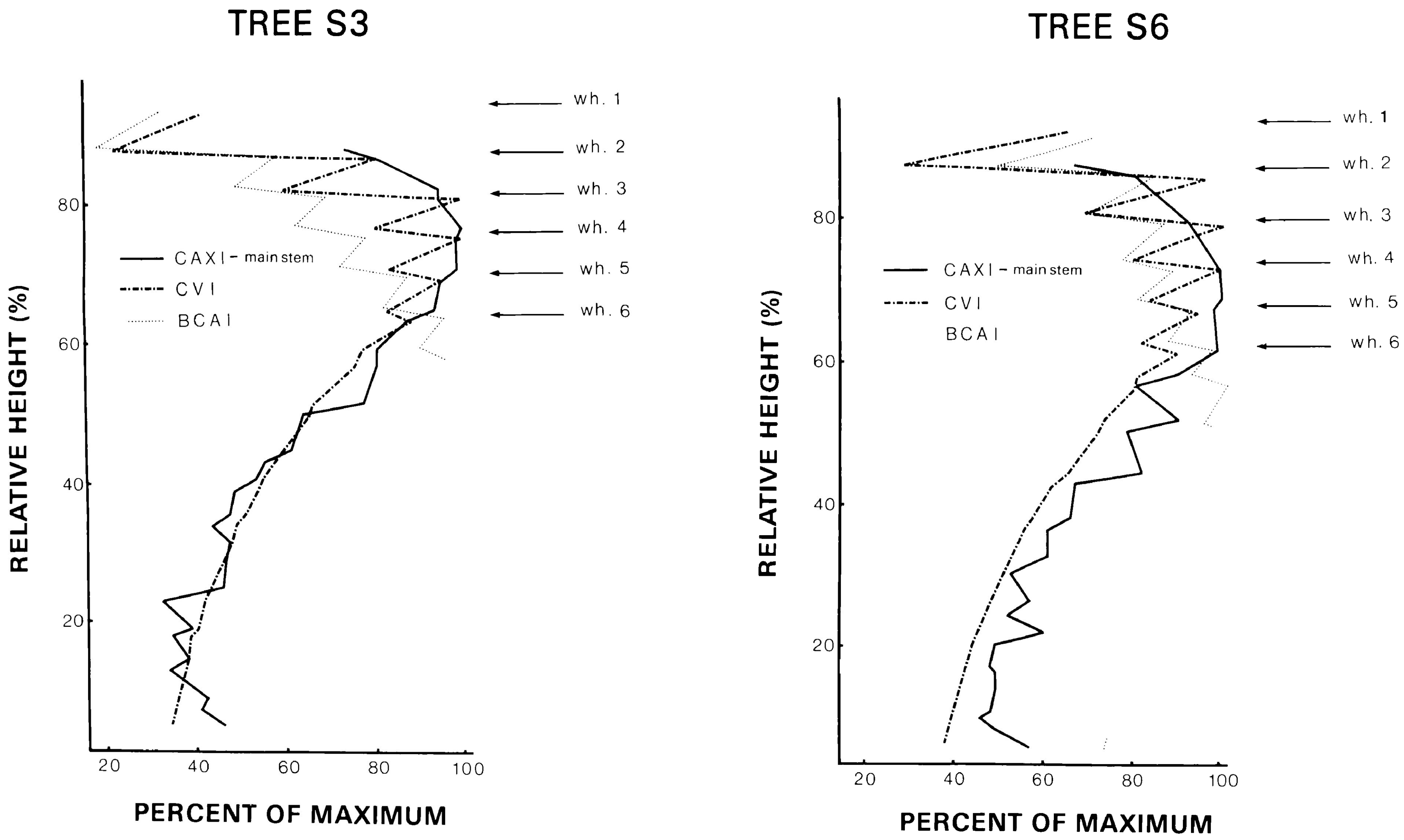


FIGURE 12. Variation of the current annual radial increment of the main stem (CAXI - main stem), crown vigor index (CVI), and Barker's crown activity index (BCAI) with relative tree height and in relation to branch whorls in 21-year-old trees S3 and S6.

whorl foliage development.

Correspondence between CVI and CAXI-main stem in mid to lower bole regions was best in 21-year-old tree S3 (Figure 12). Only at the site of butt swell did CVI noticeably underestimate CAXI-main stem. In 21-year-old tree S6 (Figure 12) and 16-year-old tree N6 (Figure 11), CVI consistently underestimated CAXI-main stem in the mid and lower bole regions. In tree S6 index values closely paralleled ring widths along the length of the tree bole. In tree N6, underestimates of CAXI-main stem gradually increased the length of the tree bole. In both trees these discrepencies increased markedly at the site of butt swell. In 16-year-old tree N1 (Figure 11) and 13 year-old tree K2 (Figure 10) mid bole correspondence was good. In the lower bole regions, below 20 percent tree height this correspondence broke down and CVI increasingly underestimated CAXI-main stem. Only in tree K4 did CVI overestimate CAXI-main stem. This is in the bole region where main stem ring widths were uncharacteristically narrow relative to trees K2, N1, N6, and the upper bole regions of trees S3 and S6.

Bole Growth Simulaton With Barker's Crown Activity Index

In the upper crown region of the 13 and 16-year-old trees (Figures 10 and 11) Barker's Crown Activity Index (BCAI) generated bole growth simulation patterns similar to those generated by the Crown Vigor Index. BCAI values followed CAXI-main stem closely but only at points immediately below branch whorls. At bole locations just above branch whorls BCAI underpredicted CAXI-main stem. The resultant zigzagging pattern continued down the bole to about the location of maximum whorl foliage development. In the 21-year-old trees BCAI greatly underpredicted CAXI-main stem throughout the length of the upper crown region. From about the sixth branch whorl downward, BCAI increasingly overestimated CAXI-main stem. BCAI also overestimated CAXI-main stem in the mid to lower bole regions of the 13 and 16 year-old trees but these overestimates were not as marked.

Statistical Comparisons Between Actual And Simulated Bole Growth Patterns

Using the transformed values, there was no significant difference between CAXI-main stem and CVI for 13-year-old tree K2 (Table 3), 16-year-old tree N1 (Table 4), and 21-year-old tree S3 (Table 5). CVI significantly overestimated CAXI-main stem in tree K4. Tree K4 had unusually narrow rings in the lower bole region. CVI significantly underestimated CAXI-main stem in trees N6 and S6. These trees had no clear maximum CAXI-main stem value. In all sample trees, Barker's crown activity index significantly overestimated CAXI-main stem.

Bole Growth Simulation With A Modified Crown Vigor Index

The ring width formed in the current growing season and measured at branch base (CAXI-branch base) was compared to relatively easily measured branch parameters. The best estimate was then substituted into the crown vigor index and a modified bole growth simulation model was produced. The coefficients of determination for relationships between CAXI-branch base and easily measured branch parameters thought to be logical estimators of

Table 3. Statistical comparison of crown vigor index (CVI) and Barker's crown activity index (BCAI) to actual main stem ring width values for 13-year-old trees K2 and K4.

Tree Number	K2		K4	
	CVI	BCAI	CVI	BCAI
Average deviation ($\bar{d}$)	-3.6	+7.6	+7.2	+18.2
Standard error ($s_{\bar{d}}$)	2.33	2.53	2.04	2.56
t statistic ($\bar{d}/s_{\bar{d}}$)	-1.52	+2.98	+3.53	+7.11
Number of paired comparisons	15	15	14	14
Significance	ns	**	**	**

ns - not significantly different

** - significantly different at the 0.01 per cent level

Table 4. Statistical comparison of crown vigor index (CVI) and Barker's crown activity index (BCAI) to actual main stem ring width values for 16-year-old trees N1 and N6.

Tree Number	N1		N6	
	CVI	BCAI	CVI	BCAI
Average deviation ($\bar{d}$)	-2.9	+10.6	-7.6	+3.6
Standard error ($s_{\bar{d}}$)	2.98	3.03	2.23	1.19
t statistic ($\bar{d}/s_{\bar{d}}$)	-0.97	+3.50	-3.43	+3.04
Number of paired comparisons	16	16	16	16
Significance	ns	**	**	**

ns - not significantly different

** - significantly different at the 0.01 per cent level

Table 5. Statistical comparison of crown vigor index (CVI) and Barker's crown activity index (BCAI) to actual main stem ring width values for 21-year-old trees S3 and S6.

Tree Number	S3		S6	
	CVI	BCAI	CVI	BCAI
Average deviation ($\bar{d}$)	+0.12	+2.32	-5.7	+15.6
Standard error ($s_{\bar{d}}$)	0.76	3.83	1.33	2.60
t statistic ($\bar{d}/s_{\bar{d}}$)	+0.16	+6.06	-4.26	6.00
Number of paired comparisons	26	26	24	24
Significance	ns	**	**	**

ns - not significantly different

** - significantly different at the 0.01 per cent level

CAXI-branch base are presented in Table 6. The equations and relevant statistics for these relationships are found in Appendix E. The best consistent estimator of CAXI-branch base throughout the live crown was the product of total branch foliage dry weight and current extension length of the primary branch (F•ΔL). One-year-old branch foliage (ΔF) and the product 1-year-old branch foliage and current branch extension length (ΔF•ΔL) gave better estimates than F•ΔL in the upper whorls but these relationships break down in whorls 7 and 8. Three branch parameters: total branch foliage dry weight (F), branch length (L), and current primary branch extension length (ΔL) gave consistent but poorer estimates of CAXI-branch base than F•ΔL. The quotient, current primary branch extension length divided by branch length (ΔL/L), gave consistently poor estimates of CAXI-branch base throughout the live crown.

The effect of using F•ΔL as an estimator of the input parameter CAXI-branch base in the Crown Vigor Index was tested. A t-test for paired compairisons was used to compare modified and unmodified CVI values. There was no significant difference between modified and unmodified bole growth simulation patterns in 13-year-old trees K2 and K4 and 21-year-old tree S6 (Table 7). Small but consistent and significant negative differences in the

Table 6. Coefficients of determination (R^2) for relationships between easily measured branch parameters and the width of the current annual growth ring measured at branch base (CAXI-branch base).

