CROWN STRUCTURE IN PLANTATION RED PINE

by

W. M. Stiell

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INTRODUCTION

The study reported here deals with the structure and development of the crowns of red pine (*Pinus resinosa* Ait.) and the distribution of foliage within the crown, and seeks a means of estimating foliar content from direct measurement of the crown's external dimensions.

While the importance of the tree's crown to development of the stem has long been acknowledged (*vide* Bennett, 1960), the nature of the relationship is not well understood, and detailed knowledge of the crown itself is limited. Most investigations relating crown size to stem size or growth treat the crown as a homogeneous solid, and little attention has been given to its internal morphology, or to its modification with age except for general changes in weight or gross dimensions. Ladefoged (1946) described the vertical distribution of dry weight of needles within the crowns of young Norway spruce (*Picea abies* (L.) Karst.), and Morris (1951) presented similar data for the current year's foliage, for flowering and non-flowering balsam fir (*Abies balsamea* (L.) Mill.). Ovington and Madgwick (1959) dissected, measured, and weighed the components of young Scots pine (*Pinus sylvestris* L.), and recorded whorl height, branch length and weight, and leaf weight by whorls for different girth classes in an even-aged stand. Lehtpere (1957) weighed and measured the branches removed from the lower crowns in a pruning experiment with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Duff and Nolan (1953, 1957, 1958) and Forward and Nolan (1961a, 1961b) have made detailed studies of ring pattern and wood increment in the stems and branches of red pine, but foliage distribution and its changes with age do not seem to have been investigated for this species.

Studies relating wood production to quantity of foliage require good estimates of crown size. But apart from the cumbersome procedure of weighing or counting the needles, or obtaining their volume by displacement, few accurate methods of estimating foliar content from direct measurement have been devised. Buchanan (1936) correlated number of needles with crown length (L) and maximum width (W), in young western white pine (*Pinus monticola* Dougl.) having crowns extending almost to the ground and the widest part at the base, as follows: thousands of needles $= 1.36LW^{1.16}$. This relationship was not investigated for closed stands. Sometimes the amount of foliage has been considered directly proportional to the volume or surface area of some solid of the same length and width as the crown, but the validity of such assumptions has not been checked. Methods of estimating crown weight from stem diameter (Kittredge, 1944; Cable, 1958), while valuable for other purposes, are obviously not appropriate where the actual crown-stem relationship is being investigated.

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This study attempts to clarify some of these points for red pine. Since modification of the crown is the first consequence of stand treatment, a better understanding of the crown's makeup and a ready index of its effective mass should lead to more intelligent silviculture.

Terms of Reference

Crown Length

Red pine crowns consist of a series of whorls of live branches, and often, below these, one or more whorls in which some branches are dead. The part containing wholly live whorls only is known as the "upper crown length" (Empire Forestry Association, 1953). This is the portion that was measured for length and width in the following study, and on which estimates of crown shape and size were based. This was necessary to obtain objective measurements, and to provide the basis for a symmetrical representation of the crown. However, since all foliage contributes to the crown's output, the weight of the needles in the partial whorls was included in the estimates of total crown weight.

Branch Size

Each stem whorl is composed of several large branches of comparable size, and may contain one or more very small branches as well. The needles on these dwarf branches were included in the total weight of foliage, but for determining the periphery of the crown the dwarf branches were ignored.

Bundle Sheaths

Except in the current year's foliage, stripping the needles usually detaches the bundle sheaths as well. Since the sheaths do not contain chlorophyll, including their weight would over-estimate the amount of effective foliage. A sample of 187 grams of green foliage was found to contain 3.74 per cent by weight of bundle sheaths, and therefore all sheaths were removed before weighing.

Phenology

Seasonal changes occurring in the crown are shoot and needle growth, and needle fall. From observations made on lateral branches for two growing seasons, and from data reported by Kienholz (1934) and Friesner (1943), the timing of these phenomena seems to be as follows: (a) shoot growth on branches may begin about the middle of May and is complete by the end of August; (b) the needles on the oldest foliage-bearing internodes remain green, and presumably productive, at least until the end of August, before turning colour and falling; (c) the needles of the next oldest internode show no colour change during the year; (d) the current year's needles probably start developing not later than the middle of May, and could increase in length, doubtless with changing productivity, at least until the middle of September. They make no further growth in subsequent years. To avoid the period when crown changes were taking place, then, no measurements were made between May 15 and September 15.

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METHODS

The study was carried out at the Petawawa Forest Experiment Station, near Pembroke, Ontario. The approach was to examine the crowns of red pine of a variety of ages, growing under similar conditions. There were two aspects of the study: (a) obtaining measurements of those few gross dimensions of the crown that can feasibly be taken from the ground without felling the tree; and (b) dissecting the crown to determine the distribution of foliage within it.

The red pine plantations chosen for study were:—

(a) Four stands, aged 8, 20, 25, and 33 years from planting, all growing at a 7×7 foot spacing, and on similar sites.

(b) Two stands aged 25 and 34 years, growing at 5×5 feet, and also on similar sites.

The soils were somewhat dry medium and fine sands of windblown or lake-laid origin. All sites were old fields.

In each stand two trees in the upper diameter classes were chosen. These were undamaged, growing at the required spacing ±0.5 foot, and without adjacent gaps. The following procedure was carried out for each sample tree:—

(1) The distance to the nearest 4 competitors was measured with a tape.

(2) True north was marked on the stem with lumber crayon.

(3) Breast height was marked and d.b.h. measured.

(4) The tree was felled.

(5) True north was marked at each live whorl.

(6) Total height and the height to every whorl was measured to the nearest tenth of a foot.

(7) The stem containing the live crown was cut into approximately 6-foot lengths, each cut being made exactly at the base of a whorl.

(8) The crown sections were transported to the workshop.

Each section, in turn, was set up vertically on a board graduated in 360 degrees, with the north mark of the section at 0 degrees. The section was supported by a wooden arm (Figure 1).

(1) The following measurements were made in each stem whorl[2]:—

(a) The length of each branch along its curve from its junction with the stem to its tip.

(b) The vertical projection from the whorl base and the horizontal projection from the stem centre, of the tip of each branch.

(c) The diameter of each branch at its point of attachment to the stem.

(d) The azimuth bearing of each branch.

(2) For each stem internode:—

(a) The mid-point d.o.b. was measured.

(b) The needles, if any, were stripped and bagged.

(3) For one representative main branch in each stem whorl:—

(a) The horizontal and vertical projections of each primary whorl were measured.

(b) The needles from each primary whorl were stripped and bagged separately. (If very few needles were found on a primary whorl,

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[2] Figure 1a indicates the crown parts and their designations.

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Figure 1. Measurement of tree section in workshop. Needles have been stripped from top whorl. Note supporting arm and azimuth board.
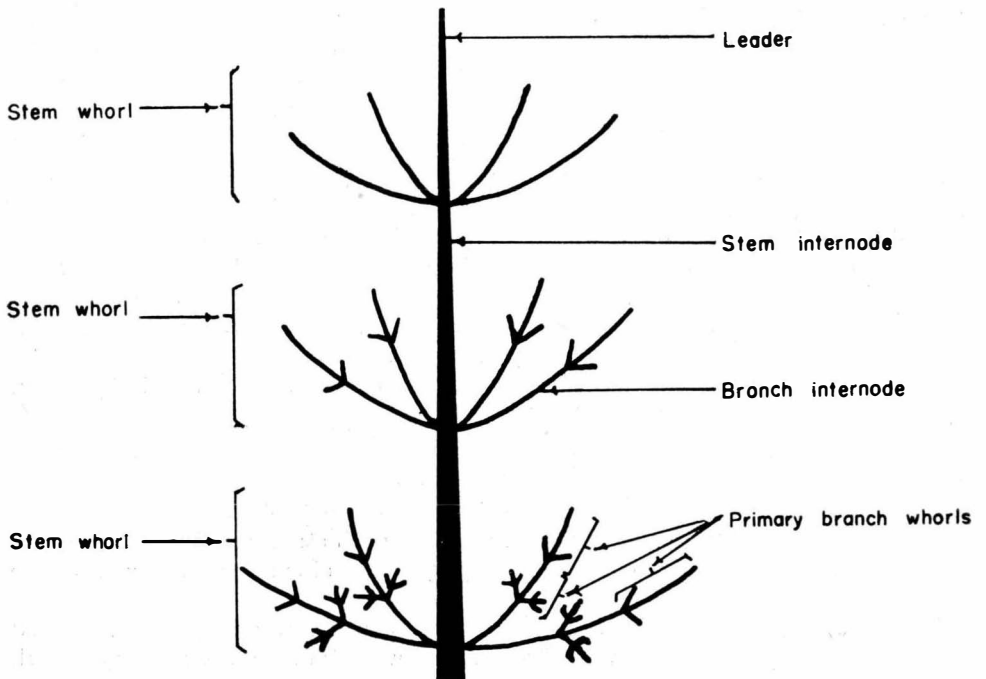

Figure 1a. Crown parts.

needles of the same year's whorl from each other branch were collected also and added to them, and the bag so marked),

(4) Needles from all dwarf branches in each stem whorl were stripped and placed in one bag.

The bags of foliage from each tree were placed at one time in a Moore cone-drying kiln, and their moisture content reduced to 5.8 per cent, as determined by oven-drying samples. Bags and contents were weighed on a direct reading balance, and a bag weight of 28 grams was deducted from each value. Oven-dry weights of the foliage were then calculated.

The dimensions of an "average" main branch in each stem whorl were computed by applying the ratio:

$$\frac{\text{mean horizontal (or vertical) projection of all branch tips}}{\text{horizontal (or vertical) projection of sample branch tip}}$$

to the primary whorl projections measured on the sample branch. The resulting co-ordinates were plotted to scale in relation to the stem, and a two-dimensional representation of the whole live crown so produced.

Average main branch length was determined, and foliage weights of the sample branch adjusted in direct proportion to its length. Total weight for a stem whorl was found by multiplying average weight by the number of main branches and then adding the weights obtained for the dwarf branches.

The location of the foliage within the crown was plotted by weight classes on the diagram (Figures 3-8). On the left side of the diagram is shown main branch shape, and the location of the primary branch whorls. On the right, the corresponding foliage weights of the whorls are indicated; these are not values for single branches, but are crown totals for all primary whorls of the same age and stem whorl. No boundaries are shown between adjacent primary whorls of the same weight class.

The shape of the crown diagram was assumed to be variously a rectangle, triangle, parabola, etc., and the equivalent areas were determined using the length and maximum width of the diagram as the basis for calculation. These area values were plotted against the actual diagram area. The figures best approximating the diagram were then considered as their circular, 3-dimensional equivalents (e.g. a triangle would be taken as a cone), and regressions of total foliage weight were calculated on their areas or volumes.

Two supplementary sets of observations were obtained as well. One tree was stripped entirely and all the needles were weighed according both to branch whorl and to year produced; all the branches of this tree were dried and weighed also. On another tree 200-needle random samples were selected from various locations and their lengths measured to the nearest tenth of an inch.

