INTERNODAL CHANGES IN RING WIDTH ALONG A RED PINE STEM

D.C.F. Fayle

Ontario Forest Research Centre
Ministry of Natural Resources
Maple, Ontario, Canada LOJ 1E0

SUMMARY

Internodal and nodal changes in ring width in a red pine (*Pinus resinosa* Ait.) stem are presented, based on measurements at 5-6 points throughout internodes of a 40-year-old codominant tree. A strong basal increase in ring width occurred within the first and second internodes from the apex. This lessened in lower internode positions, becoming a slight overall decrease below the internode of maximum width (internode 5). Within the internodes above and below the crown base, however, there was again a slight overall basal increase in ring width. Thereafter there was little change within the internodes until the region of butt swell. At the first and second nodes there was a large increase in width from one internode to the next. Changes were minimal at the next few nodes. There were consistent decreases at nodes within and for some distance below the lower crown, with the greatest decrease occurring at or near the crown base. These decreases at the nodes were greater than the increases within the internodes. Thus overall longitudinal changes in the width of the growth layer are a combination of changes within the internodes and at the nodes themselves. Associated changes in cross-sectional area and relationships to branches are also discussed.

Keywords: Ring width, internodes, nodes, growth layer.

INTRODUCTION

The common practice in stem analysis studies of radial growth based on Duff and Nolan's (1953) concepts is to measure ring widths on cross sections from the mid point of internodes, or on sections near this point. When the widths of a particular annual ring are plotted against height in the stem or internode number, a more or less smooth curve of characteristic shape is produced, representing the growth layer profile (GLP)[1]. The idealized shapes of the curve for various growing conditions were summarized by Farrar (1961). For example, in a dominant, plantation-grown conifer, the width of the annual growth layer increases for several internodes from the apex to a maximum value and then decreases. Below the crown the width of the growth layer remains fairly constant and then thickens again near the stem base. But does this curve represent what happens within the internodes? For example, does ring width for a given year increase basally in the upper internodes? Does it decrease basally -- a reverse taper -- along an internode below the point of maximum width?

Duff and Nolan (1953) measured ring widths in "the upper, median, and lower parts of the fifth internode" of one (?) red pine (Pinus resinosa Ait.). They found that "the pith tapered slightly, the first wood ring strongly and the second wood ring very slightly or not at all. The subsequent rings were found to be substantially uniform and the internode as a whole retains as it grows radially only the taper imparted to it in the first year's growth". Their concern was whether use of data from the mid point of the internode was applicable throughout the internode to calculate internodal ring volume; they concluded that use was justified because the error was small. However, information that can be derived about the detailed shape of the growth layer from their observations is minimal because measurements were limited to 5 years' growth at one internode only, no data were obtained below the point of maximum width, and graphical presentation was in terms of mean radii rather than ring widths.

Furthermore, Duff and Nolan did not comment on any changes in width at the node. But if, as they stated, ring widths are substantially uniform along the length of the internode (except the first), then there must be a definite increase in the width of the growth layer at each whorl in the upper crown and a decrease in width at whorls in the lower crown to comply with the overall shape of the growth layer described earlier.

To clarify the changes that must occur in ring width between or within internodes, ring widths were measured at 5-6 locations throughout most internodes of a 40-year-old red pine. The results are presented and discussed here.

THE MEASUREMENTS TAKEN

A codominant tree was selected in a red pine plantation established in 1937 at a 1.5 x 2.3 m spacing in Simcoe County, Ontario. The soil was a deep, well drained loamy sand.

The 15.5-m tall tree was felled in early summer 1977. The distance from the stem base to each node (branch whorl) was measured to the nearest centimetre. The stem was sectioned at the mid point of each internode; these stem segments were then suitably marked to permit 'reconstruction', placed in plastic bags and kept in cold storage for analysis.

In the laboratory, the stem segments were sectioned immediately above and below each whorl, the latter being closer to the actual node than the

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1 The node marks the start (and end) of each year's height increment and is characterized externally in red pine by a whorl of branches. An internode is the portion between successive nodes. Numbering is from the apex, with node 1 being at the base of internode 1.

former due to branch angle. Except for very short internodes, sections were also taken halfway between these nodal cuts and mid internode to give 5 sections per internode. The nodal segments were sectioned longitudinally to determine the exact location of the node and the origin (terminal or lateral bud) of each year's height growth. Height data were then corrected where necessary. Sections were also taken at the base of branches.