	Branch Parameters						
Whorl No.	F•ΔL	F	L	ΔL	ΔF	ΔL/L	ΔF•ΔL
1	0.70	0.65	0.69	0.69	0.65		0.70
2	0.73	0.69	0.71	0.73	0.82	0.04	0.88
3	0.80	0.73	0.70	0.65	0.86	0.15	0.83
4	0.73	0.69	0.53	0.46	0.80	0.09	0.87
5	0.73	0.68	0.53	0.62	0.83	0.33	0.73
6	0.87	0.66	0.46	0.81	0.80	0.53	0.86
7	0.65	0.53	0.51	0.46	0.48	0.22	0.51
8	0.91	0.72	0.63	0.75	0.44	0.60	0.64

F • ΔL	product of branch foliage dry weight and current extension length of the primary branch
F	branch foliage dry weight
L	total branch length
ΔL	current extension length of the primary branch
ΔF	one-year-old branch foliage
ΔL/L	current branch extension length divided by total branch length
ΔF • ΔL	product one-year-old branch foliage and current branch extension length

Table 7. Statistical comparison of crown vigor index values to modified crown vigor index values.

Tree Number	K2	K4	N1	N6	S3	S6
Average deviation ($\bar{d}$)	-0.47	+0.02	-0.45	-1.70	+1.40	+0.12
Standard error ($s_{\bar{d}}$)	0.37	0.46	0.18	0.25	0.36	0.27
t statistic ($\bar{d}/s_{\bar{d}}$)	-1.27	+0.04	-2.50	-6.80	+3.89	+0.44
Number of paired compairisons	18	18	21	24	35	36
Significance	ns	ns	*	**	**	ns

ns - not significantly different

* - significantly different at the 0.05 per cent level

** - significantly different at the 0.01 per cent level

bole growth simulation patterns existed in 16-year-old trees N1 and N6. The difference was significant at the 0.05 percent level in tree N1 and at the 0.01 percent level in tree N6. Differences were small, positive, and significant in 21-year-old tree S3. This difference was significant at the 0.01 percent level.

DISCUSSION

Data presented in Figures 7, 8, and 9 indicates that no clear correspondance exists between the vertical distribution of bolewood increment and the branch parameters foliage dry weight, current primary extension length, and current annual xylem increment measured at branch base. Each branch parameter, however, when considered separately by whorl exhibits a definite pattern in regards to its distribution throughout the crown. The regularity of these patterns in relation to a well defined main stem wood increment distribution suggests that an indirect relationship between crown parameters and main stem wood increment may exist.

Distribution of Bolewood Increment

In all sample trees, CAXI-main stem increased from the apex downward, reached a maximum at about the fourth branch whorl, decreased to near ground level, and then increased in the region of butt swell. This bole growth pattern is in general agreement with those found by numerous other workers (Onaka 1950a, Duff and Nolan 1953, Larson 1963, 1964, 1965, Hall 1965, Burton and Smith 1972, Beckwith and Shackelford 1976, and Barker 1981).

A passive system of xylem growth control, as defined by Larson (1965), may dominate wood production above the region of butt swell. The terminal leader and whorl branches are considered to be sources of photosynthates and growth regulators contributing to a pool of metabolites translocated downward in the stem phloem. The most productive branches are thought to be located in the upper crown (Larson 1969). As growth regulators are translocated downward the concentration of these substances builds up, presumably reaching a maximum at the point of greatest wood growth. In all sample trees maximum ring width occured near the fourth branch whorl. Declining branch production in the lower whorls coupled with growth regulator dilution with increasing phloem surface area would explain the continuous decline in ring widths on the bole below the fourth branch whorl. A second growth maximum occured in the region of butt swell. Stress induced hormone production appears to be responsible for increased growth in this region (Fayle 1976). Bending stress may also induce growth at other points along the bole, particularly in the upper crown (Barker 1981), and at points just above the uppermost branch whorls (Brown 1971). The contributory effect of stress induced hormone production to main stem wood increment, especially within the crown, is unknown.

Relation of Crown Distributed Branch Measurements to Bolewood Increment

Foliage Dry Weight

Crown foliage dry weights could not be clearly related to the level of main stem wood increment. In 13-year-old tree K2 compared to tree K4 (Figure 8) less crown foliage appears to result in narrower growth rings the length of the tree bole. The 16 and 21-year-old trees N1 (Figure 9) and S6 (Figure 10), both had comparatively smaller crown weights than sample trees of similar age i.e. trees N6 and S3 respectively. Trees N1 and S6 did not, however, show obvious differences in the level of main stem wood increment. Mar:Moller (1945; cited by Assmann 1970) showed a similar result with European beech trees (*Fagus sylvatica* L.). He found that trees with similar foliage dry weights but growing on different sites showed markedly different wood volume increments. Foliar efficiency changed with site. Tree foliage alone could not be directly related to wood increment levels.

Foliage dry weights could not be related to the distribution of main stem wood increment down the bole. The location of maximum whorl and branch foliage dry weight within the crown differed among sample trees of different ages (Figures 7, 8, and 9). The older trees carry maximum whorl foliage lower in the crown. Maximum main stem ring width, however, occured near the fourth branch whorl regardless of tree age. This implies that maximum CAXI-main stem is related to the stem apex but not to foliage dry weight distributions.

The shifting pattern of foliage dry weight distribution as trees age in relation to a somewhat static upper crown wood increment pattern, and a lack of clear relationship between foliage dry weight and level of wood increment, combine to suggest that foliage dry weight distributions alone cannot be easily used as measures of branch productivity to predict main stem ring width.

Current Extension Length of the Primary Branch

The lateral extension of tree branches grown in the current season was greatest in the upper crown and decreased progressively downward from whorl to whorl (Figure 7, 8, and 9). This is a typical pattern of branch extension growth observed in pines. Excurrent crown forms, such as this, are under strong apical control (Brown and Zimmermann 1971). The mobilization of nutrients into a branch and the subsequent extension of the shoot depends upon the capacity of the shoot to produce hormonal growth regulators. Growth regulators, particularly auxin, appear to be produced in relation to the size of the bud on the primary branch axis (Onaka 1950a). Large buds are produced in the favourable environment found high in the tree crown. This is especially true of the terminal leader. These buds produce larger amounts of auxin, create stronger nutrient sinks and outcompete the lesser nutrient sinks created by smaller buds formed in the less favourable environment in lower parts of the crown.

Bud size is highly correlated to shoot extension length (Little 1969). For this reason, the current extension length of the primary branch has been hypothesized to be a good measure of branch to bole auxin input (Barker 1981). This parameter should thus relate well to bole growth. There are, however, logical deficiencies in this argument. In pines, all the needles and virtually all the cells of next years shoot are present in the bud; a new bud is formed even before current elongation is completed (Wilson 1970). Thus, the elongation of pine shoots is partly regulated by environmental conditions of the previous year, when cell division is occuring, and partly by environmental conditions of the current year when elongation is progressing. Also, shoot elongation depends more on carbohydrate reserves accumulated during the previous year than on carbohydrate produced in the current year (Kozlowski and Keller 1966). Cambial growth, however, is primarily affected by current environmental conditions and carbohydrate reserves produced in the current years growth (Kozlowski and Kramer 1979). Significant amounts of branch extension can result even though current environmental factors suppress cambial activities in the branch and tree stem. This would add to the variability in branch extension - main stem wood increment relations.

The reliance of primary branch extension growth on carbohydrate reserves may explain the sigmoid pattern which occured when primary branch extension lengths were summed by whorl (Figure 7, 8, and 9). Extension lengths decreased rapidly from tree top to mid crown and then remained somewhat equal. In this region of little changing extension lengths, whorl foliage dry weights increased to a maximum. Below the point of maximum foliage dry weight, whorl branch extension lengths rapidly declined. It would appear that reserve carbohydrates, stored primarily in the branch foliage, maintain extension rates at successively lower points in the crown. Below the level of maximum foliage dry weight, decreased foliar efficiencies coupled with a declining leaf volume sharply reduce the surplus of carbohydrate reserves needed for optimal bud development and following year branch extension. A point in the crown is reached where branch extension may occur, due primarily to reserves, but cambial activity may not occur. Such may be the case in 21-year-old trees S3 and S6 (Figure 10). Branch extension occured in the lower whorls of these trees with no concomitant xylem growth at the branch base. Auxin and carbohydrate levels may be too low at this point to allow for cambial activity.

Primary branch extension length may be an inaccurate estimate of branch to stem auxin input and may not relate well to main stem growth for it does not take into account the translocation length from branch tip to the point of insertion into the bole. Further, it does not take into account the contibution of auxin made at other locations in the branch. The contribution of secondary branch buds, foliar organs, or expanding reproductive organs to the supply of auxins produced in the branch tip may be substantial. Furthermore, individual branches differ widely in the surface area of phloem and cambium over which these hormones are translocated and utilized. It is easy to conceive of two branches of equal extension length that contribute radically different amounts of growth regulator to the tree bole.

Growth Ring Width Formed in the Current Growing Season and Measured at Branch Base

Figures 7, 8, and 9 showed a decrease in CAXI-branch base from upper to lower crown in sample trees. I have hypothesized that the most vigorous branches are those with the most active cambium and hence are those that produce the widest growth ring. Presumably, these branches exert the greatest influence on wood growth along the tree bole.

The branches contributing most to bole growth in the sample trees may be located near the top of the tree with individual branch contribution decreasing with increasing whorl rank. Differences in the rate of decrease of branch contribution between trees most likely reflects a complex of factors which act differently upon individual trees to regulate internal physiological conditions.

The above, suggested pattern, of branch contribution to stem growth is in general agreement with inferred patterns of contribution described by Larson (1962,1969), and with direct estimates of crown productivity made by Ladefoged (1946) and Labyak and Schumacker (1954). Ladefoged pruned varying numbers of whorls from Norway spruce (<u>Picea abies</u> (L.) Karst.), took needle age and light exposure into account, and estimated that half of total assimilation occurs in the upper 4 or 5 whorls of trees with 9 to 11 whorls. Labyak and Schumacker used similar pruning methods and concluded that for loblolly pine (<u>Pinus taeda</u> L.) a branch in the top tenth of the tree contributes most to mainstem growth just below its base. In the lower half of the tree, Labyak and Schumacker determined that the contribution made by individual branches was fairly evenly distributed. This disagrees with suggested patterns of branch contibution reported in this thesis where estimates of contributions made by individual branches continually decreased in the lower crown.

Mar:Moller (1960) used Ladefoged's (1946) foliage dry weight measurements and estimated that the greatest contribution of branches occured in the fifth and sixth whorls of a tree with 11 whorls. These estimates were based primarily upon foliage dry weight distributions and do not agree with the suggested trend in branch contribution reported here.

