TENSION WOOD FORMATION FOLLOWING RELEASE OF UPLAND OAK ADVANCE REPRODUCTION[1]

J. R. Hamilton

Professor of Wood Science
Division of Forestry, West Virginia University
P.O. Box 6125, Morgantown, WV 26506-6125

C. K. Thomas

Guardsman Chemical Incorporated
High Point, NC 27261

and

K. L. Carvell

Professor of Silviculture
Division of Forestry, West Virginia University
P.O. Box 6125, Morgantown, WV 26506-6125

(Received May 1984)

ABSTRACT

Stem straightening and tension wood formation in advance red oak and white oak reproduction were studied. Saplings straightened either as a result of a lateral branch assuming dominance or by a reorientation of the leaning stem. Tension wood fibers were greater on the upper side than on the lower side of straightening stems. The greatest concentrations of tension wood fibers were in or above the stem region in which straightening took place. Tension wood fiber formation began immediately following release and continued at an increasing rate for the period studied. The ratio of upper increment width to lower increment width was greater in the zone of maximum straightening and several years after straightening had begun.

Keywords: Red oak, white oak, tension wood, advance reproduction.

INTRODUCTION

Understory seedlings frequently have nonerect stems with flat-topped crowns. Such seedlings, if they are shade-tolerant, often remain in the understory for long periods of time. If the overstory is removed, these seedlings may undergo stem straightening (Trimble 1968).

Straightened stems usually contain tension wood. Tension wood occurs on the upper side of leaning stems and is characterized by an eccentric stem cross section and an abnormal amount of gelatinous fibers. Gelatinous fibers may occur singly, in isolated groups, or in broad bands. Usually they are more abundant in broad than in narrow growth rings and may be present in one growth ring and absent from the next (Atkins and Pillow 1950). The frequency of gelatinous fibers was found to be directly related to degree of lean in *Populus* and *Salix* spp. (Berlyn 1961) and in *Acer saccharinum* and *A. rubrum* (Arganbright and Bensend 1968). On the other hand, gelatinous fibers were observed in nonleaning *P. deltoides*

[1] Approved by the Director of the Agricultural and Forestry Experiment Station as Scientific Paper No. 1877.

