Radial Growth in Forest Trees and Effects of Insect Defoliation

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IT IS WELL RECOGNIZED that radial growth in forest trees is influenced by many factors, including climatic fluctuations, site, variable stand conditions, and defoliation. Severe or prolonged insect defoliation may cause modifications of the normal ring pattern that are useful in assessing the risk of imminent mortality and the need for control action. If old surviving trees are available, the modified ring patterns may be used in the reconstruction of outbreak histories many decades after the event (Swaine and Craighead, 1924; Blais, 1954). Critical cross-dating techniques are available for assigning year dates to ring sequences from dead trees (Ghent, 1952).

The most common source of radial growth data is a core, or disc, taken low in the stem, usually at breast height. The sequence of annual rings reflects the influence of many factors during the life of the tree, and as will be noted below, not all of them are extrinsic. Even the effects of severe and prolonged defoliation cannot always be segregated clearly from the effects of other factors, if one is dependent solely on cores or discs at breast height. Growth data from other sources are helpful: e.g. (a) higher levels in the same trees, for comparison with breast height records; (b) trees of the same species in nearby areas, known to have been free from infestation during the period in question; (c) trees of other species growing in the same stand, known to be unsusceptible or only moderately susceptible to attack by the insect defoliator. Visual comparison of the growth curves resulting from these various sources may be sufficient to clarify the influence of defoliation on growth of the susceptible species (Reeks and Barter, 1951).

In an attempt to eliminate the influence of climatic fluctuations, a crude method has been used in some unpublished Canadian studies of the effects of insect defoliation. The method is dependent on growth data for a companion species not attacked by the insect. It consists in converting the growth data for the susceptible species to a series of ratios, using the corresponding yearly records for the unsusceptible species as the appropriate divisors. This simple method assumes that the two species respond similarly to environmental factors other than defoliation, and that a decline in the series of ratios is a measure of the influence of defoliation alone. These are perhaps unwarranted assumptions even for tree species growing together—in fact, in-

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teractions might well be expected. The method has not been evaluated critically, and is unlikely to be used extensively now that more sensitive methods are available.

A voluminous literature has accumulated on tree ring analysis, but reference will be made here only to a few studies that throw light on the distribution of radial increment in tree stems. Onaka (1950) reviewed the literature on the vertical distribution of radial growth, and carried out numerous observations and experiments with *Pinus densiflora* S. and Z., *Pinus thunbergii* Parl., and *Chamaecyparis obtusa* S. and Z. He reported increase in ring width from the apex to the position of maximum branch development, and decrease in the lower part of the live crown. In the branchless portion of the stem, the distribution of ring width was related to tree condition: (a) in vigorous trees with large crowns, and in open-grown trees with large crowns and short branchless stems, ring width showed little or no decrease below the crown and often increased near the roots; (b) in close-grown trees with small to medium crowns, ring width decreased to a minimum near the base of the tree, and tended to increase abruptly at the root level.

From a series of disbudding, pruning, and girdling experiments, supplemented by measurement of growth hormone in the stem, Onaka concluded that the vertical distribution of radial increment is governed by the production and distribution of growth hormone and the flow of nutritive substances; that the growth hormone is produced by growing buds, cones, new and even old needles; and that nutritive substances are manufactured chiefly by old needles in the early part of the season and by new needles later in the season.

In a mathematical analysis of periodic cross-sectional growth in loblolly pine trees subjected to differential pruning, Labyak and Schumacher (1954) show that area increment is maximum at the base of the live crown; and that the contribution of branches in the upper crown, especially in the top one-tenth of tree height, is greatest at or near the base of the branch. The contribution of branches in the lower half of the tree is more or less evenly distributed over the stem between branch base and point of root influence.

The distribution of radial increment in red pine, *Pinus resinosa* Ait., has been studied systematically by Duff and Nolan (1953). From trees 15 to 30 years of age, complete records were taken of internodal lengths and the width of all annual rings in all internodes. The assemblage of ring measurements from a single tree, when plotted (see their Fig. 5), reveals an orderly design of ring widths which can best be described in terms of three sequences as follows:

Type 1 sequence. This is the series of measurements of the width of a given ring in all the internodes in which it occurs. The most recently formed ring has normally the longest series of measurements, comprising widths for all internodes from the apex of the tree to its base. The series of ring widths, starting at the apex, rises to a maximum in the first few internodes, and then gradually declines in successive internodes toward the base. This regular pattern, repeated by successive rings as they are laid down, is attributed by Duff and Nolan to nutritional gradients in the axis, arising from the distribution of foliage and incidence of light. Random extrinsic factors cause fluctuations in type 1 sequences, but these are usually masked by the characteristic "pattern" due to intrinsic growth factors.

Type 2 sequence. This is the series of width of rings laid down annually in any one internode, corresponding to conventional sequences based on a core or disc at breast height, or any other single level in the tree. The series of ring widths, starting at the center, typically rises to a maximum in the first few rings and gradually declines in successive rings toward the periphery. The strong pattern in the early part of the sequence is derived from the pattern of the type 1 sequence and is therefore attributable to nutritional gradients. In the type 2 sequence, systematic variations in the pattern tend to obscure the effects of random extrinsic factors.

In the type 1 and type 2 sequences, the series of ring widths toward the base, or the periphery, are produced by progressively "older" cambia. At each successively lower internode in the type 1 sequence, the cambium producing the internodal section of the *same growth ring* is one year older than the cambium in the internode immediately above. Similarly, in any one internode, each successive growth ring is produced by cambium one year older than the cambium which produced the preceding growth ring. In any one internode, the *Xth* ring is therefore equally the *Xth* term of the appropriate type 1 and type 2 sequence.

Type 3 sequence. This is a unique sequence first defined by Duff and Nolan, from which the factors of cambial age and nutritional gradient are eliminated. The sequence consists of annual rings laid down by cambium of uniform age, but in successive internodes. The innermost ring in each internode from the apex downward would comprise such a sequence, based on radial increment of the year in which the leader of the tree was formed. The third ring in each internode from the third, downward, would comprise a sequence based on the product of cambium in its third growing season in each internode; and so on. The type 3 sequence is thus free from effects of nutritional gradient or cambial age, and is theoretically the best suited of the three types to portray the effects of extrinsic factors on radial growth.

Among extrinsic factors, Duff and Nolan recognize site quality and stand density, which have a systematic effect on radial growth, producing what is called "configuration" in type 3 sequences; and random variations, such as weather, which produce irregular fluctuations in the growth curve. To these, we would add a third category, neither entirely systematic nor random, but periodic and usually with cumulative effects for a period of years until the tree succumbs or recovers: we refer to serious defoliation that accompanies major outbreaks of defoliating insects.

The studies reported here had two objectives: 1) to determine whether patterns of radial growth similar to those in red pine are found in other species of comparable growth habit, as Duff and Nolan (p. 474) surmised would be the case; and 2) to determine the suitability of the various types of growth sequences as means of portraying the effects of insect defoliation on radial growth. These studies were extensions of work already in progress by the Forest Biology Division in stands of balsam fir, *Abies balsamea* (L.) Mill, var. *phanerolepis* Fern. in New Brunswick; of tamarack, *Larix laricina* (DuRoi) K. Koch, in Manitoba; and of lodgepole pine, *Pinus contorta* Dougl. var. *latifolia* Engelm. in Alberta. Balsam fir and lodgepole pine are comparable in general growth habit to red pine. However, balsam fir retains its old needles somewhat longer than red pine and lodgepole pine develops quite strong whorls of internodal branches. Tamarack differs from the other species in being deciduous; the nodal whorls of branches are less regular, and may be confused with internodal branches.