Pith and ring widths were measured on each stem and live branch section, along 2 diameters at right angles to each other, using a stereomicroscope fitted with a measuring eyepiece. Measurements were made to the nearest 0.1 and 0.04 mm for stem and branch material respectively. Average ring widths, radii and cross-sectional areas, by years, were calculated at each stem position and live branch base, and growth layer profiles (GLPs) drawn for the stem.

It became evident as analysis of data progressed that some idea of when branches had died, i.e. the location through time of the live crown base, was required. This was estimated by determining, for the 3 largest diameter branches in each whorl, when the cambium of the branch at its insertion into the stem had died (Andrews and Gill 1939). In addition, the year in which the last complete annual ring occurred near the branch base was recorded as an indication of approaching death.

After examination of the graphical data, the internodes formed during 1947-54 (2.56-7.04 m height in stem) were selected to demonstrate the typical internodal changes in ring width. The length and radial growth of these successive internodes were not affected by damage to the terminal bud and continuation of the main stem from a lateral bud or branch. They were formed after crown closure had commenced and their lengths were similar. The 1947 and 1954 internodes had progressed from the first to the 30th and 23rd positions respectively. To provide additional ring width data in the upper part of the internodes, an extra section was cut from these 8 internodes between the 2 previous upper sections, and ring widths measured.

A composite GLP of 20 internodes was constructed from the 1947-54 internode data, taking into account the relative positions of maximum width and the crown base in the calculations. Minor adjustments were necessary to match up widths in some successive internodes to form this GLP. The term 'composite' is used because the upper part of the GLP is based on rings laid down in earlier years than in the lower part of the GLP, rather than on rings laid down in the same period, as would be the case in a 'normal' GLP. Nonetheless, the pattern of internodal changes is similar.

RESULTS

Ring width

A sample of the typical longitudinal changes in ring width within 4 successive internodes as they progressed from the first to the 20th position in the stem is shown in Fig. 1. Also included are pith width and data for the lower and upper halves of the adjacent internodes to emphasize changes at the nodes themselves. These internodal and nodal changes in width are summarized in terms of a single growth layer by the composite GLP (Fig. 2, left). The region of butt swell is included at the bottom of the GLP and is based on data from the basal 2 m of the stem.

Within an internode pith width increased basally to the mid point, with little change in the lower half; minimum width occurred at the nodes (Fig. 1).

