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Crown Structure and Distribution of Biomass in a Lodgepole Pine Stand

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Abstract

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Gross dimensions and quantities of needles and branches are presented for 298 trees. Weight, diameter, length, and height relations were usually highly correlated. Needles were normally distributed along the length of branches as well as vertically through the canopy. Needle and branchwood weights for entire crowns were best estimated by the logarithmic transformation of diameters at breast height.

Keywords: *Pinus contorta*, biomass, canopy, foliage, overstory productivity, transpiration.

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INTRODUCTION

The quantity and arrangement of leaves and branches in tree crowns have long been of interest to foresters, ecologists, and plant physiologists. Much recent interest in tree crowns has been related to their efficiency in trapping and dispersing man-caused aerosols (Brady 1967). The sound-attenuating properties of tree and shrub crowns for noise control have been evaluated by Cook and van Haverbeke (1971). The potential of tree crowns as raw material for oils and pharmaceuticals is also under study (Keays 1971). Detailed crown structure information should be gathered prior to studies of forest productivity and nutrient cycling, and fuel description for fire control operations (Ovington and Madgwick 1959, Deeming and others 1974).

A characteristic need in the above interdisciplinary studies of tree crowns is for more detailed knowledge about the dimensions and quantities of foliage and branches, and interrelationships between them. The horizontal and vertical distribution of foliage and branches must also be better understood if we are to realize the full potential for organic production, energy exchange, nutrient cycling, effects of fertilization, water balance in response to climate, and similar factors. This study reports size and weight interrelations of lodgepole pine (*Pinus contorta*) needles, branches, and boles.

PREVIOUS WORK

Crown Characteristics

Branching in lodgepole pine crowns, as in most conifers, is excurrent: an undivided main stem or bole supports whorls of branches radiating outward. Stiell (1962) reported for red pine (*P. resinosa*), "The crown is by no means uniformly dense: the stem and a zone around it occupy a needle-free core up the center; there are gaps between the foliage of successive branches, both horizontally and vertically; and the weight of the foliage itself varies erratically from one branch whorl to another." Similar characteristics are apparent in lodgepole pine. Differences in site quality, spacing, and genetic factors apparently all contribute to the wide variation of crown characteristics of individual trees, and in stand development (Curtis and Reukema 1970). The growth of branches, as well as that of needles, reflects such factors as: position within the whorl, subsequent shading by neighboring branches and whorls higher in the crown, available soil nutrients, and climatic conditions (Madgwick 1967).

Needle Size and Persistence

Needle size and persistence also vary significantly with position in the crown, from tree to tree, year of formation, species, and soil fertility (Heiberg and others 1964, Hall 1966, Brix and Ebell 1969, and Smith 1972). For red pine, Madgwick (1967) reported that average weight of individual needles on branches at the base of the crown was 36 to 50 percent of the average weight of individual needles on the topmost whorl. He believed that "future effects of shading on total weights of needles may be postulated as a result of the death of growing points, the increasing ratio of respiring branch tissue to photosynthesizing needle tissue . . ." Most dendrology textbooks indicate that lodgepole pine needles persist 4 to 6 years.

Needle and Branchwood Surface Area

Needle surface area has long been used as a basic parameter for expressing physiological activities such as photosynthesis and transpiration. Surface area estimates obtained indirectly from photoelectric methods (Kramer 1937), projected surface areas (Barker 1968), volume measurements (Ronco 1969, Lopushinsky 1970), and weight measurements (Cable 1958, Mellor and Tregunna 1972) are usually linearly and highly correlated with the direct surface area measurement method used by Kozlowski and Schumacher (1943).

The surface area of branches is also an important dimension of forest stands, with implications for respiration rate, energy exchange, water balance, and nutrient cycling. Surface area of branches has been satisfactorily estimated when "conceived in terms of a basal or first-generation segment which forks into two second-generation segments of smaller diameters, each of which forks into two third-generation segments of still smaller diameters, and so forth" and then computed as conic surfaces (Whittaker and Woodwell 1967).

Crown Weight Prediction

The moisture contents of bark, sapwood, and heartwood of larger branches vary only slightly from the bottom to the top of the crown and through the year (Smith 1971, Markstrom and Hann 1972). In contrast, the water content in small branches and needles varies greatly, both diurnally and seasonally, in response to age and changing environmental factors (Gary 1971). Equations for estimating total crown weight can, however, be developed from green weights of branches and needles by establishing (and periodically updating) a relationship to more easily measured variables such as diameter at the base of live crown, and ratio of live crown length to tree height (Kittredge 1944, Storey and others 1955).

Extrapolation of individual crown weights to a land area basis generally involves (1) counting trees by species and size and/or some form of size stratification, and (2) relating the data from (1) by regression analysis to the more easily measured variables (especially d.b.h.) (Arts and Marks 1971).

Foliage and branchwood weights of individual crowns have also been satisfactorily estimated from branch diameters. First, regression constants are established relating branch diameter to weight; then diameters of all branches are measured, and predicted weights for all branches on the tree are summed (Loomis and others 1966). Difficulty in determining branch diameters in tall trees has usually limited the wide use of this method.

Weight distribution through vertical or horizontal sections of tree crowns is seldom estimated. In the few reported studies for conifers, foliage weight was apparently normally distributed both vertically through the crown and along the length of branches (Tadaki 1966, Stephens 1969).

Branch size stratification and limited sampling of various sized branches within individual crowns provides another good method for obtaining weight-size relations (Baker 1948). Stratification procedures also offer great possibilities for obtaining considerable information about branches themselves—such as frequency distribution of diameters, lengths, annual growth, needle concentrations, and other characteristics.

For lodgepole pine stands in Canada similar to those in the present study, Johnstone (1971) reported needles made up about 5 percent and branches about 6 percent of the total dry weight above 0.3-m- (1-ft) high stumps of an unthinned stand averaging about 16 cm (6.4 inches) d.b.h., 16.8 m (55 ft) tall, and about 2,470 living stems per ha. Average tree weight above the 0.3-m stump was about 78.4 kg (210 lb). In a "dog hair" stand, he reported needles averaged about 8 percent and branches about 16 percent of the aboveground dry weight for trees averaging about 5.6 cm (2.2 inches) d.b.h., 5.8 m (19 ft) tall, and about 12,350 stems per ha. Average tree weight above the 0.3-m stump was 7.3 kg (16 lb). Both stands were 100 years old.

STUDY AREA

The primary study area was in a large expanse of lodgepole pine forest about 3.2 km southeast of Foxpark, in southern Wyoming. The stand was on a gently rolling plateau about 2,743 m above m.s.l. Slopes in the area averaged less than 5 percent. The forest was thinned during the early 1940's to a spacing of about 2.3 m (7.5 ft) and about 2,000 stems per ha. A stagnant "dog hair" portion of the study stand had a stocking of about 25,000 stems per ha. All trees were about 80 years old. In the thinned stand, the height range of 285 study trees was 7.3 to 14.9 m and average height about 10.8 m (35.5 ft). The d.b.h. ranged from 6.6 to 19.8 cm and averaged 13.2 cm (5.2 inches) (fig. 1). Five "dog hair" trees were also sampled. Their average height was 7.5 m (24.5 ft), and average d.b.h. was 5.6 cm (2.2 inches).

Eight additional trees were sampled in a thinned stand, on a steep northeast-facing slope near Pingree Park, Colorado. Elevation, age, and stand structure were about the same as observed above. The area was about 80 km south of the main study area. Average height of the eight study trees was 9.4 m (31 ft) and d.b.h. was 14.7 cm (5.8 inches).

METHODS

Field measurements were made during August 1970, 1971, and 1972. All sample trees were in areas cleared to establish small openings (<0.2 ha) for other studies.

The individual trees used for various parts of the study were subjectively selected as being representative of the existing stand. For convenience of the reader and because of the number of relations studied, some statements regarding methods are also presented in the Results section. All measurements

Figure 1.—Relative size, crown form, and spacing of the study trees near Foxpark, Wyoming.

are reported as metric units. The following gross measurements were recorded for all study trees: d.b.h., total height, height to first dead whorl, and length of all-live crowns. For greater handling and sampling convenience, the all-live crowns were stratified into three height sections, and data were recorded by lower, middle, and upper crown thirds. Whorl heights were recorded for about one-third of the 298 study trees. Because measurements of surface area relations and horizontal weight distribution of needles and branchwood were extremely time consuming, they were limited to one and two trees, respectively.

In 1970, eight trees were intensively dissected and sampled. Measurements on five of the trees include whorl heights, diameter of all branches 5 cm from the bole, length of branch axes (central line of branchwood), ovendry (100°C) weight of branches and needles, vertical rise and horizontal spread of branches, and vertical angle of branches measured 15 cm from the trunk. Measurements on one tree also included total length of individual branches (axes plus length of all side branches); computed surface areas of needles, branches, and bole; and age, persistence, weight, and number of needles. The horizontal distribution of needles and branchwood weight by whorls and branch azimuth were also determined for two of the trees. Horizontal weight distribution was determined after laying all branches within each whorl side by side so as to fit on a 60-cm-wide cutting board. The branches were held in place by 10-cm-wide hinged guides, cut into 10-cm segments, ovendried, and weights obtained for needles and branches (fig. 2).

Figure 2.—Board with hinged 10-cm-wide leaves to guide cutting of branches for horizontal weight distribution of needles and branchwood.

For trees less intensively sampled in 1970, branch lengths and diameters, height of branch whorls, and their green and ovendried weights were determined for one group of 10 trees. Ovendry weights of whorls were also obtained for five trees from an adjacent "dog hair" stand. Ratios of green-to-dry weight were also determined for one group of 27 trees. Total green weight of all branches by crown thirds was also determined for another group of 49 trees (fig. 3). Their dry weights were estimated.

Figure 3.—Method of obtaining green weight of all branches in a crown section.

Eight trees were sampled in 1971 at Pingree Park to obtain ratios of green-to-dry weight and branch diameter-to-length relations in order to make relative comparisons with similar data from trees at Foxpark.

In 1972, the gross measurements for 191 trees removed to enlarge a clearing at Foxpark included d.b.h., height to first dead whorls, height to all-live whorls, and total height. Green and dry weights of selected branches were obtained for 17 trees, and were later used to estimate dry weights of the crown sections and the whole crown.

Surface areas of needles and branches were also estimated for one intensively sampled tree. The fascicles of lodgepole pine usually consist of two needles which form an approximate cylinder when pressed together. Each needle has one flat inner face and one curved outer face. Surface area was thus computed by adapting the method of Kozlowski and Schumacher (1943). The surface area of branchwood was computed from branch segments using the method of Whittaker and Woodwell (1967). All branch segments were assumed to be a frustum of a cone. The basic formula used for determining surface area of branch segments was:

$$S = \pi(r_1 + r_2)\sqrt{\ell^2 + (r_1 - r_2)^2}$$

where S is surface area, r is radius, and ℓ is length. The surface areas of the branch segments were summed to obtain a surface area estimate of individual branches. Bole surface area was determined for increments corresponding to the whorl height using the formula above.