The distribution pattern of current annual xylem increment measured as ring width at branch base throughout the crowns of sample trees were similar to concomitant distribution patterns of current primary branch extension lengths (Figure 7, 8, and 9). Both patterns showed a general decreasing trend from tree apex to live crown base. Wilson (1970) has suggested that increase in the length of a shoot is indirectly related to the increase in its diameter. Wilson submits that an increase in branch extension length corresponds to an increase in branch foliage. This foliage has more stored material for both extension growth and apical bud formation. Branches able to produce and mobilize the greatest amounts of reserve materials also produce the greatest extension lengths and next years buds. These branches are able to synthesize large amounts of growth regulators essential for the stimulation of cambial activity. The fact that CAXI-branch base measurements deeased rapidly below maximum foliage dry weight would seem to suggest that foliage plays an important role in supplementing levels of growth hormones and reserve materials in branches. These substances directly affect levels of growth.

Bole Growth Simulation

Bole Growth Simulation with the Crown Vigor Index

The crown vigor index is only one of many possible models simulating bole growth. It is based on a number of logical assumptions which are combined mathematically to produce a simplified representation of a passive system of bole growth control. CVI may not be the best representation of the system but it is thought to be an improvement over the models of Beckwith and Shackelford (1976) and Barker (1981).

The best CVI simulation model resulted when the index distribution parameter was raised to the exponent 1/2. This was similar to Barker's crown activity index where the denominator of the index was also raised to 1/2. Why 1/2 works better than other exponents raises questions about the nature of the physiological system operating to control wood growth. Many authors have recognized a relationship between metabolic activities of organisms and their surface area raised to some power (Von Bertalanffy 1957, McMahon 1973). The value of the exponent depends upon the organism being investigated. Since the distribution parameter in the crown vigor index is a measure of surface area, the fact that it is raised to the power 1/2 is biologically interesting. This is particularly in light of the fact that the crown vigor index is dimensionless. Further study is needed to determine the significance of the exponent 1/2.

Evidence that the model is a reasonable representation of the real system comes from comparisons of simulated bolewood increment distributions to actual bolewood increment measurements. The radial growth of tree S3 correlated well with the crown vigor index when each was expressed relative to its maximum value. S3 was a 21-year-old tree and one of the oldest trees studied. Considering that the model only takes into account the passive system of xylem growth control, the fact that CVI worked best for older trees made sense. Large, older, open-grown trees are less influenced by internal stress conditions resulting from windsway than younger trees. In younger trees, the area of the lower bole were under-predicted whereas prediction in the lower bole of tree S3 was good.

Unfortunately tree S6 was not predicted very well. Noticable was the fact that bole growth was systematically underestimated. This systematic error may be the result of an error inherent in the experimental technique. It must be remembered that for the sake of comparison all values of the simulated and actual bole growth were transformed to make the bole growth patterns comparable. All calculations hinge upon the maximum recorded value. It is assumed, therefore, that if the actual maximum value is in error the whole bole growth pattern will be altered. This was probably what happened not only in tree S6 but also in 16-year-old tree N6 where similar systematic underpredictions were noted. The evidence for thinking that the true maximum was not detected comes from the fact that no clear maximum ring width value could be detected for these trees. This may be due to the nature of the sampling technique where samples were measured only above and below branch whorls. If maximum ring widths occurred at places other than these sampling points, maximum ring width would not be detected. To remedy this situation more samples in the area of suspected maximum ring width would have to be taken.

The most striking pattern exhibited by the CVI index was the zigzaging appearance in the upper crown of simulated trees (Figures 10, 11, and 12). In truly passive systems of xylem growth, the terminal leader and branches are the only sources of growth hormone input. Since these substances are distributed and metabolized over an increasing cambial surface area, a pattern such as this would be expected. Two things could alter this basic pattern in real trees. 1. Localized stress in the lower portions of stem internodes may stimulate metabolites to be mobilized and thus promote growth in these regions as suggested by Brown (1971), or 2. the stem cambium or adjacent tissue may produce its own growth hormones, independent of localized stress conditions, as suggested by Mirov (1941). Either way there is strong evidence that an active growth system is influencing xylem growth distribution. Another anomolous site of growth is in the region of butt swell. Fayle (1976) has recently implicated local bending stress to explain the phenomenon of butt swell.

An interesting, irregular, pattern of growth was located in the lower region of the bole of tree K4. Ring widths decreased rapidly from maximum in this region. The crown vigor index over estimated bole growth in this region. The reason bole growth decreased to such an extent in this bole region may be due to an extremely small crown (Figure 8). Growth hormones may be in sufficient supply to stimulate bole growth but without a sufficient complement of carbohydrates growth does not occur. Therefore, an index which predicts growth hormone concentrations overpredicts the actual bole growth. Even though hormone sinks may be prevailent remain throughout the tree there may beno metabolite to supply the demand. Other factors such as water, light, nutrients, etc. may be limiting to growth but whether these factors influence growth directly or indirectly by affecting growth hormone synthesis is not known.

In general, CVI bole growth simulations of actual bole growth measurements are good. This supports the idea that a passive system of xylem growth control is the dominant physiological system regulating main stem wood formation in red pine.

Bole Growth Simulation with Barker's Crown Activity Index

The crown vigor index is a model derived primarily from both Barker's (1981) crown activity index and Beckwith and Shackelford's (1976) crown growth index. Barker's CAI is presented in Figures 10, 11, and 12 along with the crown vigor index. Beckwith and Shackelford's index was not presented because the rate of extension of the primary branch necessary for the calculation of their index was not available. Beckwith and Shackelford's original crown growth model did not work and was modified to include measures of foliage dry weight as well as measures of branch extension. The ability of this modified model to accurately predict bole growth is questionable.

Barker's model differed from the CVI model in two ways. The input parameter of Barker's model was the primary branch extension length as opposed to current annual xylem increment measured at branch base; and the distribution parameter was the distance to point of bole growth whereas CVI used cambial surface area. Further, Barker measured main stem ring width at consistent distances down the tree bole whereas the CVI measured bole growth in relation to branch whorls. Differences in simulation patterns resulted in the differences in the above mentioned changes even though primary constructs in the models remained the same.

The results as indicated in Figures 10, 11, and 12 suggested that the parameters used in Barker's index were not as satisfactory as those used in CVI. The fact that the CVI index has better predictive powers suggests that the parameters used in the CVI model better estimate the real system's important components. The argument that Barker's estimates of system components was not the best is further supported by the fact that I can logically explain anomalies resulting from CVI simulations of actual main stem ring width patterns. Barker's model predictions do not make sense even though his model is based on a similar set of assumptions. On the older trees, where influences of localized stress are least apparent, Barker's model does the poorest. In all other cases Barker's model underpredicts actual bole growth which would not be expected in a model simulating a passive system of wood growth control.

Bole Growth Simulation with the Modified Crown Vigor Index

If indeed CAXI-branch base is an improved measure of branch to bolewood contribution, then estimates of this parameter may say something about the influence of other branch parameters on bole growth. The best consistent estimate of CAXI-branch base throughout the live crown of red pine was the product of total branch foliage dry weight and current primary branch extension length. This supports Beckwith and Shackelfords hypothesis that the foliage of branches produces hormones in sufficient quantities to make a significant contribution to basipetally moving auxins emanating primarily from the bud and elongating shoot. The fact that 1-year-old foliage dry weight and the product 1-year-old foliage and current primary branch extension length gave consistently better results in the upper crown indicate the importance of new foliage in producing and supplying growth hormones to upper crown branches. New foliage less affects branch contribution in the lower whorls.

Total foliage dry weight may not be a good predictor of basal branch growth primarily because the efficiency of foliage changes markedly down the crown. This means that foliage in the lower whorls is less productive and supplies the stem with less metabolites and auxin even though the weight of foliage may be increasing. Also, foliage is the producer of photosynthate which is not hypothesized to be the limiting factor in wood growth.

Current primary branch extension length was also a mediochre predictor of CAXI-branch base probably because it does not take translocation path into account. Although it represents the primary source of growth hormone production, it discounts the contribution made by the leaves. The total length of a branch was a poor estimator of CAXI-branch base probably because it assumes that all years prior to the current one contributed to how productive the branch was in the current year. Although there is a feedback mechanism operating in branch growth, the current year's environment plays a major role in determining what the branch is doing this year.

Current primary branch extension length divided by total branch length was a consistently poor estimator of CAXI-branch base. It was thought that the translocation length of a branch plays a major role in basal branch growth. Total branch length, however, may be too crude a parameter estimating internal physiological processes of hormone distribution and utilization. It therefore may distort any relationship which might exist between the branch extension length and total branch length measurements.

Table 14 indicates that there are significant differences between modified and unmodified CVI bole growth patterns in trees N1, N6 and S3. The fact that the modified CVI gave consistent smaller results than the original CVI for trees N1 and N6 indicates that these trees are more productive than the prediction equation makes them out to be. The regression equations which estimate CAXI-branch base must underpredict CAXI-branch base for these trees. This consistently affects bolewood increment prediction down the tree bole. Similarly, the modified CVI is consistently higher than CVI values indicating that the regression equations overpredict CAXI-branch base for this tree. It should be noted that the difference between the curves was very small as was indicated by the small average deviation values indicated in Table 7. The reason the curves are significantly different lies in the fact that the t-test tests for consistent differences in paired values and does not consider the size of the difference.

Models like the crown vigor index are interesting for two reasons. First, they may eventually lead to growth response simulation systems which provide the kind of quantitative information that forest managers need to design optimal silvicultural prescriptions. For example, growth simulation techniques might be used to optimize the initial spacing of plantations, thinning schedules and pruning treatments. Practical management objectives might be met efficiently with great saving of time and money. Secondly, crown growth models may further clarify our insight into complex biological relationships between the crown and growth of the bole. With refinement, the crown vigor index may provide information needed to elucidate the interaction between the dual active - passive system of xylem growth control. Eventually it may be possible to develope a model incorporating both the active - passive systems. But, before a more accurate representation of the physiological system of wood growth can be procured, more information is need about: the existance of growth regulator distribution along branches and main stem; and the mechanism of growth regulator control of cambial activity.

LITERATURE CITED

Abeles, F.B. 1973. Ethylene In Plant Biology. Academic Press, New York.

Adams, A.E. 1970. Camera and lens. The creative approach. Morgan and Morgan Inc., New York. 304 pp.

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. Res. Exp. Stn., St. Paul, Minnesota.

Asher, W.C. 1968. Response of pine seedlings to mechanical stimulation. Nature (Lond.) 217:134-136.

Assmann, E. 1970. The Principles of Forest Yield Study. Permagon Press, New York. 506 pp.

Barker, J.E. 1981. Bole growth patterns of Pinus radiata D.Don. in relation to fertilaization, bending stress, and crown growth. N.Z. J. For. Sci. In press.