In referring to the several growth sequences in the following sections of this paper, we employ the following descriptive terminology; *oblique* sequence, equivalent to type 1 of Duff and Nolan; *horizontal* sequence, equivalent to type 2; and *vertical* sequence, equivalent to type 3.

We are indebted to our colleagues in the Forest Biology laboratories at Fredericton, Winnipeg, and Calgary for advice, criticism, and assistance during the investigations reported here; and to M. L. Prebble, Chief of the Forest Biology Division, for suggesting this co-ordinated study in widely separated parts of Canada, and for

editorial assistance in preparation of the manuscript.

Growth in Balsam Fir

Studies of radial growth of balsam fir were carried out by D. G. Mott in the Green River and Kedgwick watersheds in northwestern New Brunswick, in conjunction with long-term investigations of the ecology of the spruce budworm, *Choristoneura fumiferana* (Clem.).

Tree selection. For the investigation of growth sequences in balsam fir, trees were selected from two of the predominant age classes found in this part of the boreal forest region: immature stands of nearly pure balsam fir arising after the 1912-20 outbreak of the spruce budworm; and mature (80-year-old) stands of balsam fir with a small content of white spruce, *Picea glauca* (Moench) Voss. Both stand types are well stocked. White birch, *Betula papyrifera* Marsh., a minor component of these stands, was killed by "birch dieback" prior to the present outbreak of the spruce budworm. Since 1949, most of the susceptible stands of the spruce-fir association in northern New Brunswick have been subjected to repeated defoliation by the spruce budworm.

Tree A (Fig. 1) was a young, fully foliated balsam fir from the immature stand. It was representative of the codominant crown class, was 5.7 inches in diameter at breast height, and 43 feet in height. Tree B (Fig. 2) was a defoliated balsam fir, representative of the codominant crown class in the mature stand. It was 9.0 inches in diameter and 61 feet in height. Tree B died in 1954, following complete defoliation of the new growth each year from 1951 to 1954 and 65 percent defoliation in 1950.

In addition, less intensive growth measurements are presented for five trees from the immature undefoliated stand from which Tree A was taken, and on five trees from a comparable young stand which had experienced defoliation by the budworm from 1950 to 1954, to the extent of 20, 45, 91, 98, and 98 percent of the current new growth, respectively.

Growth measurement. Discs were taken from the midpoint of each internode, which could easily be identified by the whorls of branches, or the branch stubs or scars in trunk sections within or close to the crown. In lower parts of the trunk, frequent splitting was required to determine nodal points. Ring growth was measured to the nearest 0.13 mm. along two average radii in each disc, each ring width being thus the average of two measurements.

Growth sequences. The typical pattern of the *oblique* sequence is shown in four rings of tree A (Fig. 1a). This pattern occurs in balsam fir trees with crowns of moderate fullness, growing under conditions of moderate competition. Its gross features are the rapid increase of ring width to a maximum in the third to seventh internode from the apex of the tree, and the gradual decline of ring width in successively lower internodes. Deviations from the typical pattern are not uncommon. One of them is shown in Fig. 2a, where the 1945 ring of mature tree B maintained its width just short of the maximum in the 4th to the 25th internodes. Maintenance of ring width at the lower internodes was associated with well developed crowns and more exposed growing conditions in the mature stand.

Curves of the *horizontal* sequence for balsam fir (Figs. 1b, 2b) show the effect of the pattern of the oblique sequence, namely, increase in the width of successive rings at a given level in the tree to a maximum a few years after the internode is formed, and then gradual decline in rings laid down later in the same internode.

Curves of the *vertical* sequence (Figs. 1c, 2c) show no obvious pattern, but irregular fluctuations due to flowering, drought, and defoliation. The younger tree (Fig. 1c) had not yet produced heavy crops of flowers, but the older one had. The depressing effect of flower production on radial increment is clearly seen in the

