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THE POSITION OF ECCENTRIC STEM GROWTH AND TENSION WOOD IN LEANING RED OAK TREES[1]

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ABSTRACT

Eccentric growth (maximum radial increment) in the stems of leaning or straight red oak trees (Quercus rubra L.) occurs below the zone of maximum crown development. Tension wood is always found on the upper side of leaning stems. Most stems lean naturally and have maximum crown development on the under side of the lean, but those that have been tipped by external agencies such as high winds usually have maximum crown development on the upper side of the lean. Therefore, eccentricity and tension wood coincide only in the latter case.

INTRODUCTION

Red oak trees (Quercus rubra L.) dominate many of the older natural stands on the better sites at the Harvard Forest, Petersham, Massachusetts. All these oaks lean to some degree, most have eccentric crowns and both eccentric radial growth and tension wood are common in such stems. The present study was designed to test the value of field measurements of lean, crown distribution and external eccentricity for assessing in individual red oak stems the location of eccentric radial growth and tension wood.

Eccentric growth has been attributed to uneven crown distribution around the stem (Jaccard, 1915; Tischendorf, 1943) and to a reaction in response to mechanical stimuli such as wind sway or compression of the cambium due to the weight of the leaning tree (Grossenbacher, 1915; Engler, 1918, 1924; Jacobs, 1945). Tension wood, on the other hand, forms on the upper side of leaning stems, presumably due to a gravitational stimulus (Wardrop, 1964). The locations of eccentric growth and tension wood are usually found to coincide, but there are cases reported where they are on the opposite sides of branches or leaning stems (Marra, 1942; Wardrop, 1964; White, 1962). The relationship between eccentric growth and tension wood, if any, is not well known because most investigators have studied primarily tension wood and only incidentally noted the eccentric growth. In this paper, the location of eccentric growth is emphasized to stress that it seems to be a phenomenon separate from the formation of tension wood.

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MATERIALS AND METHODS

The trees studied were located in compartments PH I and PH III of the Harvard Forest. Red oak trees, 60 to 70 years old, 10 to 15 inches in diameter 4.5 feet above ground level and about 70 feet tall are dominant in the stand; red maple trees (Acer rubrum L.) are abundant. The oaks are primarily of seedling origin, having originally developed under an old field white pine stand (Pinus strobus L.). About 20 percent of the dominant and codominant trees were tilted in the 1938 hurricane and the most severely damaged trees were subsequently removed in salvage operations.

Data were collected intensively from 4 trees and extensively from 54 trees, in two separate surveys. Of the four intensively studied trees, three leaned naturally and the fourth had been tipped by the 1938 hurricane. Of the three, one was almost vertical, one leaned moderately and one leaned strongly, the hurricane-tipped tree leaned strongly (Table 1).

Height feet	Lean in degrees			
	Tree 1	Tree 2	Tree 3	Tree 4
2	1	7	2	24
4	2	9	11	24
6	1	13	13	18
8	2	9	13	19
10	2	5	15	19
12	1	3	15	14
14	1	1	14	12
16	1	1	6	11
18	5	1	25	6
20	2	2	20	4
22	1	2	18	0
24	2	2	20	0
26	1	3	24	0

Table 1. Lean in degrees at two foot intervals up the stem for the four trees studied intensively.

Lean from the vertical was measured in degrees at breast height for all of the trees and additionally, for the four trees, at two foot intervals up the stem to the first live branch in the crown. Direction of lean was also noted. Crown eccentricity was estimated by judging the distribution and size of the few (usually 5 to 10) major branches in the crown. Crown projections were found to be of little value because most of the trees were leaning. The most successful technique was to map from the ground the direction of the branches relative to the stem and to note their relative size.

The eccentricity of the stems was expressed as a percentage using the expression $(\frac{\text{max. diameter} - \text{min. diameter}}{\text{max. diameter}} \times 100)$, where radial measurements could be substituted for diameters when determining internal eccentricity. External diameter measurements were made to the nearest 0.1 inch outside the bark using calipers. Internal radius measurements from the pith to the bark were made from transverse disks taken from the four individual trees. A further measure of eccentricity was obtained by comparing the width of the last 10 growth rings from increment cores taken at different positions around the stem at breast height.