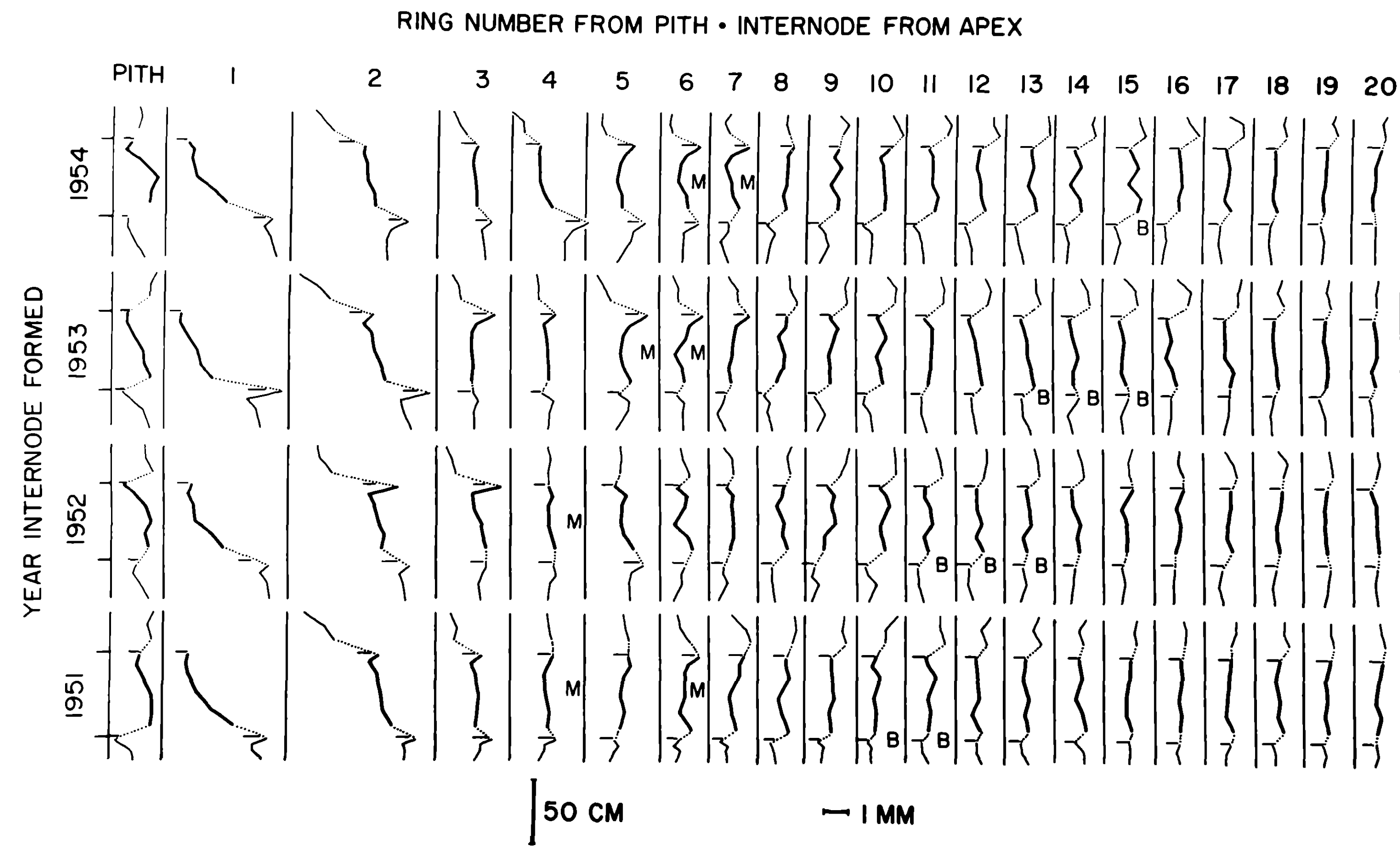

Fig. 1 Changes in ring width along the 1951-54 internodes for the first 20 rings. Part of individual GLPs can be 'seen' in the upper left to lower right diagonals, e.g. the upper part of the 1954 GLP consists of 1954 internode 1, 1953 internode 2, 1952 internode 3, 1951 internode 4 (maximum ring width at the mid point), etc. The yearly locations of maximum ring width (M) and the crown base (B) are indicated.