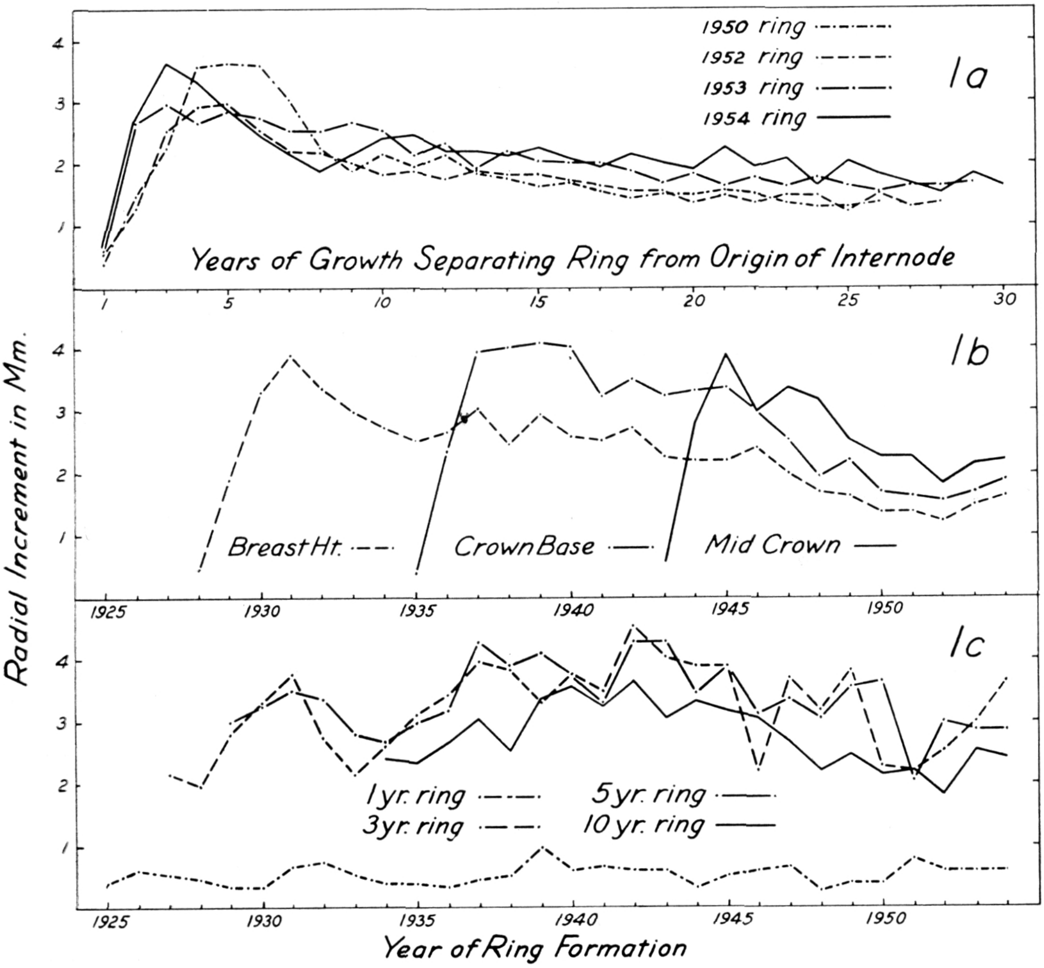

FIGURE 1. *Curves of radial growth in young, undefoliated balsam fir (tree A). Fig. 1a: curves of the oblique sequence for the 1950, 1952, 1953 and 1954 growth rings. Fig. 1b: curves of the horizontal sequence at the breast height, lower-crown and mid-crown levels. Fig. 1c: curves of the vertical sequence for the 1-, 3-, 5-, and 10-year rings. To show the pattern of the oblique sequence more clearly (Fig. 1a), all curves of this sequence have been aligned to a common scale on the X-axis, by using the abscissal scale "years of growth separating ring from origin of internode"—the ring formed in the year of internode formation being assigned number 1 in the series. If the internode numbers of the tree at time of felling had been used as the abscissal scale, the curves would be separated in the chart. The curve for the 1950 ring would start at the internode formed in 1950, the curve for the 1952 ring in the internode formed in 1952, and so on.*

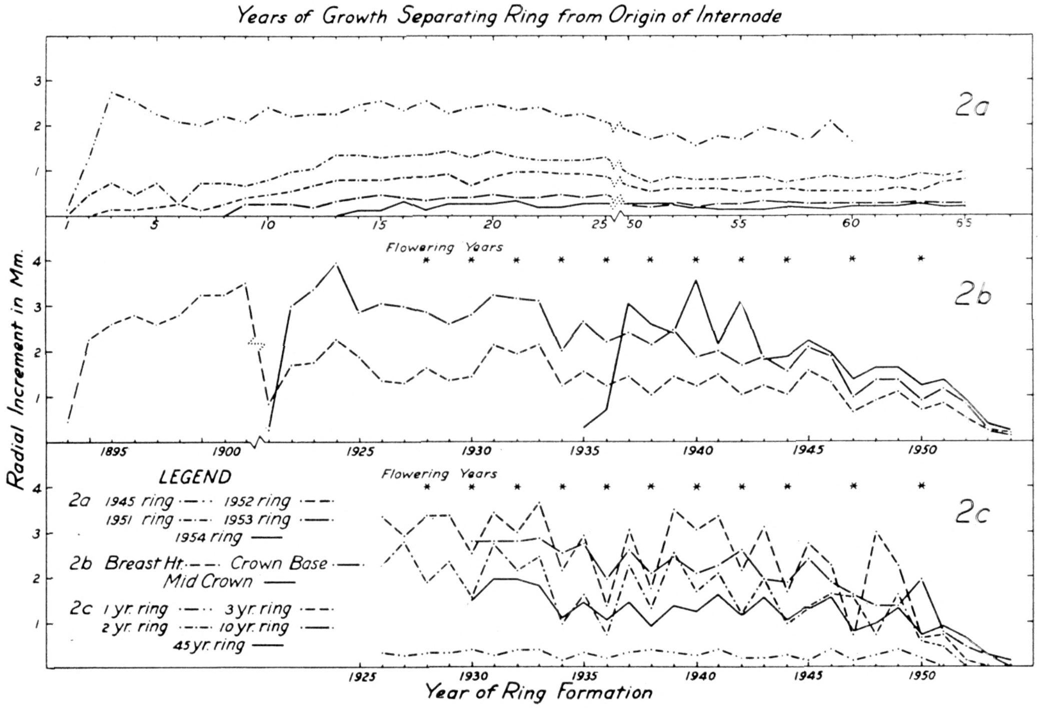

FIGURE 2. *Curves of radial growth in mature, defoliated balsam fir (tree B). Fig. 2a: curves of the oblique sequence for the 1945, 1951, 1952, 1953 and 1954 growth rings. Fig. 2b: curves of the horizontal sequence at the breast height, crown-base, and mid-crown levels. Fig. 2c: curves of the vertical sequence for the 1-, 2-, 3-, 10-, and 45-year rings. Years of staminate flower production are marked in Figs. 2b and 2c.*

curves of the vertical sequence (Fig. 2c), and to a somewhat lesser extent in the curves of the horizontal sequence (Fig. 2b). Morris (1951) has described several other effects of heavy flowering in balsam fir, including reduction of needle length and total foliage production.

Subnormal June rainfall, characteristic of northern New Brunswick from 1943 to 1948 (Greenbank, 1956), undoubtedly contributed to decline of growth in balsam fir stands at that time (Figs. 1c, 2c). However, the effect of drought was much less clearcut than that of frequent flowering and of defoliation after 1950.

Influence of budworm defoliation. Injury by this insect occurs in May and June. Mining of old needles and feeding on staminate flowers occur early in the spring before the vegetative buds have burst. Later, the larvae feed in the opening vegetative buds and destroy the newly-appearing foliage, and, when populations of the budworm are high, some of the older foliage as well. Damage is more severe in the tops of trees. The apex of the tree, the upper branches, and the tips of the lower branches begin to die after the third year of complete or almost complete defoliation of current foliage. Tree mortality generally begins after the fifth year of severe defoliation (Belyea, 1952).

Seasonal and periodic increment of defoliated trees has been reported by Swaine and Craighead (1924), Belyea (1952), and Blais (1954), in the form of curves of the horizontal sequence, usually at breast height in the tree. Reduction of radial growth at breast height is first apparent one to three years after the first defoliation, and the growing period is progressively shortened by successive annual defoliations (Belyea, 1952). Effects of defoliation are seen in all three sequences of the mature tree (Fig. 2). Curves of the oblique sequence for the 1951 to 1954 rings (Fig. 2a) show a general reduction as contrasted with the pre-outbreak ring of 1945. Other effects of defoliation are lack of the characteristic maximum width in the upper internodes, and complete absence of the annual ring in the top of the tree for a progressively greater number of internodes as the defoliation continued in 1952 and later. In the year of death (1954), the current ring was very narrow from the 14th internode to the bottom of the stem, and was absent above the 14th internode.

Curves of the horizontal sequence (Fig. 2b) show great reduction of the 1952-54 rings laid down at the three levels. However, the influence of defoliation is confounded by the effects of flowering and the gradual decline of radial growth inherent in this type of sequence. The significance of growth reduction could be inferred if nearby stands of comparable age and density, free from budworm attack, were available for ring-growth studies. However, uninfested stands of susceptible age are uncommon during an active, widespread infestation. Since effects of budworm defoliation on ring growth are most severely and quickly reflected in the top of the tree, discs from the uppermost internodes should be included in series for careful study if accurate appraisal is to be expected from growth curves of the horizontal sequence.

Curves of the vertical sequence (Fig. 2c) reflect the effect of defoliation in various degrees. There was a general decline in all curves after 1950. The 45th ring declined gradually, but still had a measurable width in 1954 (this occurred in the 45th internode from the top of the tree). The 10th ring declined to zero in 1954, and the first- to third-ring sequence declined to zero in 1951, 1952, and 1953 respectively. These curves show the serious consequences of defoliation on ring growth in the upper internodes, but not so clearly as the curves of the oblique sequence (Fig. 2a).