The incidence of tension wood was determined from microscopic observation of transverse sections 30 microns thick. Sections were cut on a sliding microtome, stained with safranin and fast green and mounted as permanent microslides. Unlignified walls of the fibers in tension wood areas stained green, while the normal, lignified fibers stained red.

RESULTS

It became clear during the course of this study that leaning red oak trees can be separated into two groups, those tipped by the 1938 hurricane and those that have apparently grown naturally into leaning positions (Fig. 1). Trees that lean naturally are by far the most common in the stand investigated. Wind-tipped trees could be identified readily because of the mound formed by the raised portion of the root system and because many of the branches become reoriented after the tipping so that they grow vertically (Fig. 1 E). As a result of reorientation of the branches, and the extension of new branches upwards, wind-tipped trees have their crowns predominantly on the upper side of the lean.

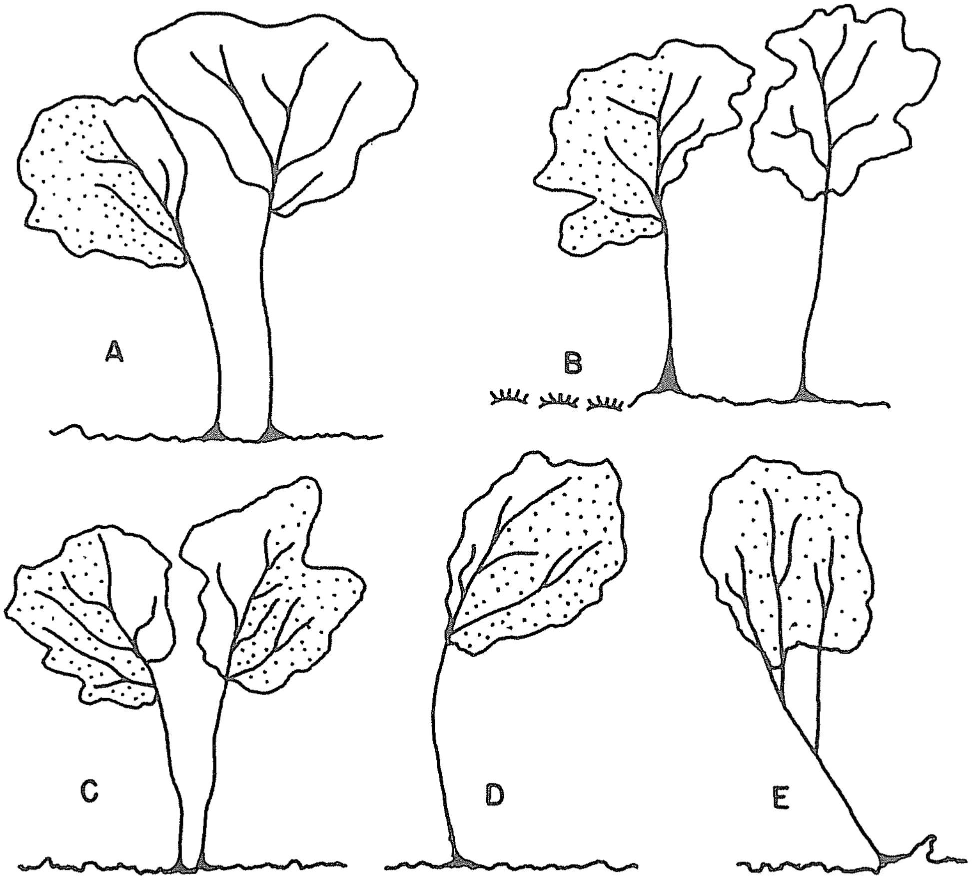


Figure 1. Diagrams of some types of leaning red oak trees. The better lighted portion of the crowns are stippled, A- a smaller tree growing out from under a larger one, B- a tree growing at the edge of a swamp, C- two trees growing close together, D- a "recurved" tree, E- a tree that was tipped in the 1938 hurricane and shows a windthrow mound.

