CHARACTERISTICS OF WOUND-ASSOCIATED WOOD OF YELLOW-POPLAR (*LIRIODENDRON TULIPIFERA* L.)[1]

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ABSTRACT

Selected anatomical characteristics and specific gravity of yellow-poplar wood formed after wounding and adjacent to the wound were compared to similar characteristics of yellow-poplar wood formed before and after wounding and away from the wound. The wood formed immediately after wounding was similar anatomically to the barrier zones described for other species. Vessel volume, vessel diameter, percentage of vessel multiples, and vessel element length were significantly lower in wound-associated wood, while ray volume, ray density, and specific gravity were significantly greater. Such changes in the vessel system would result in a decrease in conductivity in the wounded area, while the increase in parenchyma would increase the potential for manufacture of fungitoxic compounds. With increasing radial distance from the wound area, the anatomical features of the wound-associated wood gradually approached those of normal wood, although by four years after wounding, the wood still had not returned to normal. The specific gravity stayed significantly greater.

Keywords: *Liriodendron tulipifera* L., yellow-poplar, barrier zones, wood anatomy, wounding, discoloration and decay.

INTRODUCTION

Wounds extending into the wood of branches, stems, or roots of a tree create an opportunity for the initiation of discoloration and decay. Trees respond to wounds biochemically and anatomically to isolate or "compartmentalize" the wounded area (Shigo and Marx 1977; Shigo 1980). Xylem cells produced by the vascular cambium form a "barrier zone," which prevents the spread of microorganisms into the xylem formed after wounding (Tippet and Shigo 1981). Ana-

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TABLE 1. *Characteristics of trees used for characterization of wound-associated wood.*

Trees	DBH (cm)	Height (m)	Aggregate column of discoloration and decay (cm)	Discoloration and decay class
Mn	23	20	162	minimum
Av	19	20	320	average
Mx	26	22	538	maximum

tomically distinct barrier zones have been described for the hardwoods: black walnut, maple, birch, beech, and sweetgum. The cells in such barrier zones differ from normal xylem cells in size, shape, relative proportions, and orientation (Sharon 1973; Moore 1978; Mulhern et al. 1979; Bauch et al. 1980; Smith 1980; Rademacher et al. 1984). With the increasing mechanization of silvicultural and harvesting operations, the likelihood of tree injury is increasing. Wound-associated wood is abnormal wood and its presence, while of adaptive significance to the tree, has a negative effect on wood quality.

Detailed knowledge of the anatomical characteristics of wound-associated wood is based on the examination of only a few species. Changes in tissue composition and cellular dimensions are quantified only for maple, birch, and beech (Bauch et al. 1980; Rademacher et al. 1984). Yellow-poplar lends itself to a detailed study of such changes as its anatomy, like that of maple and birch, is relatively simple for a hardwood. Yellow-poplar wood is comprised chiefly of vessels, ray parenchyma, and fibers; longitudinal parenchyma is confined to the growth ring boundaries. *Liriodendron* belongs to the magnolia family (Magnoliaceae), and is considered more primitive than the other species examined. Study of the wound-associated wood of this species will expand our knowledge of the wound response. The extent of the discoloration and decay associated with wounding is apparently under genetic control in yellow-poplar (Lowerts and Kellison 1981). If anatomical characteristics can be used to predict resistance to development of discoloration and decay following wounding, then it would be possible to incorporate selection for effective compartmentalization into a breeding program for yellow-poplar.

Yellow-poplar (*Liriodendron tulipifera* L.) wood is of commercial importance in the southeastern United States, and its use in construction is expanding. A barrier zone has been observed in wound-associated wood of yellow-poplar (Shortle and Cowling 1978), but was described only as an area of incompletely differentiated cells. This paper provides further details of the wound-associated wood of yellow-poplar.

MATERIALS AND METHODS

In May 1978, seventy-two yellow-poplar trees were artificially wounded at approximately 0.9 m and 1.8 m up the tree bole from average ground level. At those heights, the wounds were inflicted in each quadrant of the bole to a depth of approximately 10 cm by an electric drill with a bit diameter of 1.3 cm. In small diameter trees, there was some overlap of wound holes. In summer 1979, thirty-six of these trees were harvested to determine the heritability of resistance to discoloration and decay (Lowerts and Kellison 1981).