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

Bowen, M.R. and P.F. Wareing 1971. Further investigations into hormone-directed transport in stems. Planta 99:120-132.

Boyd, J.D. 1977. Basic cause of differentiation of tension wood and compression wood. Aust. For. Res. 7:121-143.

Brown, C.L. 1970. Physiology of wood formation in conifers. Wood Sci. 3:8-22.

Brown, C.L. and M.H. Zimmermann 1971. Trees structure and function. Springer-Verlag, New York. 336p.

Brown, K.M. 1971. Xylem growth distribution in certain species of open-grown conifers. Ph.D. Dissertation. Purdue University. 82p.

Brown, K.M. and A.C. Leopold 1973. Ethylene and the regulation of growth in pine. Can. J. For. Res. 3:143-145.

Bunge, M.A. 1967. Scientific Research II. The Search For Truth. Springer-Verlag, New York. 374 pp.

Burstrom, H.G. 1979. In search of a plant growth paradigm. Am. J. Bot. 66:98-104.

Burton, J.D. amd D.M. Smith 1972. Guying to prevent wind sway influences in loblolly pine growth and wood properties. U.S.D.A. For. Serv. Res. Pap. SO-80. 8p.

Busgen, M. and E. Munch 1929. The Structure and Life of Forest Trees. (transl. by T. Thompson), 3rd ed. Wiley, New York. 436p.

Camus, G. 1949. Recherches sur le role des bourgeons dans les phenomenes de morphogenese. Rev. Cytol. Biol. Veg. 11:1-199.

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

Chatfield, C. 1975. Statistics for Technology. Chapman and Hall Ltd., London. 359 pp.

Clayton, J.S., Ehrlich, W.A., Cann, D.B., Day, J.H., and I.B. Marshall. 1977. Soils of Canada. Vol. 1. Soil report. Res. Br. Can. Dept. Agr. 243 pp.

Denne, M.P. and J.E. Wilson 1977. Some quantitative effects of indoleacetic acid on the wood productionand tracheid dimensions of Picea. Planta 134:223-228.

Doerner, K. 1966. Stress and hormone interrelationship in branch growth. Plant Physiol. 41:614-616.

Duff, G.H. and N.J. Nolan. 1953. Growth and morphogenesis in the Canadian forest species. I. The controls of cambial and apical activity in Pinus resinosa Ait. Can. J. Bot. 31:471-513.

Duff, G.H. and N.J. Nolan 1957. Growth and morphogenesis in the Canadian forest species. II. Specific increments and their relation to the quantity and activity of growth in Pinus resinosa Ait. Can. J. Bot. 35:327-372.

Duff, G.H. and N.J. Nolan 1961. Growth and morphogenesis in the Canadian forest species. IV. Radial growth in branches and main axis of Pinus resinosa Ait. under conditions of open growth, suppression, and release. Can. J. Bot. 39:385-409.

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

Farrar, J.L. and W. Fan 1970. Induction of tracheid development in decapitated jack pine seedlings (Pinus banksiana Lamb.) with indole-3-acetic acid and gibberellic acid. Annu. Rep. Fac. For. Dep. Bot. Univ. Toronto. 8p.

Fayle, D.C.F. 1976. Stem sway affects ring width and compression wood formation in exposed root bases. Forest Sci. 22:193-194.

Goodwin, P.B. and P.E. Cansfield 1967. The control of branch growth on potato tubers: III The basis of correlative inhibition. J. Exp. Bot. 18(55): 297-307.

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

Gregory, F.G. and J.A. Veale 1957. A reassessment of the problem of apical dominance. Symp. Soc. Exp. Biol. 11:2-20.

Hall, G.S. 1965. Wood increment and crown distribution relationships in red pine. Forest Sci. 11:438-448.

Hall, G.S. 1967. Some mechanical and nutritional aspects of cambial increment distribution in red pine. Ph.D. Dissertation. Yale University. 127p.

Hejnowicz, A. and M. Tomaszewski 1969. Growth regulators and wood formation in Pinus silvestris. Physiol. Plant. 22:984-992.

Jacobs, M.R. 1954. The effect of wind sway on the form and development of Pinus radiata D.Don. Aust. J. Bot. 2:35-51.

Kozlowski, T.T. 1971a. Growth and development of trees. Vol. 1, Academic Press, New York. 443p.

Kozlowski, T.T. 1971b. Growth and development of trees. Vol. 2, Academic Press, New York.

Kozlowski, T.T. and Keller, T. 1966. Food relations of woody plants. Bot. Rev. 32:293-382.

Kozlowski, T.T. and C.H. Winget. 1964. The role of reserves in leaves, branches, stems and roots on shoot growth of red pine. Am. J. Bot. 51:522-529.

Kramer, P.J. and T.T. Kozlowski 1979. Physiology of woody plants. Academic Press, New York. 811p.

Labyak, L.F. and F.X. Schumacker 1954. The contribution of its branches to the main stem growth of loblolly pine. J. of For. 52:333-337.

Ladefoged, K. 1946. [The importance of individual parts of the crown, in Norway spruce, from the point of view of increment production.] Forstl. Forsogsv. Danm. 16:365-400. [cited from For. Abstr. 7:2097.]

Larson, P.R. 1962. Auxin gradients and the regulation of cambial activity. In: Tree growth. (T.T. Kozlowski ed.) pp. 97-117. The Ronald Press Co., New York.

Larson, P.R. 1963. Stem form development in forest trees. Forest Sci. Monograph 5, 42p.

Larson, P.R. 1964. Some indirect effects of environment on wood formation. In: The formation of wood in forest trees. (M.H. Zimmerman, ed.), pp.345-365. Academic Press, New York.

Larson, P.R. 1965. Stem form of young Larix as influenced by wind and pruning. Forest Sci. 11: 412-424.

Larson, P.R. 1969. Wood formation and the concept of wood quality. Yale Sch. For. Bull. 74.

Leopold, A.C., Brown, K.M., and F.H. Emerson. 1972 Ethylene in the wood of stressed trees. Hort. Sci. 7:175.

Little, C.H.A. 1969. Apical dominance in long shoots of white pine (Pinus strobus). Can. J. Bot. 48:239-253.

Little, C.H.A. 1975. Inhibition of cambial activity in Abies balsamea by internal water stress: role of abscisic acid. Can. J. Bot. 53:1805-1810.

Little, C.H.A. and J.M. Bonga 1974. Rest in the cambium of Abies balsamea. Can. J. Bot. 52:1723-1730.

Little, C.H.A. and D.C. Eidt 1968. Effect of abscisic acid on budbreak and transpiration in woody species. Nature (Lond.) 220:498-499.

Little, C.H.A. and D.C. Eidt 1970. Relationship between transpiration and cambial activity in Abies balsamea. Can. J. Bot. 48:1027-1028.

Mar:Moller, C. 1960. The influence of pruning on the growth of conifers. Forestry 33:37-53.

McGraw, D.C. 1973. An investigation into the role of gibberellins in apical dominance in the Cupressaceae. MSc. Thesis. University of Calgary, Calgary, Alberta.

McMahon, T. 1973. Size and shape in biology. Science 197:1201-1204.

Milthorpe, F.L. and J. Moorby 1969. Vascular transport and its significance in plant growth. Ann. Rev. of Plant Physiol. 20:117-138.

Mirov, N.T. 1941. Distribution of growth hormone in shoots of two species of pine. J. Forest. 39: 457-464.

Mitchell, H.L. 1972. How peg helps the hobbyist who works with wood. U.S.D.A. For. Serv. For. Prod. Div. 20 pp.

Morris, D.A. and P.J. Winfield 1972. Kinetin transport to axillary buds of dwarf pea (Pisum sativum L.). J. Exp. Bot. 23:346-355.

Mullins, M.G. 1970. Hormone directed transport of assimilates in decapitated internodes of Phaseolus vulgaris L. Ann. Bot. 34:897-909.

Myers, C.A. 1963. Vertical distribution of annual increment in thinned ponderosa pine. For. Sci. 9:394-404.

Nelson, C.D. 1964. the production and translocation of photosynthate -C14 in conifers. In: 'The Formation of Wood in Forest Trees', (M.H. Zimmermann ed.), pp. 243-257. Academic press, New York.

Onaka, F. 1950a. The longitudinal distribution of radial increments in trees. Bull. Kyoto Univ. Forests 18:1-53.

Onaka, F. 1950b. The effects of defoliation, disbudding, girdling and other treatments upon growth, especially radial growth in evergreen conifers. Bull. Kyoto Univ. Forests 18:55-95.

Patrick, J.W. 1976. Hormone-directed transport of metabolites. In: 'Transport and Transfer Processes In Plants', (I.F. Wardlaw and J.B. Passioura, eds.), pp. 433-446, Academic Press, New York.

Patrick, J.W. and D.J. Woolley 1973. Auxin physiology of decapitated stems of Phaseolus vulgaris L. treated with indole-3yl-acetic acid. J. Exp. Bot. 24:949-957.

Pharis, R.P. and G.G. Kuo 1977. Physiology of gibberellins in conifers. Can. J. For. Res. 7:299-325.

Pharis, R.P., Ruddat, M., Phillips, C.C., and E. Heftmann 1965. Gibberellin growth retardants and apical dominance in arizona cypress. Naturwissenschaften 52:88-89.

Phillips, I.D.J. 1968. Nitrogen, phosphorus, and potassium distribution in relation to apical dominance in dwarf pea (Phaseolus vulgaris v.c. Canadian Wonder). J. Exp. Bot. 19:617-627.

Phillips, I.D.A. 1969. Apical dominance. In: The physiology of plant growth and development. (M.B. Wilkins ed.) pp. 165-202. McGraw-Hill, London.

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

Plonski, W.L. 1974. Normal yield tables (Metric). Ontario Ministry of Natural Resources. 40 pp.

Quirk, J.T., Smith, D.M., and F. Freese 1975. Effect of mechanical stress on growth and anatomical structure of red pine (Pinus resinosa Ait.): torque stress. Can J. For. Res. 5:691-699.

Reich, F.P. and K.K. Ching 1970. Influence of bending stress on wood formation of young douglas fir. Holzforschung 24(2):68-70.

Roberts, L.W. 1969. The initiation of xylem differentiation. Bot. Rev. 35:201-250.

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

Shea, S.R. and K.A. Armson. 1972. Stem analysis of jack pine (Pinus banksiana, Lamb.): Techniques and concepts. Can J. For. Res. 2:392-406.

Shepherd, K.R. and K.S. Rowan 1967. Indoleacetic acid in cambial tissue of radiata pine. Aust. J. Biol. Sci. 20:637-646.