RESULTS AND DISCUSSION

Crown Component Relations

Differences in sites, spacing, environment, and other factors all contribute to wide variation of crown characteristics. Figure 4 illustrates the wide variability of the crown length parameter and the lower and upper limits of the canopy for one intensively sampled group of 10 trees.

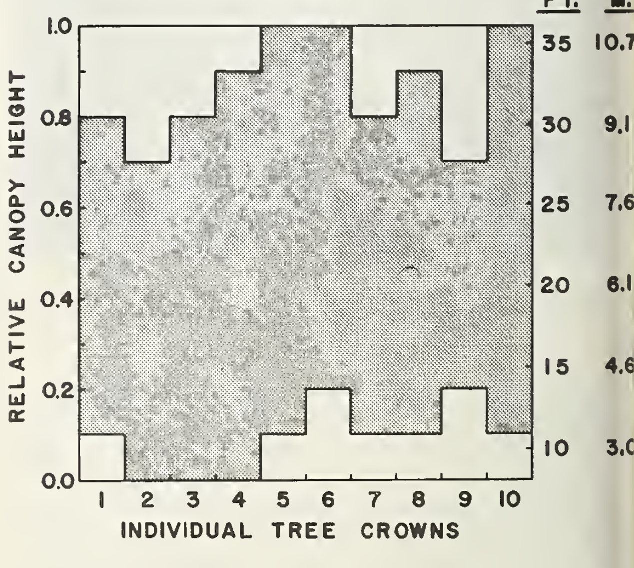


Figure 4.—Representation of a 10-tree canopy and crown length variability.

Crown Length, Height, and Bole Diameter

Average height and standard deviation to the first dead whorls for 285 trees in the thinned stand at Foxpark was 1.7 ± 0.4 m. For the five trees in the adjacent "dog hair" stand, average height to the first dead whorls was 1.4 m. Many of the dead branches were more than 40 years old in both stands. Dimensions and weights of dead branches were not determined.

Height to the live crown and its standard deviation averaged 4.6 ± 0.9 m for the thinned stand, and height averaged 4.5 m for the "dog hair" trees. Crown length and tree height were significantly correlated with d.b.h., but were probably not the consequence of common factors such as quality of light. The sample correlations between live crown length and d.b.h. and tree height and d.b.h. accounted for 36 to 56 percent of the total variation, respectively. In a two-way average relationship between crown length and tree height, the regression equation accounted for 48 percent of the variation. Average crown length and average length-to-height ratio for 285 trees in the thinned stand, five "dog hair" trees, and eight trees at Pingree Park were as follows:

	Crown length	Ratio crown length to tree height
	m	
Foxpark thinned trees	6.2	0.576
Foxpark "dog hair" trees	2.7	.353
Pingree Park trees	6.2	.661

Branching Characteristics

Two types of branches were consistently observed in the annual whorls of all study trees. The main (nodal) or larger branches in the whorls developed from the lateral buds at the apex of each leader. Internodal branches were usually much smaller and developed later in the growing season from buds distributed along the leader (fig. 5). Similar branch development is common to many conifers (Stiell 1969). No attempt was made to measure the two types of whorl branches separately. The number of live whorls for the Foxpark trees averaged 27. Number of branches per annual whorl ranged from one to eight and averaged 4.1. The ratio of foliage to branchwood weight increased from the lower crown section (one-third of crown) upward. An example based on averages for 10 trees was:

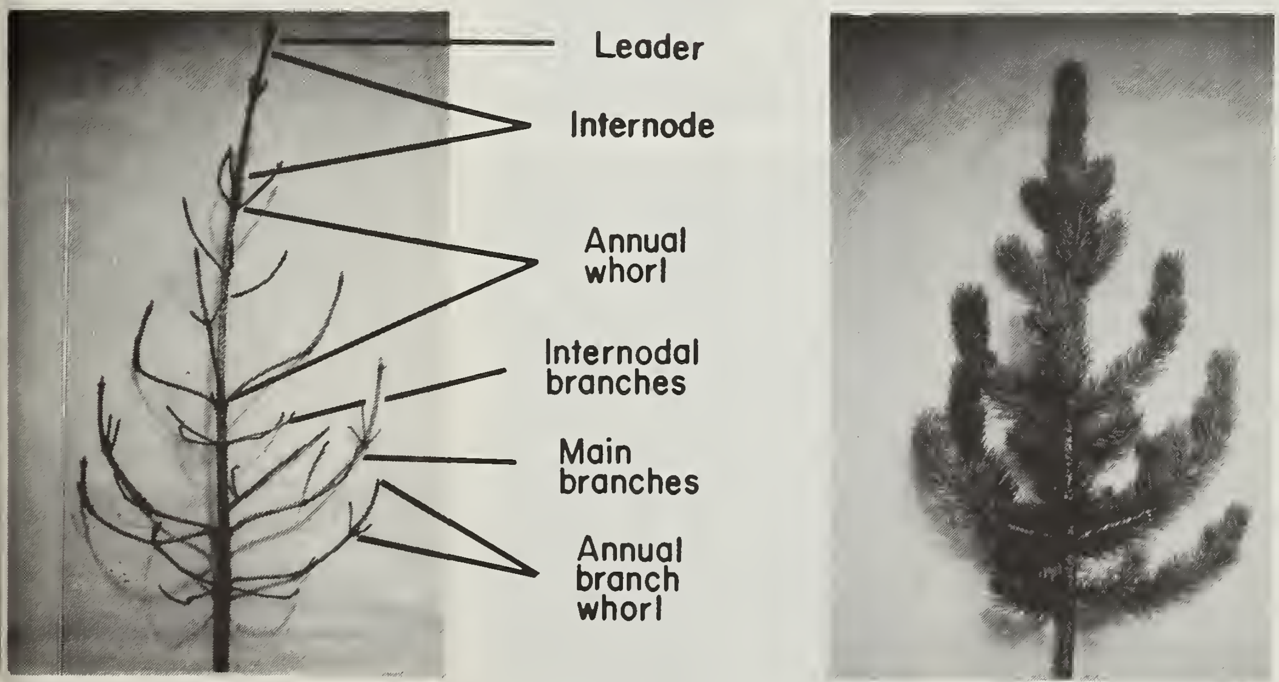


Figure 5.—Position of branch components on a lodgepole pine sapling.

Crown position	Weight ratio, needles to branchwood
Upper	1.6
Middle	1.5
Lower	1.0

The decreasing foliage per whorl or branch appeared highly dependent on light quantity and quality; the light environment apparently accounted for the low needle-to-branch ratio in the lower crowns (Stiell 1962). The more active growth and extension of branches higher in the crown or in the canopy eventually shades out the needles on the lowest whorls, and branches die.

Radial Spread and Vertical Rise of Branches

There was no significant difference among numbers of branches or radial distribution of branches between quadrants within crown sections or between trees. Stiell (1962) also reported no significant departure from radial symmetry of branches of red pines in a plantation.

Branch tips, regardless of age or position in the crown, generally pointed upward (fig. 6). Branches were relatively straight and longer in the lower half of most crowns, and their extension was mainly horizontal. In the upper crowns the branches were shorter, were pointed upward, and had less curvature near the branch tips. Apart from being dependent on

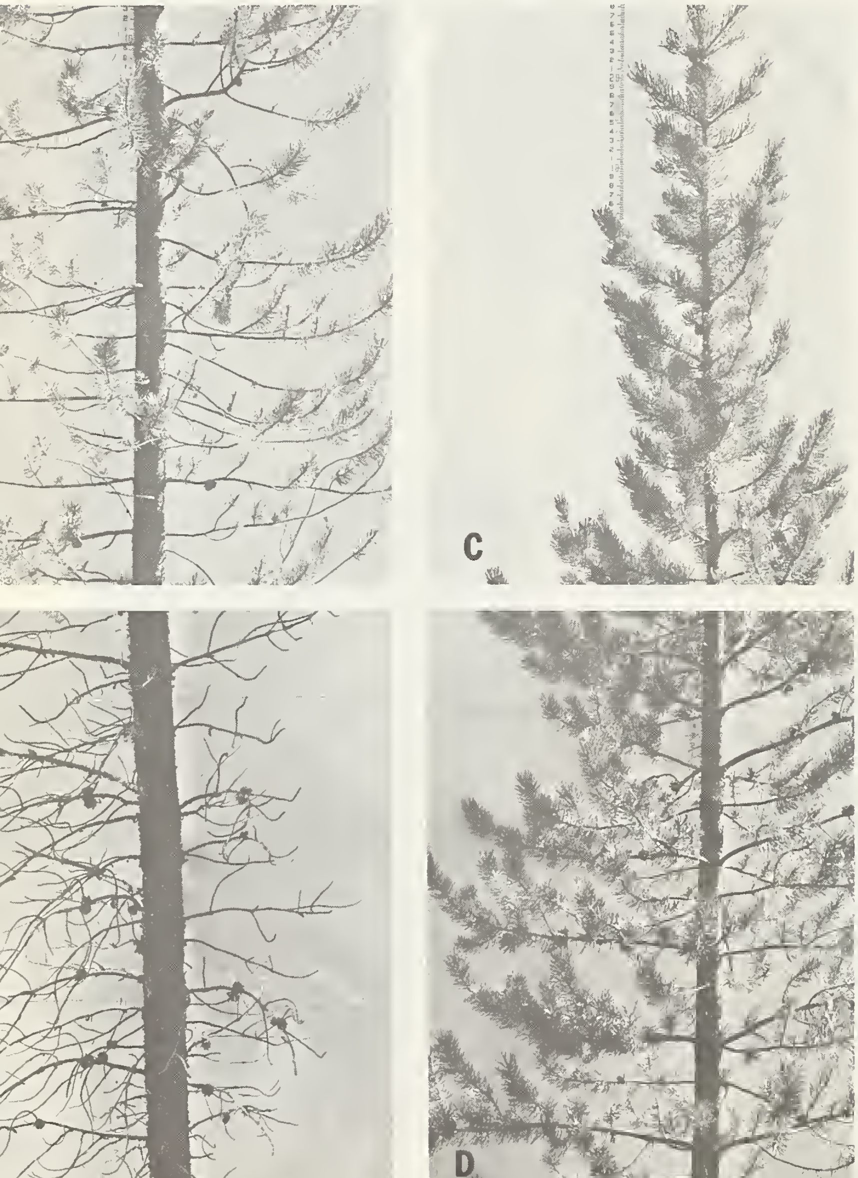


Figure 6.—Horizontal spread and vertical rise of branches on a 10-m lodgepole pine: **A**, lower crown; **B**, dead branches; **C**, upper crown sections; and **D**, middle crown. Length of crown sections about 2 m.

length, the relations between horizontal spread and vertical rise of branches were highly variable and poorly correlated. As was evident from the photographs in figure 6, the angles between the bole and the branches were steeper from the younger and shorter branches in the upper crown sections (fig. 7).