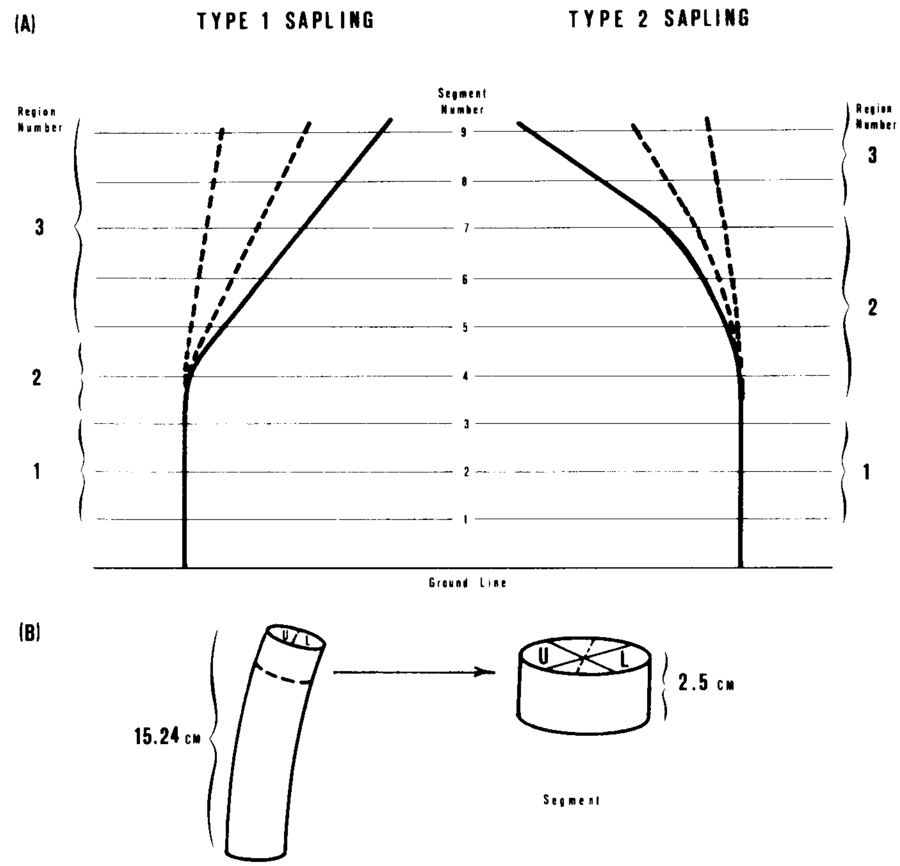

FIG. 1. The sapling sampling plan. (A) Segments were equally spaced along the stems and assigned to regions 1, 2 or 3 depending on the location involved in stem straightening. (B) Data were collected on wedges taken from the upper and lower stem halves.

(Isebrands and Bensend 1972). Cano-Capri and Burkhart (1974) could not detect a change in the frequency of gelatinous fibers associated with increasing degree of lean in *Quercus falcata.* They did observe, however, a change in the distribution of such fibers between the lower and upper sides of leaning stems. Even though there are many inconsistencies in the literature, the occurrence of gelatinous fibers is considered to be the best indication of the presence of tension wood.

In 1963, following a heavy single-tree selection cutting in a mixed-northern hardwood stand, fifty understory oak seedlings or seedling-sprouts were identified and classified, according to vigor, erectness of stem, and crown type (Carvell 1967). Height measurements and photographs were taken in 1964, 1965, and 1966. These data and photographs were used to track seedling development after release. Many of the seedlings regained vigor and exhibited stem straightening. Stem straightening came about as a result of a lateral branch assuming dominance and becoming the erect stem or by the main stem becoming more nearly vertical. In the first instance we expected that tension wood would be formed in very localized stem areas, whereas in the latter case extensive areas of the stem would show tension wood.

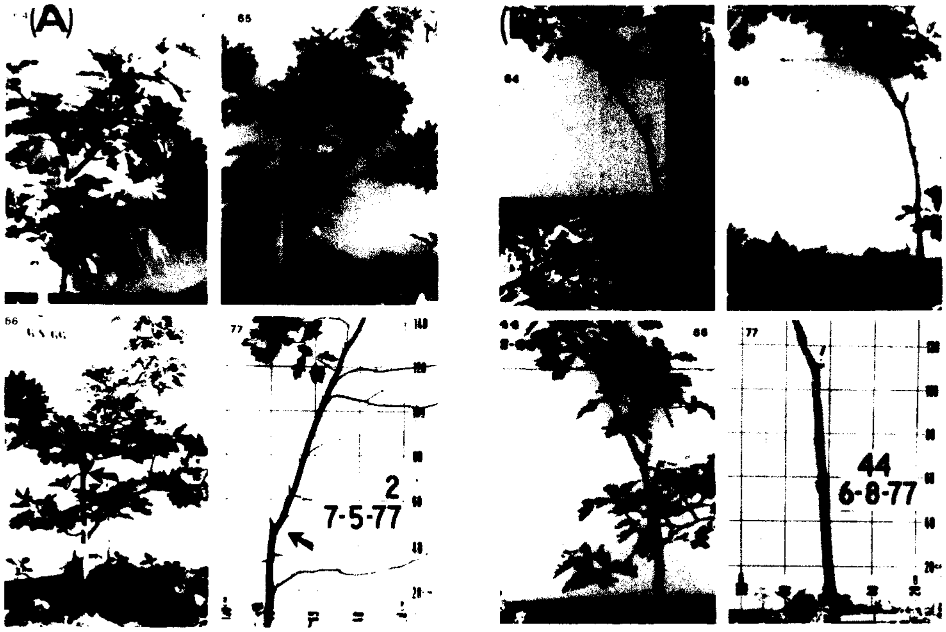

FIG. 2. The two methods of stem reorientation. (A) Type I sapling in which a lateral branch assumed dominance, and (B) Type II sapling in which reorientation occurred over an extended portion of the stem.