RESULTS

The basic data for the sample trees are summarized in Table 1. Relative heights and crown sizes and shapes are shown in Figure 2. At the 7-foot spacing, sizes ranged from small trees with almost full-length crowns, which had not quite closed laterally, up to 60-foot trees with the base of their crowns 40 feet above ground. The younger age groups were not available at the 5-foot spacing.

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Table 1—Summary of tree data

Stand No.	Tree No.	Years Planted	Average Spacing (Feet)	D.b.h. (Ins.)	Total Ht. (Feet)	Ht. to Crown (Feet)	Crown Length (Feet)	Ht. to Widest Part of Crown (Feet)	Diameter at Widest Part (Feet)	No. Wholly Live Whorls (and Partially Live)	Oven Dry Weight Foliage (Grams)
1	13	8	7.2	2.45	10.5	0.7	9.8	2.0	6.8	8(+1)	3,527
1	14	8	7.0	1.89	9.2	0.2	9.0	2.4	6.8	9(+0)	3,664
2	10	20	7.0	5.89	28.6	10.5	18.1	17.8	9.6	9(+1)	9,390
2	17	20	7.1	6.40	26.0	5.9	20.1	16.6	9.4	12(+0)	9,675
3	11	25	7.1	7.40	45.8	29.1	16.7	33.7	10.0	9(+2)	7,804
3	12	25	6.8	6.48	45.8	28.2	17.6	33.9	9.6	9(+1)	7,704
4	15	33	7.4	8.35	58.7	39.4	19.3	44.6	11.0	12(+1)	10,461
4	16	33	7.4	8.47	55.7	34.0	21.7	40.4	11.0	14(+1)	12,582
5	20	25	5.0	4.53	38.5	22.8	15.7	29.7	6.4	10(+1)	2,829
5	21	25	5.0	4.33	38.2	24.8	13.4	29.6	6.0	8(+1)	3,250
6	18	34	5.4	6.45	54.2	38.5	15.7	45.5	6.2	12(+1)	4,584
6	19	34	4.9	6.38	51.6	36.6	15.0	42.8	7.8	12(+2)	4,845
					SUPPLEMENTARY SAMPLE						
2	23	20	7.0	5.40	30.1	13.9	16.2			8(+1)	
2	24	20	7.0	6.60	29.6	12.6	17.0			9(+2)	

("Crown" refers to wholly live whorls only)
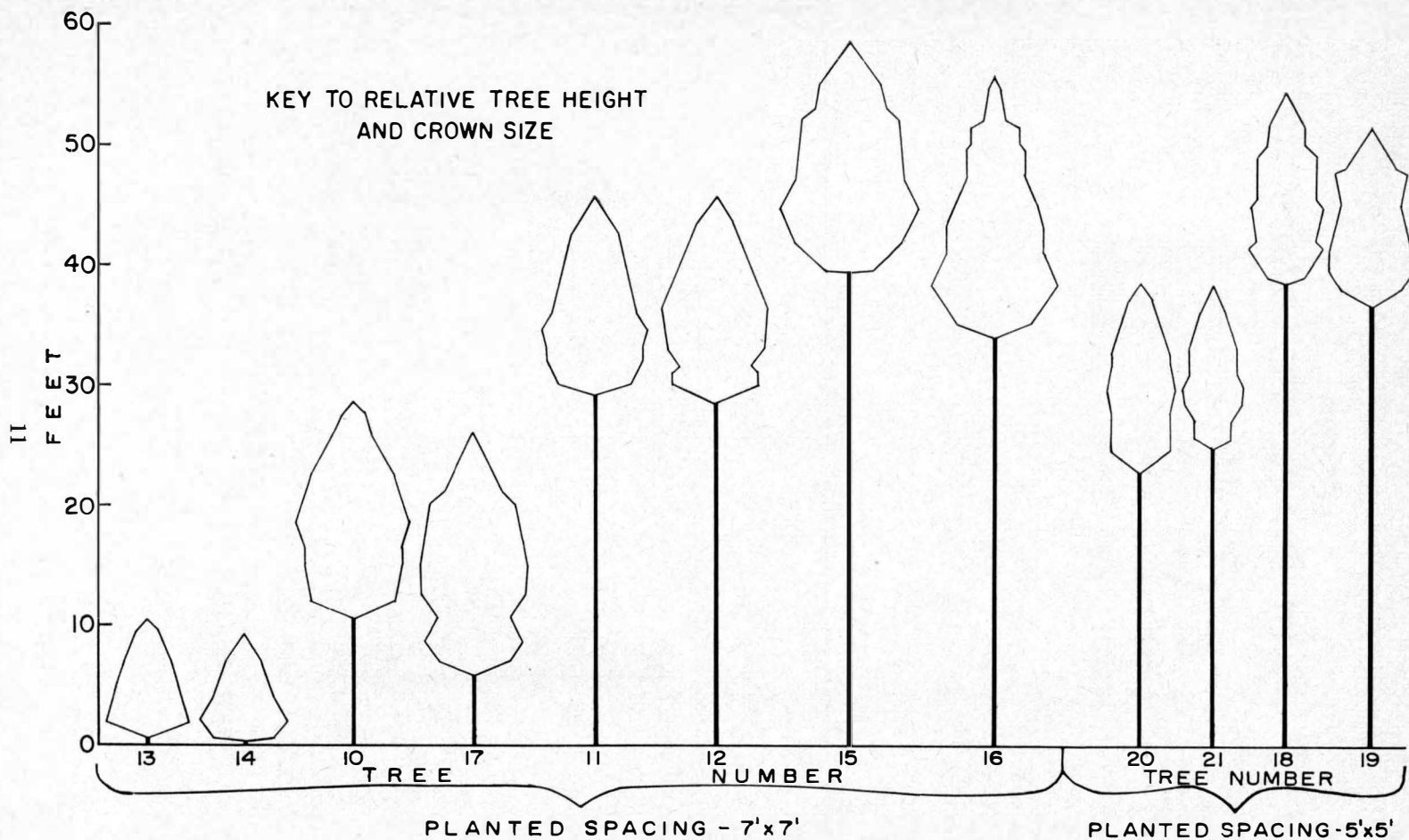
KEY TO RELATIVE TREE HEIGHT
AND CROWN SIZE

Figure 2.

LEGEND
OVEN–DRY FOLIAGE WEIGHTS

I–50 Gms........
51–200 Gms......
201–500 Gms......
501–1100 Gms......

15 FEET

—10—

—5—

4 3 2 1 0 1 2 3 4   4 3 2 1 0 1 2 3 4

FEET

TREE No. 13   TREE No. 14

Figure 3.

40 FEET

— 35 —

— 30 —

— 25 —

— 20 —

— 15 —

— 10 —

— 5 —

5 4 3 2 1 0 1 2 3 4 5   5 4 3 2 1 0 1 2 3 4 5

FEET

TREE No. 10   TREE No. 17

Figure 4.

13

50 FEET

—45—

—40—

—35—

—30—

—25—

—10—

—5—

0

FEET

5 4 3 2 1 0 1 2 3 4 5   5 4 3 2 1 0 1 2 3 4 5

TREE No. 11   TREE No. 12

Figure 5.

14

60 FEET

—55—

—50—

-45—

—40—

—35—

—30—

—5—

6 5 4 3 2 1 0 1 2 3 4 5 6   5 4 3 2 1 0 1 2 3 4 5
FEET

TREE No.15   TREE No.16

Figure 6.

15

40 FEET

—35—
—30—
—25—
—20—
—15—
—10—
—5—
0

4 3 2 1 0 1 2 3 4   4 3 2 1 0 1 2 3 4
FEET

TREE No. 20   TREE No. 21

Figure 7.

16

55 FEET

—50—

—45—

—40—

—35—

—15—

—10—

—5—

0

4 3 2 1 0 1 2 3 4   4 3 2 1 0 1 2 3 4

FEET

TREE No. 18   TREE No. 19

Figure 8.