In the lower crown sections, lower branch angles were also apparent for the older and longer branches. The negative angles in figure 7 show that some branches were pointed downward. The angle or general position of older branches in the lower and middle crown sections were apparently succeedingly influenced by the annual weight and length increments of new growth and competition for space and light. Stiell (1962) observed similar patterns for red pine, where new lateral branches were nearly vertical. He noted that increasing needle numbers displaced branches outward, and that succeeding annual growth weighed them down. Over time, weight stress was removed by needle cast, and branches responded by curving upwards and eventually reflexing their tips.

Branch Diameter-to-Length and Age

Branch diameter and length were highly correlated at both Foxpark and Pingree Park. The correlation coefficient between lengths and diameters for 493 normally developed branches on five trees at Foxpark was 0.93, and 0.84 for 89 branches from eight trees at Pingree Park. The equation for the regression of branch length (axis) on branch diameter for the Foxpark trees was:

$$\hat{Y} = -11.30 + 68.76X$$

where $\hat{Y}$ was estimated branch length (axis) in cm and X was branch diameter in cm.

Measuring the total length of branches was time consuming because of the number of secondary, tertiary, and other divisions of the branchlets. To gain some knowledge of the spatial quality of branch length, however, the total length of all branchlets was determined for one tree at Foxpark. Figure 8 shows the regressions between branch diameters and

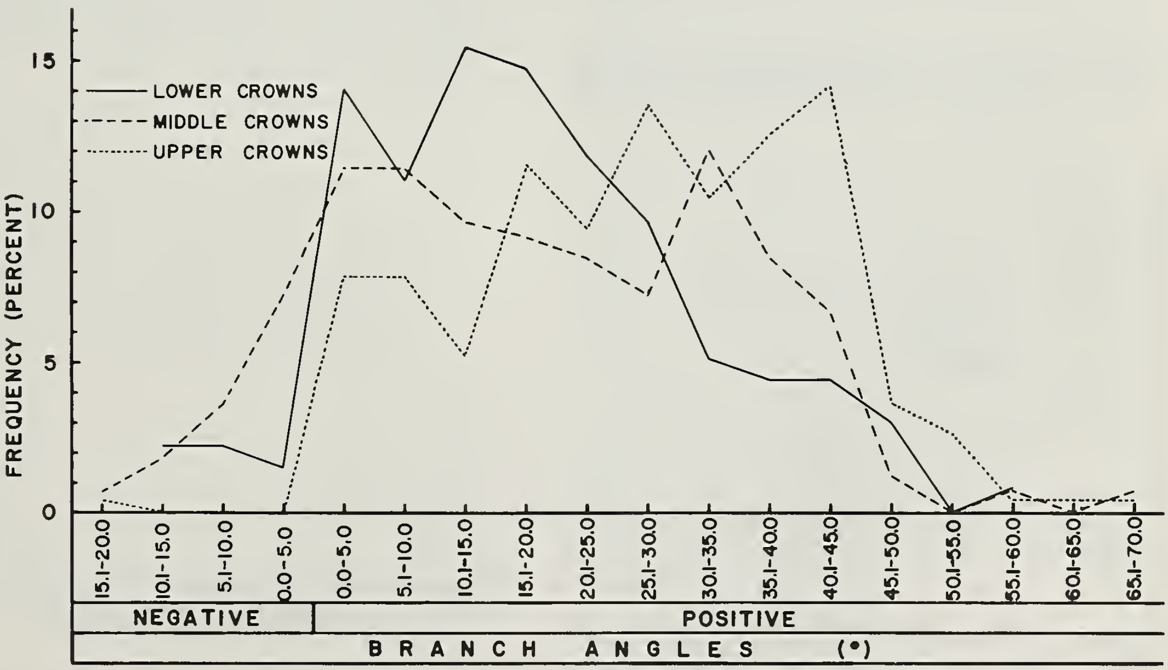


Figure 7.—Frequency distribution of branch angles (measured 15 cm from bole) for 493 branches on 5 trees.

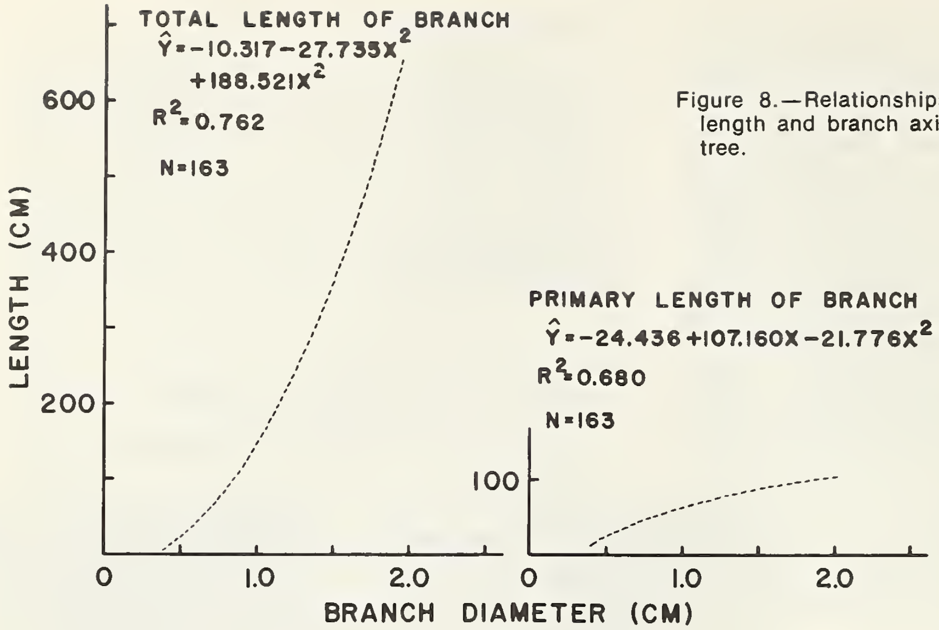


Figure 8.—Relationships between diameter and total length and branch axis length for 163 branches on 1 tree.

primary length (branch axis) of branches, and total length of the same branches. Of the 163 branches on the study tree, 50 were unbranched. The "straight" branches were mainly the smaller internodal and current-year branches; length was usually less than 40 cm. On the average, total length for individual branches was about three times greater than primary branch length, and ranged up to six times greater.

Branch environment apparently had more influence on growth than did age. Branch age (years since development), for all branches on 10 trees at Foxpark, was very poorly correlated with either average or longest branch length, or with branch diameter (r values<0.2). Other general relationships —such as that between primary length and total length of branches (sum of all side branchlets) for 163 branches on one tree—were highly correlated, however (fig. 9). Regression analysis accounted for about 77 percent of the variation, and provided a qualitative measure of total length of branches for all reaches of the crown.

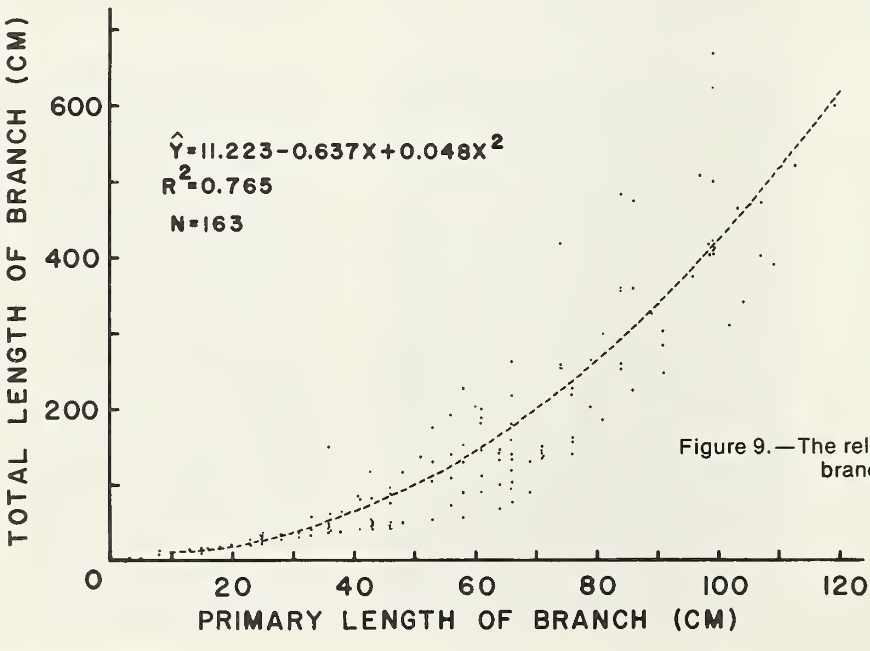


Figure 9.—The relationship of primary and total length of branches for 1 tree at Foxpark.

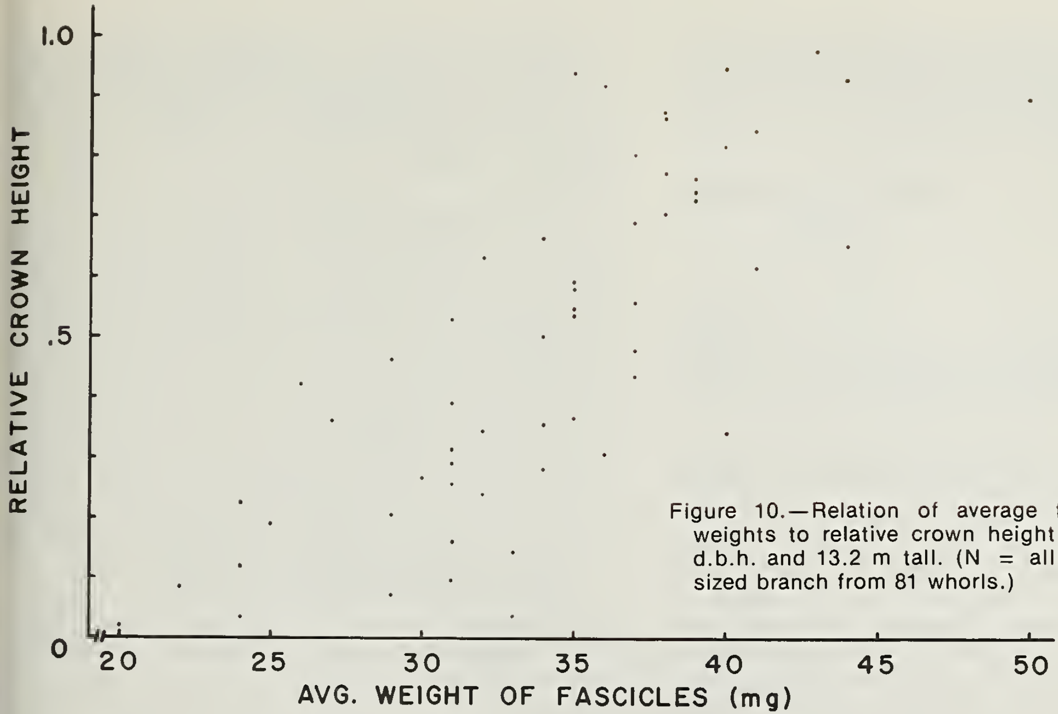


Figure 10.—Relation of average fascicle (2 needles) weights to relative crown height for one tree 13 cm d.b.h. and 13.2 m tall. (N = all needles on median-sized branch from 81 whorls.)