Nine of the remaining thirty-six trees were felled and dissected in the field

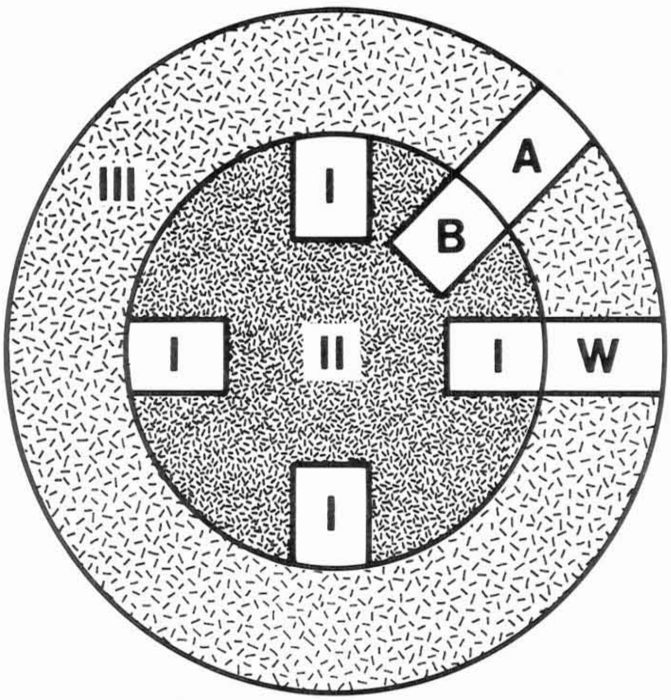

FIG. 1. Location of wood blocks within each wood disk. W = wood formed after wounding and radial to the wound hole, B = wood formed *before* wounding and away from the wound area, A = wood formed *after* wounding and away from the wound area. I = wound hole, II = wood formed before wounding, III = wood formed after wounding.

during January 1982. The nine trees were 22 years old, with an average diameter (DBH) of 18.9 cm and an average height of 19.3 m. The length of the column of discoloration and decay associated with each wound was measured to the nearest 2.5 cm. The lengths were then summed to determine the aggregate column length for a tree.

The trees with the minimum, average, and maximum aggregate column length (Table 1) were selected for study to determine which, if any, wood anatomical features might affect the extent of discoloration and decay (Lowerts 1983). A wood disk, approximately 2.5 cm thick, containing the four wound areas was sectioned from both wound heights in each tree.

A band saw was used to cut three wood blocks W, A, and B (2.5 cm thick) from each wood disk (see Fig. 1). Wood block W contained the four growth rings formed after wounding and radial to the wound hole. Wood blocks A and B were selected from nondiscolored, nondecayed areas of each disk, away from the wound areas and without any evident development of a barrier zone. Wood block A contained four growth rings of wood formed after wounding and wood block B contained four growth rings of wood formed before wounding.

Laboratory procedure

Each growth ring in each wood block was separated for determination of the following features: mean vessel diameter; proportion of vessel multiples; specific gravity; growth ring width; the percent composition of vessels, fibers, and ray parenchyma cells; ray density; and fiber length.

The specific gravity of each growth ring was determined using the maximum moisture content method (Smith 1954). Prior to the measurement of specific gravity, each growth ring was placed in a Soxhlet extractor for 24 hours with a 2:1 solution of benzene and alcohol, followed by a 12-hour water wash. Extractives soluble in alcohol-benzene were removed from each growth ring by this procedure.

A sledge microtome was used to cut a transverse section (24 μm thick) from each growth ring. The proportion of vessel multiples and cell types, vessel diameter, and ray density were measured microscopically from the center of each growth ring. Within each growth ring of yellow-poplar, there is a continuum of cellular dimension change from springwood to summerwood (Taylor 1965). By limiting all measures to the center of each growth ring, it was assumed that the measure of each wood anatomical feature would be comparable from ring to ring.

The percent volume composition of vessels, fibers, and ray parenchyma cells was determined from a transverse section following the procedure used by Taylor (1965) and Hosseinzadeh (1980). This procedure utilized a Leitz microscope equipped with a six-spindle integrating eyepiece with a movable transect line and a measuring line perpendicular to the transect line in a 100-unit square. Rotation of any spindle results in a movement of the measuring line and the distance moved was recorded by the spindle rotated. A different spindle was used for each cell type. The accumulated distance traversed for each cell type was expressed as a percentage of the total distance traversed. The percentage figure is equivalent to the area or volume percentage occupied by the different cell types (Hosseinzadeh 1980).

The proportion of vessel multiples (two or more vessels with common walls) was determined from a superimposed 0.08 mm^2 grid placed over the center of each growth ring in five randomly selected areas. All solitary and multiple vessels falling within the grid were counted. Tangential vessel diameter was determined by measuring 50 vessels. Growth ring width was determined to the nearest tenth (0.1 mm) millimeter.

Vessel element and fiber lengths from each growth ring were measured from macerations. The wood was macerated in a mixture of 1:1 30% hydrogen peroxide and glacial acetic acid at a temperature of 60 C for 24 hours. The bull's eye method of Hart and Swindel (1967) was used to randomly select and then measure the length of 50 fibers to the nearest 0.01 mm.