17
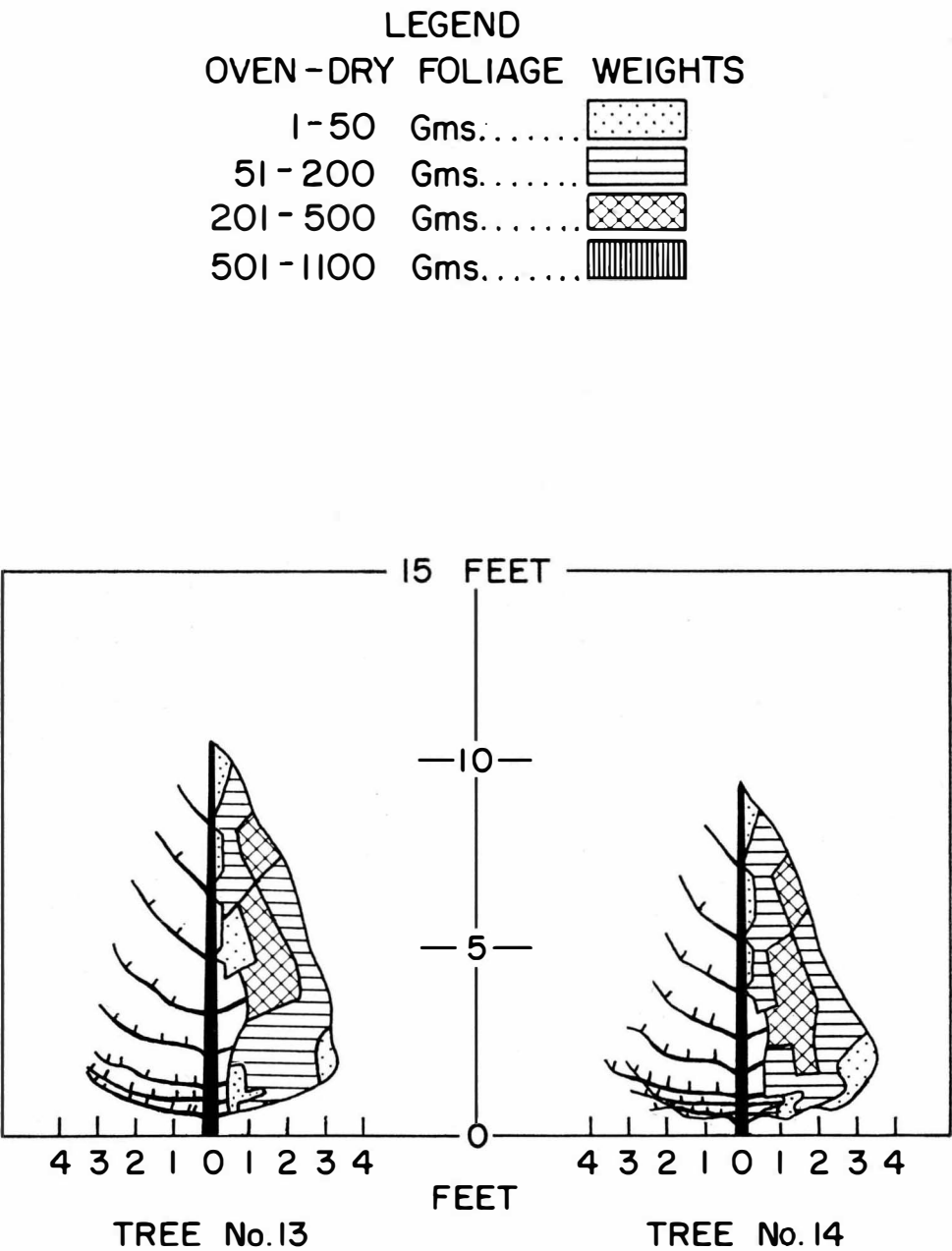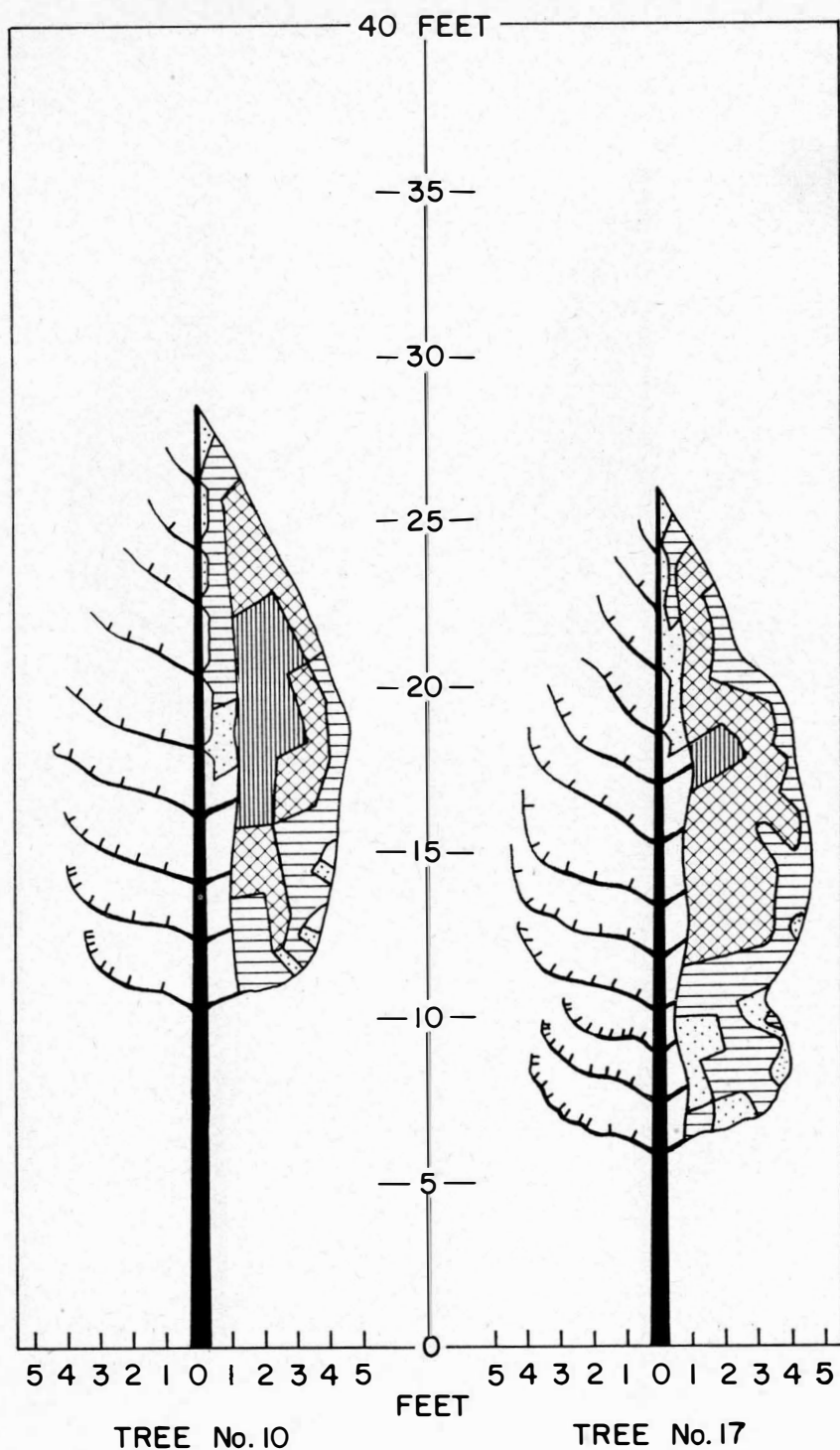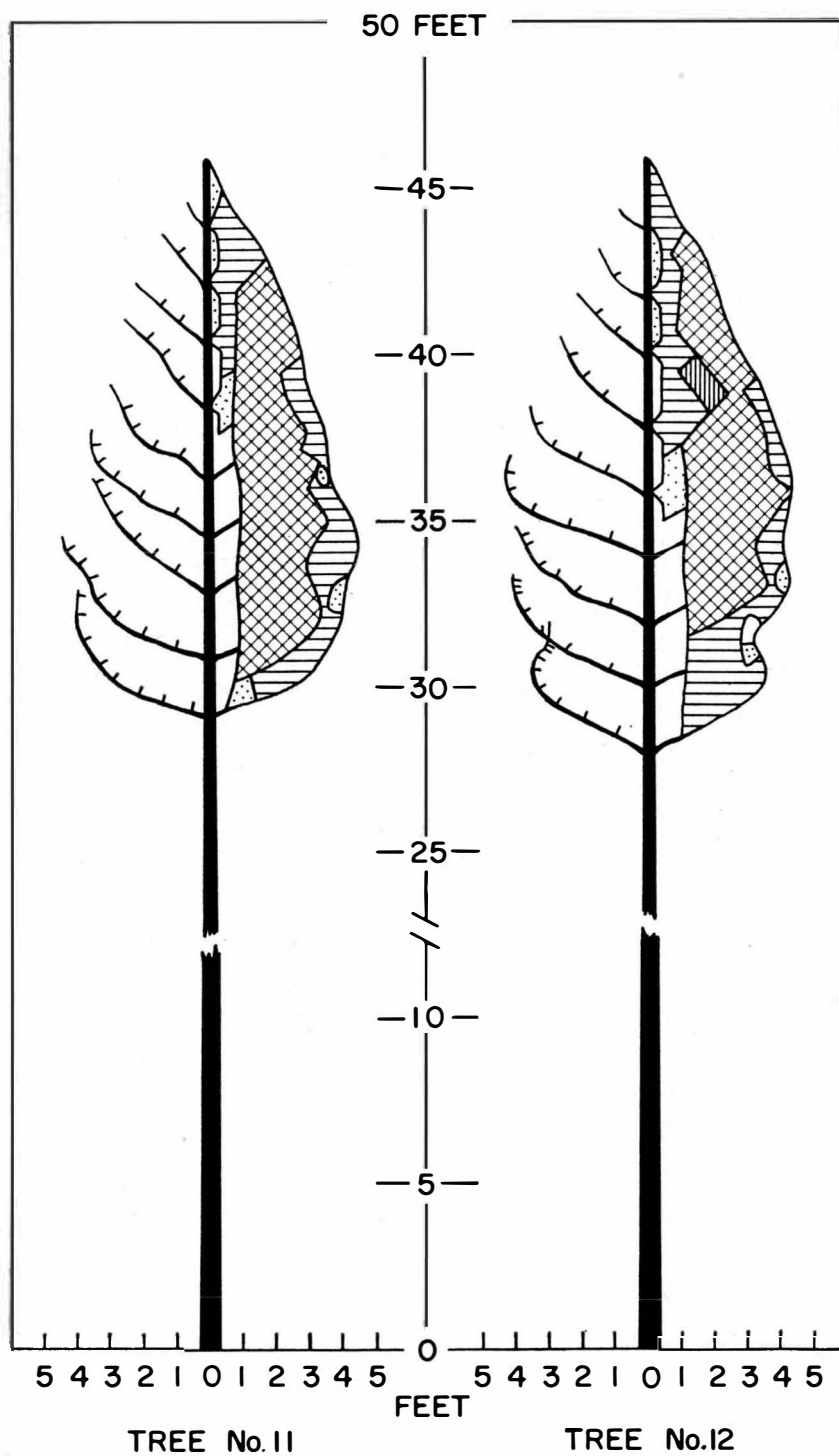
Branches

The number of wholly live whorls per tree ranged from 8 to 14 (Table 1). Average numbers increased slightly with age at both spacings, but considerable differences occurred between the trees of some pairs. Partially live whorls averaged one per tree.

There was no evident association of branch numbers with position of the whorl, except for Trees 13 and 14 which still retained their juvenile two-branched whorls at the base of the crown (Appendix 1). Nor did the average numbers per whorl seem to be related to age of the tree. Numbers of main branches varied from 2 to 8 per whorl and averaged 5 or 6 for most trees. The ratio of dwarf to main branches was 1:9. Except for Trees 13 and 14, total numbers of branches per tree were fairly similar for all ages.