Stiell, W.M. 1969. Stem growth reaction in young red pine to the removal of single branch whorls. Can. J. Bot. 47:1251-1256.

Svenonius, B. and E. Olausson. 1975. The variation in annual rings of trees. Some methodical problems. Geologiska Foreningens i Stockholm Forhandligar. 97:174-179.

Thinmann, K.V. 1934. Studies of the growth hormones of plants. VI. J. Gen. Physiol. 18:23-24.

Thinmann, K.V. 1965. Toward an endocrinology of higher plants. Recent Prog. Horm. Res. 21:579-596.

Thinmann, K.V. 1974. Fifty years of plant hormone research. Plant Physiol. 54:450-453.

Tomaszewski, M. 1970. Auxin-gibberellin intractons in apical dominance. Bull. Acad. Pol. Sci. Ser. Sci. Biol. 18:364-372.

Ursino, D.J. 1973. The translocation of 14C - photosynthate in single tree progeny of white spruce (Picea glauca (Moench) Voss.). Can. J. For. Res. 3:315-318.

Ursino, D.J., Nelson, C.D., and G. Krotkov. 1968. Seasonal changes in the distribution of photoassimilated 14C in young pine plants. Plant Physiol. 43:845-852.

Venning, F.D. 1949. Stimulation by wind motion of collenchyma formation in celery particles. Bot. Gaz. 110:511-514.

Von Bertalanffy, L. 1957. Quantitative laws in metabolism and growth. Quart. Rev. of Biol. 32:217-231.

Walker, W.S. 1960. The effects of mechanical stimulation and etiolation on the collenchyma of Datura stromonium. Am. J. Bot. 47:717-724.

Wardlaw, I.F. and D.C. Mortimer 1970. Carbohydrate movement in pea plants in relation to axillary bud growth and vascular development. Can. J. Bot. 48:229-237.

Wareing, P.F. 1958. The physiology of cambial activity. Jour. Inst. Wood Sci. 1:34-42.

Wareing, P.F. and J. Patrick 1973. Source-sink relations and the partition of assimilates in the plant. (J.P. Cooper, ed.) pp. 481-499. Cambridge Univ. Press, Cambridge.

Wareing, P.F., Hanney, C.E.A., and J. Digby 1964. The role of endogenous hormones in cambial activity and xylem differentiation. In: The formation of wood in forest trees. (M.H. Zimmermann ed.) pp. 323-344. Academic Press, New York.

Westing, A.H. 1965. Formation and function of compression wood in gymnosperms. Bot. Rev. 31: 381-480.

Westing, A.H. 1968. Formation and function of compression wood in gymnosperms. II. Bot. Rev. 34:51-78.

Whitmore, F.W. and R. Zahner 1966. Development of the xylem ring in young red pine trees. For. Sci. 12:198-210.

Wickson, M. and K.V. Thimann 1958. The antagonism of auxin and kinetin in apical dominance. Physiol. Plant. 11:62-74.

Wilcox, H. 1962. Cambial growth characteristics. In: Tree growth. (T.T. Kozlowski ed.) pp.57-88. The Ronald Press Co., New York.

Wilson, B.F. 1970. The growing tree. The Univ. of Mass. Press, Amherst. 152p.

Wilson, B.F. 1981. Apical control of diameter growth in white pine. For. Sci. 27:95-101.

Wilson, B.F., Wodzicki, T. and R. Zahner 1966. Differentiation of cambial derivatives: Proposed terminology. Forest Sci. 12:438-440.

Wodzicki, T.J. and A.B. Wodzicki 1973. Auxin stimulation of cambial activity in Pinus silvestris. II. dependence upon basipetal transport. Physiol. Plant. 29:288-292.

Wodzicki, T.J. and S. Zajaczkowski 1974. Effects of auxin on xylem tracheid differentiation in decapitated stems of Pinus silvestris L. and its interactions with some vitamins and growth regulators. Acta. Soc. Bot. Pol. 43:129-148.

Young, H.E. and P.J. Kramer. 1952. The effect of pruning on the height and diameter growth of Loblolly pine. J. Forest. 50:474-479.

Zajaczkowski, S. 1973. Auxin stimulation of cambial activity in Pinus silvestris. I. The differential cambial response. Physiol. Plant. 29:281-287.

Zajaczkowski, S. and T.J. Wodzicki 1975. Inhibition and requirement of natural stimulator for cambial xylem production in isolated stem segments of Pinus silvestris. Physiol. Plant. 33:71-74.

Zoltai, S.C. 1965. Glacial features of the Quetico-Nipigon area, Ontario. Contrib. No. 64-14, Res. Br., Ont. Dept. Lands and Forests.

APPENDIX A

Estimation of Site Index for the Sapawe, Nym Lake, and Kawene Study Areas.

Estimation of Site Index Values for the Sapawe, Nym Lake, and Kawene Study Areas

Alban (1979) suggests two useful methods, based on height growth, for estimating site index in young red pine stands. The method to be used depends upon the age and the height of the tree on the site to be evaluated. Method 1 is used for young red pine stands with at least two whorls above 8 ft. (2.43 m). This was the case at the Sapawe and Nym Lake study sites. Method 2 is used in stands with less than two whorls above 8 ft. This method of site evaluation applied to the Kawene study area.

Method 1

Steps for estimating site index values using Method 1 are as follows:

1. Beginning at the first whorl above 8 ft. measure the next 5 years growth ie. the 5 internodes extending to the 6 whorl above 8 feet. (A 5 year height growth measurement will give good results, but as little as 2 years will give a fair estimate.)
2. Divide this length by the number of internodes measured to get the average growth in feet per year.

3. Read the corresponding site index below:

Average Annual Height Growth (feet)	(meters)	Site Index Age 50 (feet)	(meters)
0.8	0.24	38	11.6
1.0	0.30	46	14.0
1.2	0.37	52	15.8
1.4	0.43	56	17.1
1.6	0.49	61	18.6
1.8	0.55	65	19.8
2.0	0.61	68	20.7
2.2	0.67	72	21.9
2.4	0.73	76	23.2

4. Repeat process for all sample trees and find the average site index.

Method 2

1. Beginning at the first whorl above breast height (4.5 ft., 1.76 m), measure to the uppermost whorl.

2. Divide this length by the number of internodes measured to set the average growth per year.

3. Read the site index table below:

Average Annual Height Growth (feet)	(meters)	Site Index Age 50 (feet)	(meters)
0.6	0.18	40	12.2
0.8	0.24	47	14.3
1.0	0.31	52	15.8
1.2	0.38	57	17.4
1.4	0.44	61	18.6
1.6	0.49	65	19.8
1.8	0.55	69	21.0
2.0	0.61	72	21.9
2.2	0.67	76	23.2

4. Repeat the process for all sample trees and find the average site index.

Site index estimates for the 24 study trees at Kawene, Nym Lake and Sapawe are presented in Table A3, A4, and A5 respectively.

Table A3. Average annual height growth and related site index values for eight sampled trees at Kawene.

Tree No.	Ave. Annual Ht. Growth (ft)	(m)	Site Index Age 50 (ft)	(m)
		KAWENE		
K1	1.5	0.45	63	18.9
K2	1.9	0.56	70	21.2
K3	1.8	0.56	69	21.1
K4	1.9	0.58	71	21.7
K5	2.2	0.65	76	22.9
K6	1.5	0.48	63	19.0
K7	1.6	0.48	65	19.5
K8	2.1	0.64	75	22.7

Table A4. Average annual height growth and related site index values for eight sampled trees at Nym Lake.

Tree No.	Ave. Annual Ht. Growth (ft)	(m)	Site Index Age 50 (ft)	(m)
		NYM LAKE		
N1	2.3	0.69	74	22.4
N2	2.2	0.68	72	22.3
N3	2.2	0.67	72	22.0
N4	2.4	0.74	76	23.3
N5	2.3	0.69	74	22.4
N6	2.1	0.65	70	21.6
N7	2.2	0.68	72	22.1
N8	2.0	0.62	68	20.9

Table A5. Average annual height growth and related site index values for eight sampled trees at Sapawe.

Tree No.	Ave. Annual Ht. Growth (ft)	(m)	Site Index Age 50 (ft)	(m)
		SAPAWE		
S1	2.0	0.61	68	20.8
S2	2.0	0.59	68	20.5
S3	1.8	0.54	65	19.4
S4	2.0	0.61	68	20.8
S5	1.6	0.49	61	18.4
S6	2.1	0.63	70	21.2
S7	1.7	0.53	64	19.2
S8	1.6	0.49	61	18.5

APPENDIX B

Summary of Error Analysis For Growth Ring Width Measurements.

Summary of Error Analysis for Growth Ring Width Measurements

Table B1 summarizes the mean ring width and standard error computations for each of the enlarged branch disc negatives. Figure B1 illustrates the relationship between image diameter and the standard error of its measurement. The small numbers placed beside each point represent the approximate section magnifications. These are directly related to the image diameters. Figure B1 indicates a decrease in the standard error of measurement with both increase in the projected image size and decrease in the size of the photographed section.

Table B1. Mean ring width and associated standard error for three different diameter branch sections calculated at different magnifications.

Section No.[†]	Section Diameter (cm)	Magnification	Image Diameter (cm)	Mean Ring Width (mm)[††]	Standard Error
S3 2-4	1.04	5.14	5.3	2.15	0.0116
S3 2-4	1.04	10.02	10.4	2.11	0.0051
S3 2-4	1.04	15.10	15.8	2.10	0.0057
K4 4-1	1.73	5.06	8.7	1.88	0.0131
K4 4-1	1.73	10.13	17.7	1.88	0.0084
K4 4-1	1.73	15.09	26.6	1.89	0.0054
S1 5-1	2.51	5.09	12.8	2.10	0.0137
S1 5-1	2.51	10.07	25.5	2.38	0.0084

[†] section numbers represent tree, whorl, and branch number respectively.

[††] calculation based on 30 independant measurements.