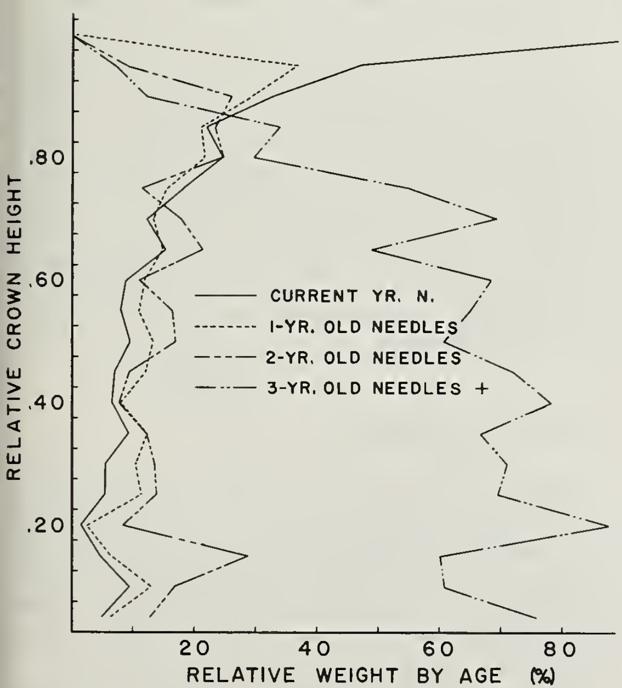


Figure 11.—Age distribution of needle fascicles scaled to percent of ovendry weight and relative crown height. Data for one tree (see fig. 10).

Needle Persistence, Distribution, and Size

Before average values can be applied to needle size and weight, we must learn more about their distribution and variability within the crowns and in the canopy. The reported trend (Madgwick 1967) of increasing weight of fascicles with height in the crown was carefully documented for one tree 13 cm d.b.h. and 13.2 m tall (fig. 10). Analysis of the relative distribution of needle ages for the median-sized branch from annual whorls on the same tree showed that the quantity of needles 3 yr of age and older was greatest in the lower quarter of the crown and least in the upper quarter (fig. 11). The weight percentages of current-year, 1- and 2-yr-old needles were highest in the upper quarter of the crown. The relative weight percentages of the younger needles were about the same through most of the middle and lower sections of the crown, with a tendency for lower weight percentage of current-year needles. The age distribution of fascicles for the whole tree, based on ovendried weights, was:

Needle age	Percent of total weight
Current year	10.7
1 year	12.6
2 years	14.3
3 years and older	62.4

Needle lengths and their standard deviations for a sample of 100 fascicles randomly collected from the composited foliage of 10 trees at Foxpark, and from eight trees at Pingree Park were:

Site	Average needle length (*mm*)
Foxpark	49.6 ± 7.7
Pingree Park	40.9 ± 8.7

The coefficient of variation for length was 16 percent at Foxpark and 21 percent at Pingree Park. Needle lengths were significantly different between the two areas.

Average fascicle weight computed from 100 samples, each consisting of 100 fascicles of all ages and from all sections of one tree at Foxpark, was 0.034 ± 0.009 gram. The coefficient of variation for weight was about 26 percent and indicates the large range of needle sizes. Smith (1972), working with Douglas-fir (*Pseudotsuga menziesii*), reported an average coefficient of variation of about 12 percent for needle length. He also believed the wide variation in weight and persistence within and between trees should be considered in documenting future studies.

Surface Area of Needles, Branches, and Bole

The total surface area for 25 branch and 25 bole fascicles was estimated from five diameter measurements taken at equidistant intervals along each fascicle from base to tip (Kozlowski and Schumacher 1943). The average total surface area was computed to be 304 mm^2 per branch fascicle and 441 mm^2 for fascicles on the upper bole.

The total surface area of needle fascicles was estimated for a sample of 170 branches on one 13-cm-diameter and 13.2-m-tall tree. Total surface area was determined as follows:

number of fascicles (computed from weight)
× average surface area per fascicle

Total surface area of branch fascicles were highly correlated with both branch diameter ($r = 0.95$) and branch weight ($r = 0.95$). The regression equation using branch diameters (<2.5 cm) to estimate total surface area of fascicles was:

$$\hat{Y} = -0.104X + 0.359X^2$$

where $\hat{Y}$ was estimated total area (m^2) of needle fascicles on the branch and X was diameter in cm. With further sampling on additional trees to establish regression constants, the use of other variables such as d.b.h. and crown length would probably be satisfactory for indirectly estimating needle surface area for entire trees.

Surface area of the branchwood was also computed for the 170 branches by the segment method of Whittaker and Woodwell (1967). Cumulative curves were plotted for surface area of needles, branches, and bole section of the crown for the sample tree (fig. 12).

An estimated 144,000 two-needle fascicles were contained within the crown. If all needles on the one tree were placed end to end, they would reach nearly 14.5 km (9 mi)! Assuming the tree was average for the stand, the needle or leaf area index defined as the ratio of total needle surface area of all trees to unit of ground area (m^2/m^2) was about 8. Moir and Francis (1972) reported a leaf area index of 4.3 for a low-productivity lodgepole pine stand in Colorado of about the same age and density as the stand at Foxpark. They also reported a leaf area index of 14 for a stand of moderately high productivity and twice the density but the same age as the Foxpark stand.

The 50 percent level of cumulative bole surface area, because of upward taper, was located in the lower third of the crown. For needles and branches, the 50 percent level of total surface area was reached near midcrown, and suggested a normal distribution of surface area within the crown region. Needle surfaces accounted for about 82 percent of the total calculated surface area.

Weight Relations of Needles and Branches

In destructive tree sampling, it is usually easier to obtain dry weights of leaves and branches than to measure their actual sizes or numbers. The component weight relations, once developed, offer a simple indirect method to obtain considerable information about various hard-to-measure branch parameters. Weight component relations of branches are readily adapted to simulation and other types of studies that seek to evaluate and maximize organic production in response to climate, fertilization, and similar relationships.

Green vs. Dry Weight

Moisture percentage of needles plus branchwood was plotted in relation to relative crown height for 234 whorls on 10 trees at Foxpark (fig. 13). The samples were taken during one day in August 1970. The higher average moisture content in the upper crown section was due to a higher proportion of needles and younger and succulent branchwood.

It was impractical to dry and weigh all branches on all trees for dry weight determination. However, good estimates of branch dry weights were obtained after sampling a few trees because of the generally excellent correlation between green and ovendry

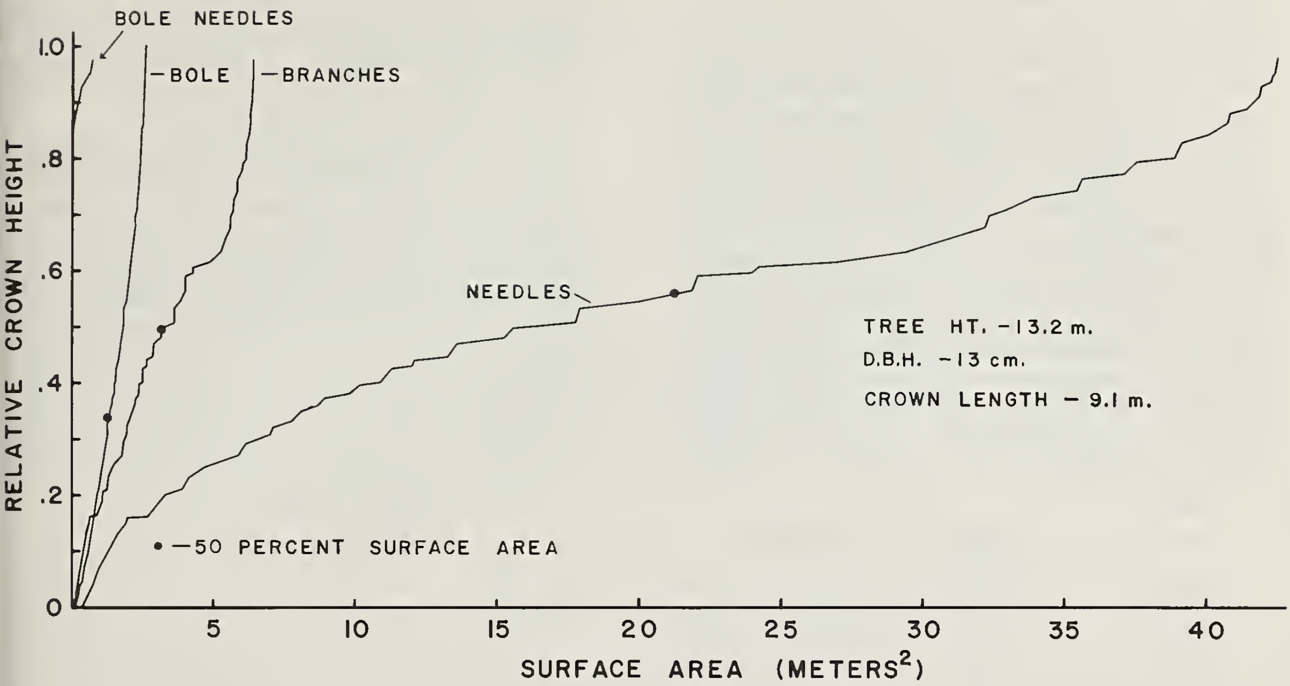
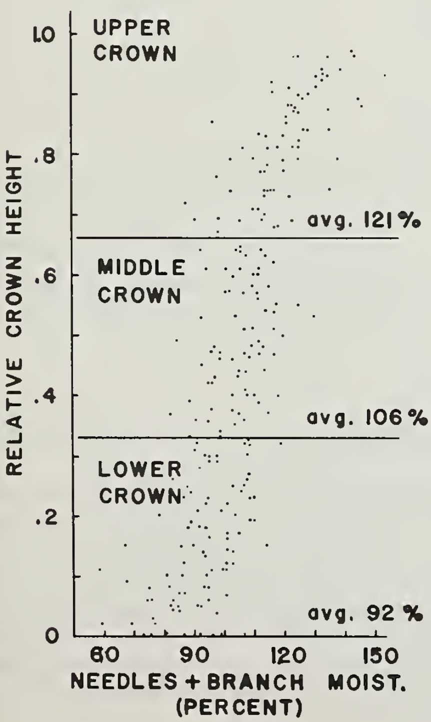