PROCEDURE

In 1977, twenty-six of the original seedlings with flat-topped crowns, of which a photographic record had been maintained, were examined. By comparing the photographic record with visual evidence in the field, nine of the 26 living saplings were determined to have undergone stem straightening. These nine, and two control saplings that had been erect since 1964, comprised the study material.

The original upper surface of the lean of each sapling, determined from the photographs, was marked. The tree stem was also marked at intervals of 15.24 cm to a distance of 1.2 m above the ground line.

The eleven study saplings were cut by sawing slightly below the ground line, and transported to the laboratory where they were dissected according to the plan shown in Fig. 1. At each interval a segment 2.5 cm long was cut beginning at the ground line. They are referred to as segments one through nine in this paper. When a branch or other defect occurred at one of the preselected segments, the segment was taken 2.5 cm higher. Each sapling was divided into three regions to indicate whether a given segment was located above, region 3, within, region 2, or below, region 1, the observed area of the stem reorientation.

Estimation of stem reorientation

The degree of lean of each stem was determined from photographs taken in 1964, 1965, 1966, and 1977. The actual vertical could only be estimated in the 1964, 1965, and 1966 photographs. A square grid background held vertically behind the saplings made it easier to determine the degree of lean in the 1977 photographs.

The photographs indicated that straightening came about in two distinct ways (Fig. 2). Type I saplings exhibited a definite point of reorientation, which was occasioned by a lateral branch assuming apical dominance and subsequently becoming the main stem. Three saplings under went this type of straightening. Type II saplings exhibited main stems, which underwent upward bending over a large portion of their stems. Six saplings were designated Type II. Two erect saplings (the controls) were designated Type III.

Specimen preparation

After softening in boiling water, each segment was separated into the upper and lower stem halves, based on the direction of straightening. A wedge extending from the pith to the bark was prepared from each half and stored in equal parts of glycerin and 70% ethanol.

Transverse sections, 14 μm thick were cut from each wedge using a sliding microtome. The sections were affixed to glass slides using 1% gelatin and formalin and allowed to dry 24 hours at 60 C. The sections were then differentially stained with 1% aqueous safranin 0 and 1% alcoholic fast green (FCF) by the method of Berlyn and Miksche (1976). Staining time varied from 4 to 5 hours for safranin and 30 to 60 seconds for fast green, depending on the time required to obtain proper color differentiation. This combination of dyes causes the walls of normal wood fibers to stain red because of the presence of lignin, and the unlignified inner wall layer of tension wood fibers to stain green.

Data collection

The total age of each sapling was determined by counting growth rings at the ground line cross section. All other data were taken from paired upper and lower stem segments. Ring widths were measured and recorded to the nearest 0.1 mm.

The occurrence of tension wood fibers was estimated using a combination of earlier methods described by Atkins and Pillow (1950), Terrell (1952), and Kaeiser (1955). These authors devised frequency classes as a means of visually determining the percentage of tension wood fibers in a microscopic field of view. The number of tension wood fibers in each growth ring was expressed as a percentage of the total number of fibers and subjectively assigned to one of five frequency classes. These classes were 0, 25, 50, 75, and 100%. In some growth rings, up to three frequency classes were assigned because of the extreme variability in the occurrence of tension wood fibers across increments. For each frequency class, the distribution of tension wood fibers was found by means of a dot-grid system. The percentages of tension wood fibers were obtained as the product of frequency (f) and distribution (d) where:

$$\text{Percent Tension Wood Fibers} = \frac{\sum_{n=1}^{5} (f_n \times d_n)}{\text{total dots counted}} \times 100 \qquad (1)$$