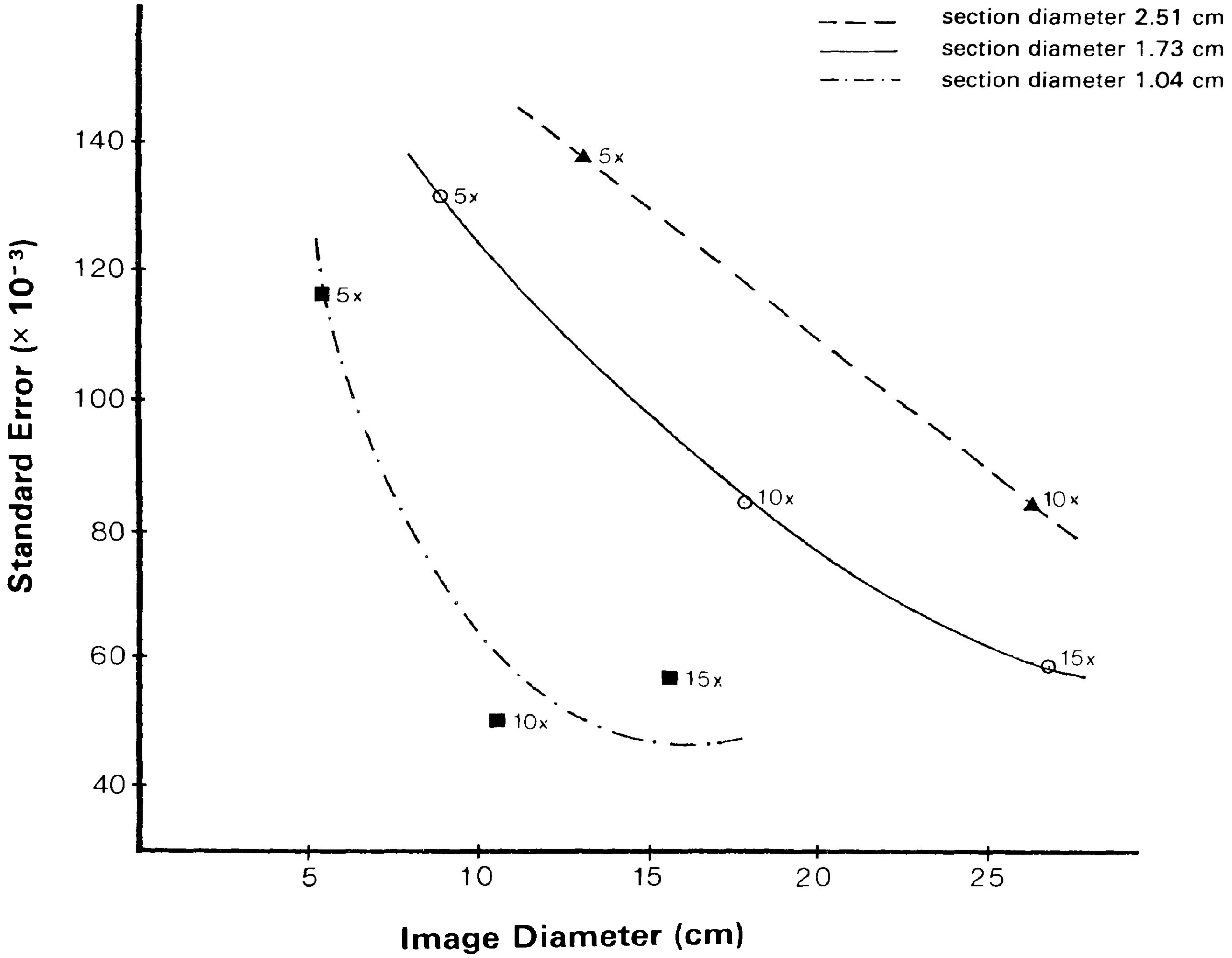


FIGURE B1. Relationship between the image diameter of three enlarged branch section photograph negatives and the standard deviation of their measurements at 5×, 10× and 15× magnification.

APPENDIX C

Data Transformations: Observed Ring Width, Crown Vigor Index and Barker's Crown Activity Index Transformed to Percent Maximum; Tree Height Converted to Relative Tree Height.

Table D1. Data transformations for Tree K2.

Bole Section No.	Distance from Apex (m)	Relative Height (%)	ΔR_s† (mm)	ΔR_s as % max. ΔR_s	Crown Vigor Index	CV Index As % max. CV Index	Crown Activity Index	CA Index as % max. CA Index
1	0.71	83.3	0.40	52.2	0.058	68.6	39.7	90.1
2*	1.27	70.1	0.58	76.4	0.028	33.7	25.9	58.9
3	1.42	66.6	0.69	91.0	0.074	88.5	39.1	88.9
4*	1.88	55.8	0.72	94.8	0.058	68.9	33.5	76.1
5	2.02	52.5	0.74	97.3	0.083	98.8	41.8	94.8
6*	2.30	45.9	0.76	100.0	0.072	85.4	39.1	88.7
7	2.44	42.6	0.73	96.1	0.084	100.0	44.0	100.0
8	2.74	35.5	0.70	92.9	0.074	88.4	41.6	94.4
9	2.89	32.0	0.61	81.1	0.076	90.7	43.4	98.7
10	3.11	26.8	0.64	84.9	0.071	84.2	41.9	95.2
11	3.26	23.3	0.62	82.0	0.069	82.5	41.2	93.7
12	3.45	18.8	0.64	84.4	0.066	78.2	40.1	91.1
13	3.59	15.5	0.63	83.2	0.063	75.5	39.5	89.7
14	3.77	11.3	0.61	80.9	0.060	72.1	38.6	87.6
15	3.95	7.1	0.63	82.6	0.058	69.1	37.8	85.7
16	4.04	4.9	0.60	79.8	0.057	67.6	37.3	84.8
17	4.16	2.1	0.61	80.2	0.055	65.7	36.8	83.6
18	4.25	0.0	0.60	79.1	0.054	64.4	36.4	82.7

† Current annual radial increment measured along the main stem (CAXI- main stem).

* points excluded from t-test - for explaination see page 55

Table D2. Data transformations for Tree K4.

Bole Section No.	Distance from Apex (m)	Relative Height (%)	ΔR_S[†] (mm)	ΔR_S as % max. ΔR_S	Crown Vigor Index	CV Index As % max. CV Index	Crown Activity Index	CA Index as % max. CA Index
1	0.69	82.5	0.38	56.3	0.046	69.2	29.7	83.2
2*	1.22	69.1	0.51	75.7	0.024	35.9	20.1	56.3
3	1.35	65.8	0.61	91.5	0.065	98.2	35.7	100.0
4*	1.80	54.4	0.64	94.8	0.051	77.3	30.4	85.2
5	1.93	51.1	0.67	100.0	0.065	98.4	35.3	98.8
6*	2.26	42.8	0.66	97.9	0.057	85.9	32.5	91.0
7	2.40	39.2	0.61	92.1	0.066	100.0	35.5	99.5
8	2.64	33.2	0.61	91.2	0.060	90.9	33.8	94.8
9	2.79	29.4	0.50	74.4	0.060	90.6	35.0	97.8
10	2.94	25.6	0.46	68.0	0.057	85.9	34.0	95.3
11	3.08	22.0	0.48	71.0	0.056	84.4	34.2	95.6
12	3.17	19.8	0.47	70.3	0.055	82.1	33.7	94.3
13	3.30	16.5	0.46	68.5	0.053	79.8	33.4	93.7
14	3.44	12.9	0.45	67.2	0.051	76.8	32.8	91.7
15	3.57	9.6	0.44	65.5	0.049	74.3	32.2	90.1
16	3.74	5.3	0.47	69.9	0.047	71.2	31.4	88.1
17	3.83	3.0	0.46	69.1	0.046	69.6	31.1	87.0
18*	3.95	0.0	0.52	78.3	0.045	67.6	30.6	86.1

[†] Current annual radial increment measured along the main stem (CAXI- main stem).

* points excluded from t-test - for explaination see page 55

Table D3. Data transformations for Tree N1.

Bole Section No.	Distance from Apex (m)	Relative Height (%)	ΔR_s [†] (mm)	ΔR_s as % max. ΔR_s	Crown Vigor Index	CV Index as % max. CV Index	Crown Activity Index	CA Index as % max. CA Index
1	0.71	85.7	0.43	47.0	0.063	77.2	46.0	99.2
2*	1.30	73.7	0.64	69.9	0.029	35.1	30.0	64.6
3	1.45	70.7	0.77	84.1	0.078	95.3	44.9	96.8
4*	2.01	59.4	0.82	89.4	0.056	69.0	37.7	81.3
5	2.16	56.4	0.85	93.5	0.076	93.0	44.2	95.3
6*	2.52	49.1	0.91	100.0	0.065	79.5	40.9	88.1
7	2.69	45.7	0.90	98.0	0.082	100.0	46.3	99.9
8*	3.10	37.4	0.85	92.8	0.070	86.3	43.2	93.2
9	3.26	34.1	0.83	90.8	0.076	92.5	46.4	100.0
10	3.57	27.9	0.73	79.6	0.069	84.6	44.4	95.7
11	3.73	24.7	0.80	87.0	0.069	84.1	45.5	98.1
12	3.90	21.2	0.80	87.4	0.066	80.5	44.5	96.0
13	4.05	18.2	0.77	84.0	0.064	78.4	44.2	95.4
14	4.19	15.4	0.78	85.3	0.062	75.8	43.5	93.9
15	4.29	13.3	0.72	78.7	0.061	74.3	43.3	93.3
16	4.42	10.7	0.77	83.8	0.059	72.3	42.6	92.0
17	4.55	8.1	0.75	81.8	0.057	70.3	42.0	90.7
18	4.63	6.5	0.79	86.7	0.056	69.2	41.7	89.9
19	4.76	3.8	0.78	85.5	0.055	67.4	41.1	88.7
20	4.82	2.6	0.78	85.5	0.054	66.6	40.9	88.2

Table D3. (Continued)

Bole Section No.	Distance from Apex (m)	Relative Height (%)	ΔR_s (mm)	ΔR_s as % max. ΔR_s	Crown Vigor Index	CV Index as % max. CV Index	Crown Activity Index	CA Index as % max. CA Index
21*	4.95	0.0	0.80	87.8	0.053	64.9	40.4	87.1

‡ Current annual radial increment measured along the main stem (CAXI- main stem).

* points excluded from t-test - for explaination see page 55

Table D4. Data transformations for Tree N6.