Complete curves of the oblique sequence require measurements of each designated ring in each internode. However, since the pattern is essentially linear below the internodes of maximum ring width, an outline of the pattern may be obtained by measuring ring widths in each of the upper 10 or more internodes (to obtain the point of inflection), and thereafter at selected intervals, for example, every 10th or 15th internode. Oblique-type curves based on average ring measurements of five balsam fir trees, partially sampled in this manner and representing a young uninfested stand, are shown in Fig. 3a. All curves show the typical pattern of rapid rise in the upper internodes, gradual decline thereafter, and butt swell in the lowest part of the tree. Fig. 3b shows similarly abbreviated oblique-type curves for five trees from an infested stand. Progressive ring reduction occurred throughout the stem as the budworm defoliation continued from year to year. The consequences in this young stand were less drastic by 1954 than in the mature stand represented by Fig. 2.

Development of oblique-type curves based solely on measurement of selected internodes, will often be adequate to detect the effect of defoliation. The substantial saving of time arising from partial study of individual trees will permit more extensive sampling of stands, on the basis of tree size, crown class, defoliation history, and so on.

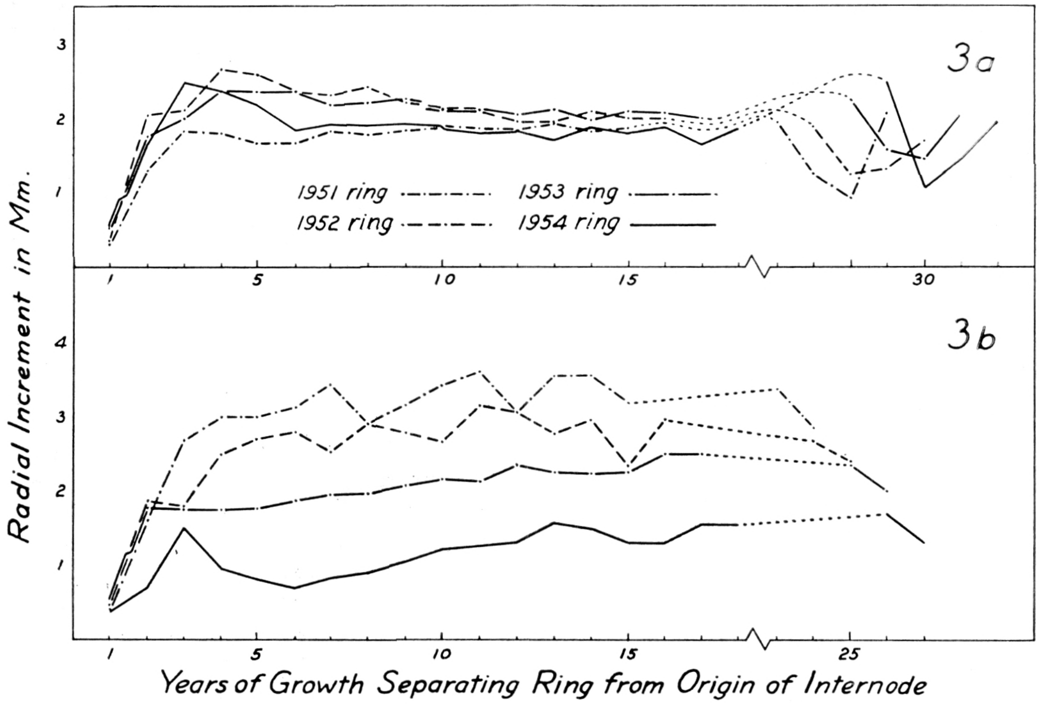

FIGURE 3. *Average curves of the oblique sequence for the 1951, 1952, 1953 and 1954 rings, based on partial sampling of the ring widths in 5 young, undefoliated balsam fir trees (Fig. 3a) and 5 young, defoliated trees (Fig. 3b).*

Growth in Tamarack

Radial and terminal growth of tamarack were studied by L. D. Nairn in Manitoba, as part of a series of investigations on the larch sawfly, *Pristiphora erichsonii* (Htg.).

Tree selection. For the investigation of growth sequences in tamarack, representative trees were selected from each of two tamarack stands in southeastern Manitoba, at the end of the 1953 growing season. These stands, as well as all others in the region, had been infested by the larch sawfly during recent years.

Tree C (Fig. 6) was 47 years old at the 1-foot level, was 5.1 inches in diameter at breast height, and 52 feet in height. It was representative of the dominant crown class of a dense, even-aged 50-year-old stand growing on a dry site near West Hawk Lake in the Whiteshell Forest Reserve. Tamarack, averaging 5 inches in diameter and 50 feet in height, comprised 90 percent of the stand; black spruce (*Picea mariana* (Mill.) B.S.P.), averaging 4 inches in diameter and 35 feet in height, made up the remaining 10 percent of the stand. Tree D was representative of the codominant crown class of a 30-year-old pure tamarack stand, and was situated at the edge of a small clearing in the stand. Both trees were given the same analytical treatment. Since the same results and conclusions are drawn from the two trees, curves are given here only for tree C.

Growth measurement. Radial and linear growth was recorded in every internode throughout the length of the stem. The upper four or five nodes were readily identified by the branch whorls, but difficulty was encountered in locating nodes in lower parts of the stem owing to the prominent development of internodal branches (Fig. 4). This problem was solved by locating the approximate position of the nodal points from the difference in ring counts in a series of discs along the stem. The stem was split in these regions and the nodes located by careful examination of the pith (Fig. 5). A disc was removed from every internode but its location was governed by the remaining unsplit portions of the internode. The annual rings were measured[1] and averaged for three radii on each disc. A complete record of the radial growth throughout the entire length of the stem was obtained and any desired sequence could readily be obtained from the data.

[1]Ring widths were originally measured to the nearest 0.01 inch. Rings of less than 0.01 inch were given a plus (+) rating but were valued at 0.005 inch in the calculations. In the interest of uniformity with other parts of this paper, the measurements have been converted to the metric system.

FIGURE 4. *Growth habit of tamarack, showing incomplete whorls of nodal branches and prominent development of internodal branches.*

FIGURE 5. *Nodal point in the pith of tamarack.*

Growth sequences. Typical *oblique* sequences are shown for the 1924, 1944, and 1947 rings in Fig. 6a. The width of each ring reaches a maximum at about the third or fourth internode, gradually declines in the following 10 to 20 internodes, and maintains a rather uniform low rate in the lower levels of the stem. Curves for the 1949, 1951, and 1953 rings are affected by sawfly defoliation and are referred to in a later section.