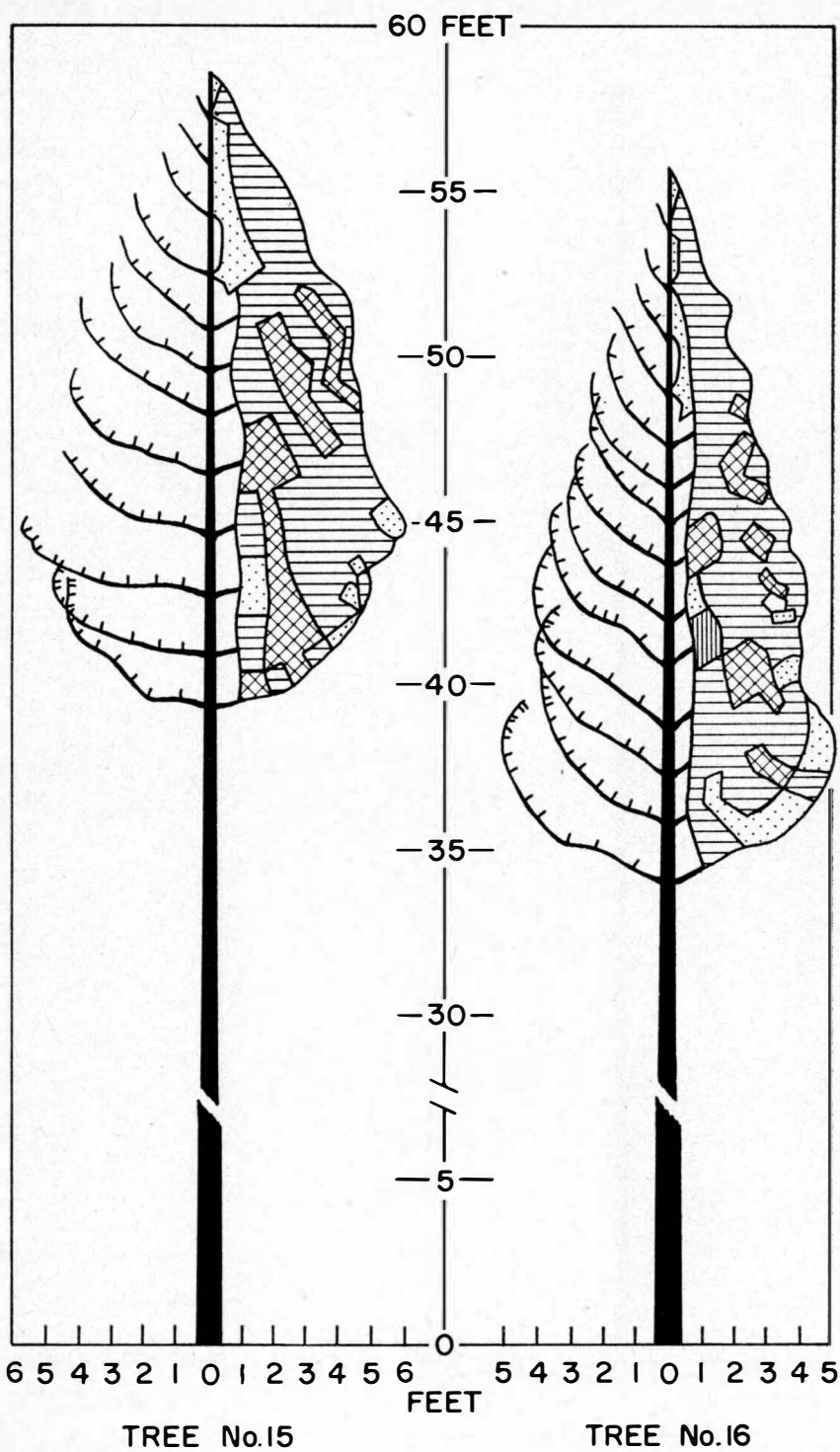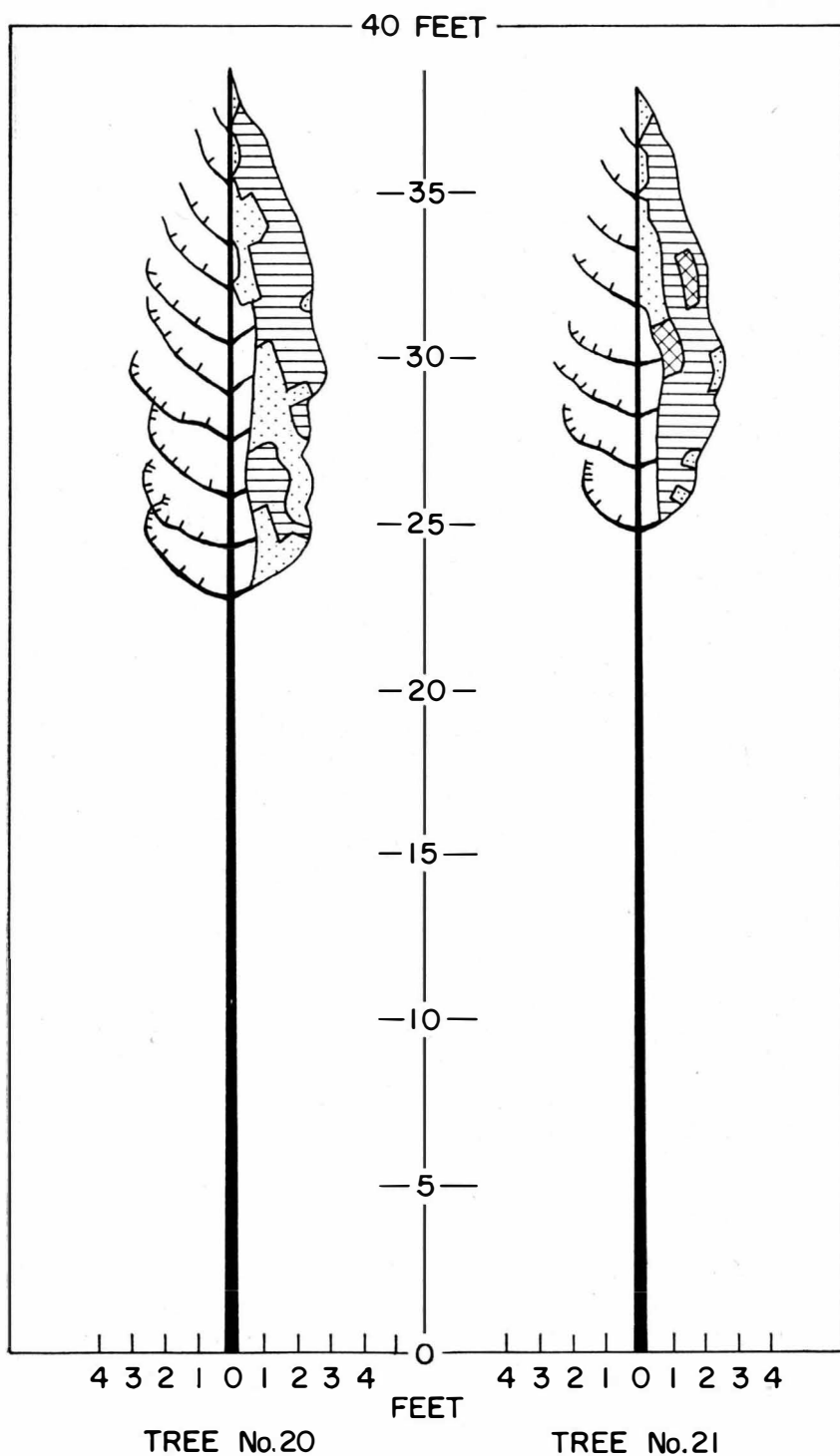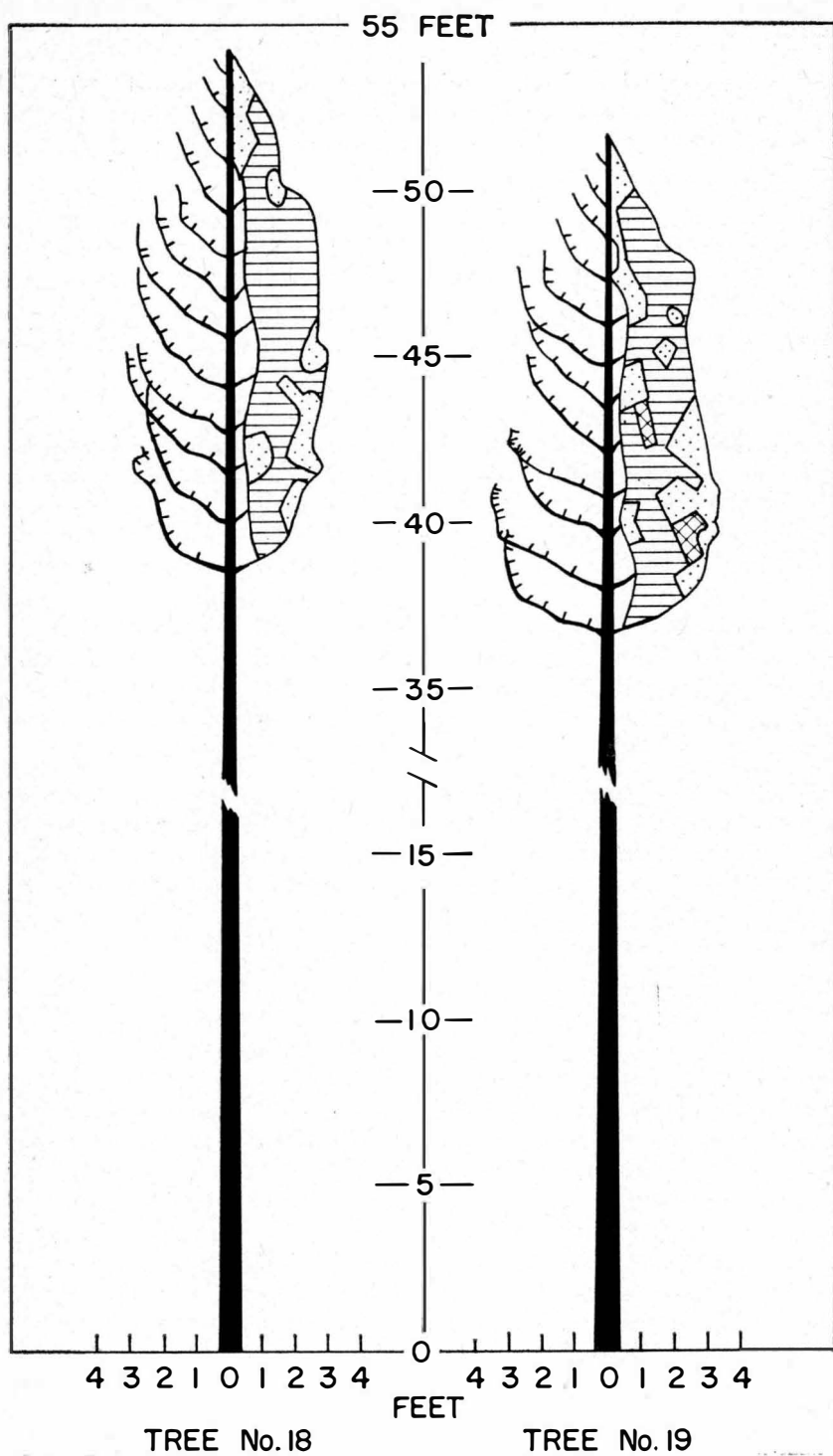Radial distribution of branches is shown in Appendix 2. Somewhat fewer than average branches were located in the west quadrant and more than the average in the south quadrant. A finer breakdown into 40-degree sectors (Appendix 3) indicates quite similar numbers except for the 286-325 degree sector (approximately northwest) which had considerably fewer branches than some other sectors. The local prevailing wind is northwest (Anon., 1952), and this may produce less favourable conditions for branch initiation or survival in that exposure. Despite the low branch count for the northwest sector, a chi-square test indicated no significant departure from a distribution of equal numbers in all sectors when the data are considered as a whole. Radial symmetry of branches is therefore considered to be closely approximated, at least numerically.

Little increase in branch basal diameter was found below the third to fifth whorl from the top, and branches in the oldest whorls were seldom the thickest (Appendix 4). The largest average branch diameter was 1.21 inches for the 8-year-old whorl of Tree 15; average diameter of the 12-year-old whorl of the same tree was 1.09 inches. Only the branches of Tree 23 were weighed, but maximum weight for this specimen was reached in the sixth whorl (Appendix 5).

Branches pointed generally upwards. The inner (and greater) length of a branch was fairly straight; the angle formed with the stem was usually greater for branches further down the crown, some of which approached the horizontal. The outer part of a branch curved upward often becoming vertical, or nearly so, towards the tip. The ends of some lower branches actually curved inwards towards the stem, overlapping the next higher whorl (Figures 3-9). Branch shape seems to be controlled largely by foliage weight. A new lateral shoot is nearly vertical, but the expansion of its needles displaces it outwards, and the added foliage of successive shoots weigh it down still more. The branch thus becomes a series of internodes under stress. Later, when the oldest needles along the inner branch fall, some of the stress is released and the branch responds by curving upwards and eventually reflexing the tip. This can be demonstrated on a young branch by removing the inner foliage.