Figure 12.—Cumulative curves of estimated total surface area of needles, branches, and bole sections for one tree.



weight. Equations for estimating dry weight were developed from the green and ovendried weights of all branches in the 234 whorls mentioned above and from 89 branches taken from eight trees at Pingree Park in August 1971:

Foxpark	$\hat{Y} = 2.18 + 0.49X$
Pingree Park	$\hat{Y} = -0.24 + 0.52X$

where $\hat{Y}$ was estimated dry weight of needles plus branches, and X was green weight of needles plus branches. Weights were in grams. Both regressions accounted for more than 99 percent of the sample variation, and their slopes were not significantly different. The high correlations indicated the regressions were generally applicable for all branches from both the lower and upper crown sections, and varying moisture content had little apparent effect on dry weight estimation. The regression constants for dry weight estimation should be recomputed occasionally because of seasonal changes in moisture contents.

Figure 13.—Needle-plus-branch moisture in relation to relative crown height for 234 whorls on 10 trees at Foxpark. Percent moisture determined as:

$$\frac{\text{green weight - ovendry weight}}{\text{ovendry weight}} \times 100.$$

Needle vs. Branch Weight

The time and labor required to separate needles from green branchwood is usually prohibitive. However, in the present study, reliable estimates of dry needle weights were obtained from regression analyses that utilized branch weights (needles plus branchwood). Regression equations were developed after ovendrying and weighing sample branches. Branchwood was separated from needles and discarded. Needles were easily stripped from branches after a few hours of drying at 100°C. The needles were again ovendried and weighed to determine the respective quantities of needles. The regression equations for branches up to 500 grams dry weight and from crown sections of five intensively sampled trees were as follows:

Crown position	Branches	Equation
	No.	
Lower	136	$\hat{Y} = 1.42 + 0.48X$
Middle	167	$\hat{Y} = 2.20 + 0.57X$
Upper	190	$\hat{Y} = 0.66 + 0.58X$

where $\hat{Y}$ was estimated dry weight of needles, and X was dry weight of needles plus branchwood in grams. Each of the above equations accounted for more than 95 percent of the total variation. The regression coefficient for the lower crown section indicated fewer needles per unit of branchwood, but was not significantly different from regression coefficients for the middle and upper crown sections.

The general applicability of the above equations for estimating dry weight of needles was tested by subjectively selecting one sample branch from each of 53 trees. A wide array of sizes was sampled; 15 of the branches (ovendried needles plus branchwood) weighed between 500 and 800 grams. The constants for the equation were similar to the ones shown above, and the regression accounted for 94 percent of the variation:

$$\hat{Y} = 0.87 + 0.48X$$

where $\hat{Y}$ was estimated dry weight of needles, and X was dry weight of needles plus branchwood.

Diameter vs. Length of Branches

Nondestructive estimates of branch weight are often required for growth and fuel-accumulation studies. In young forest stands, branch diameters and length of branch axes can be obtained relatively easily and repeated over time to provide an indirect method for estimating weight or weight changes of branches. Branch diameters are more easily obtained and the relation of diameter to weight of needles plus branchwood for 89 sample branches from Pingree Park is shown in figure 14. Branch diameter was related to weight for five trees at Foxpark in about the same manner as shown in figure 14.

There was little apparent change in diameter-weight relations for branches from various heights in the crowns. Although the data in figure 14 may not be generally applicable for trees taller than about 15 m for insect-damaged trees or for trees on all sites, they do indicate that individual weights of live branches can be quantified by nondestructive methods.

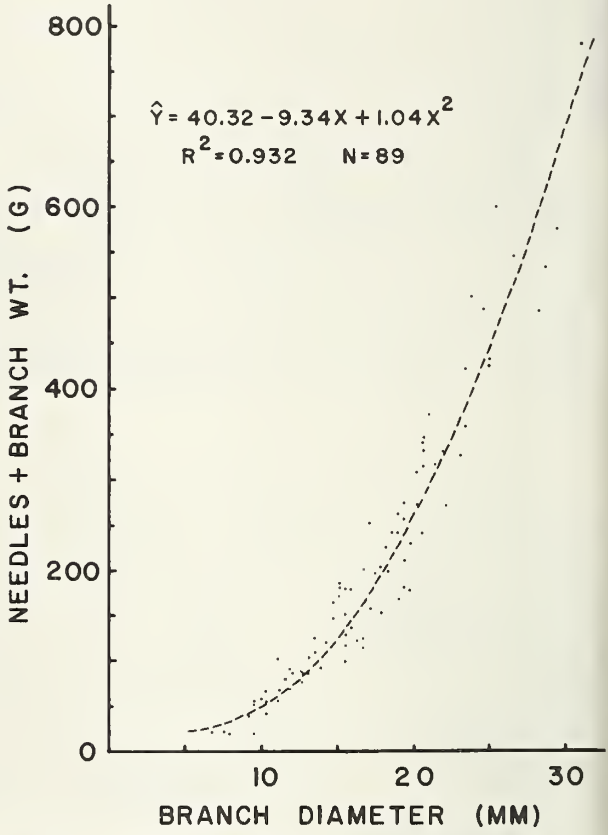


Figure 14.—The relation of branch diameters to dry weight of needles plus branchwood.

Distribution of Needles and Branch Weight

General observations of lodgepole pine and other conifers reveal both horizontal and vertical differences in the space distribution of needles and branches. Near the top of the crowns, the relative amounts of needles and branchwood are small due to the young age of the branches. In the midcrown region, the branches are larger, have more side branchlets, and support more needles. Below the midcrown region, needles and branch quantities are decreased by mortality, apparently because of decreasing light quality.

Weight Distribution Along Branches

The branches on two trees were studied to obtain better knowledge of the horizontal weight distribution of needles and branchwood. One tree had branches ranging up to 1.4 m in length; maximum lengths on the second tree were about 1.1 m. The sample unit consisted of all branches in an annual whorl. The average percent weight distribution of needles and branchwood was plotted as a function of 0.1-m increments of the branches (figs. 15, 16).

The average weight distribution of needles along the branches within all crown sections of both trees clearly indicated the expected region of low needle density near the bole. Needle concentration was maximum near the average midlength of the branches and in the zone of maximum branching. The arrow pointers in figure 15 show that 50 percent of the needle weight was usually reached near the midlength of the branches, which suggests a symmetrical "bell shape" or normal distribution pattern. In the upper crown sections of both trees, the region of highest needle concentration was nearer to the bole than in the middle and lower crown regions. The maximum weight percentage of the needles remained near the midlength of the shorter and younger branches, however, which had undergone little needle cast and secondary branching.

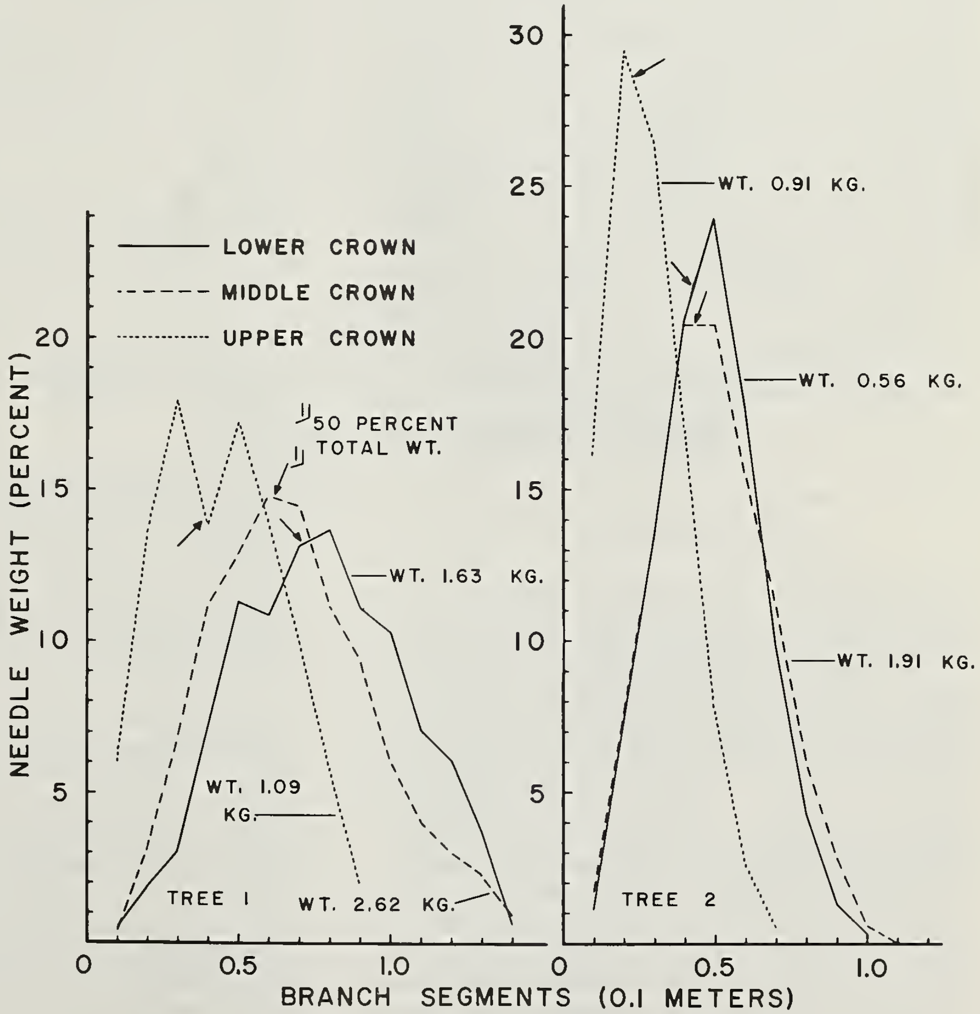


Figure 15.—Average horizontal weight distribution of needles along branches in three crown sections of two trees.