Bole Section No.	Distance from Apex (m)	Relative Height (%)	ΔR_s (mm)	ΔR_s[†] as % max. ΔR_s	Crown Vigor Index	CV Index as % max. CV Index	Crown Activity Index	CA Index as % max CA Index
1	0.74	87.2	0.55	64.3	0.056	72.0	32.3	75.9
2*	1.29	77.7	0.66	76.8	0.027	35.0	22.4	52.8
3	1.43	75.3	0.84	97.9	0.073	93.8	38.6	90.7
4*	2.00	65.5	0.84	97.4	0.053	68.3	32.3	75.9
5	2.15	62.9	0.78	90.2	0.077	99.0	39.7	93.3
6*	2.57	55.6	0.86	100.0	0.064	82.2	36.3	85.3
7	2.72	53.0	0.84	97.9	0.078	100.0	41.2	96.7
8*	3.17	45.2	0.82	94.9	0.067	85.6	38.2	89.7
9	3.32	42.7	0.84	07.9	0.074	95.6	42.1	99.0
10	3.58	38.2	0.82	94.8	0.069	88.5	40.6	95.4
11	3.78	34.7	0.81	93.9	0.070	89.3	42.6	100.0
12	4.15	28.3	0.80	92.5	0.063	81.3	40.7	95.7
13	4.31	25.6	0.76	87.8	0.063	80.4	40.8	95.9
14	4.61	20.4	0.73	84.7	0.059	75.3	39.5	92.8
15	4.76	17.8	0.73	85.2	0.057	73.5	39.0	91.6
16	4.95	14.5	0.76	88.2	0.055	70.8	38.3	89.9
17	5.08	12.3	0.68	78.6	0.054	69.0	37.8	88.8
18	5.24	9.5	0.71	82.7	0.052	67.0	37.2	87.5
19	5.37	7.2	0.74	85.7	0.051	65.5	36.8	86.5
20	5.51	4.8	0.73	84.9	0.050	63.9	36.4	85.4

Table D4. (Continued)

Bole Section No.	Distance from Apex (m)	Relative Height (%)	ΔR_s (mm)	ΔR_s as % max. ΔR_s	Crown Vigor Index	CV Index as % max. CV Index	Crown Activity Index	CA Index as % max. CA Index
21*	5.61	3.1	0.78	90.5	0.049	62.8	36.0	84.6
22*	5.64	2.6	0.78	90.5	0.049	62.4	35.9	84.4
23*	5.75	0.7	0.78	90.8	0.048	61.2	35.6	83.6
24*	5.79	0.0	0.78	90.9	0.047	60.8	35.5	83.4

† Current annual radial increment measured along the main stem (CAXI- main stem).

* points excluded from t-test - for explaination see page 55

Table D5. Data transformations for Tree S3.

Bole Section No.	Distance from Apex (m)	Relative Height (%)	ΔR_s[†] (mm)	ΔR_s as % max. ΔR_s	Crown Vigor Index	CV Index as % max. CV Index	Crown Activity Index	CA Index as % max. CA Index
1	0.64	93.2			0.039	46.1	13.4	37.1
2*	1.12	88.1	0.66	75.7	0.024	28.2	8.7	24.0
3	1.26	86.8	0.73	83.3	0.070	82.4	22.4	62.0
4*	1.66	82.4	0.83	95.2	0.054	63.9	19.4	53.6
5	1.82	80.7	0.83	95.1	0.085	100.0	26.3	72.7
6*	2.26	76.0	0.87	100.0	0.069	81.6	23.7	65.5
7	2.40	74.5	0.86	99.0	0.085	99.9	29.1	80.5
8*	2.80	70.3	0.86	98.9	0.072	85.0	27.1	74.9
9	2.99	68.3	0.83	95.0	0.081	95.2	32.3	89.1
10*	3.37	64.2	0.82	94.0	0.072	84.3	30.5	84.4
11	3.55	62.3	0.77	88.0	0.075	88.5	35.0	96.9
12	3.94	58.2	0.71	81.9	0.068	79.6	33.4	92.4
13	4.15	55.9	0.71	81.6	0.066	77.7	36.2	100.0
14	4.66	50.5	0.69	79.1	0.059	69.3	34.3	94.9
15	4.84	48.6	0.58	67.0	0.058	68.2	35.4	97.9
16	5.27	44.1	0.56	64.4	0.053	62.9	34.1	94.2
17	5.45	42.1	0.51	58.5	0.052	60.9	33.6	92.7
18	5.72	39.3	0.50	57.2	0.049	58.2	32.8	90.7
19	5.88	37.6	0.46	52.6	0.048	56.7	32.4	89.6
20	6.23	33.9	0.45	51.4	0.046	53.7	31.6	87.2

Table D5. (Continued)

Bole Section No.	Distance from Apex (m)	Relative Height (%)	ΔR_s (mm)	ΔR_s as % max. ΔR_s	Crown Vigor Index	CV Index as % max. CV Index	Crown Activity Index	CA Index as % max. CA Index
21	6.39	32.2	0.42	47.8	0.044	52.5	31.2	86.2
22	6.58	30.2	0.45	51.5	0.043	51.2	30.8	85.1
23	6.85	27.9	0.44	50.1	0.042	49.3	30.2	83.5
24	7.20	23.6	0.43	49.8	0.040	47.2	29.5	81.6
25	7.39	21.6	0.33	38.0	0.039	46.1	29.2	80.6
26	7.77	17.5	0.37	42.9	0.037	44.1	28.5	78.8
27	7.92	15.9	0.34	39.0	0.037	43.4	28.2	78.0
28	8.19	13.1	0.37	42.3	0.036	42.2	27.8	76.8
29	8.33	11.6	0.33	38.2	0.035	41.6	27.6	76.2
30	8.59	8.8	0.38	43.3	0.034	40.5	27.2	75.1
31	8.73	7.3	0.40	45.8	0.034	40.0	27.0	74.6
32*	8.89	5.6	0.39	45.0	0.033	39.3	26.8	73.9
33*	9.05	3.9	0.42	47.7	0.033	38.7	26.5	73.3
34*	9.20	2.3	0.43	49.2	0.032	38.2	26.3	72.8
35*	9.33	1.0	0.45	51.2	0.032	37.7	26.0	71.8
36*	9.42	GND$^{\text{II}}$	0.45	51.2	NC*		NC	

† Current annual radial increment measured along the main stem (CAXI- main stem).

* points excluded from t-test - for explaination see page 55

Table D6. Data transformations for Tree S6.

Bole Section No.	Distance from Apex (m)	Relative Height (%)	$\Delta R_s^{\dagger}$ (mm)	ΔR_s as % max. ΔR_s	Crown Vigor Index	CV Index as % max. CV Index	Crown Activity Index	CA Index as % max. CA Index
1	0.73	92.5			0.057	66.8	35.5	76.6
2*	1.24	87.2	0.57	68.8	0.028	32.7	24.4	52.6
3	1.38	85.8	0.68	81.5	0.082	95.7	38.9	83.8
4*	1.86	80.9	0.75	90.3	0.060	70.5	32.9	70.9
5	2.03	79.1	0.78	93.3	0.086	100.0	40.1	86.4
6*	2.48	74.5	0.81	97.2	0.070	81.3	36.1	77.9
7	2.63	72.9	0.82	99.2	0.084	98.6	40.8	88.0
8*	3.07	68.4	0.83	100.0	0.072	84.0	37.8	81.4
9	3.23	66.8	0.81	97.6	0.081	94.1	42.6	91.9
10*	3.61	62.9			0.071	83.3	40.4	87.1
11	3.76	61.3	0.82	98.8	0.077	89.7	44.8	96.6
12	4.13	57.5	0.75	90.2	0.070	81.7	42.8	92.3
13	4.29	55.9	0.68	81.9	0.070	82.3	46.0	99.2
14	4.74	51.2	0.75	90.6	0.064	74.7	43.9	94.6
15	4.89	49.7	0.67	80.1	0.063	74.1	46.4	100.0
16	5.45	43.9	0.69	83.3	0.057	66.8	44.0	95.0
17	5.63	42.1	0.57	68.8	0.055	64.8	43.4	93.6
18	6.12	37.0	0.57	68.2	0.051	59.9	41.7	89.9
19	6.30	35.2	0.52	63.2	0.050	58.3	41.1	88.7
20	6.70	31.1	0.52	63.1	0.047	55.0	39.9	86.1

Table D6. (Continued)

Bole Section No.	Distance from Apex (m)	Relative Height (%)	ΔR_s (mm)	ΔR_s as % max. ΔR_s	Crown Vigor Index	CV Index as % max. CV Index	Crown Activity Index	CA Index as % max. CA Index
21	6.93	28.7	0.46	55.7	0.046	53.3	39.3	84.7
22	7.33	24.6	0.49	59.5	0.043	50.7	38.2	82.5
23	7.49	22.9	0.46	55.2	0.043	49.7	37.8	81.6
24	7.75	20.3	0.52	62.2	0.041	48.2	37.2	80.3
25	7.94	18.3	0.43	52.3	0.040	47.2	36.8	79.4
26	8.20	15.6	0.42	51.1	0.039	45.9	36.2	78.2
27	8.35	14.1	0.43	52.2	0.039	45.2	35.9	77.5
28	8.58	11.7	0.43	52.3	0.038	44.1	35.5	76.5
29	8.70	10.5			0.037	43.6	35.2	76.0
30	8.84	9.0	0.43	51.4	0.037	43.0	34.9	75.4
31	8.98	7.6	0.41	49.8	0.036	42.4	34.7	74.8
32*	9.12	6.2	0.44	52.4	0.036	41.9	34.4	74.2
33*	9.32	4.1	0.49	59.3	0.035	41.1	34.1	73.5
34*	9.44	2.9	0.54	65.0	0.034	40.6	33.8	72.9
35*	9.72	GND$^{\Pi}$	0.58	70.0	NC*		NC	

† **Current annual** radial increment measured along the main stem (CAXI- main stem).
* points excluded from t-test - for explaination see page 55

APPENDIX D

Calculations for Barker's Crown Activity Index.

Calculations for Barker's Crown Activity Index

The crown activity index is calculated for a number of points along the tree bole which correspond with data from disc measurements. The crown influence factor is calculated as:

$$BCAI_i = \sum_{j=1}^{N} \sum_{k=1}^{n_j} \frac{I_{jk}}{(h_j - h_i + L_{jk})^{\frac{1}{2}}}$$

where: N = total number of branch whorls above a bole section

n_j = number of branches in the jth whorl

I_{jk} = yearly length increment of the kth branch in the jth whorl

h_j = height of jth whorl

h_i = height of ith bole cross-section

L_{jk} = branch length at the end of the growing season

$BCAI_i$ = relative contribution of all whorls above the ith bole cross-section to growth at the ith disc

The index assumes that branch length growth during the year being considered is a reasonable representation of the relative stimulatory contribution to the bole. In addition, the effect of a branch is assumed to decline with distance from the branch down the bole.

APPENDIX E

Regression Equations and Important Statistics for Relationships Between the Width of the Current Annual Growth Ring Measured at Branch Base, and Various Branch Parameters; Whorls One to Eight.

Table E1. Whorl one: regression equations and important statistics between the width of the current annual growth ring measured at branch base (CAXI- branch base) and various branch parameters.