Horizontal sequences for the 1-, 16-, 33-, and 43-foot levels are shown in Fig. 6b. The curves for the upper three levels attain their maximum in the third to thirteenth rings from the pith, and then decline abruptly. The normal decline of the horizontal-type sequence is in this case greatly hastened by increasing competition within the stand, and by sawfly defoliation during the past five or six years of the growth record. The curve for the 1-foot level conforms with the others in the recent decline, and it also shows the typical pattern during the first five years. Its fluctuations during the intermediate period suggest

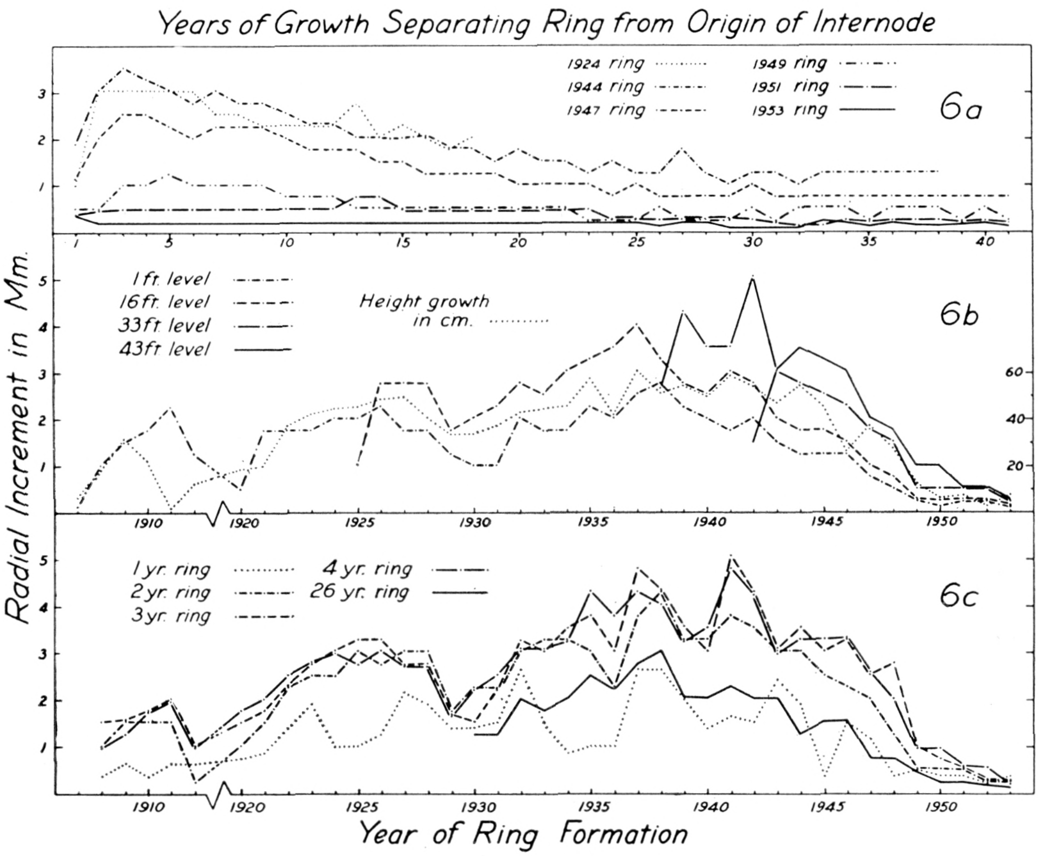

FIGURE 6. *Curves of radial growth in young tamarack (tree C). Fig. 6a: curves of the oblique sequence for the 1924, 1944, 1947, 1949, 1951, and 1953 growth rings. Fig. 6b: curves of the horizontal sequence at the 1-, 16-, 33-, and 43-foot levels. Height growth also shown, ordinate scale in cm. at right. Fig. 6c: curves of the vertical sequence for the 1-, 2-, 3-, 4-, and 26-year rings. Tree defoliated by the larch sawfly from 1947 to 1953.*

quite variable, but on the whole, good growing conditions until 1938.

Vertical sequences for the 1-, 2-, 3-, 4-, and 26-year rings are shown in Fig. 6c. The width of the 1-year ring, produced in each internode during the year of internode formation, is quite variable throughout the length of the internode, owing to taper of pith and xylem in the tree terminal. For reasons described earlier, it was not possible to make growth measurements in tamarack at the same relative points in different internodes, and this inconsistency in point of measurement casts doubt on the validity of the vertical sequence for the 1-year ring. This objection does not apply to sequences of rings laid down at a greater distance from the pith, because the effect of taper within the internode is largely absent after the year of internode formation.

Curves for the 2-, 3-, 4-, and 26-year rings are devoid of obvious pattern, yet show great consistency in their year-to-year fluctuations. These vertical sequence curves also vary consistently with the horizontal sequence curves for the same tree (Fig. 6b). Correlation between the vertical sequences and the horizontal sequence at the 1-foot level (which, among horizontal sequences, is least influenced by intrinsic growth pattern) is stronger for the vertical sequences based on rings at a greater distance from the pith (Table 1).

Annual height growth in Tree C (Fig. 6b) was measured as the distance between successive nodal points in the pith. A positive and significant correlation was found between annual height growth and radial growth as recorded in vertical sequences, as well as in the horizontal sequence at the 1-foot level in the stem (Table 2). Among the vertical sequences, that based on the ring nearest the pith was most strongly correlated with height growth, and there was a general decline in the degree of correlation as distance of the ring from the pith increased. The lowest correlation with height growth was shown by radial growth of the horizontal sequence. Duff and Nolan (1953) have shown that terminal growth is influenced by extrinsic as well as intrinsic factors. Among the former must be included factors that operate during the year of bud formation, and others that operate during the year of shoot elongation. On the basis of the correlation coefficients shown in Table 2 (similar results were obtained in tamarack tree D), from about 48 to 85 percent (r^2) of the variation in annual height growth of tree C may be

TABLE 1. Correlation between annual radial growth (horizontal sequence) at the one-foot level and various vertical sequences in Tamarack (tree C).

Vertical Sequences (based on indicated ring from pith)	n	r^1
2	44	.790
4	44	.784
6	42	.681
9	39	.771
16	30	.867
26	22	.978

[1]All coefficients significant at 1 percent level.

TABLE 2. Correlation between annual height growth (internodal length) and radial growth as expressed in various sequences in tamarack.

Sequence Type	Ring No.	n	r^1
Vertical	2	44	.921
"	4	44	.860
"	6	42	.822
"	9	39	.844
"	16	32	.888
"	26	22	.736
Horizontal (1-foot level)	2-47	44	.696

[1]All coefficients significant at 1 percent level.

attributed to variations in factors that caused concurrent fluctuations in radial growth.

Influence of sawfly defoliation. A recent outbreak of the larch sawfly affected most of the tamarack stands in western Canada after 1940. The larvae feed from the extremities of the branches inward and the peak period of feeding generally occurs in July. The needles are first consumed at the top of the trees and at the periphery of the crown. Complete defoliation is common in severe infestations. Annual radial growth of tamarack is almost complete in Manitoba before seasonal defoliation is at its peak. The effect of defoliation on radial increment is not apparent during the first year of an infestation. Severe defoliation of a healthy tree is followed by refoliation later in the same summer. Defoliation in successive years causes reduced production of foliage and shoots, death of lower branches and scattered tips, and ultimately the death of upper branches and, occasionally, the entire tree.