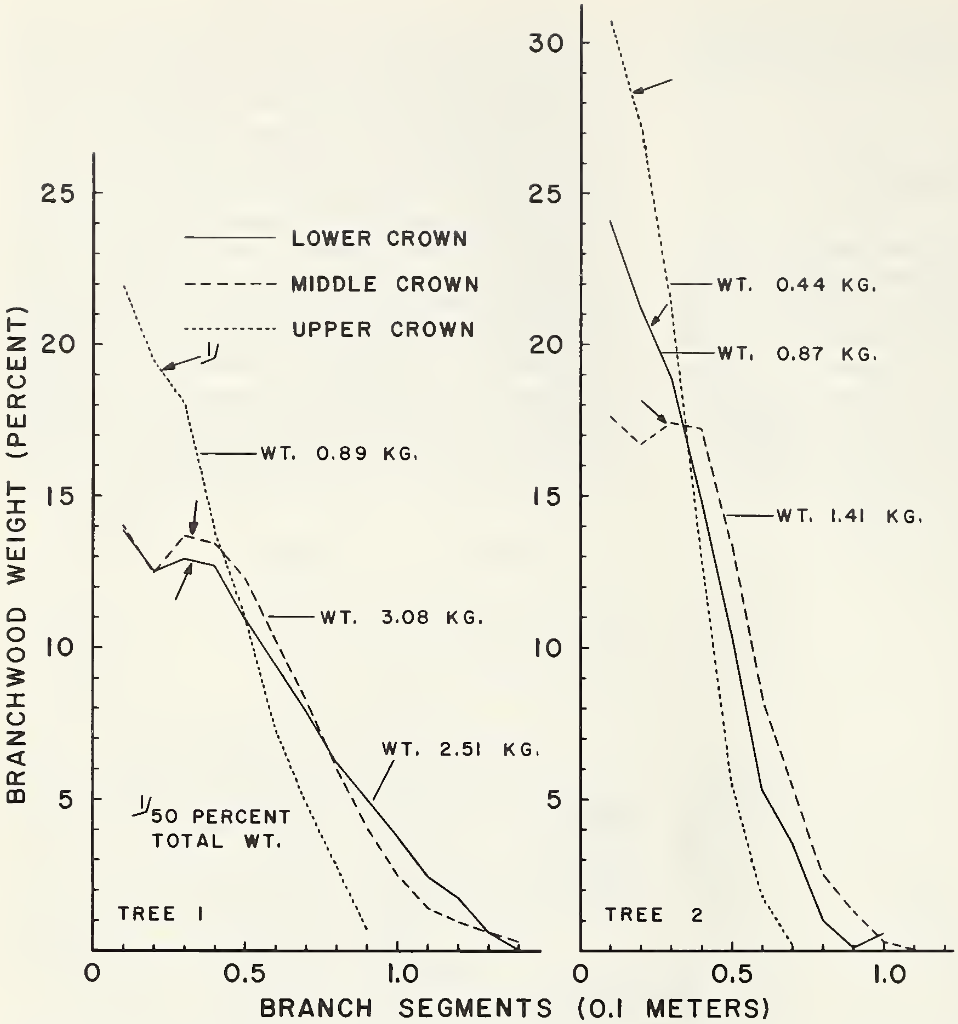


Figure 16.—Average horizontal weight distribution of branchwood in three crown sections of two trees.

The patterns of needle weight concentrations were about the same in both trees. However, the volume distribution of needles along and around the branches could not be quantitatively inferred from the weight distribution data. The distribution of needles on individual branches appears highly dependent upon variables such as light quality, position within the crown, competition for space from branches above and from neighboring trees, age and growth vigor of branches, and branching forms.

In contrast to needle weight distribution, average weights of the 0.1-m branchwood segments were highest near the bole and decreased steadily to the branch tips (fig. 16). The occurrence of secondary branching in the lower and middle crown regions was evidenced by the slight weight increase in the lower and middle crown sections of tree No. 1 and the middle crown section of tree No. 2. On the average, 50 percent or more of the branchwood weight in all crown sections was contained within the first 30 percent of the branch length.

Vertical Weight Distribution in the Crown

The variability of weight distribution associated with the lower, middle, and upper crown sections of 100 trees in the even-aged stand at Foxpark is shown in figure 17. The height range of the trees, which was relatively narrow, had little apparent effect on weight percentage distribution within the individual crowns. The coefficient of variation ($S/\bar{X}$) for crown weight (needles plus branchwood) percentages was highest in the upper crown sections, apparently the result of varying tree heights and branch sizes, and relative exposure and shading within the canopy. The

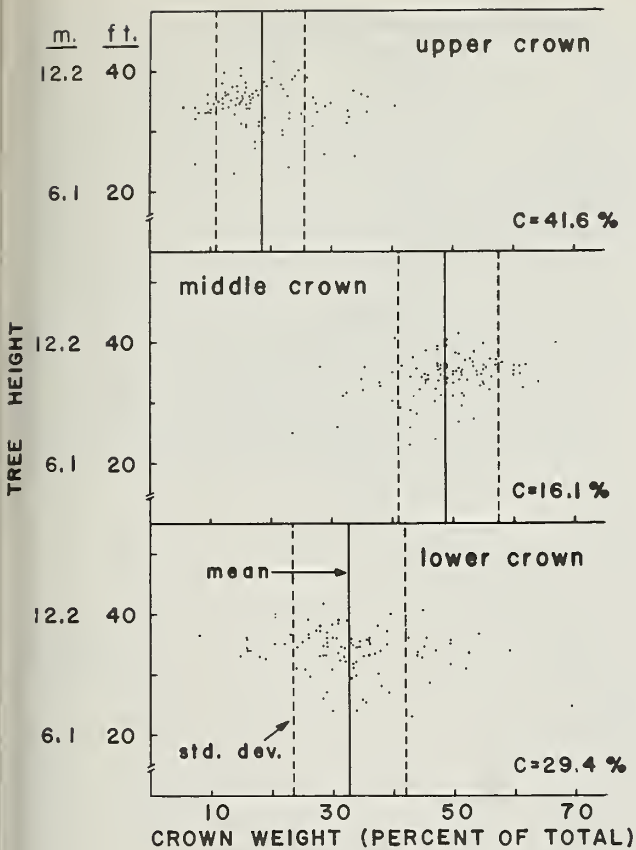


Figure 17.—Weight percentages of needles plus branches in the lower, middle, and upper crown sections for 100 trees.

average vertical distribution of needles plus branch weights within the crown sections followed a normal distribution curve. The general pattern was gradually increasing branch weight from the lower to midcrown region, and then more rapid decrease of weight from midcrown to the upper crown.

Since the stand canopy is the whole collection of crowns of various widths and lengths, it is usually of greater interest than the crowns of individual trees. The weight distribution within the canopy formed by a sample of 10 trees at Foxpark was computed by two empirical methods. The distribution of needle and branch weights was also compared to normal distribution curves. The ranges of heights and crown lengths for the 10 trees were previously illustrated in figure 4.

In the first method, live crown length of each tree was divided into 10 equal parts. Length of the crown segments varied from tree to tree. Weights of the branch whorls for each tree were then mathematically apportioned to the 10 crown height sections. The needle plus branch weights for similarly positioned crown height sections for each of the 10 trees were then summed. Average percentages of total weight were computed for each of the 10 crown height sections and plotted as to height in the average crown or canopy (fig. 18A).

In the second method, the canopy zone was assumed to start at the lowest all-live whorl and stop at the apex of the tallest tree. As previously seen in figure 4, the maximum lower and upper height limits of the canopy were on different trees. The canopy depth, based on the 10 crowns, was then divided into 10 equal height sections. Branch weights of the 10 trees were then mathematically apportioned according to relative height in the normalized canopy. The apportioned weights within each of the 10 sections of the canopy were summed, and percentages of total canopy weight computed (fig. 18B).

Both empirical methods of determining crown weight distribution agreed well with the observed values for crown weight percentages and the expected or theoretical frequencies of a normal distribution. Chi-square values for both methods showed probabilities greater than 30 chances out of 100; no real departure from normality was indicated. For the first method of average values (fig. 18A), the apparent canopy depth was compressed about 1.2 m on both the bottom and top. Averaging of branch weights for both short and long crowns indicated greater skew of weight distribution to the lower part of the canopy. The relative average canopy height at the point of theoretical maximum value for weight distribution was also about 60 cm lower than that observed for the lower-upper height range canopy method. The values in figure 18B apparently provided a better characterization of the canopy weight distribution, since the whole depth range (lower and upper height values) of the canopy was used.

Crown Weight Estimates

Crown weights are generally estimated by regression techniques that utilize measurements of bole diameters or branch diameters (Kittredge 1944, Loomis and others 1966, Madgwick 1971). Another good but seldom used method is to stratify branches into classes such as crown position, age, and size, and then select the median branch for weight estimation (Baker 1948).

Table 1 summarizes selected equations for the relation of crown weights (Y) to d.b.h. and other commonly measured stem and crown variables (X) for 117 trees at Foxpark. The equations with d.b.h. or diameter at start of live crown accounted for more sampling variation than the combined variables of tree height and crown length. As seen in table 1, including tree height (eq. 6) and crown length (eq. 5) with untransformed d.b.h. did not increase percent of variation accounted for. In Canada, Kiil (1971)

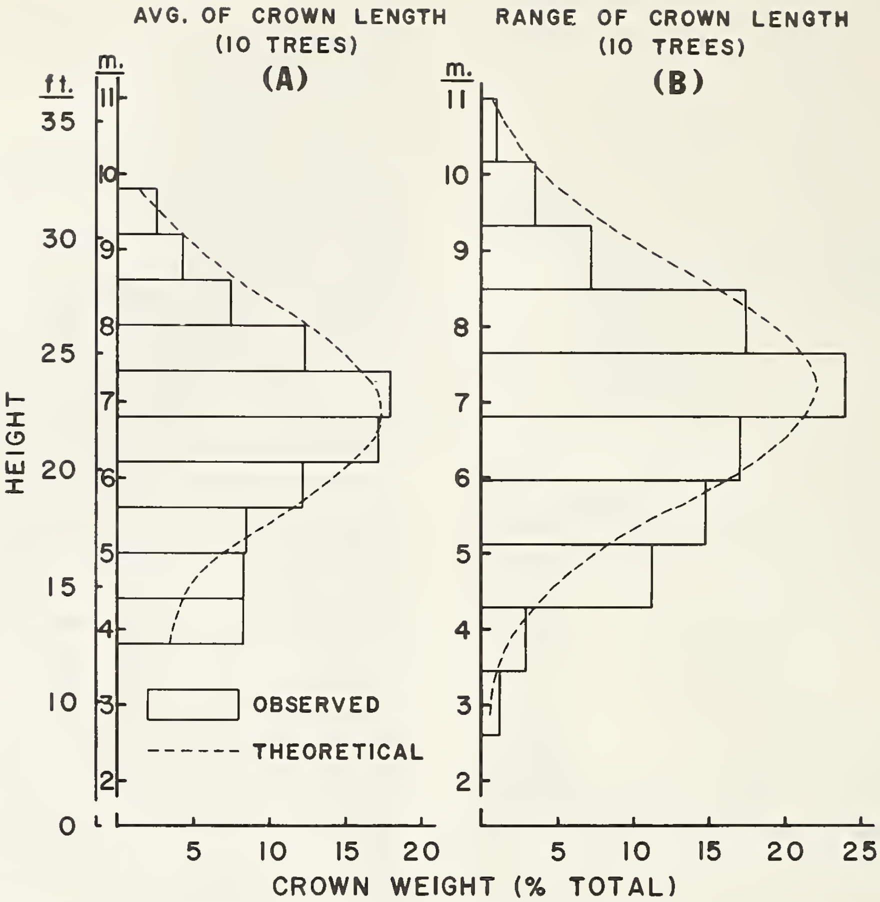


Figure 18.—Vertical weight distribution of needles plus branchwood for 10 height sections as computed for (A) average crown height, and (B) canopy averaged over maximum lower-upper height range of crowns.