Secondary branches often occurred in pairs, arising in both the vertical and horizontal planes. In the upper part of the crown the secondary branches were fairly well distributed around the main branch but further down tended to turn upwards, and in the lowest whorls all projected above the branch (Figure 9).
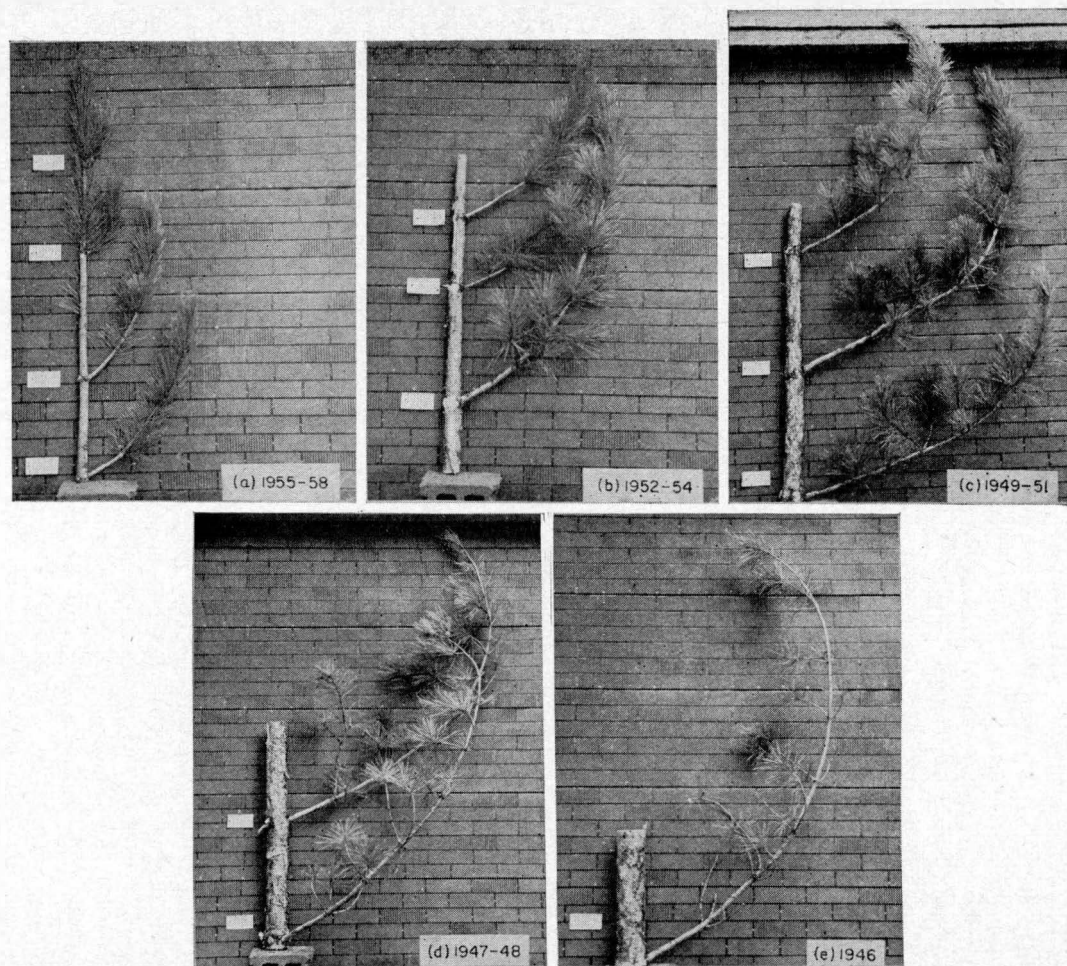
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Figure 9. Crown "profile" showing characteristic branch formation from whorls in upper crown (a) to base (e).

Foliage

Needle length was extremely variable, even within the same crown, as shown by the samples from Tree 24, where the range was from 2.0 to 5.8 inches (Appendix 6). There was no particular pattern of needle length from one main whorl to another, except in the two partial whorls where the current year's needles were both shorter and thinner. Needles from the same main whorl, but formed in different years, showed a slight decrease in average length with age; however, no correlation was found between needle length and precipitation or hours of sunshine for either the same growing season in which the needles were formed or for the previous season. There did not appear to be any association between needle lengths of foliage formed in the same year on different secondary branches of the same main whorl. Since it had been found that needle length does not increase after the first year, age of secondary branch and position in the tree (perhaps through shading effects) may both influence needle size.

Figures 3 to 8 are schematic representations of foliage distribution, in which the amounts found at each branch whorl have been plotted as though occurring horizontally from that node out to the next, and vertically half-way both upwards and downwards to the next branch. Thus needle-free branch internodes (except for those next to the stem), and spaces between the foliage of adjacent branch whorls and branches, have not been shown. The distribution of foliage by whorls is shown in Appendix 7. For each whorl the needles occurring on the stem internode, main branch internodes, secondary branches, and dwarf branches, are all included.

Needles usually were borne only on the last three stem internodes (Figure 9), although Tree 21 retained needles on the 4-year-old internode (Figure 7). Stem internode needles accounted for up to 3.5 per cent of the total foliage weight in the lighter-crowned trees (Appendix 8). Dwarf branches contributed very little foliage—over one per cent of the crown total in only one tree (Appendix 8). Partial whorls in most trees contained less than 3 per cent of the total foliage, although in Trees 15 and 19 they contained 7 per cent (Appendix 7).

The bulk of the foliage was found on the main branches of the fully live whorls. Needles were borne on secondary branches, and on the main branch internodes as well—although usually only on the last 4 or 5 years' growth. Figure 10, which shows a branch from a 1954 stem whorl, illustrates the usual foliage distribution in the middle and upper crown. In the lower whorls, needles occurred as mere tufts on the ends of main and secondary branches (Figure 9).

Foliage weight increased from the top downwards, tended to remain more or less constant for 4 or 5 whorls in most trees, and then diminished towards the base of the crown (Appendix 7). In most trees, these few whorls contained between half and three-quarters of the total foliage. No generalization regarding the horizontal distribution of foliage weight in the crowns is possible, owing to the extreme variability encountered between trees (Figures 3-8). It is apparent, though, that foliage density is less in the trees at the 5-foot spacing.

With respect to distribution of foliage by age, information is available only for Tree 23 (Appendix 5). This tree carried needles up to 5 years old, but 85 per cent (by weight) had been formed in the last 3 years. Needles produced in a given year were generally most abundant in the main whorls formed 2 to 4 years earlier. The oldest whorls had relatively few young needles. In all complete whorls except the lowest the foliage outweighed the branches, and foliage accounted for 54.7 per cent of the dry crown weight.
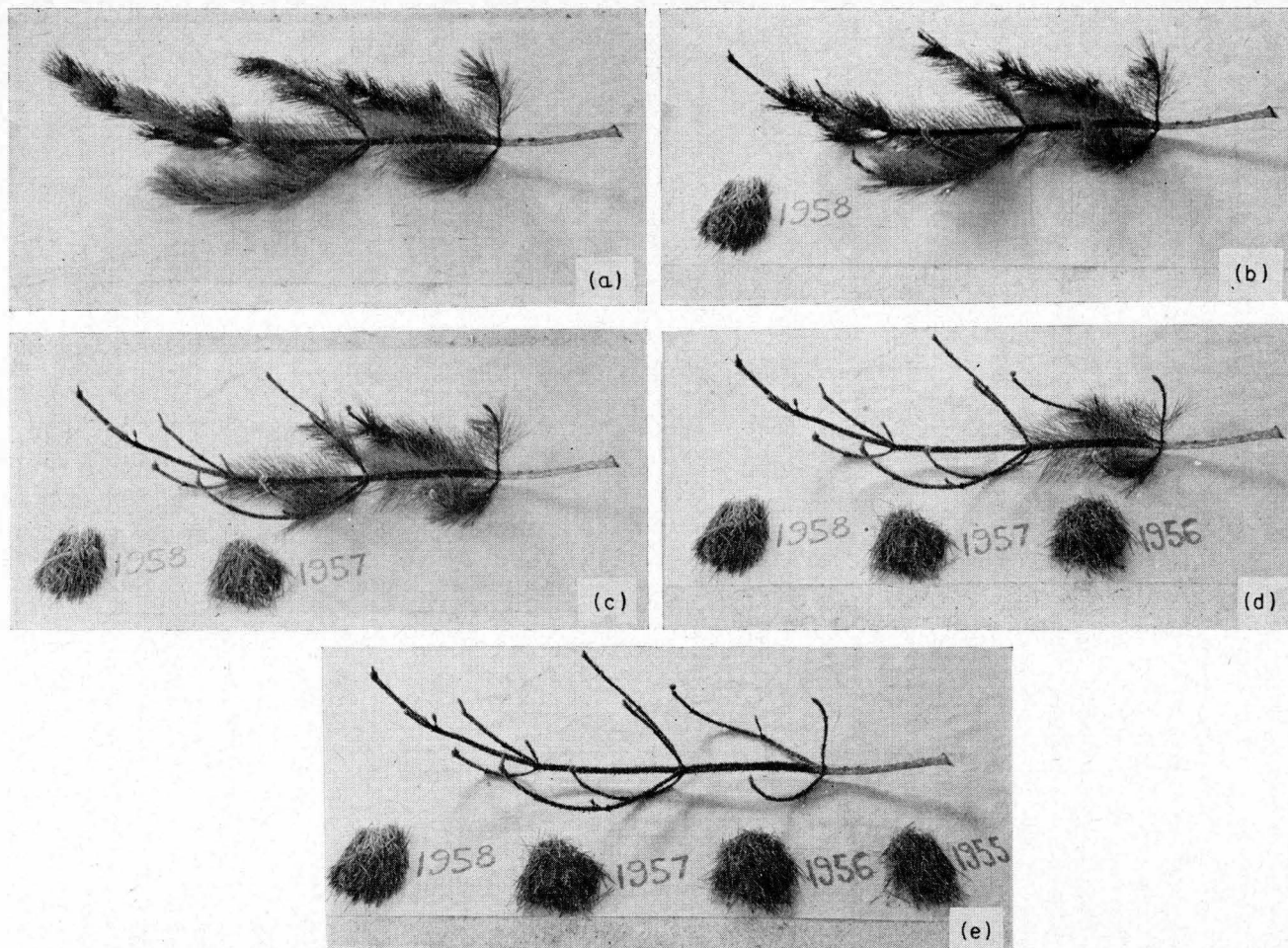
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Figure 10. Branch from 1954 whorl showing positions and amounts of foliage produced each year.

Crowns

The tops of all crowns were elongated and convex. In trees 13 and 14, where closure had not taken place, crown width increased almost to the base. In all other trees maximum width occurred considerably higher, whence the crown tapered gradually to the base, giving it a somewhat spindle shape.

It was found that areas of the crown profile diagrams (Figures 3-8) could be approximated almost exactly by assuming a triangular shape for the portion above the plane of maximum width, and a rectangular shape for the portion below it. The relationship was $\hat{Y}=0.926X+3.45$, with the correlation co-efficient (r) = 0.996. Good estimates of the area were obtained also by assuming the shape to be a parabola or an ellipse. Since the crown has been shown to be radially symmetrical, its solid form, at least in outline, should correspond to the 3-dimensional counterparts of these figures. However, the crown is by no means uniformly dense: the stem and a zone around it occupy a needle-free core up the centre; 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. Accordingly, while crown foliage weight might be expected to vary with crown size as represented by a geometrical shape of similar gross dimensions, the relationship probably would not be proportionate.