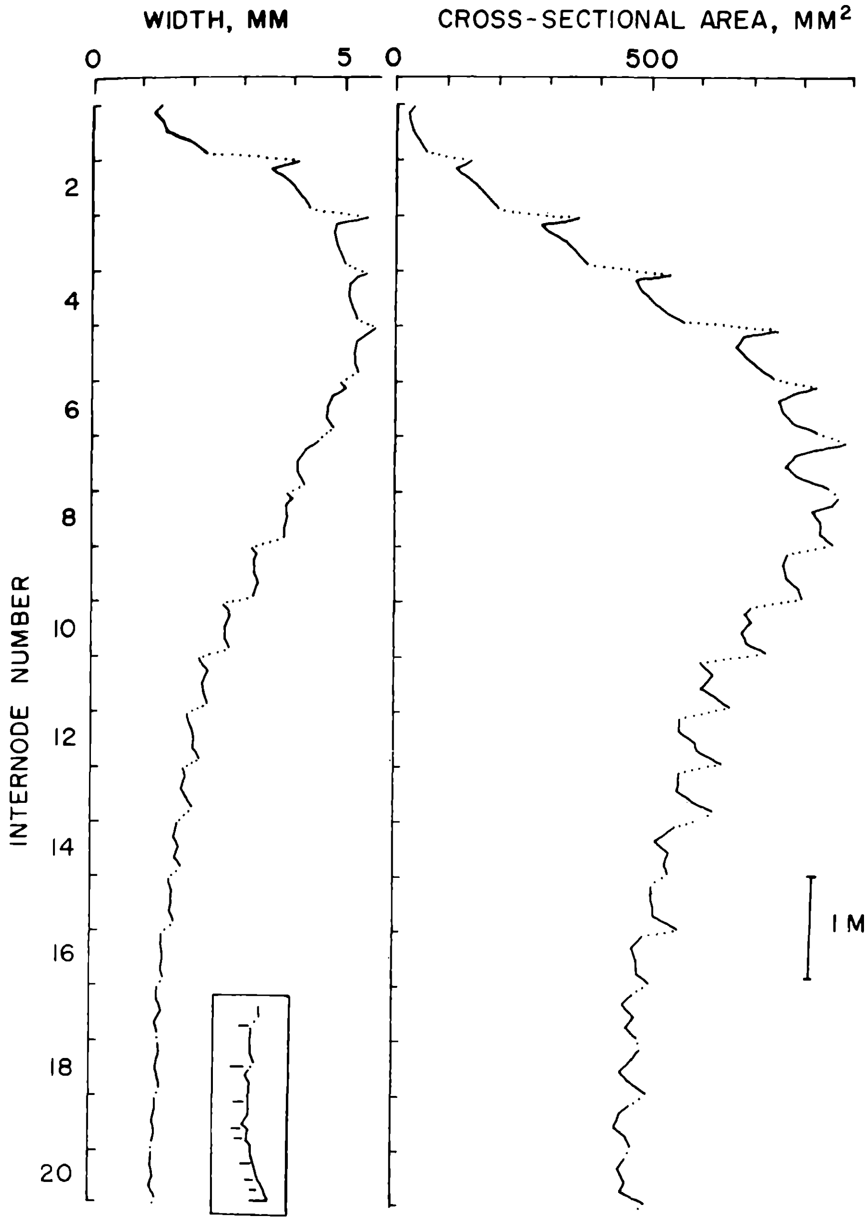

Fig. 2 The composite GLPs for ring width (left) and cross-sectional area (right) based on data from the 1947-54 internodes. Internodes 1 to 8 were derived from those years in which maximum width of the individual growth layers occurred in the 4th or 5th internode from the apex. The lower internodes were based on position above or below the estimated crown base (from 4 above to 9 below), rather than number from the apex. An 'overlap' occurred at position 4 (and 3) above the crown base with internode 8 (and 9) respectively

In general, ring width within an internode switched with time (internode number or ring number from pith) from a basal increase, to a basal decrease, to a basal increase again, and finally to a negligible difference in width. The internode numbers, however, in which these switches occurred was not necessarily the same, but do relate to the locations of maximum ring width and the base of the live crown. Likewise, there were also changes in width from above to below the nodes. Initially, ring width increased at the node but then decreased, with eventually minimal differences occurring. (It should be pointed out that the sampling positions, being at constant distances above and below the nodes, changed with time in relation to the branch axes due to the angle and thickening of the branches.)

More specifically, a marked basal increase in ring width occurred in the first and second internode positions, averaging around 70 and 20% respectively. This basal increase declined over the next few internodes (Figs. 1 and 2), with a correspondingly larger portion of the upper part of the internodes developing a basal decrease in width. For a few internodes below the one in which maximum width of the growth layer occurred (at the mid point of the internode) there was usually a slight overall decrease in width basally (average of 5%), but in the internodes near the crown base there was once again a slight overall basal increase. The latter was maintained for several internodes below the crown base, after which there was little change along the internode.

At the first node there was a marked increase in width from above to below the node, averaging about 70%, with an average 25% increase at the second node. At the next several nodes associated with maximum width of the growth layer, differences in width were variable, but this changed to a definite decrease at nodes in the lower crown. This decrease in width was greatest (averaging about 20%) near the crown base, and dropped to less than 5% about 5 nodes below the crown base.

Examination of changes at the nodes in <u>all</u> growth layers formed during the life of the tree showed that the maximum decrease could occur at the estimated crown base, or somewhat above or below it. The rate of decline of branches in the lower crown, and the accuracy of estimating the crown base, may influence the coincidence of these two points.

Indentations often occurred in the periphery of the annual rings above and below branch whorls throughout the stem and were the results of longitudinal 'grooves' that developed in the stem in line with the branch axes. I will discuss these grooves in a later paper, but of interest here is that when measured immediately above the node, the average ring width in line with the branches (indentations) expressed as a percentage of the average ring width in between the branches, reached a minimum about the time the branches in that whorl apparently died.