Table 1.--Relation of total needles plus branchwood weight (Y), in kilograms, to selected items and crown variables (X) for 117 trees

Variables		Regression equations	Variation accounted for (R^2)
			Percent
D.b.h., X_1	(1)	$Y = -10.594 + 1.528X_1$	78
Diameter, base live crown, X_2	(2)	$Y = -8.727 + 1.656X_2$	78
Crown length, X_3	(3)	$Y = -3.809 + 2.070X_3$	33
Tree height, X_4	(4)	$Y = -17.672 + 2.538X_4$	44
D.b.h. × crown length, $X_1 \cdot X_3$	(5)	$Y = -2.442 + 0.145\ (X_1 \cdot X_3)$	68
D.b.h. × tree height, $X_1 \cdot X_4$	(6)	$Y = -5.204 + 0.105\ (X_1 \cdot X_4)$	74
D.b.h.^{2} × tree height, $X_1^2 \cdot X_4$	(7)	$Y = -0.833 + 0.005\ (X_1^2 \cdot X_4)$	80
D.b.h. × d.b.h.^{2}, X_1^3	(8)	$Y = +0.605 + 0.004\ (X_1^3)$	83
D.b.h. + d.b.h.^{2}, $X_1 + X_1^2$	(9)	$Y = -3.300 + 0.154X_1 + 0.061X_1^2$	82
Log d.b.h., X_1	(10)	$Y = +0.0047X_1^{2.916}$	91

established regression constants, and found that crown weights of lodgepole pine could be estimated from aerial photographs with the same degree of accuracy as tree heights and crown widths.

The allometric function (d.b.h.^{2} × tree height, or D^2H, eq. 7, table 1) only slightly improved the regression estimate over the single-variable d.b.h. equation. The formula D^2H, generally proportional to stem volume, is used worldwide for the estimation of biomass (Crow 1971).

Of the several variables used in table 1, the curvilinear function d.b.h.^{3} (eq. 8) accounted for 83 percent of sample variation, was slightly superior to the allometric function (eq. 7), and was more convenient to use because tree height was not required. All the single-variable equations with diameter as an independent variable were satisfactory for estimating total needle and branch weight of a crown. The logarithmic (base 10) transformation of d.b.h. (X) and needle plus branch weight (Y) best described the functional relationship, and accounted for 91 percent of the sampling variation (eq. 10).

The regression of dry weight of needles plus branches on d.b.h. for 117 trees was plotted with 95 percent confidence limits for individual and mean tree weights (fig. 19). A larger range of tree diameters would perhaps narrow the confidence bands and decrease the variance for crown weight estimates. The figure also demonstrates high correlation between diameter and weight, and the reliability of d.b.h. for predicting crown weights.

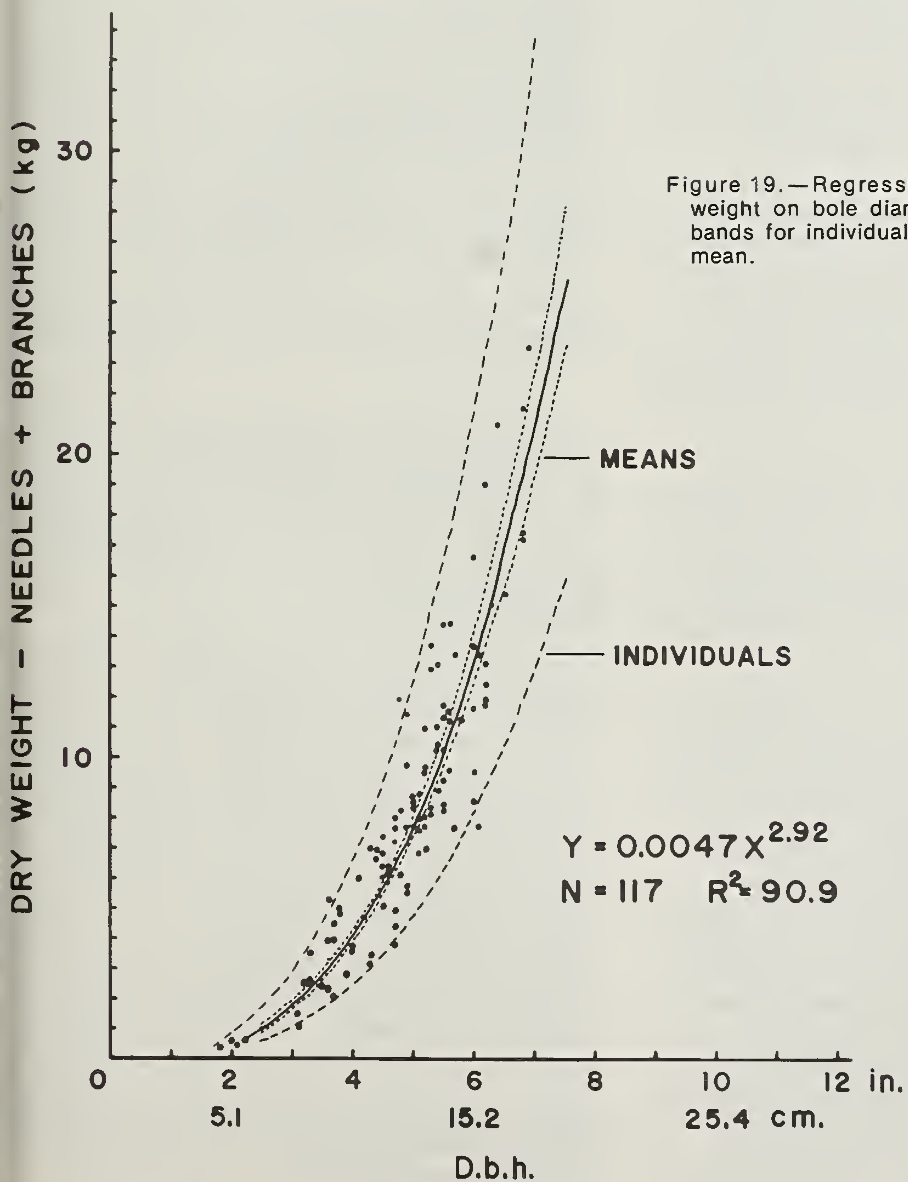


Figure 19.—Regression of needle-plus-branchwood weight on bole diameter, with 95 percent confidence bands for individual observations and the population mean.

SUMMARY AND CONCLUSIONS

The horizontal and vertical distribution of needles and branches, their quantities, and their interrelations must be better understood if we are to manage our forests for maximum production of wood fiber. This study reports various relationships between needles, branch components, and boles for 298 trees, and methods of estimating biomass from these relationships.

Height to live crown averaged about 4.6 m for all trees. The crown length to height ratio was 0.58 at Foxpark, 0.66 at Pingree Park, and about 0.35 in the "dog hair" stand. Crown length was weakly correlated with d.b.h. and tree height; it was apparently more dependent upon spacing and light.

Individual branches per annual whorl ranged from 1 to 8, and averaged about 4. Average length or axis for 493 live branches on five trees at Foxpark was 46 cm, and maximum length was about 1.5 m. Total length of individual branches averaged about three times greater than their axes.

Analysis of variance indicated no significant departure from radial symmetry in branch numbers or among directional quadrants within lower, middle, and upper crown sections for two study trees. Branch angles were steeper in the upper crowns. Older branches in the lower and middle crown sections had lower angles and were succeedingly influenced by annual weight increments, and branch tips were reflexed upward.

There was an apparent trend of decreasing weight of individual fascicles from the top to the bottom of the crown. The current year, 1-, and 2-year-old needle age classes each accounted for 10 to 14 percent of the total weight of needles. Needles 3 years and older accounted for about 62 percent of total needle weight.

For one 13-cm-diameter, 13.2-m-tall tree, about 50 percent of the cumulative branch surface area and about 42 percent of the needle surface area was in the lower half of the crown. Total surface area was about 42.5 m^2 for needles, 6.4 m^2 for crown branches, and 2.6 m^2 for the crown bole section.

Weights of needles and branches were very useful for obtaining information on component relations within the crowns of felled trees. Weighing was practical because the moisture content of branches did not vary significantly from the bottom to the top of the crowns, and thus, there was excellent correlation between green and ovendry weights. The regression of green weight on dry weight usually accounted for 95 percent of the sampling variation. When weights of needles and branches were estimated indirectly from branch diameters, regression equations showed that about 90 percent of the sampling variation was accounted for.

Except in the upper crown sections, there were relatively few needles near the bole. Maximum needle concentrations were near the midlength of the branches and/or in the zone of maximum branching. Generally, needle weight was normally distributed along the length of branches in the lower and middle crown sections. In the upper crown sections, higher needle concentrations near the bole were due mainly to younger branches which had undergone little needle cast or secondary branching.

On the average, more than 50 percent of the weight of branchwood was contained in the first 30 percent of branch length for all crown sections.

Crown weight (needles plus branchwood) for a sample of 100 trees gradually increased from the lower to midcrown region, and then decreased through the upper crown region. The vertical weight distribution of needles and branches through the canopy of 10 intensively studied trees was symmetrical and followed a normal distribution curve. Once the constants for characteristic normal distribution curves are established for lodgepole pine, it should be possible to characterize the canopy over large areas by various indirect methods. One indirect method relates the mass of needles and branches to reduction in windspeed ratios for various heights in a canopy (Cionco 1972).