The dimensions used were those readily measured from the ground—crown length, greatest crown width, and distance from crown base to widest part. These were measurements of the actual crowns, and were not taken from the profile diagrams. A number of straight-line regressions were derived showing good correlation between foliage weight and such values as the volume of the crown with the upper part considered as a cone and the lower part considered as a cylinder; the volume of the crown considered as two cones (one inverted); the surface area of the crown considered as two cones; and the volume of the crown considered as an ellipsoid. One of the best examples was the regression of foliage weight in grams (W) on the volume of the crown considered as paraboloid, in cubic feet (V), which could be expressed as $W = 10.62V + 1403.5$, with $r = 0.978$ (significant at the one per cent level). An excellent, if empirical, relationship was also found between foliage weight and the product of the length and the width of the crown in square feet (A), expressed as $W = 54.0A - 836.4$, for which $r = 0.970$. The value most out of line in these relationships is that for Tree 20, which evidently had a very low-density crown in comparison with its dimensions (Appendices 9 and 10).

DISCUSSION

These small samples are not intended to demonstrate precisely the morphogenesis of individual crowns. Trees 11 and 12, for example, appear to have rather small crowns for their age in comparison with those of Trees 10 and 17. Yet different stands of unknown provenance are represented, and both variation between and within populations may account for some crown differences. The purpose, rather, is to show whether significant changes do occur with age under controlled stand conditions.

It appears that once closure is complete the rate of crown enlargement, in terms of diameter and length, is reduced, and provided stocking remained unaltered, might eventually cease. However, this situation has not been reached in the trees studied here, and it is clear that quite small increments in crown

dimension permit substantial gains in foliage weight. As an example, Tree 23 was evidently still increasing in weight. It gained 2312 gm. of needles in 1959, but presumably could lose only 1130 gm. at the end of the same year—i.e. the combined weight of the 1955 and 1956 needles plus the remainder of the foliage in the partial whorl (Appendix 5). Numbers of live whorls may fluctuate from year to year but probably remain fairly constant. There are two mechanisms resulting in mortality of the basal whorls. By one, the lowest branches fail to produce new foliage so that the oldest needles die without being replaced; mortality ensuing from this cause takes place in the autumn. By the other process, the considerable extension of shoots and new foliage of higher branches during the summer may be sufficient to shade out the needles on the lowest whorls during the growing season. Thus while the formation of a new whorl at the top of the tree is an annual occurrence, mortality at the base of the crown proceeds more erratically.

When crown weight is plotted over d.b.h., it can be seen that for a given stem diameter the crowns of trees at the 5-foot spacing are lighter than those at the 7-foot spacing. Thus two populations are represented, and no single expression for estimating crown weight from d.b.h., as developed by Kittredge (1944), could be derived to apply to more than one spacing.

The foliage of each pair of trees showed remarkably similar weights, yet their crown configurations differed considerably. This was due mainly to differences in numbers of live whorls; but since the lower whorls carried relatively little foliage, total weight was not greatly influenced.

This variability in whorl numbers for trees of similar height and diameter may be significant in pruning. The practice of removing an equal number of whorls, for example, would in effect be a very unequal treatment. Appendix 7 indicates the range, within pairs, of the proportion of total crown weight contained in the lowest 3 live whorls. In this sample, probably only Trees 10 and 17 would be considered for pruning. Removing the lowest 3 whorls in each case would take 28 per cent of the foliage of Tree 10, but only 17 per cent of Tree 17. A more equable approach would be to use per cent of crown length, or per cent of number of whorls (Appendices 11 and 12). Pruning the lowest 30 per cent of the crown would take 26 per cent of the foliage weight of Tree 10, and 24 per cent of Tree 17.

The regressions derived here make it possible, from simple crown measurements, to estimate foliage production for individual trees, and for stands as well, and by periodic remeasurement to determine the foliage required to produce given wood increments.

It should be pointed out that these regressions are merely expressions of total foliage weight; no attempt has been made to account for possible variations in productivity of different parts of the crown. Factors operating here might be age and density of foliage and light conditions. The increase in foliage weight for several whorls from the top down, and the decrease towards the base of the crown, are in accord with the type of nutrition gradient in the cambium proposed by Duff and Nolan (1953). The present study provides no evidence on specific stem growth-foliage relationships, but the contribution of a given whorl to stem increment may depend on the ratio of its foliage weight to its branch weight—i.e. a given amount of branch wood may require a given amount of foliage to sustain it, with the surplus nurturing the stem.

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SUMMARY

A study of red pine crown structure was made in 6 plantations at the Petawawa Forest Experiment Station, representing 4 ages (8 to 34 years) and 2 spacings (5×5 and 7×7 feet). The crowns of 12 trees were dissected, the branches were measured, and samples of foliage from each whorl were dried and weighed. Observations of needle age and length were made on two other trees. Diagrams of the crowns were prepared, showing branch formation and foliage distribution.

Numbers of wholly live whorls per tree ranged from 8 to 14, showing considerable variation between trees of the same size. Following crown closure the number of whorls probably stays fairly constant. Partially live whorls at the base of the crown averaged one per tree. Except in the youngest trees, whose crowns had not closed, there was no evident association of number of branches per whorl with whorl position or with tree age. There were 5 or 6 main branches per whorl on most trees. About equal numbers of branches were found on all trees, except the youngest. Dwarf branches made up about 10 per cent of the branch total. Branches were distributed equally on all sides of a tree. There was little increase in branch thickness below the third to fifth whorl from the top. Branches in the top of the crown made an acute angle with the stem; further down they were more horizontal owing to the weight of foliage; branches near the base freed of the weight of the older foliage turned upwards and inwards.

Needle length was very variable, even within the same branch and year of formation, and may be influenced by position in tree and age of secondary branch. Current year's needles were shortest and thinnest in the lowest whorl. Bundle sheaths accounted for about 3.7 per cent of the green weight of foliage. Needles were borne on the last three stem internodes, accounting for up to 3.5 per cent of total foliage dry weight. Dwarf branches contributed less than one per cent of the foliage weight of most trees. Partial whorls contained up to 7 per cent of total foliage, usually less than 3 per cent. Most foliage was found on the main branches of the fully live whorls. Foliage weight increased from the top downwards, remained constant for 4 or 5 whorls in most trees, and then diminished towards the base of the crown. Horizontal distribution of foliage was very variable. Crowns at the 5×5 spacing were sparser and more elongated than those of the same age at 7×7 feet. Needles up to 5 years old were found on one tree, but 85 per cent were 3 years old or less. On this tree the foliage outweighed the branches in all but the lowest complete whorl.

The relationship of dry foliage weight in grams (W) to the family of circular solids with common length and diameter could be expressed by straight-line regressions with good correlation; e.g. the relation to the volume of the crown considered as a paraboloid, in cubic feet (V), was $W = 10.62V + 1403.5$, with $r = 0.978$. A good relationship was also found with the product of the length and the greatest width of the crown in square feet (A), as follows: $W = 54.0A - 836.4$. These regressions applied to the full range of data for trees 10 feet to 60 feet tall. They should be useful in calculating per tree and per acre foliage weights and, by remeasurements, in estimating the foliage required to produce given wood increments.

Owing to variability in numbers of whorls for trees of similar size, a policy of pruning an equal number of whorls would remove quite different proportions of the total foliage. A more equable treatment would be to remove a certain per cent of crown length or per cent of number of whorls.

APPENDICES

Appendix 1—*Branches per whorl

Tree No.	1959	1958	1957	1956	1955	1954	1953	1952	1951	1950	1949	1948	1947	1946	Total	Mean
13	8(+0)	7(+1)	4(+0)	5(+0)	4(+0)	4(+0)	2(+0)	2(+0)							36(+ 1)=37	4.5(+0.1)
14	5(+3)	5(+3)	5(+0)	5(+0)	4(+0)	2(+0)	2(+0)	2(+0)	2(+0)						32(+ 6)=38	3.6(+0.7)
10	7(+0)	8(+0)	8(+0)	8(+0)	8(+0)	6(+0)	6(+0)	6(+0)	7(+0)						64(+ 0)=64	7.1(+0)
17	8(+0)	6(+0)	5(+1)	5(+0)	5(+0)	6(+0)	6(+1)	6(+1)	4(+0)	5(+1)	8(+0)	6(+0)			70(+ 4)=74	5.8(+0.3)
11	6(+0)	5(+1)	6(+1)	6(+2)	5(+2)	5(+2)	6(+0)	6(+0)	5(+0)						50(+ 8)=58	5.6(+0.9)
12	7(+0)	5(+1)	5(+0)	6(+1)	6(+1)	6(+1)	7(+1)	6(+1)	7(+0)						55(+ 6)=61	6.1(+0.7)
15	5(+1)	4(+1)	5(+1)	4(+2)	4(+0)	4(+1)	4(+1)	6(+0)	5(+1)	5(+0)	4(+0)	4(+0)			54(+ 8)=62	4.5(+0.7)
16	6(+0)	5(+1)	4(+0)	3(+0)	4(+0)	4(+1)	4(+2)	5(+0)	5(+0)	4(+0)	4(+1)	5(+1)	6(+0)	4(+0)	63(+ 6)=69	4.5(+0.4)
20	5(+0)	5(+0)	3(+1)	5(+1)	4(+1)	4(+0)	5(+1)	4(+1)	5(+1)	5(+0)					45(+ 6)=51	4.5(+0.6)
21	5(+0)	5(+1)	4(+1)	6(+2)	6(+0)	4(+1)	6(+0)	5(+1)							41(+ 6)=47	5.1(+0.8)
18	4(+1)	3(+2)	4(+1)	7(+0)	4(+0)	4(+2)	4(+0)	6(+1)	4(+0)	6(+1)	4(+1)	4(+0)			54(+ 9)=63	4.5(+0.8)
19	5(+0)	3(+3)	3(+2)	4(+2)	5(+0)	5(+0)	5(+0)	5(+2)	5(+0)	5(+1)	5(+0)	5(+0)			55(+10)=65	4.6(+0.8)
															Mean 51.6(+5.8)=57.4	

* Main (+ dwarf)

Appendix 2—Distribution of *branches by cardinal direction

Tree	Quadrant				Total
	North (316°–45°)	East (46°–135°)	South (136°–225°)	West (226°–315°)	
13	9(+0)	9(+1)	12(+0)	6(+0)	36(+1)
14	8(+1)	7(+1)	9(+2)	8(+2)	32(+6)
10	16(+0)	17(+0)	15(+0)	16(+0)	64(+0)
17	15(+1)	19(+2)	17(+1)	19(+0)	70(+4)
11	13(+4)	14(+2)	11(+2)	12(+0)	50(+8)
12	15(+1)	14(+0)	14(+3)	12(+2)	55(+6)
15	14(+3)	13(+3)	16(+1)	11(+1)	54(+8)
16	16(+1)	17(+2)	16(+3)	14(+0)	63(+6)
20	10(+1)	10(+2)	12(+2)	13(+1)	45(+6)
21	10(+1)	9(+2)	13(+2)	9(+1)	41(+6)
18	14(+2)	13(+4)	14(+2)	13(+1)	54(+9)
19	14(+4)	15(+1)	14(+2)	12(+3)	55(+10)
	154(+19)	157(+20)	163(+20)	145(+11)	619(+70)