Defoliation was light from 1939 to 1946 in the tamarack stand in which tree C grew. Defoliation was recorded annually during the period 1947-1953, with results as follows:

Year	percent of defoliation	Year	percent of defoliation
1947	15	1951	45
1948	45	1952	90
1949	70	1953	75
1950	60		

The influence of defoliation may be seen in the several sequences of Fig. 6. Curves of the oblique sequence for 1949, 1951, and 1953 (Fig. 6a) show greatly reduced increment throughout the entire bole; in the last two of these there is complete obliteration of the characteristic maximum ring width near the top of the tree. Competition within the stand reduced radial increment whereas repeated defoliation by the larch sawfly eliminated the differential in growth rate normally reflected in greater ring width in the upper internodes. In oblique sequences for other years (not illustrated) there were inconsistencies in pattern, such as lack of a prominent maximum width in the upper internodes, or maintenance of uniform width in lower internodes. This suggests that such extrinsic factors as competition, drought, seed production, and defoliation affect the distribution of radial increment along the bole in different ways.

Curves of the horizontal sequence (Fig. 6b) reflect the influence of intrinsic factors causing pattern, extrinsic factors causing configuration, and random extrinsic factors. The effect of defoliation after 1947 cannot readily be separated from the effects of other factors which were operative as early as 1939 or 1940 (curves for 1- and 16-foot levels). Curves for successive ring widths at the 33- and 43-foot levels decline rapidly from their early maxima (1942 and 1944 respectively), the rate of decline being well established before larch sawfly defoliation became severe. The chief characteristic of the curves of the horizontal sequence during the later years is the minimal growth rate at all levels. The curves of this sequence do not permit identification of the year which first reflects the effects of defoliation, nor any clear evaluation of the extent of reduction due to defoliation in the later years.

Variation in curves of the vertical sequence (Fig. 6c) are, by definition, due exclusively to extrinsic factors. However, there is no clear distinction between the effects of competition, which was operative in the early 1940's, and of defoliation, which became severe six or seven years later.

This test of the three growth sequences in tamarack has been complicated by both the increasing competition in the stand and the absence of check trees free from sawfly defoliation during recent years. Under these handicaps, the horizontal and vertical sequences show the combined effect of competition and defoliation upon radial increment. Only the successive curves of the oblique sequence (Fig. 6a) show clearly a distinctive effect of severe defoliation, namely, elimination of the typical growth pattern of a given ring in the upper internodal sections of the stem.

Growth in Lodgepole Pine

Studies of radial growth of lodgepole pine were carried out by J. A. Cook as part of a series of investigations on the lodgepole needle miner, *Recurvaria starki.*, Free., in the region of Banff National Park, Alberta.

Tree selection. Two trees, among many studied, were selected for illustration of growth sequences in lodgepole pine. These trees were free from mechanical injury, frost or grazing damage, and abnormal competition, and were representative of the stands from which they were taken. Their crowns were well formed with distribution of the branches in regular whorls.

Tree E grew in a moderately dense, pure stand on a gently inclined slope near valley bottom in Kootenay National Park. The tree was 25 years old and 33 feet in height, with crown depth about two-thirds of tree height. So far as is known, there have been no insect infestations of sufficient intensity to cause defoliation during the life of young stands in this locality.

Tree F grew on the border of a mature, 100- to 110-year-old lodgepole pine stand on a 10 percent southwest slope in the Bow Valley near Lake Louise, in Banff National Park. The tree was 40 years old and 30 feet in height, with a well developed and regular crown. The area from which tree F was taken supported very heavy infestations of the lodgepole needle miner for several years.

Growth measurement. In lodgepole pine, there are commonly one or two, and occasionally three, internodal whorls of branches. Radial growth tends to be distorted in the immediate vicinity of the internodal branches, but this effect disappears about 1 to 1½ inches from the branch base. The pith has a moderate taper within a single internode, and the width of the first ring narrows quite strongly toward the apex. To avoid variability from these sources, ring measurements were made on discs taken one-third of the internodal length from the base. This point of measurement was always below the lowermost whorl of internodal branches. The average width of each ring was based on measurements in four radii of the disc.

Growth sequences. Representative *oblique* sequences for uninfested tree E are shown in Fig. 7a. The width of each growth ring increases to a maximum in the then third to sixth internode from the apex, and gradually decreases at lower points in the stem. Differences in the height of the various curves reflect the influence of external factors such as competition and weather. Reduced width of the 1954 ring, in comparison with those laid down earlier, is suggestive of increasing competition within the stand, but the evidence is not strong. Random seasonal variations in climate could equally be responsible for the observed differences in width of successive rings.

Fig. 7b shows *horizontal* sequences at the 4-, 6-, and 13-foot levels in tree E. At any one level, the maximum width is usually found in about the fifth ring from the pith. Secondary peaks in later rings (e.g., the 1947 and 1948 rings at the 6-foot level) during particular years, are indicative of sufficiently good growing conditions to override the typical pattern of the horizontal sequence.

The curves of the *vertical* sequence (Fig. 7c) illustrate the general trend referred to as "configuration." The trend for tree E is a gradual increase until about 1948 and a gradual decrease thereafter which probably resulted from increased stand competition. Sharper fluctuations which do not change the over-all trend