Statistical analysis

Analysis of variance procedures were used on a fixed model with the following main effects: tree, wound height, and wood block. Means, standard deviations, and simple linear correlations were determined for specific gravity, growth ring width, and each wood anatomical feature. This paper will discuss the anatomical differences among and within the wood blocks (A, B, W) and the wood block by tree and wood block by height interactions. The variation of specific gravity, growth ring width, and wood anatomical features among individual trees and their correlation with the extent of discoloration and decay was the subject of a separate discussion (Lowerts 1983).

TABLE 2. *Summary of results of analysis of variance showing probability level of* F *for specific gravity, growth ring width, and all wood anatomical features.*

Sources of variation	Degrees of freedom	Specific gravity	Vessel volume	Fiber volume	Ray parenchyma volume	Ray density
Tree	2	0.1276 ns	0.0029**	0.0001**	0.1159 ns	0.0387*
Height	1	0.004**	0.1638 ns	0.1820 ns	0.6089 ns	0.5581 ns
Wood block	2	0.0001**	0.0001**	0.0001**	0.0001**	0.0001**
Wood block × tree	4	0.0002**	0.5486 ns	0.1816 ns	0.1879 ns	0.3597 ns
Wood block × height	2	0.4931 ns	0.4616 ns	0.6133 ns	0.7311 ns	0.5987 ns

Sources of variation	Degrees of freedom	Vessel diameter	Vessel multiple percentage	Fiber lengths	Vessel element length	Growth ring width
Tree	2	0.3333 ns	0.3845 ns	0.2262 ns	0.0082*	0.1713 ns
Height	1	0.9189 ns	0.3161 ns	0.9891 ns	0.2694 ns	0.8880 ns
Wood block	2	0.0001**	0.0001**	0.0001**	0.0001**	0.1350 ns
Wood block × tree	4	0.0467*	0.2748 ns	0.0610 ns	0.8318 ns	0.6716 ns
Wood block × height	2	0.6075 ns	0.3255 ns	0.9160 ns	0.7205 ns	0.8812 ns

* = significant at 0.05 probability level.
** = significant at 0.01 probability level.
ns = not significant.

OBSERVATIONS AND RESULTS

The variation of all features examined between wood blocks A, B, and W was comparable at each height within each tree. None of the features displayed a significant wood block by height interaction (Table 2). Consequently, the variation among and within wood blocks was analyzed on a mean basis regardless of wound height. The comparison of wound-associated wood (W) to wood formed away from the wound and before (B) and after (A) wounding was done using the mean of measurements for the 4 growth rings in each wood block (the mean of 24 sets of measurements). There was a significant wood block by tree interaction for specific gravity and vessel diameter. In all three trees, wood block W had the largest specific gravity and smallest vessel diameters. Specific gravity and vessel diameters in wood blocks A and B were not significantly different in any tree, although their rank order changed. Each data point in Figs. 16–20 represents the mean of six sets of measurements, two per tree.

Highly significant wood anatomical and specific gravity differences existed among the wood blocks (Table 2). The cell dimensions and tissue percentages, and specific gravity of wood block W were significantly different from those of wood blocks A or B (Table 3). The proportions of fibers, fiber length, and vessel multiples were the only variables that displayed significant differences between wood blocks A and B (Table 3).

One obvious feature of wound-associated wood is the profound alteration of cell orientation. Figure 2 shows normal wood of yellow-poplar, Figs. 3 and 4 show wood formed subsequent to wounding at the wound area. Cross sections (as defined relative to the tree's axis) of wound-associated wood resemble longitudinal sections as the fibers and vessel elements are oriented perpendicular or near-perpendicular to the tree's long axis.

The tissue immediately adjacent to the wound appears to be a band of parenchyma and can be considered the "barrier zone." A distinctive feature of wound-