*Main (+ dwarf)

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Appendix 3—*Branch distribution by 40° sectors

Tree No.	326°–5°	6°–45°	46°–85°	86°–125°	126°–165°	166°–205°	206°–245°	246°–285°	286°–325°	Total
13	2(+0)	5(+0)	4(+0)	4(+1)	4(+0)	4(+0)	5(+0)	3(+0)	5(+0)	36(+1)
14	2(+0)	5(+1)	2(+0)	5(+1)	3(+1)	5(+0)	3(+1)	4(+0)	3(+2)	32(+6)
10	8(+0)	8(+0)	9(+0)	7(+0)	7(+0)	7(+0)	6(+0)	6(+0)	6(+0)	64(+0)
17	5(+1)	9(+0)	10(+0)	5(+1)	10(+2)	8(+0)	10(+0)	7(+0)	6(+0)	70(+4)
11	8(+2)	5(+1)	5(+1)	7(+1)	7(+1)	5(+0)	3(+1)	6(+0)	4(+1)	50(+8)
12	6(+0)	7(+1)	6(+0)	7(+0)	6(+0)	8(+2)	6(+2)	3(+1)	6(+0)	55(+6)
15	7(+0)	7(+2)	6(+2)	6(+0)	6(+1)	7(+0)	5(+2)	9(+0)	1(+1)	54(+8)
16	4(+1)	11(+0)	3(+2)	13(+0)	3(+1)	8(+1)	8(+1)	8(+0)	5(+0)	63(+6)
20	5(+1)	5(+0)	7(+0)	2(+2)	6(+0)	4(+2)	7(+0)	5(+0)	4(+1)	45(+6)
21	4(+1)	5(+0)	5(+1)	4(+0)	4(+3)	5(+0)	5(+0)	6(+0)	3(+1)	41(+6)
18	4(+0)	9(+2)	4(+1)	9(+3)	2(+1)	10(+1)	5(+0)	8(+0)	3(+1)	54(+9)
19	9(+1)	4(+3)	7(+1)	6(+0)	7(+0)	6(+1)	7(+2)	6(+1)	3(+1)	55(+10)
	64(+7)	80(+10)	68(+8)	75(+9)	65(+10)	77(+7)	70(+9)	71(+2)	49(+8)	619(+70)

* Main (+ dwarf)

Appendix 4—Average length (feet) and basal diameter (inches)—main branches

Whorl	Tree 13		Tree 14		Tree 10		Tree 17		Tree 11		Tree 12		Tree 15		Tree 16		Tree 20		Tree 21		Tree 18		Tree 19	
	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D
1959		0.48		0.55		0.51		0.42						0.47		0.38		0.35		0.42		0.30		0.24
1958	2.17	0.69	2.30	0.74	1.94	0.60	1.88	0.46	1.92	0.58	2.00	0.65	1.55	0.52	1.50	0.47	1.54	0.52	1.64	0.56	1.17	0.42	0.98	0.36
1957	2.90	0.81	2.48	0.70	2.94	0.72	2.86	0.76	2.74	0.75	2.80	0.74	2.65	0.70	1.87	0.58	2.27	0.61	2.05	0.59	1.92	0.50	1.70	0.45
1956	3.30	0.78	2.88	0.66	3.90	0.87	3.38	0.80	3.77	0.86	3.82	0.90	3.57	0.81	3.10	0.72	2.96	0.69	2.57	0.62	2.80	0.63	2.55	0.63
1955	3.48	0.79	3.18	0.78	4.58	0.88	4.70	0.82	4.20	0.91	4.65	0.98	4.00	0.92	3.80	0.90	3.52	0.70	2.80	0.58	2.70	0.62	2.97	0.69
1954	3.25	0.70	3.95	0.86	5.58	0.97	5.32	1.10	4.70	0.91	5.32	0.98	4.77	0.99	4.23	0.86	3.82	0.69	3.32	0.63	4.05	0.82	4.13	0.82
1953	3.75	0.76	3.65	0.78	4.92	0.88	5.77	1.03	5.60	1.00	5.20	0.89	5.70	0.99	4.68	0.90	3.92	0.75	2.88	0.58	4.77	0.91	3.65	0.74
1952	3.80	0.82	3.40	0.66	5.06	0.96	5.95	1.02	6.24	1.04	5.67	0.98	5.88	1.21	5.15	0.88	4.20	0.75	3.12	0.64	4.78	0.89	4.42	0.79
1951			2.80	0.51	4.23	0.88	5.32	1.00	6.42	0.99	5.15	0.90	6.34	1.06	6.18	1.02	4.10	0.69			3.90	0.75	3.90	0.70
1950							3.52	0.61					7.00	1.06	6.92	1.15	4.26	0.67			5.50	0.84	4.18	0.71
1949							4.64	0.88					6.80	1.03	7.52	1.16					5.48	0.85	5.15	0.85
1948							5.48	1.00					7.12	1.09	7.78	1.05					4.85	0.76	4.94	0.78
1947															7.82	1.04								
1946															8.43	1.09								

Main whorl	Foliage, by year formed												Branches	
	1959		1958		1957		1956		1955		Total			
	Gm.	%	Gm.	%	Gm.	%	Gm.	%	Gm.	%	Gm.	%	Gm.	%
1959	132	1.9	—	—	—	—	—	—	—	—	132	1.9	50	0.9
1958	233	3.4	127	1.9	—	—	—	—	—	—	360	5.3	175	3.1
1957	495	7.3	268	3.9	67	1.0	—	—	—	—	830	12.2	431	7.6
1956	413	6.1	343	5.0	219	3.2	18	0.3	—	—	993	14.6	557	9.9
1955	398	5.8	340	5.0	343	5.0	160	2.3	2	—	1243	18.1	755	13.4
1954	355	5.2	367	5.4	411	6.0	298	4.4	54	0.8	1485	21.8	1110	19.6
1953	176	2.6	276	4.1	331	4.9	234	3.4	40	0.6	1057	15.6	972	17.2
1952	93	1.4	74	1.1	223	3.3	149	2.2	6	0.1	545	8.1	1004	17.8
*1951	17	0.2	30	0.4	68	1.0	46	0.7	5	0.1	166	2.4	594	10.5
Total	2312	33.9	1825	26.8	1662	24.4	905	13.3	107	1.6	6811	100.0	5648	100.0

*partial whorl

Appendix 6—Variation in needle length (inches)—Tree 24

(a) *Between stem whorls—needles formed same year (1959)*

Whorl	Range	Mean
1959	4.0–4.6	4.2
1958	4.1–5.1	4.6
1957	3.8–4.7	4.2
1956	4.3–5.3	4.7
1955	4.3–5.4	4.8
1954	3.2–5.3	4.7
1953	3.4–5.6	4.6
1952	2.6–5.8	4.4
1951	2.9–5.2	4.3
*1950	2.2–3.9	2.8
*1949	2.0–4.1	3.0

*partial whorls

(b) *Within one whorl (1954)—needles formed different years*

Year formed	Range	Mean
1959	3.2–5.3	4.7
1958	2.6–5.5	4.8
1957	3.9–4.9	4.4
1956	3.6–4.8	4.1
1955	3.5–4.7	4.0

(c) *Within one whorl (1954)—needles formed same year (1959)*

Secondary Branch	Range	Mean
1959	3.8–4.9	4.4
1958	3.8–4.8	4.3
1957	3.0–5.0	4.0
1956	3.3–4.9	4.2
1955	3.8–5.5	4.7

Appendix 7—Foliage weight—distribution by whorls

Whorl		Tree 13 %	Tree 13 Cum.	Tree 14 %	Tree 14 Cum.	Tree 10 %	Tree 10 Cum.	Tree 17 %	Tree 17 Cum.	Tree 11 %	Tree 11 Cum.	Tree 12 %	Tree 12 Cum.	Tree 15 %	Tree 15 Cum.	Tree 16 %	Tree 16 Cum.	Tree 20 %	Tree 20 Cum.	Tree 21 %	Tree 21 Cum.	Tree 18 %	Tree 18 Cum.	Tree 19 %	Tree 19 Cum.
1	1959	4.8	100.0	3.8	100.0	1.8	100.0	1.7	100.0	1.6	100.0	2.3	100.0	0.9	100.0	1.1	100.0	3.1	100.0	2.8	100.0	0.9	100.0	1.1	100.0
2	1958	14.2	95.2	11.2	96.2	5.3	98.2	3.3	98.3	4.1	98.4	5.3	97.7	1.6	99.1	2.2	98.9	6.9	96.9	6.4	97.2	2.3	99.1	2.2	98.9
3	1957	15.2	81.0	16.8	85.0	8.8	92.9	4.9	95.0	9.0	94.3	9.2	92.4	3.8	97.5	2.6	96.7	6.8	90.0	6.5	90.8	3.2	96.8	3.3	96.7
4	1956	22.9	65.8	15.8	68.2	18.3	84.1	7.6	90.1	14.9	85.3	18.7	83.2	4.7	93.7	3.1	94.1	16.1	83.2	16.6	84.3	6.5	93.6	6.4	93.4
5	1955	15.9	42.9	17.8	52.4	22.0	65.8	12.2	82.5	13.5	70.4	15.2	64.5	4.5	89.0	4.3	91.0	13.7	67.1	17.4	67.7	5.9	87.1	5.4	87.0
6	1954	9.8	27.0	14.6	34.6	15.4	43.8	15.9	70.3	14.3	56.9	16.4	49.3	8.0	84.5	6.6	86.7	9.9	53.4	12.0	50.3	11.6	81.2	7.5	81.6
7	1953	6.5	17.2	8.4	20.0	13.6	28.4	16.7	54.4	15.2	42.6	17.4	32.9	9.3	76.5	8.5	80.1	12.2	43.5	22.1	38.3	10.8	69.6	6.1	74.1
8	1952	8.9	10.7	8.0	11.6	8.8	14.8	14.1	37.7	14.9	27.4	6.9	15.5	18.2	67.2	10.1	71.6	12.2	31.3	12.6	16.2	13.9	58.8	23.3	68.0
9	1951	*(1.8)	(1.8)	3.6	3.6	3.4	6.0	6.5	23.6	7.4	12.5	8.4	8.6	15.6	49.0	9.6	61.5	11.3	19.1	(3.6)	(3.6)	11.7	44.9	8.2	44.7
10	1950					(2.6)	(2.6)	3.3	17.1	(4.4)	(5.1)	(0.2)	(0.2)	8.3	33.4	14.0	51.9	7.7	7.8			15.1	33.2	8.9	36.5
11	1949							8.1	13.8	(0.7)	(0.7)			9.1	25.1	11.2	37.9	(0.1)	(0.1)			9.7	18.1	11.2	27.6
12	1948							5.7	5.7					8.9	16.0	11.3	26.7					7.2	8.4	9.5	16.4
13	1947													(7.1)	(7.1)	9.1	15.4					(1.2)	(1.2)	(6.2)	(6.9)
14	1946															3.7	6.3							(0.7)	(0.7)
15	1945															(2.6)	(2.6)								
Lowest 3 live whorls			27.0		20.0		28.4		17.1		42.6		32.9		33.4		26.7		31.3		50.3		33.2		36.5