Trees that lean naturally apparently do so as a result of a growth habit characterized by a relatively weak expression of apical dominance and by a relatively strong phototropism. The crowns of 77 percent of the naturally leaning trees were better developed on the lower, better lighted side of the lean (Fig. 1 A-D). The main stem develops from the most vigorous of the competing terminal shoots, and because this shoot has usually grown towards an opening in the forest canopy, the stem develops a lean towards such an opening. Engler (1918, 1924) has suggested that large woody stems may also bend phototropically towards a light source, but we have no data with which to assess his hypothesis. A few general types of leaning red oak trees are diagrammed in Fig. 1. Because the character of the stand constantly changes during the life of a tree, the crown may have shifted in more than one direction over the years. These changes result in trees which lean in different directions at different heights, and also at different angles to the vertical at different heights (Table 1). Note that of the four trees studied in detail, only the wind-tipped tree shows the gradual decrease in lean with increasing height presumably due to righting of the younger portions of the stem through the action of tension wood. The trees that leaned naturally, on the other hand, leaned at about the same angle throughout their whole height.

Measurements of disks from the four trees intensively studied showed that internal eccentricity was always greater than external eccentricity (Fig. 2). If the trunk was eccentrically shaped there was always internal eccentricity, however, nearly round sections seldom had the pith in the geometrical center of the stem. The photograph in Fig. 3 and the diagram in Fig. 4 show one way in which highly eccentric internal growth can produce a round stem when the maximum radial increment is always on the same radius; another way is shown in the photograph in Fig. 5 and the diagram in Fig. 6 where the zone of maximum radial increment shifts around the stem. Engler (1918) illustrates a similar cross section to that in Fig. 5. The zone of maximum growth may not always move in one particular direction. In some trees successive 10 year zones of maximum radial increment appear to be distributed randomly in the disks, or there may even be two zones of equal maximum radial increment on opposite sides of the stem during a period of 10 years in the same disk. In addition, the pattern of the distribution of maximum radial increment may be different at different levels in the stem; a stem may have grown eccentrically at some levels and not at others, or on different sides of the stem at different levels during the same 10 years.