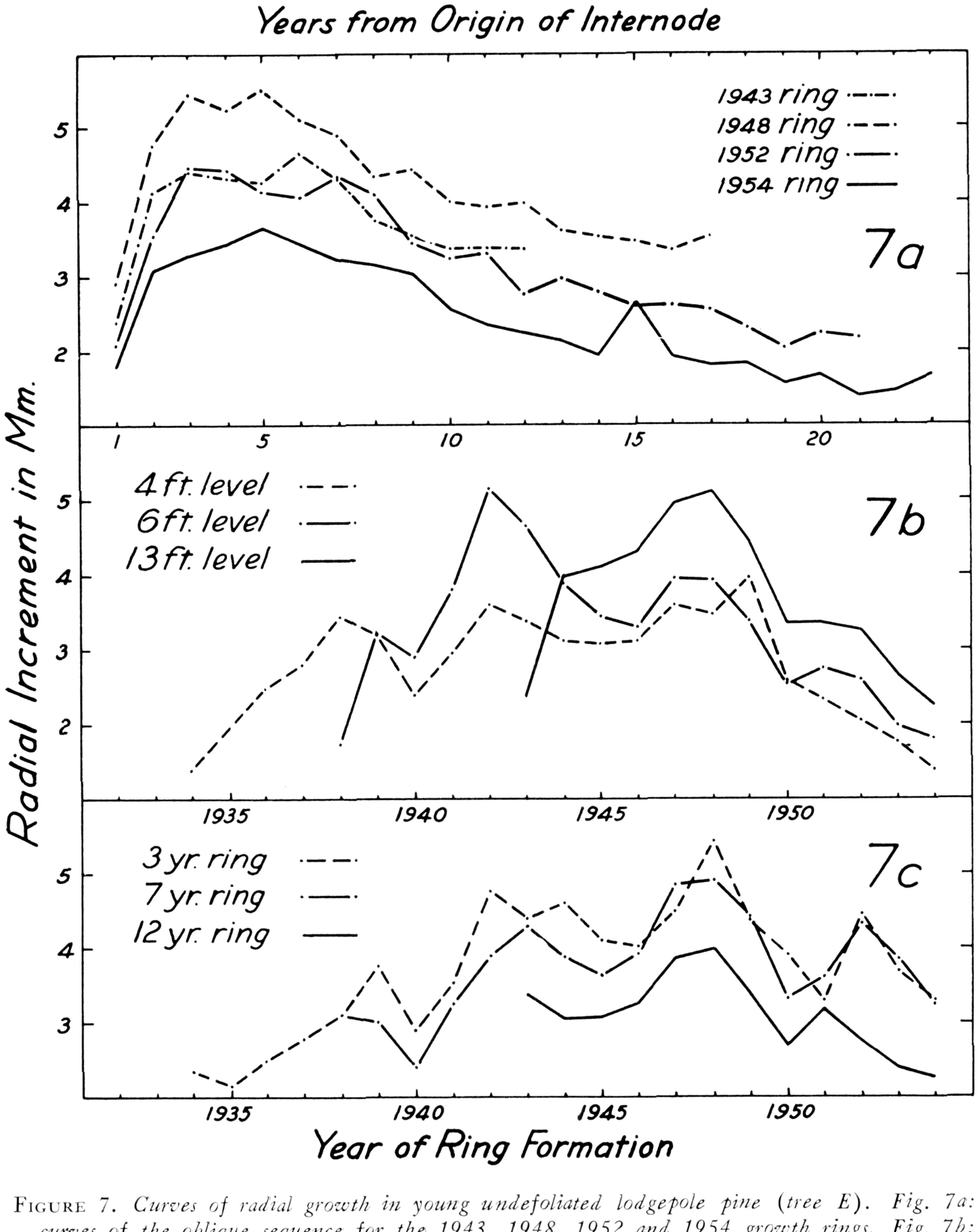

FIGURE 7. *Curves of radial growth in young undefoliated lodgepole pine (tree E). Fig. 7a: curves of the oblique sequence for the 1943, 1948, 1952 and 1954 growth rings. Fig. 7b: curves of the horizontal sequence at the 4-, 6-, and 13-foot levels. Fig. 7c: curves of the vertical sequence for the 3-, 7-, and 12-year rings.*

materially are probably the result of random weather factors.

Influence of needle miner defoliation. The lodgepole pine needle miner has a 2-year life cycle. Larval development extends over a 21-month period in three succeeding summers, and during this time each larva usually destroys three needles (Stark, 1954). The needle miner infestation is generally heaviest in the upper crown and in the younger needles. The gradual but cumulative loss of needles leads to reduced radial increment. Current studies indicate that defoliation of 40 to 50 percent is necessary to have a measurable effect on radial increment, and that the reduction of increment first appears about two years after defoliation (Stark and Cook, 1957).

The infestation was first noted in the Lake Louise area in 1942 (Hopping, 1946), but subsequent defoliation studies indicated that the infestation probably started in the 1930's (Stark and Cook, 1957). Owing to its size and position in the stand, tree F was possibly attacked some years later than the mature stand in the immediate vicinity. The infestation in this area declined after 1948, and was almost eliminated by severe climatic conditions in the winter of 1949-50 (Henson *et al.*, 1954). Since that time the needle-miner population has remained very low.

Figure 8 shows curves of the various sequences for tree F. Among the curves of the oblique sequence (Fig. 8a), that for 1938 precedes the infestation. The 1943 ring, formed in the early stages of the outbreak, lacks the typical maximum width in the upper internodes. The greatly depressed 1948 ring shows the full effect of progressive defoliation. Although the 1954 ring shows some improvement following the decline of the needle miner, the weakened condition of the upper crown is evident in the flattened growth curve for the topmost internodes. If curves for all rings were introduced into Fig. 8a, there would be a more gradual merging of the curves of the pre-infestation and the infestation periods, each curve being influenced by intrinsic as well as external factors. Even with the full complement of curves, some doubt remains as to the year in which the influence of defoliation was first reflected in the curve of ring growth.

Curves of the horizontal sequence for the 4-, 10-, and 16-foot levels (Fig. 8b) show the gross effects of defoliation, namely, several years of decline leading to minimal growth in the period 1947-1951, and slight recovery in 1952 to 1954 following reduction of the needle miner population. The first consistent and sustained reduction in the three curves occurred in 1943, and one might attribute this to the effects of defoliation in 1942, or earlier. However, from the evidence of horizontal sequence curves alone, this interpretation would be open to question: a similar decline might be initiated by growth pattern (see growth curves, 1949 to 1954, in undefoliated tree E, Fig. 7b), or confused with the effects of unfavorable growing conditions.

Curves of the vertical sequence for tree F (Fig. 8c) show an upward trend in the configuration until 1942, where there is a sharp break and a decided downward trend to a low point between 1946 and 1952. Later, the curves rise again. Only severe and prolonged defoliation by the lodgepole needle miner can account for the great depression of growth after 1942. If tree F had not suffered needle miner attack, it is reasonable to expect that the general growth trend would have been similar to that which prevailed before 1942, and to the growth trend in uninfested tree F after 1942. Therefore, 1943 can be accepted with reasonable assurance as the first year of radial increment reduction due to defoliation by the needle miner. If the configuration trend is properly evaluated, it is possible to define the first year of increment reduction due to defoliation as well as the period of severely depressed growth. Confusion due to the influence of random climatic fluctuations can be eliminated to a large extent by careful appraisal

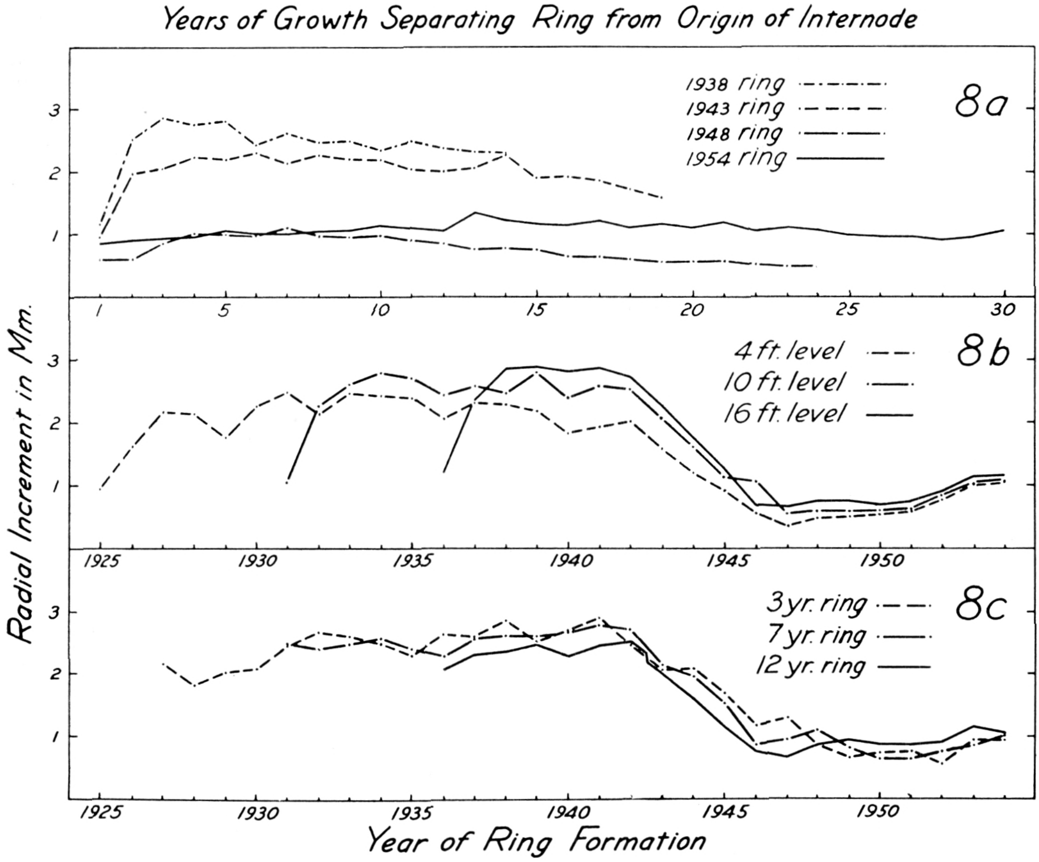

FIGURE 8. *Curves of radial growth in young, defoliated lodgepole pine (tree F). Fig. 8a: curves of the oblique sequence for the 1938, 1943, 1948 and 1954 growth rings. Fig. 8b: curves of the horizontal sequence at the 4-, 10-, and 16-foot levels. Fig. 8c: curves of the vertical sequence for the 3-, 7-, and 12-year rings.*