Where internodes had been influenced by damage to the terminal and development of a replacement leader from a lateral bud or existing branch, the GLP narrowed in the internode below the 'replacement' internode. This can be seen in Fig. 3 in the 1958 and 1959 GLPs below the 1956 internode, and in the 1962 and 1963 GLPs below the 1960 internode. In time, the normal changes in width along the GLP are resumed. The change in shape of the GLP may not be so much a reduction in ring width in the lower internode as an increase in width in the replacement internode with the development of reaction wood. Adjustments in the longitudinal and radial distributions of secondary thickening would occur as the replacement internode became vertical and remaining curvatures in the stem were infilled. In addition, branch development in the whorl below the damaged one may have been stimulated somewhat by the lessened development of the latter.

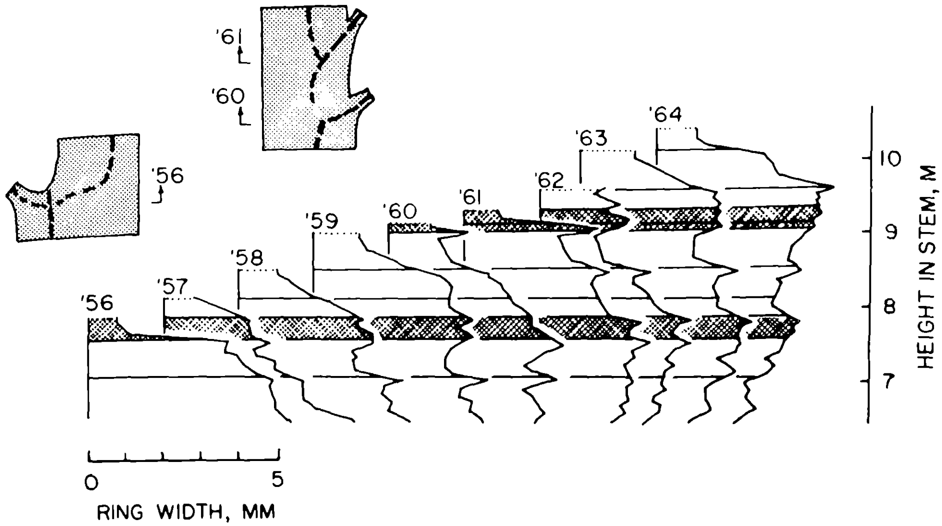

Fig. 3 The upper portion of the 1956-64 GLPs in which the internodes formed in 1956 and 1960-61 (shaded) were derived from lateral rather than terminal buds. The nodes at these points of lateral takeover are shown diagrammatically.

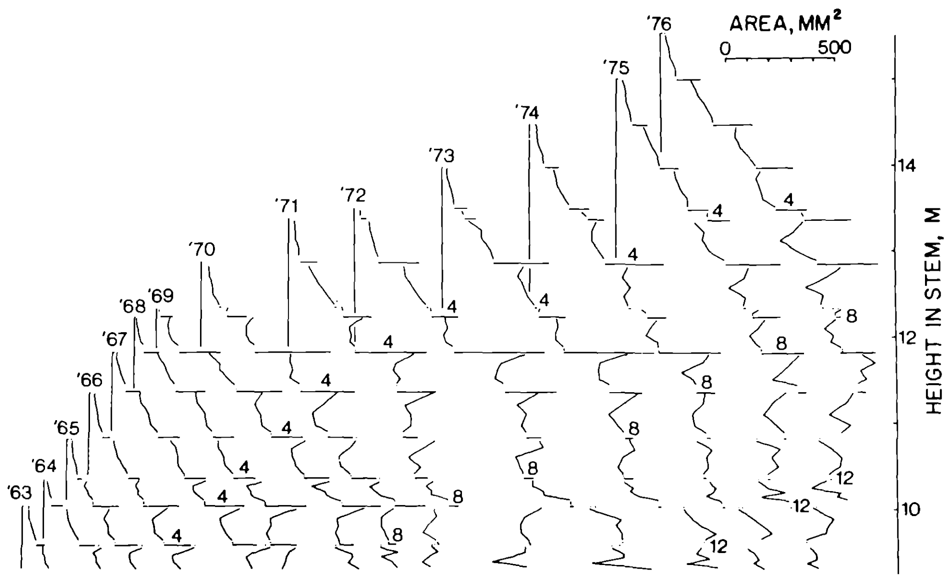

Fig. 4 Annual cross-sectional area in the stem and at the base of branches (horizontal mark, every 4th whorl numbered) for the portion of stem with live branches at felling.