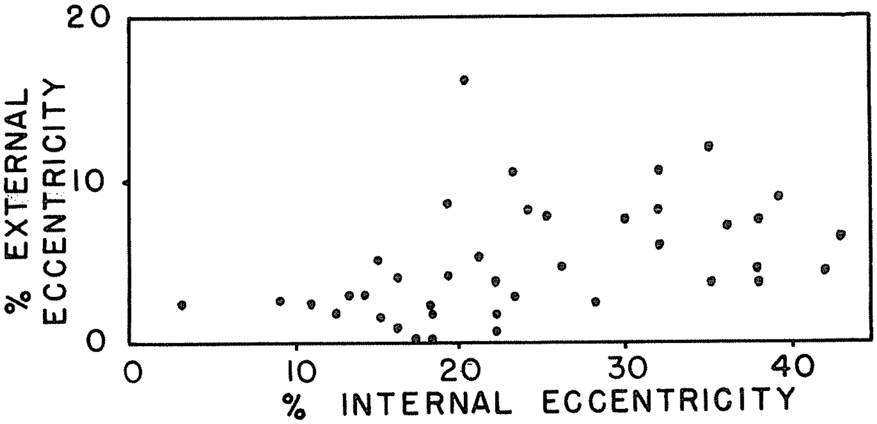
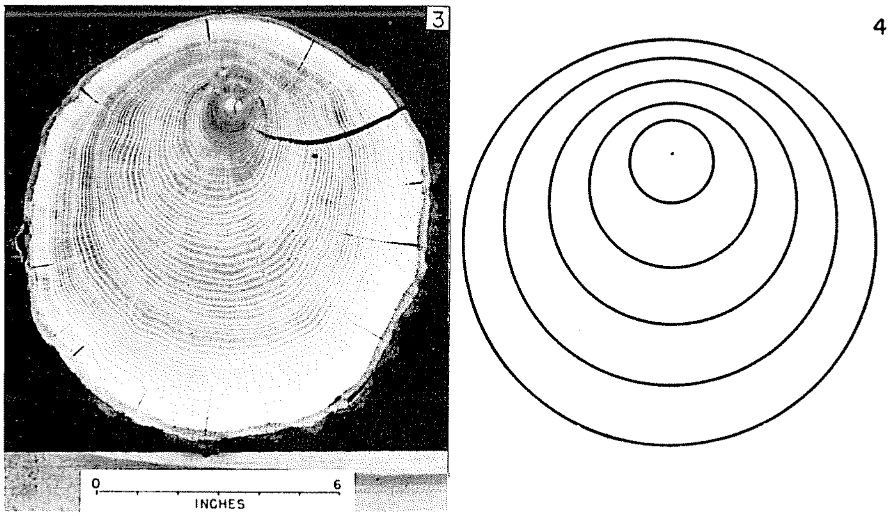
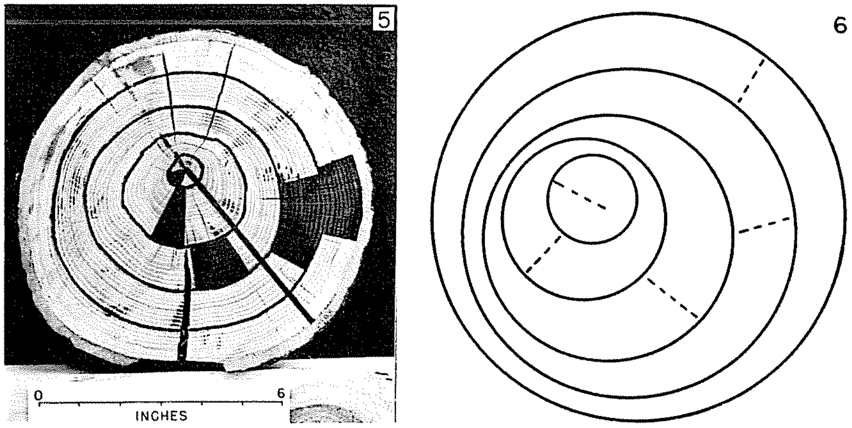


Figure 2. The relationship of external eccentricity measured outside the bark to internal eccentricity measured from pith to bark in disks cut at two foot height intervals from four trees.



Figures 3, 4. Figure 3. Transverse disk cut from the stem of a naturally leaning tree where the maximum radial increment has consistently been on the under side of the lean. Figure 4. Diagram showing how eccentric internal growth as in Fig. 3 can produce a round stem.



Figures 5, 6. Figure 5. Transverse disk from the stem of a naturally leaning tree where the maximum radial increment has shifted around the stem in successive 10 year intervals. Blackened areas mark zone of maximum radial increment. The maximum internal radius is marked in black. Figure 6. Diagram showing how shifting internal eccentricity as in Figure 5 can produce a round stem.

Tension wood was found on the upper side of both wind-tipped and naturally leaning trees. It was distributed in patches rather than as one continuous tissue. The tension wood seemed to be present generally throughout the upper side of leaning stems, most densely along the upper radius, and absent on the lower side of the stem. Tension wood could be detected positively only by relatively tedious microscopic examination of stained sections of wood, so its location was checked in only a few disks selected from the four intensively studied trees. Straight trees (leaning 2 degrees or less) were essentially free of tension wood, but the actual threshold angle of lean required for the formation of tension wood was not determined. In contrast to the predictable location of tension wood, eccentric growth was predominantly on the lower sides of stems that leaned naturally, but on the upper sides of the stems of wind-tipped trees. Disks from wind-tipped trees showed regular concentric growth rings until 1938, the period when the tree was relatively vertical, but in succeeding years the rings were highly eccentric on the upper side of the lean in all disks analyzed (Fig. 7, Table 2).