of the over-all trend in contrast with these minor departures.

Summary and Conclusions

These studies have shown that the distribution of radial growth in balsam fir, tamarack, and lodgepole pine trees growing in natural stands, follows the patterns described by Duff and Nolan (1953) for plantation-grown red pine. In the *oblique* sequence (Type 1 of Duff and Nolan), the width of a given ring, measured in the successive internodes throughout the length of the stem, rises to a maximum in the first few internodes below the apex of the tree, and then gradually declines in successively lower internodes. This pattern is repeated in successive rings as the tree grows in height and diameter.

In the *horizontal* sequence (Type 2 of Duff and Nolan), the width of successive annual rings from the pith to the periphery of the stem reaches a maximum among rings laid down very early at any given height in the tree, and then declines gradually throughout the remaining rings at that level. This attribute of the horizontal sequence follows naturally from the inherent growth characteristics of the tree as expressed in the pattern of the oblique sequence. Typically, the number of the ring having maximum width in the horizontal sequence would correspond to the number of the internode having maximum ring width in the oblique sequence. The early portions of oblique and horizontal sequences are dominated by inherent growth patterns attributed by Duff and Nolan to the influence of nutritional gradients in the tree.

In the vertical sequence (Type 3 of Duff and Nolan), each year's radial growth is the width, in a given internode, of a ring produced by cambium of uniform age. For example, a vertical sequence based on the 3-year ring would be made up of the following terms: the outside ring in the 3rd internode from the top of the tree, for the current year; the 3rd ring in the 4th internode, for the current year less one; the 3rd ring in the 5th internode, for the current year less two; and so on. Similar sequences may be based on any given ring from the pith. The vertical sequence is thus free from the effects of nutritional gradients in the tree, and hence, from inherent pattern; and it may show more clearly than do the oblique and horizontal sequences the effects of certain extrinsic factors, such as climatic fluctuations, changing competition within the stand, defoliation, and incidence of heavy flowering. The influence of recurrent flowering on ring growth of balsam fir is shown in the vertical sequences of Fig. 2c.

The influence of insect defoliation on radial growth was of particular interest in this study. In balsam fir trees defoliated by the spruce budworm, the reduction of radial growth shows up in growth sequences of all three types (Fig. 2). The oblique sequences portray the extent of the progressive reduction throughout the entire stem. In the early years of severe defoliation, the characteristic maximum ring width in the upper internodes is suppressed; later, the ring in the upper part of the stem is completely obliterated for a progressively greater number of internodes. The horizontal sequences at mid-crown and lower crown levels show great reduction of the most recent rings, but effects of defoliation are confounded in part by inherent pattern and by other extrinsic factors such as flowering. The vertical sequences show great reduction of all rings and early obliteration of radial growth in the rings of youngest cambial age, as a result of budworm defoliation. This is consistent with conclusions drawn from the oblique sequences but is not so clearly portrayed, owing to the more involved make-up of the vertical sequence.

The ability of the three sequences to portray the earliest influence of defoliation on radial growth is also of interest. Defoliation of the new foliage of the balsam fir tree illustrated in Fig. 2 was about 65 percent in 1950, and 100 percent in each of the following four years. The oblique sequence shows a marked effect on radial increment in 1951; the horizontal sequence at mid-crown and lower levels, shows a possible effect on radial increment in 1952; and the vertical sequence shows elimination of the 1-year ring in 1951, and similar results for 2-, 3-, and 10-year rings in later years. Sequences of the oblique type appear to be the most useful in portraying the influence of budworm defoliation on radial increment in balsam fir.

In tamarack trees defoliated by the larch sawfly, reduction of radial growth is evident in curves of all three sequences (Fig. 6). The oblique sequences have advantages similar to those detected in the analysis of balsam fir defoliated by the spruce budworm. The horizontal sequences show great reduction at various levels in the stem, but the first evidence of reduction due to defoliation is confounded by pattern and fluctuations in extrinsic factors other than defoliation. The vertical sequences show the great sensitivity of the rings formed by young cambium to fluctuations in extrinsic factors, but the effects of increasing competition and of defoliation are confused in the growth curves.

In lodgepole pine trees defoliated by the lodgepole pine needle miner (Fig. 8), oblique sequences give the best portrayal of growth reductions throughout the stem. However, in the trees studied there was a gradual decrease in the height of oblique-type curves throughout the outbreak period and it was not possible to detect which ring showed the first effects of needle-miner attack. Vertical sequences are superior to horizontal sequences as an indicator of the earliest year of ring reduction due to defoliation.

Growth sequences of the oblique type appear to have peculiar advantages in studying the effects of insect defoliators on radial growth of conifers, especially where injury is more severe in the tops of the trees. Conventional sequences of the horizontal type are less useful; for if taken at low levels in the stem where radial growth is approaching its characteristic minimum, growth fluctuations are less sensitive to environmental changes; and if taken at high levels in the stem, effects of defoliation are likely to be confused with effects of pattern. Sequences of the vertical type have a theoretical advantage over those of the other two types, owing to removal of the effects of pattern. Effects of defoliation and other extrinsic factors should be most clearly portrayed in sequences of rings laid down by "young" cambia, which produces rings of maximum width. In practice, if the object is not only to obtain a measurement of the effect of defoliation over a period of years, but also to detect the first year showing the effect, sequences of both the oblique and vertical types would be desirable. The same series of discs from the internodal points will supply the data for both types.

In preparing sequences of the oblique and vertical types, it is unnecessary to measure all ring widths in all internodes. In oblique sequences, the width of each ring to be studied should be measured in each of the upper 10 or more internodes to establish the growth curve above the point of typical maximum; but to establish the level and shape of the curve at lower points in the stem, ring measurements in every tenth or fifteenth internode should suffice. In vertical sequences, the longest series can be prepared for rings laid down by "young" cambia, i.e., the 1-, 2-, and 3-year sequences, and these are also most sensitive to changing environmental conditions. In preparing growth curves of the vertical sequence type, each year during the period of special interest should be represented by ring measurements in the appropriate internodes, but earlier or later periods could be represented by ring measurements in conveniently selected internodes. Further studies are being made of the usefulness of partial growth sequences in balsam fir, tamarack, and lodgepole pine.

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