Cross-sectional area

Maximum cross-sectional area of the composite growth layer occurred about internode 8 (Fig. 2, right), i.e. lower than maximum ring width but above the crown base -- about three quarters of the way down the crown. Within internodes, cross-sectional area usually increased basally, with the decline in area below internode 8 being brought about by the decrease at the nodes.

Cross-sectional areas of the 1963 to 1976 growth layers for the portion of stem with live crown at felling are shown in Fig. 4 with the total branch annual cross-sectional area indicated at each node. Generally, there is a direct relationship between the branch cross-sectional area and the increase in cross sectional area of the stem from above to below the node; the branch area, however, is usually somewhat greater than the stem area increase. The decrease in cross-sectional area of the stem coincides with minimal branch areas -- discontinuous rings were common at the branch bases from the 10th whorl position onwards and branches were approaching death.

DISCUSSION AND CONCLUSIONS

The detailed changes in ring width within internodes (Fig. 1) and along the growth layer (Fig. 2) confirm Duff and Nolan's (1953) statement concerning the slight taper of the pith and strong taper (a 70% increase in width basally) of the first ring from the pith in an internode. However, their statements about the later rings -- very slight or no taper in the second ring and substantially uniform width along an internode of subsequent rings -- appear oversimplified. Furthermore, definite changes in width occur at the nodes, a point they did not examine.

Based on the composite growth layer in which maximum width occurred in internode 5 and the crown base about node 11, ring widths in the second internode showed a definite basal increase (20%), with a similar increase at the node itself. Indeed, a basal increase had occurred in the second internode position during the last 35 years for the tree analysed. (The lowermost internodes were not measured at frequent enough intervals to confirm the pattern in the early years.) A slight basal increase of about 4% occurred in internodes 3 and 4, with little change at the nodes. Below the internode of maximum width, however, there tended to be a slight basal decrease in width (5%) within several internodes, i.e. a reverse taper, with a further decrease at the nodes. But within the internodes in the region of the crown base, ring width once again increased basally. However, this was more than offset by the decrease at the nodes, resulting in an overall decrease in the width of the growth layer. Lower down the stem, the change at the nodes and within the internodes lessened, being negligible by internode and node 25.

The basal increase in width of the pith and of the innermost rings imparts a basal increase in diameter to the internode. As noted by Duff and Nolan, this taper is retained by the internode as a whole in later years. Also, with time, a slight swelling occurs at the nodes (branch whorls).

The changes in ring width along the internode and from above to below a node may be the combined effects of the changing contribution of the branches in the whorl to stem growth, the interruption to transport of materials straight through the node, realignment of transport channels and possibly mechanical requirements. The greater growth at the bottom than at the top of the first two internodes may be related to the contribution of the internodal needles (Kozlowski and Winget 1964, Larson 1964) and the influence of wind-induced bending stress (Larson 1964, 1965). In the lower crown the basal increase in width in an internode and the decrease in width to the internode below may be due to some constriction to the downward movement of assimilates in the phloem by the branch bases and the negligible contribution by branches in the node as they die to stem growth below the node. In time, the pathways around the branches are readjusted and the interruption by the branch bases is reduced as the stem circumference increases, so that changes along and between internodes become negligible. Stiell (1969) concluded that growth in an internode just above the crown base may be influenced by whorls above and below it, whereas growth in an internode within the crown was primarily affected by the whorl immediately above it.

Although the growth layer started to decrease in width at a point in the crown where branch growth was still active, cross-sectional area was still increasing (Fig. 2). It continued to increase approximately in relation to the cross-sectional area of the branches at each node (Fig. 4). The increase appeared to end at about the point where the annual cross-sectional area of the branches was very small and discontinuous rings became common at their base.

The shape of the growth layer derived solely from measurements at the mid point of internodes is an idealized shape. However, changes in width within an internode do not negate the use of data from the mid point of the internode to calculate internodal ring volumes. Use of data from close to the upper or lower end of the internode, however, would be less suitable than from both ends together or from the mid point alone. In addition, the changes in width within internodes and at nodes should be considered in studies of cambial activity and branch contribution.

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