Weights of entire crowns were estimated from the regression of weight on several combinations of easily measured variables. Equations with d.b.h. accounted for more sampling variation than both tree height and crown length. Logarithmic transformations of d.b.h. and crown weight best described the functional relationship, and accounted for 90 percent of the sampling variation.

The major problems in measuring needles and branchwood result from the great diversity within and between trees. Thus "the most accurate sampling methods would be to sample a large number of trees covering the size range present in the stand and determine regression equations relating dry weight . . . to certain linear dimensions" (Ovington and Madgwick 1959). Not all available data were used in quantifying relationships in the present study, nor were all possible combinations of the variables reported. The high correlations found between the various needle and branch variables strongly indicate that many indirect and nondestructive techniques can be used to quantify changes in both short- and long-term structure and productivity for one tree or for a whole stand. Nondestructive dimensioning systems and techniques will require calibration against some easily measured tree variable for the range of expected tree sizes.

LITERATURE CITED

Arts, H. W., and P. L. Marks.
1971. A summary table of biomass and net annual primary production in forest ecosystems of the world. Forest biomass studies. Working group on forest biomass studies. Sect. 25, Growth and Yield. 15th Int. Union For. Res. Organ. Congr. [Gainesville, Fla., Mar. 1971]. Univ. Maine Press, p. 3-32.

Baker, Frederick S.
1948. A short method of determining leaf area and volume growth in pine trees. Hilgardia 18(8):335-356.

Barker, H.
1968. Methods of measuring leaf surface area of some conifers. Canada Dep. For. Rural Develop., For. Branch, Dep. Pub. 1219, 6 p.

Brady, N. D., ed.
1967. Agriculture and the quality of our environment. Am. Assoc. Advance. Soc., AAAS Pub. 85, 460 p., Wash., D.C.

Brix, H., and L. F. Ebell.
1969. Effects of nitrogen fertilization on growth, leaf area, and photosynthesis rate in Douglas-fir. For. Sci. 15:189-196.

Cable, Dwight R.
1958. Estimating surface area of ponderosa pine foliage in central Arizona. For. Sci. 4:45-49.

Cionco, R. M.
1972. A wind-profile index for canopy flow. Boundary-Layer Meteorol. 3:225-263.

Cook, David I., and David F. van Haverbeke.
1971. Trees and shrubs for noise abatement. Neb. Agric. Exp. Stn. Res. Bull. 246, 77 p.

Crow, Thomas R.
1971. Estimation of biomass in an even-aged stand —and "mean tree" techniques. Forest Biomass Studies. Working Group on Forest Biomass Studies. Sect. 25, Growth and Yield. 15th Int. Union For. Res. Organ. Congr. [Gainesville, Fla., Mar. 1971]. Univ. Maine Press, p. 35-48.

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

Deeming, John E., James W. Lancaster, Michael A. Fosberg, R. William Furman, and Mark J. Schroeder.
1974. The national fire danger rating system. USDA For. Serv. Res. Pap. RM-84, rev. 53 p. Rocky Mt. For. and Range Exp. Stn., Fort Collins, Colo.

Gary, Howard L.
1971. Seasonal and diurnal changes in moisture contents and water deficits of Engelmann spruce needles. Bot. Gaz. 132:327-332.

Hall, Gavin S.
1966. Age distribution of needles in red pine crowns. For. Sci. 12:369-371.

Heiberg, S. O., H. A. I. Madgwick, and A. L. Leaf.
1964. Some long-time effects of fertilization on red pine plantations. For. Sci. 10:17-23.

Johnstone, W. D.
1971. Total standing crop and tree component distributions in three stands of 100-year-old lodgepole pine. Forest Biomass Studies. Working Group on Forest Biomass Studies. Sect. 25, Growth and Yield. 15th Int. Union For. Res. Organ. Congr. [Gainesville, Fla., Mar. 1971]. Univ. Maine Press, p. 81-89.

Keays, J. L.
1971. Complete-tree utilization, an analysis of the literature. Part II: Foliage. For. Prod. Lab., Can. For. Serv., Dep. Fish. and For. Info. Rep. VP-X-70, Vancouver, B.C. 94 p.

Kiil, A. D.
1971. Estimating weights of tree components of lodgepole pine from large-scale aerial photographs. Can. J. For. Res. 1:193-194.

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

Kozlowski, Theodore T., and Francis X. Schumacher.
1943. Estimation of stomated foliar surface of pines. Plant Physiol. 18:122-127.

Kramer, P. J.
1937. An improved photo-electric apparatus for measuring leaf areas. Am. J. Bot. 24:375-376.

Loomis, Robert M., Robert E. Phares, and John S. Crosby.
1966. Estimating foliage and branchwood quantities in shortleaf pine. For. Sci. 12:30-39.

Lopushinsky, W.
1970. Relationship of needle surface area to needle volume in ponderosa pine and lodgepole pine. USDA For. Serv. Res. Note PNW-126, 4 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Madgwick, H. A. I.
1967. Some factors affecting the vertical distribution of foliage in pine canopies **In** Symp. Primary Productivity and Mineral Cycling in Natural Ecosystems. AAAS. 13th Annu. Meet. [New York City, N.Y., Dec. 1967]. Univ. Maine Press. p. 223-245.

Madgwick, H. A. I.
1971. The accuracy and precision of estimates of the dry matter in stems, branches, and foliage in an old-field *Pinus virginiana* stand. Forest Biomass Studies. Working Group on Forest Biomass Studies. Sect. 25, Growth and Yield. 15th Int. Union For. Res. Organ. Congr. [Gainesville, Fla., Mar. 1971]. Univ. Maine Press, p. 105-109.

Markstrom, Donald C., and Robert A. Hann.
1972. Seasonal variation in wood permeability and stem moisture content of three Rocky Mountain softwoods. USDA For. Serv. Res. Note RM-212, 7 p. Rocky Mt. For. and Range Exp. Stn., Fort Collins, Colo.

Mellor, G. E., and E. G. Tregunna.
1972. The relationship between leaf area and dry weight of three conifer species grown on three sources of nitrogen. Can. J. For. Res. 2:377-379.

Moir, W. H., and R. Francis.
1972. Foliage biomass and surface area in three *Pinus contorta* plots in Colorado. For. Sci. 18:41-45.

Ovington, J. D., and H. A. I. Madgwick.
1959. Distribution of organic matter and plant nutrients in a plantation of Scots pine. For. Sci. 5:344-355.

Ronco, Frank.
1969. Volumeter for estimating quantity of conifer foliage. USDA For. Serv. Res. Note RM-133, 2 p. Rocky Mt. For. and Range Exp. Stn., Fort Collins, Colo.

Smith, J. Harry G.
1971. Bases for sampling and simulation in studies of tree and stand weights. Forest Biomass Studies. Working Group on Forest Biomass Studies. Sect. 25, Growth and Yield. 15th Int. Union For. Res. Organ. Congr. [Gainesville, Fla., Mar. 1971]. Univ. Maine Press, p. 139-149.

Smith, J. Harry G.
1972. Persistence, size, and weight of needles on Douglas-fir and western hemlock branches. Can. J. For. Res. 2:173-178.

Stephens, G. R.
1969. Productivity of red pine, 1. Foliage distribution in tree crown and stand canopy. Agric. Meteorol. 6:275-282.

Stiell, W. M.
1962. Crown structure in plantation red pine. Can. Dep. For., For. Res. Branch Tech. Note 122, 36 p.

Stiell, W. M.
1969. Crown development in white spruce plantations. Can. Dep. Fish and For., For. Branch Pub. 1249, 12 p.

Storey, Theodore G., W. L. Fons, and F. M. Sauer.
1955. Crown characteristics of several coniferous tree species. U.S. Dep. Agric. For. Serv., Div. For. Fire Res. Interim Tech. Rep. AFSWP-416, 93 p. Washington, D.C.

Tadaki, Yoshiya.
1966. Some discussions on the leaf biomass of forest stands and trees. Bull. Gov. For. Exp. Stn. 184:135-161. Tokyo, Japan.

Whittaker, R. H., and G. M. Woodwell.
1967. Surface area relations of woody plants and forest conditions. Am. J. Bot. 54:931-939.

Gary, Howard L.
1976. Crown structure and distribution of biomass in a lodgepole pine stand. USDA For. Serv. Res. Pap. RM-165, 20 p. Rocky Mt. For. and Range Exp. Stn., Fort Collins, Colo.

Gross dimensions and quantities of needles and branches are presented for 298 trees. Weight, diameter, length, and height relations were usually highly correlated. Needles were normally distributed along the length of branches as well as vertically through the canopy. Needle and branchwood weights for entire crowns were best estimated by the logarithmic transformation of diameters at breast height.
Keywords: *Pinus contorta,* biomass, canopy, foliage, overstory productivity, transpiration.

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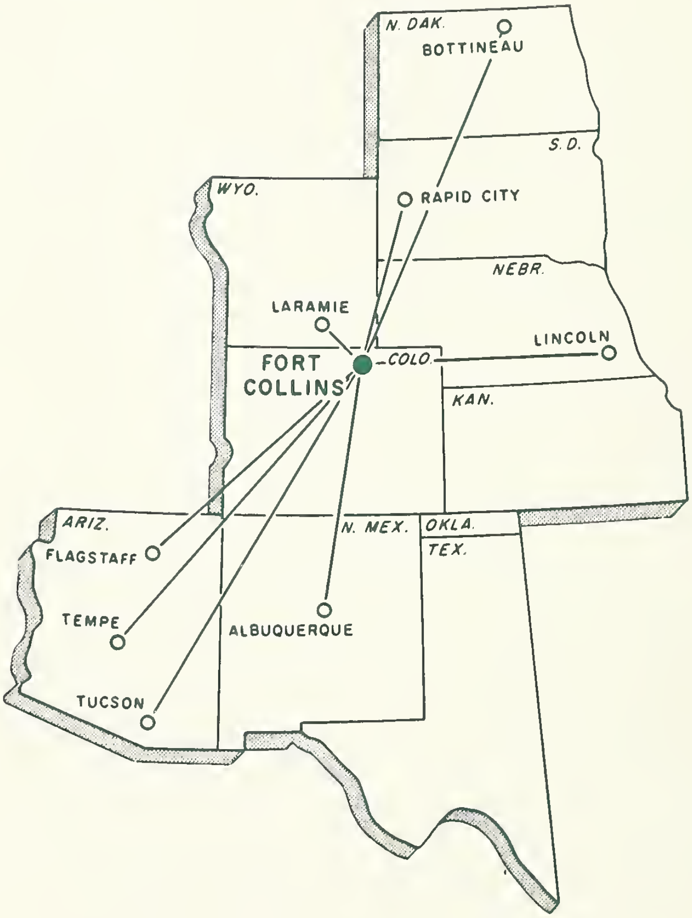
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