For example, a growth ring may have been assigned two frequency classes of 25 and 50. If, when using dot-grid system, it was found that there were 66 units in frequency class 25 and 34 units in frequency class 50 then:

TABLE 1. *Characteristics of the saplings by type, segments within regions and extent of lean for the four study years.*

Sapling type	Region 1	Region 2	Region 3	Lean 1964	Lean 1965	Lean 1966	Lean 1977
		Segment number			*Degrees*		
I	1, 2, 3	4	5, 6, 7, 8, 9	40	40	34	21
I	1, 2, 3, 4	5, 6	7, 8, 9	40	40	20	12
I	1, 2, 3	4, 5	6, 7, 8, 9	37	40	36	14
II		1, 2, 3, 4, 5, 6, 7	8, 9	30	30	27	8
II	1	2, 3, 4, 5	6, 7, 8, 9	60	44	12	−6
II	1	2, 3, 4, 5	6, 7, 8, 9	23	17	15	5
II		1, 2, 3, 4, 5	6, 7, 8, 9	34	34	6	11
II	1, 2, 3	4, 5, 6, 7	8, 9	27	26	21	21
II	1	2, 3, 4, 5, 6	7, 8, 9	30	30	13	−3
III		No reorientation		3	5	3	3
III		No reorientation		1	0	0	0

$$\text{Percent Tension Wood Fibers} = \frac{25(66) + 50(34)}{66 + 34} \times 100 = 33.5\%$$

Both northern red oak (*Quercus rubra* L.) and white oak (*Quercus alba* L.) saplings were included in the study, and the data for the two species were combined for analysis purposes. This combination appeared to be acceptable since the literature available to the authors made no reference to a difference in response to lean between the two species. In addition, the fine structure of the two species is quite similar. Light microscopical studies by Williams (1942) revealed no differences between the two species except for the character of tyloses. Wheeler and Thomas (1981) concluded that, for the most part, the ultrastructural characteristics of the two woods are similar.

Statistical analysis

Statistical comparisons were made using a linear model in the analysis of variance. Tension wood fiber formation and growth increment width were the two dependent variables studied. One aspect of the analysis compared the difference of percentage of tension wood fibers and increment widths between the upper and lower stem segments. The former was expressed as Percent T_U − Percent T_L; and

TABLE 2. *Average difference in percentage of tension wood fibers between upper and lower stem halves by sapling type and region.*

Type		Region	
	Percent		*Percent*
I	14 NS	1	14 NS
II	24*	2	21**
III	9 NS	3	24**

* Significant at 0.05 level of probability.
** Significant at 0.01 level of probability.
NS = Not significant.

TABLE 3. *Average difference in the percentage of tension wood fibers between upper and lower stem halves for nine years following release.*

Year	Age class		Percent	All class comparisons
1			10	1 vs. 2*
2	1		5	1 vs. 3**
3			7	2 vs. 3 NS
		Average	7.3	
4			12	
5	2		22	
6			29	
		Average	21.0	
7			32	
8	3		28	
9			32	
		Average	30.7	

* Significant at the 0.05 level of probability.
** Significant at the 0.01 level of probability.
NS = Not significant.

the latter was compared using the ratio of upper to lower width $\frac{I_U}{I_L}$. Comparisons were made between saplings for the average of the data from the three types, three regions, and also by regions within types.

The data, determined on all microscopic sections within a region, were averaged by year starting with 1962. Nine consecutive years from this date were examined and designated year one through year nine. When no data for 1962 were available, because of insufficient sapling height, the first growth increment from the pith was designated year one, a procedure that permitted data from one section to be averaged with data from another section. This method, designated as a Type III sequence by Duff and Nolan (1953), removes certain intrinsic variables that may contribute to errors in growth increment measurements. It effectively assigns new growth to year one, which is the first year following release. This removes the potential for statistical error that would result from averaging new rapid growth with slower growth at a lower location in the sapling.