* ( )=partial whorl

Appendix 8—Foliage distribution outside main branches

Tree No.	Stem Internodes		Dwarf Branches	
	Weight (gm.)	% Total Foliage	Weight (gm.)	% Total Foliage
13	82	2.3	—	—
14	79	2.3	7	0.2
10	99	1.1	38	0.4
17	83	0.9	31	0.3
11	93	1.2	132	1.7
12	127	1.6	25	0.3
15	76	0.7	62	0.6
16	107	0.9	123	1.0
20	98	3.5	18	0.6
21	101	3.1	13	0.4
18	49	1.1	28	0.6
19	54	1.1	24	0.5

REGRESSION OF CROWN WEIGHT ON CROWN PARABOLIC VOLUME

$$W = 10.62V + 1403.5$$
$$r = 0.978$$
$$S_{y.x} = 731.6$$
$$S_b = 0.72$$
$$t = 14.72$$
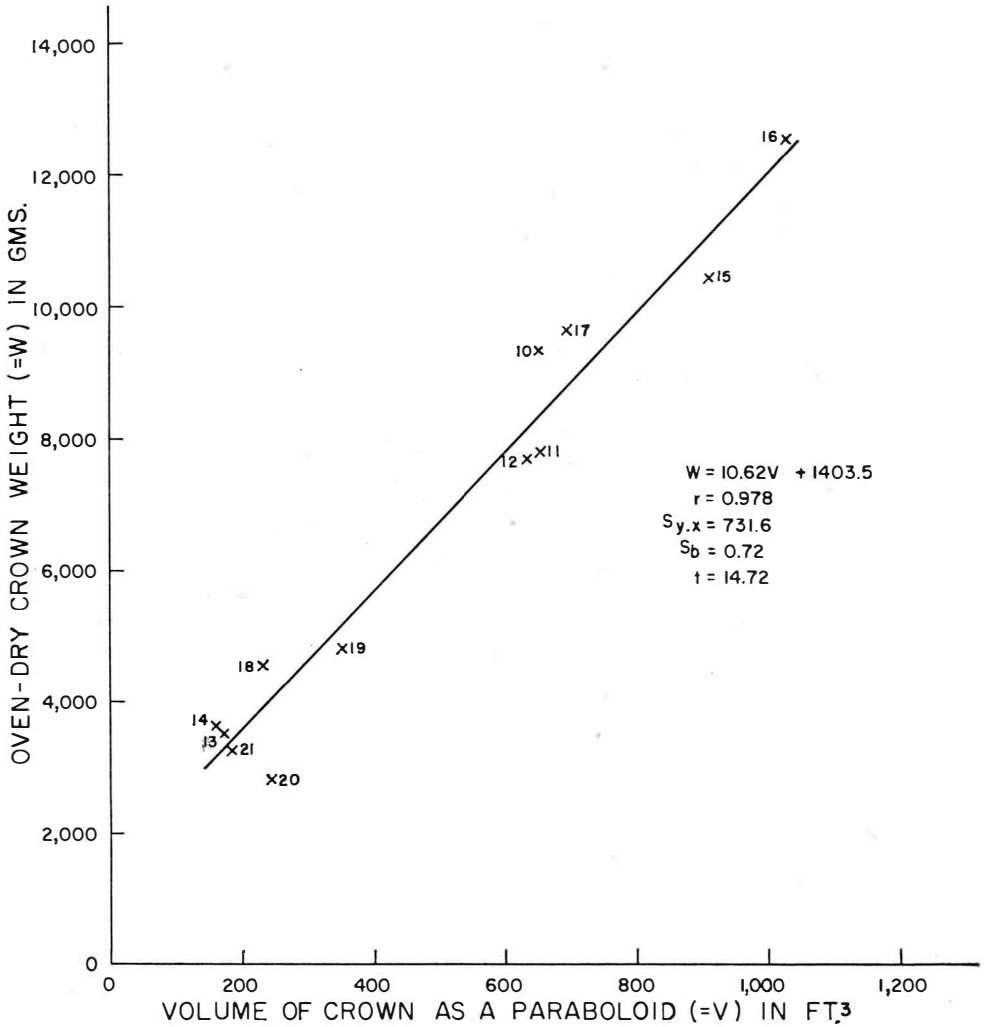
REGRESSION OF CROWN WEIGHT ON LENGTH x WIDTH OF CROWN.

$$W = 54.0A - 836.4$$
$$r = 0.970$$
$$S_{y.x} = 846.6$$
$$S_b = 4.28$$
$$t = 12.6$$

OVEN-DRY CROWN WEIGHT (=W) IN GMS.

CROWN LENGTH x WIDTH (=A) IN FT.^{2}
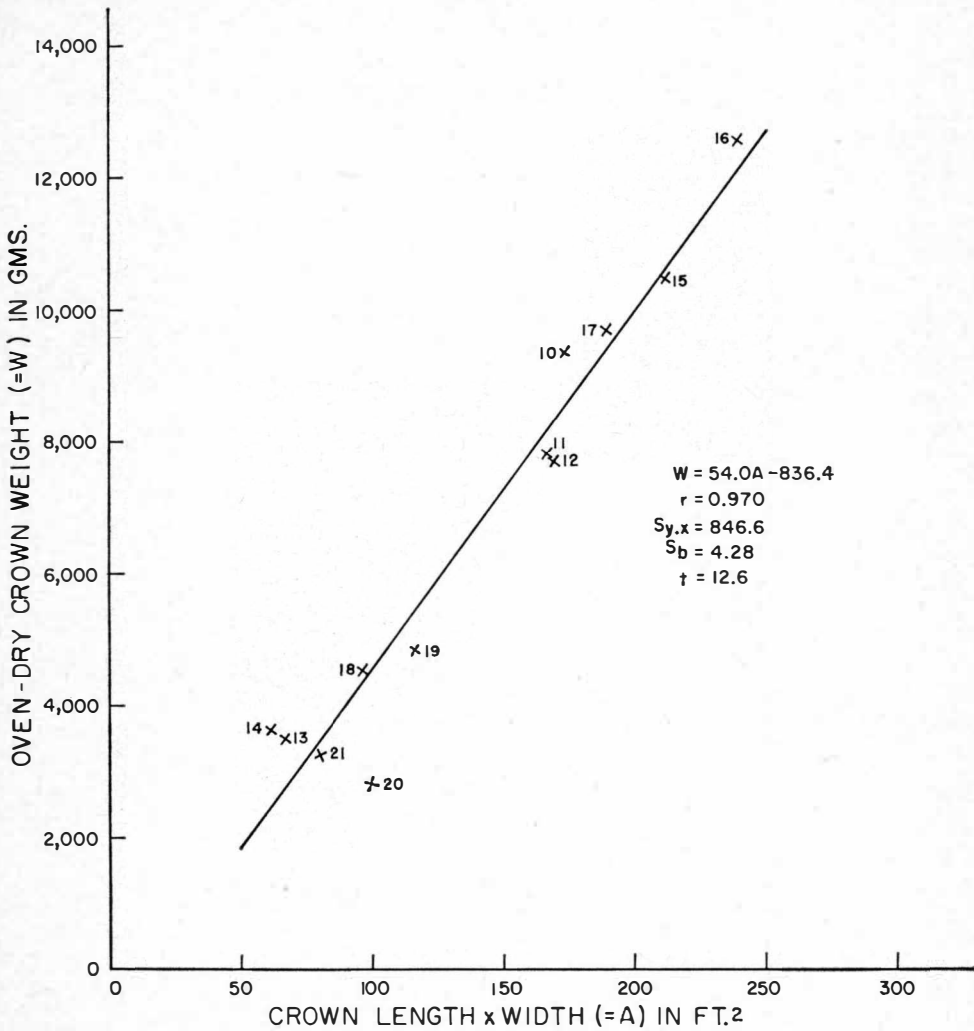
Appendix 11—**Weight of foliage—cumulative per cent from the base

*Length of Crown-Cumulative % from Base	Tree 13	Tree 14	Tree 10	Tree 17	Tree 11	Tree 12	Tree 15	Tree 16	Tree 20	Tree 21	Tree 18	Tree 19
10	20.2	22.2	5.2	7.6	11.8	7.8	17.2	8.3	7.9	10.7	8.9	16.1
20	33.3	40.2	13.9	16.0	24.7	14.1	26.8	22.0	19.3	27.0	22.4	26.9
30	47.5	56.8	26.1	23.6	39.2	27.1	37.9	36.8	30.0	42.0	37.5	37.6
40	61.4	68.6	39.6	41.8	52.8	43.7	55.0	54.2	42.9	52.8	53.0	50.0
50	72.0	79.1	56.2	60.0	64.2	58.0	71.9	69.2	53.7	65.2	68.4	70.2
60	80.8	87.4	73.0	76.8	76.2	72.0	84.7	83.8	67.3	79.8	81.8	78.5
70	88.4	92.9	86.6	87.3	87.9	85.7	90.0	91.4	84.0	87.7	87.5	85.8
80	95.6	97.0	94.5	93.7	95.4	93.5	94.6	95.2	90.1	92.7	93.8	93.4
90	97.9	98.7	98.8	97.6	98.9	98.0	98.7	98.2	96.9	97.8	97.2	97.3

* Includes wholly live crown only.

** Includes foliage from partial whorls.

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Appendix 12—**Foliage weight by whorls—cumulative per cent from the base

*Number Whorls- Cumulative % from Base	Tree 13	Tree 14	Tree 10	Tree 17	Tree 11	Tree 12	Tree 15	Tree 16	Tree 20	Tree 21	Tree 18	Tree 19
10	8.5	3.0	5.2	7.1	10.8	7.6	17.9	10.2	7.8	14.0	10.1	18.1
20	14.6	9.9	12.9	15.1	23.9	14.1	28.8	24.4	19.1	30.1	24.2	31.0
30	21.0	17.4	24.1	21.1	27.9	27.2	42.9	40.9	31.3	43.0	40.0	41.3
40	30.0	28.8	37.5	34.7	51.1	42.5	63.7	58.1	43.5	53.8	55.8	63.0
50	42.5	43.0	54.9	54.8	63.5	56.7	76.8	72.0	53.4	67.0	69.8	74.2
60	61.0	58.5	73.4	73.0	76.2	71.8	85.3	83.2	67.1	80.2	82.6	83.0
70	74.9	73.2	86.8	86.0	88.2	86.0	91.0	90.4	83.2	88.2	90.0	90.0
80	86.8	87.4	93.9	93.2	95.3	93.4	96.1	94.8	90.0	93.4	95.7	95.2
90	96.0	96.5	98.3	98.3	98.8	98.0	99.2	98.0	96.9	98.0	99.0	98.9

* Wholly live whorls only.
** Includes foliage from partial whorls.

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