Independent[†] Variable	Equation to Calculate Dependent Variable ΔR_b (CAXI- branch base)	Sample Size (N)	Coefficient of Determination (R^2)	Standard Error ($S_{y/x}$)	F Value
$F \cdot \Delta L$	$\Delta R_b = 0.11 + (1.3 \times 10^{-4})\ F \cdot \Delta L$	63	0.70	0.024	146.0
F	$\Delta R_b = 0.073 + 0.0078\ F$	63	0.65	0.027	112.0
ΔL	$\Delta R_b = 0.034 + 0.0039\ \Delta L$	63	0.69	0.025	134.9

[†] $F \cdot \Delta L$	product of branch foliage dry weight and current extension length of the primary branch
F	branch foliage dry weight
ΔL	current extension length of the primary branch

Table E2. Whorl two: regression equations and important statistics between the width of the current annual growth ring measured at branch base (CAXI- branch base) and various branch parameters.

Independent Variable[†]	Equation to Calculate Dependent Variable ΔR_b (CAXI- branch base)	Sample Size (N)	Coefficient of Determination (R^2)	Standard Error ($S_{y/x}$)	F Value
$F \cdot \Delta L$	$\Delta R_b = 0.094 + (5.1 \times 10^{-5})\ F \cdot \Delta L$	85	0.73	0.029	222.1
F	$\Delta R_b = 0.069 + 0.0024\ F$	86	0.69	0.031	186.3
L	$\Delta R_b = 0.023 + 0.0028\ L$	86	0.71	0.030	203.4
ΔL	$\Delta R_b = 0.042 + 0.0067\ \Delta L$	86	0.73	0.029	229.4
ΔF	$\Delta R_b = 0.066 + 0.0037\ \Delta F$	11	0.82	0.026	39.9
$\Delta L/L$	$\Delta R_b = 0.26 + -0.18(\Delta L/L)$	86	0.04	0.054	3.8
$\Delta F \cdot \Delta L$	$\Delta R\ = 0.092 + (8.2 \times 10^{-5})\ \Delta F \cdot \Delta L$	16	0.88	0.021	66.5

[†] $F \cdot \Delta L$	product of branch foliage dry weight and current extension length of the primary branch
F	branch foliage dry weight
L	total branch length
ΔL	current extension length of the primary branch
ΔF	one year-old branch foliage
$\Delta L/L$	current branch extension length divided by total branch length
$\Delta F \cdot \Delta L$	product one year-old branch foliage and current branch extension length

Table E3. Whorl three: regression equations and important statistics between the width of the current annual growth ring measured at branch base (CAXI- branch base) and various branch parameters.

Independent[†] Variable	Equation to Calculate Dependent Variable ΔR_b (CAXI- branch base)	Sample Size (N)	Coefficient of Determination (R^2)	Standard Error ($S_{y/x}$)	F Value
$F \cdot \Delta L$	$\Delta R_b = 0.095 + (3.4 \times 10^{-5}) F \cdot \Delta L$	91	0.80	0.024	346.6
F	$\Delta R_b = 0.070 + 0.0012 F$	91	0.73	0.028	239.7
L	$\Delta R_b = 0.045 + 0.0023 L$	91	0.70	0.029	210.3
ΔL	$\Delta R_b = 0.029 + 0.0060 \Delta L$	91	0.65	0.031	167.5
ΔF	$\Delta R_b = 0.078 + 0.0022 \Delta F$	16	0.86	0.020	89.3
$\Delta L/L$	$\Delta R_b = 0.087 + 0.38 (\Delta L/L)$	91	0.15	0.049	15.3
$\Delta F \cdot \Delta L$	$\Delta R_b = 0.11 + (5.4 \times 10^{-5}) \Delta F \cdot \Delta L$	16	0.83	0.022	69.8

[†] See descriptions of independant variables in Table E2.

Table E4. Whorl four: regression equations and important statistics between the width of the current annual growth ring measured at branch base (CAXI- branch base) and various branch parameters.

Independent[†] Variable	Equation to Calculate Dependent Variable ΔR_b (CAXI- branch base)	Sample Size (N)	Coefficient of Determination (R^2)	Standard Error ($S_{y/x}$)	F Value
$F \cdot \Delta L$	$\Delta R_b = 0.068 + (2.8 \times 10^{-5})\ F \cdot \Delta L$	80	0.73	0.030	208.5
F	$\Delta R_b = 0.045 + 0.00076\ F$	80	0.69	0.032	174.4
L	$\Delta R_b = 0.094 + 0.0021\ L$	80	0.53	0.040	87.9
ΔL	$\Delta R_b = 0.0044 + 0.0076\ \Delta L$	80	0.46	0.043	65.6
ΔF	$\Delta R_b = 0.069 + 0.0018\ \Delta F$	32	0.80	0.026	119.4
$\Delta L/L$	$\Delta R_b = 0.081 + 0.46\ (\Delta L/L)$	80	0.09	0.056	7.4
$\Delta F \cdot \Delta L$	$\Delta R_b = 0.089 + (6.4 \times 10^{-5})\ \Delta F \cdot \Delta L$	32	0.87	0.029	93.4

[†] See descriptions of independant variables in Table E2.

Table E5. Whorl five: regression equations and important statistics between the width of the current annual growth ring measured at branch base (CAXI- branch base) and various branch parameters.

Independent Variable[†]	Equation to Calculate Dependent Variable ΔR_b (CAXI- branch base)	Sample Size (N)	Coefficient of Determination (R^2)	Standard Error ($S_{y/x}$)	F Value
$F \cdot \Delta L$	$\Delta R_b = 0.036 + (1.9 \times 10^{-5})\ F \cdot \Delta L$	87	0.73	0.026	229.5
F	$\Delta R_b = 0.012 + 0.00048\ F$	87	0.68	0.028	177.0
L	$\Delta R_b = 0.080 + 0.0013\ L$	87	0.53	0.034	95.1
ΔL	$\Delta R_b = 0.0048 + 0.0061\ \Delta L$	87	0.62	0.030	142.8
ΔF	$\Delta R_b = 0.018 + 0.0020\ \Delta F$	17	0.83	0.018	72.9
$\Delta L/L$	$\Delta R_b = 0.0015 + 0.73\ (\Delta L/L)$	87	0.33	0.040	43.5
$\Delta F \cdot \Delta L$	$\Delta R_b = 0.040 + (7.2 \times 10^{-5})\ \Delta F \cdot \Delta L$	17	0.73	0.022	41.6

[†] See descriptions of independant variables in Table E2.

Table E6. Whorl six: regression equations and important statistics between the width of the current annual growth ring measured at branch base (CAXI- branch base) and various branch parameters.

Independent Variable[†]	Equation to Calculate Dependent Variable ΔR_b (CAXI- branch base)	Sample Size (N)	Coefficient of Determination (R^2)	Standard Error ($S_{y/x}$)	F Value
$F \cdot \Delta L$	$\Delta R_b = 0.014 + (1.5\text{x}10^{-5})\ F \cdot \Delta L$	56	0.87	0.014	350.4
F	$\Delta R_b = 0.083 + 0.00036\ F$	56	0.66	0.022	107.0
L	$\Delta R_b = 0.058 + 0.00081\ L$	56	0.46	0.028	46.3
ΔL	$\Delta R_b = 0.013 + 0.0052\ \Delta L$	56	0.81	0.017	224.4
ΔF	$\Delta R_b = 0.0050 + 0.0018\ \Delta F$	14	0.80	0.018	49.2
$\Delta L/L$	$\Delta R_b = 0.020 + 0.82\ (\Delta L/L)$	56	0.53	0.027	60.4
$\Delta F \cdot \Delta L$	$\Delta R_b = 0.022 + (6.2\text{x}10^{-5})\ \Delta F \cdot \Delta L$	14	0.86	0.015	74.7

[†] See descriptions of independant variables in Table E2.

Table E7. Whorl seven: regression equations and important statistics between the width of the current annual growth ring measured at branch base (CAXI- branch base) and various branch parameters.

Independent[†] Variable	Equation to Calculate Dependent Variable ΔR_b (CAXI- branch base)	Sample Size (N)	Coefficient of Determination (R^2)	Standard Error ($S_{y/x}$)	F Value
$F \cdot \Delta L$	$\Delta R_b = 0.011 + (7.6x10^{6})\ F \cdot \Delta L$	31	0.65	0.013	54.8
F	$\Delta R_b = -0.0045 + 0.00019\ F$	31	0.53	0.015	34.3
L	$\Delta R_b = 0.035 + 0.00045\ L$	32	0.51	0.016	30.9
ΔL	$\Delta R_b = 0.0058 + 0.0022\ \Delta L$	32	0.46	0.016	25.9
ΔF	$\Delta R_b = 0.015 + 0.00066\ \Delta F$	8	0.48	0.011	5.6
$\Delta L/L$	$\Delta R_b = 0.0084 + 0.33\ (\Delta L/L)$	32	0.22	0.020	8.6
$\Delta F \cdot \Delta L$	$\Delta R_b = 0.019 + (3.3x10^{-5})\ \Delta F \cdot \Delta L$	8	0.51	0.011	6.3

[†] See descriptions of independant variables in Table E2.

Table E8. Whorl eight: regression equations and important statistics between the width of the current annual growth ring measured at branch base (CAXI- branch base) and various branch parameters.

Independent[†] Variable	Equation to Calculate Dependent Variable ΔR_b (CAXI- branch base)	Sample Size (N)	Coefficient of Determination (R^2)	Standard Error ($S_{y/x}$)	F Value
$F \cdot \Delta L$	$\Delta R_b = 0.0047 + (7.5x10^{-6})\ F \cdot \Delta L$	14	0.91	0.0052	120.2
F	$\Delta R_b = 0.017 + 0.00019\ F$	15	0.72	0.0089	32.8
L	$\Delta R_b = 0.044 + 0.00040\ L$	15	0.63	0.010	22.5
ΔL	$\Delta R_b = 0.0049 + 0.0029\ \Delta L$	15	0.75	0.0083	39.9
ΔF	$\Delta R_b = 0.010 + 0.00077\ \Delta F$	8	0.44	0.0064	4.8
$\Delta L/L$	$\Delta R_b = 0.013 + 0.69\ (\Delta L/L)$	15	0.60	0.010	19.8
$\Delta F \cdot \Delta L$	$\Delta R_b = 0.014 + (5.2x10^{-5})\ \Delta F \cdot \Delta L$	8	0.64	0.0051	10.9

[†] See descriptions of independant variables in Table E2.