To study changes over the 9-year time interval, years were grouped into age classes. Class 1 included years one, two, and three. Class 2 consisted of years four, five, and six, and Class 3 was made up of years seven, eight, and nine.

RESULTS AND DISCUSSION

Reorientation of stems

The location and extent of reorientation for each of the saplings studied are given in Table 1. Type I saplings, those in which a lateral branch assumed dominance and became the main stem, underwent a change in orientation from an average lean of 39° to one of 33° during the three years immediately following release and after 13 years exhibited an average lean of 16°. Note should be made of the fact that only one or two segments were considered to be in region 2 because reorientation occurred in a restricted area of the stems.

Most Type II saplings responded very dramatically to release. The average lean

TABLE 4. *Analysis of variance of tension wood fiber differences between upper and lower stem halves by type, region, and year.*

Source	df	SS	MS	F	
Type	2	6,094.8538	3,047.4269	0.65	NS
error	8	37,583.4329	4,697.9291		
Region	2	2,163.1598	1,081.5799	0.58	NS
Region/type	2	6,967.9560	3,483.9780	1.87	NS
error	12	22,380.6736	1,865.0561		
Year	8	14,165.3849	1,770.6731	4.16	**
Year/type	16	4,773.2766	298.3298	0.70	NS
Year/region	16	4,002.7186	250.1699	0.59	NS
Year/region/type	16	3,667.3626	229.2102	0.54	NS
error	160	68,035.6704	425.2229		

** Significant 1% level.
NS = Not significant.

was 34° in 1964 and 15° in 1977. Two saplings in this group exhibited negative lean, i.e., leaned in a direction opposite to the original direction. This overcorrection was thought to be the result of changing openings in the forest canopy. The number of segments considered to be in the zone of reorientation ranged between four and seven and encompassed a considerably broader area than was observed in Type I saplings. The reorientation did not begin at the ground line in all saplings of this type. In one, no reorientation occurred below 45 cm and in three others orientation did not occur at the lowest segment.

Occurrence of tension wood fibers

Tension wood fibers were observed in both the upper and lower stem halves of the segments of all saplings when grouped by type or region. In each instance there was a greater number on the upper side of stems (Table 2). There were differences associated with both sapling type and region. Their significance was examined by means of Fisher's t test. Tension wood fibers were significantly more abundant in the upper segment halves than in the lower segment halves in Type II but not in Type I and III saplings. The greatest difference occurred in the saplings exhibiting the greatest degree of straightening. The difference between

TABLE 5. *Average ratio of upper to lower growth increment width by type, region, and age class.*

Type		Region		Age class		
	Ratio		*Ratio*		*Year*	*Ratio*
I	1.2	1	1.1		1	1.1
II	1.1	2	1.2	1	2	1.1
III	1.1	3	1.1		3	1.1
					4	1.1
				2	5	1.1
					6	1.2
					7	1.2
				3	8	1.2
					9	1.2

TABLE 6. *Analysis of variance. Test of increment width ratio of upper to lower stem segment.*

Source	df	SS	MS	*F*	
Type	2	1.0658	0.5342	1.17	NS
error	8	3.6514	0.4564		
Region	2	0.5340	0.2670	0.41	NS
Region/type	2	2.6429	1.3215	2.04	NS
error	12	7.7619	0.6468		
Year	8	0.2318	0.0292	0.49	NS
Year/type	16	1.2186	0.0760	1.28	NS
Year/region	16	0.8095	0.0506	0.85	NS
Year/region/type	16	0.9971	0.0623	1.05	NS
error	160	9.5164	0.0595		

NS = Not significant.

segment halves was also influenced by region. The difference was significantly greater in regions 2 and 3.

The change in the occurrence of tension wood fibers over time was also examined (Table 3). The difference between the upper and lower halves of segments increased with time following release from less than 10% in the early years to approximately 30% later. The significance of this change over time was tested, comparing the average percent difference for three age classes, by means of a *t* test. The difference in the frequency of tension wood fibers was significantly less in the early years of release than in later years.