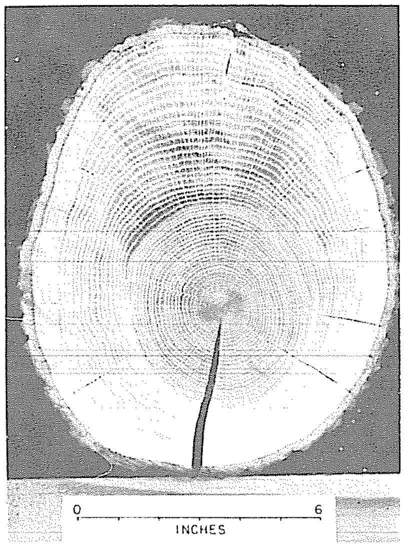


Figure 7. Transverse section from the stem of a tree that was tipped by the 1938 hurricane. Growth rings are relatively concentric until 1938, rings produced after 1938 are eccentric on the upper side of the present lean.

	Location of eccentricity			
Tree number	Upper quadrant	Lower quadrant	Adjacent quadrant	Total
1	7	1	5	13
2	6	3	4	13
3	0	10	0	10
4	10	0	0	10

Table 2. The location of the longest radius from pith to bark in the disks from the four sample trees in relation to the lean at the point at which the disks were taken.

A survey of the relationship between lean and eccentric growth (determined from increment borings taken at breast height) showed that the location of eccentric growth in naturally leaning trees was not as closely related to lean, but that 58 percent of these trees had greater growth in the last 10 years on the under side of the lean (Table 3). In the four individual trees the location of eccentric growth on the under side of the lean was more marked in those trees with most severe lean; in fact, the two trees that were leaning only slightly had the greatest growth predominantly on the upper side of the lean (Table 2).

	Number of leaning trees with			
Location of eccentricity with respect to lean	Symetrical crown	Crown on upper side	Crown on lower side	Total
Lower side	1	2	11	14
Upper side	3	0	5	8
No ecc.	1	0	1	2
Total	5	2	17	24

Table 3. Eccentricity based on the last 10 years radial increment at breast height on the upper and lower sides of leaning trees in relation to the eccentricity of the crown.

In 12 of the 24 trees in the survey of the relation of stem eccentricity to lean, there was a good correspondence between stem and crown eccentricities. The increment cores for this survey had been taken, however, on the underside of the lean and as has been pointed out, the direction of the lean and the direction of the shifting, eccentric crown frequently do not coincide. Thus a second survey was made using the distribution of the crown as the sold criterion for locating increment cores.

In the second survey, all from naturally leaning trees, 87 percent of the cores taken from beneath the zone of maximum crown development showed more growth during the past 10 years than did cores from the same trees taken from beneath the area of minimum crown development (Table 4). In many of the trees minimum crown development

	Number of trees	Percent eccentricity			
		0.1-5.0	5.1-10.0	10.1-20.0	20.1+
Trees with eccentricity on crown side	24	1(4.3)	9	3	11
Trees with eccentricity on non-crown side	4	0	0	3	1
Trees with no eccentricity	2	0	0	0	0
Total	30	1	9	6	12

Table 4. Eccentricity based on the last 10 years radial increment at breast height beneath the zones of minimum and maximum crown development.

was not directly opposite maximum crown development, so that the two cores were not taken directly opposite each other. The percent eccentricity of this 87 percent ranged from 3.4 to 42.0 with an average of 18.2. Trees in the survey were chosen only if there was a noticeable eccentricity of the crown (about half the trees in the stand), but the amount of crown eccentricity and degree of lean varied considerably. In only one-third of the trees did the position of maximum crown development coincide with the underside of the lean, but in most cases the eccentricity of the crown was within 90 degrees of the direction of the lean.

Two of the four trees that had maximum growth on the side of the stem with minimum crown development (Table 4), had recurved. They leaned in one direction at the base, higher up they straightened, and at the tip they were leaning in the opposite direction with the crown on the underside of the upper lean (Fig. 1 D). Disks cut from one of these trees showed that maximum growth had occurred on the underside of the lower lean throughout the life of the tree, but higher up the location of the maximum 10 year radial increments was variable, the later ones predominantly on the side of the present maximum crown development, the underside of the upper lean.