A comparison of percent tension wood fibers between sapling types, regions and years was made using analysis of variance (Table 4). There was no significant effect of types or regions, but there was a significant effect of year. The lack of significance of two of the main sources of variation and all of the interactions is probably due to the small sample size. Combining of the two species for analysis purposes also may have contributed to the lack of significance. Analysis of variance was also performed using stem reorientation as the covariate. The results were similar to those in Table 4; therefore, the simpler model was chosen for all analyses. The significant year effect was due to the small values during the initial years following release (Table 3).

Growth increment width

The ratio between growth increment widths in upper and lower stem segments $\frac{I_U}{I_L}$ was determined. The arithmetic means of this ratio or type, region, and age class are found in Table 5.

The ratios show that the increments were wider in (1) the upper half of the segments, (2) Type I saplings, (3) region 2, and (4) in age Class 3 segments. There is a suggestion that ratios increase with age following release.

In the analysis of variance for growth increment ratios, no significant variation was detected at the 5% confidence level for any of the comparisons that were made (Table 6). In addition, no difference was found using the analysis of the more complex model with stem reorientation as a covariant.

CONCLUSION

During a period of stem reorientation, a greater percentage of tension wood fibers occurred on the upper side of the stem segments than on the lower side. The greatest percentage of tension wood fibers occurred in and above the regions in the stem in which reorientation took place. Tension wood fiber production varied with time. More fibers were produced in the latter six years studied than in the first three years following release. Increment widths were not greatly affected by stem straightening, but the ratio between increment widths on the upper and lower side increased as stem straightening occurred.

REFERENCES

ATKINS, V., AND M. Y. PILLOW. 1950. Occurrence of gelatinous fibers and their effect upon properties of hardwood species. Proc. Forest Products Research Society, 254–264.

ARGANBRIGHT, D. G., AND D. W. BENSEND. 1968. Relationship of gelatinous fiber development to tree lean in soft maple. Wood Sci. 1(1):37–40.

BERLYN, G. P. 1961. Factors affecting the incidence of reaction tissue in *Populus deltoides.* Iowa State J. Sci. 35(3):367–424.

———, AND J. P. MIKSCHE. 1976. Botanical microtechnique and cytochemistry. The Iowa State University Press, Ames, Iowa.

CANO-CAPRI, J., AND L. F. BURKHART. 1974. Distribution of gelatinous fibers as related to lean in southern red oak. Wood Sci. 7(2):135–136.

CARVELL, K. L. 1967. The response of understory oak seedlings to release after partial cutting. W. Va. Univ. Agr. Exp. Sta. Bull. 553. 20 pp.

DUFF, G. H., AND N. J. NOLAN. 1953. Growth and morphogenesis in the Canadian forest species. Can. J. Bot. 31:471–513.

ISEBRANDS, J. G., AND D. W. BENSEND. 1972. Incidence and structure of gelatinous fibers within rapid-growing eastern cottonwood. Wood Fiber 4(2):61–71.

KAEISER, M. 1955. Frequency and distribution of gelatinous fibers in eastern cottonwood. Amer. J. Bot. 42(3):331–334.

TERRELL, B. Z. 1952. Distribution of tension wood and its relation to longitudinal shrinkage in aspen. USDA For. Ser. Res. Paper, R1917. 6 pp.

TRIMBLE, G. R. 1968. Form recovery by understory sugar maple under even-aged management. USDA For. Serv. Res. Note, NE-89. 8 pp.

WHEELER, E. A., AND R. J. THOMAS. 1981. Ultrastructural characteristics of mature wood of southern red oak (*Quercus falcata* Michx.) and white oak (*Quercus alba* L.). Wood Fiber 13(3):169–181.

WILLIAMS, S. 1942. Secondary vascular tissues of oaks indigenous to the United States III. A comparative anatomical study of the wood of Leucobalanus and Erythrobalanus. Bull. Torrey Bot. Club 69:115–129.