A major problem in estimating the distribution of the crown, or at least of the active portion of the crown, was in judging the relative vigor of the large lower branches. Longitudinal ridges form on the stem below large vigorous branches, but longitudinal grooves may form under dying branches (Münch, 1937). Dead large branches are common at the base of the crowns, usually on the less well lighted side of the crown. Once the branch is completely dead the grooves begin to fill in. The irregular outlines of many growth rings (Fig. 3, 5, 7) are probably due to this cycle of branch decline and death and the associated cycle of ridge and groove formation. Unfortunately the presence of a ridge under a branch does not guarantee that the current annual rings on the ridge are still wide, because the branch may already be declining in vigor.

DISCUSSION

Field observations can be used to judge the location of eccentric growth and tension wood in red oak with considerable accuracy. Tension wood occurs on the upper side of leaning stems, while the zone of maximum eccentric growth in a leaning or straight tree usually occurs below the area of maximum crown development. External eccentricity when present reflects internal eccentricity, but because many virtually round trees are highly eccentric internally, this measurement is of limited value. The only situation where tension wood and eccentric growth usually coincide is in trees that have been suddenly tipped by some catastrophic agency where the crown has proliferated on the upper side of the lean. In most leaning trees there has been no sudden change in the angle of lean and the crown is best developed on the under side of the lean so tension wood and eccentric growth do not coincide. Engler (1918) illustrated an exactly comparable distribution of eccentric growth in naturally leaning as opposed to snow-tipped birch and ash trees. He attributed eccentric growth on the underside of the lean, however, to longitudinal compression of the cambium and that on the upper side of the lean to geotropic stimuli.

Although it is relatively easy to measure lean in the field, estimation of crown eccentricity presents some difficulties. Unless the branches are obviously unevenly distributed around the stem it is necessary to map the distribution fairly accurately to determine whether the crown is eccentric. It is particularly difficult to assess the relative activity of large branches. Some of the lower ones may be dying and actually depressing growth below them while others are active and stimulating growth. From a practical point of view, when it is difficult to judge the eccentricity of the crown, stem eccentricity (at least of the last ten years) probably will be slight.

In trees that lean in only one direction, maximum eccentric growth occurs under the most active portion of the crown and could be presumed to result from hormones and assimilates moving preferentially down this side of the tree, but in "S" shaped or recurved trees the eccentric growth may be on different sides of the stem at different heights. Engler (1918) found that the maximum increment in "S" shaped ash and birch stems was always on the concave side of the curves. He ascribed this distribution of growth to the compressive stimulus to the cambium in the concave bends. In oaks that leaned in opposite directions at different heights eccentric growth was, however, not consistently on the concave side of bends nor was it consistently on the upper or lower side of the lean. There does not seem to be, at present, a satisfactory explanation for the distribution of cambial activity in these trees with complex leans and thus, perhaps, even for the distribution in trees with simple leans. Local mechanical stimulation of the cambium as suggested by Engler (1918) may play a role, but on the other hand there may be a gravitational redistribution of hormones as has been postulated for the formation of tension wood (Wardrop, 1964). Although the movement of materials from the crown down the stem is strongly suggested by the results of this and other studies, eccentricities observed in stems cannot be explained by the straight downward movement of materials from the crown.

The eccentric growth of the crown seems to be involved in the production of leaning stems, and thus secondarily in the formation of tension wood, and also in the eccentric growth of these stems. Thus, the obvious silvicultural recommendation for avoiding these defects is to thin oak stands to maintain an evenly distributed crown. Such "Danish high thinning" has been practiced for about 40 years on one 55-year-old hardwood stand at the Harvard Forest. Compared to unmanaged stands there is a much higher frequency of straight oak stems with relatively evenly distributed crowns. None of these trees has been cut recently, but one can assume that they have grown relatively concentrically.

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