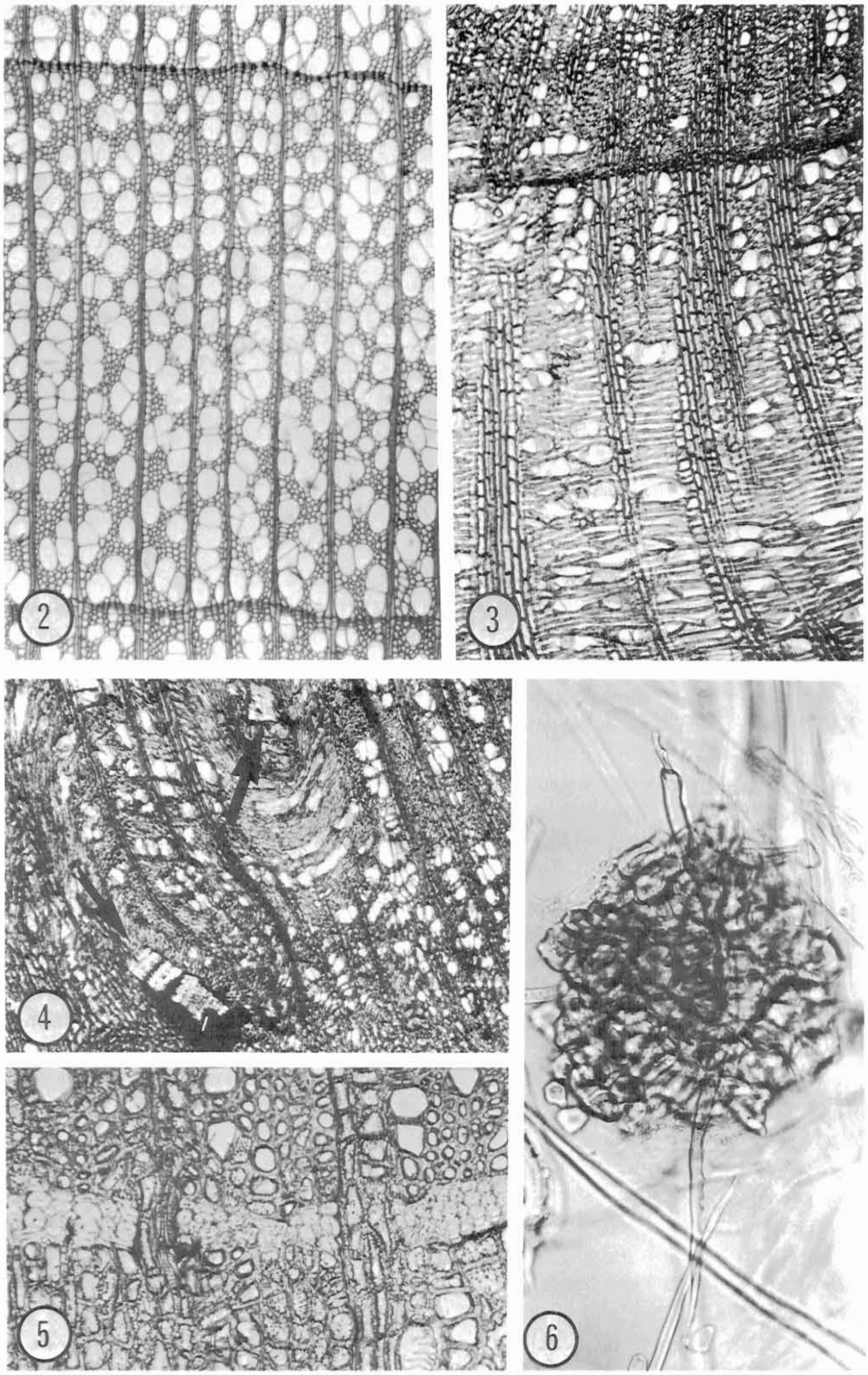
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TABLE 3. *Mean values[1,2] and standard deviations[3] of wood blocks W, A, and B, for specific gravity, growth ring width and all wood anatomical features.*

	Wood blocks		
	W	A	B
Growth ring width (mm)	6.5 (3.0) a	5.1 (2.0) a	5.4 (2.2) a
Specific gravity	0.49 (0.03) a	0.41 (0.03) b	0.41 (0.03) b
Vessel diameter (μm)	57.73 (4.94) b	70.16 (4.00) a	69.98 (3.36) a
Vessel multiple percentage	34.38 (11.03) c	50.83 (9.57) a	41.52 (10.64) b
Vessel element length (mm)	0.60 (0.15) c	0.86 (0.05) a	0.82 (0.07) a
Vessel volume	25.94 (7.84) b	36.10 (5.56) a	33.94 (6.57) a
Fiber length (mm)	1.52 (0.27) c	1.93 (0.11) a	1.81 (0.10) b
Fiber volume	54.69 (7.62) a	50.83 (4.75) b	54.16 (5.68) a
Ray parenchyma volume	19.31 (5.11) a	13.05 (2.59) b	11.89 (2.52) b
Ray density	6.5 (0.8) a	5.3 (0.5) b	5.4 (0.3) b

[1] = wood block mean values are the average of each wood block in each height.
[2] = values for a feature that have the same letters do not differ significantly ($P = 0.05$) according to Duncan's Multiple Range Test.
[3] = standard deviation in parentheses.

associated tissue is the presence of sclereids (Figs. 4–7). These sclereids occur in clusters; the tangential continuity of the sclereid clusters is variable (compare Figs. 4 and 5). When the sclereid containing tissue was macerated, the sclereids tended to stay in clumps, rather than separating (Fig. 6). Individual sclereids were thick-walled, not elongated, and had short arms (Fig. 7).

Vessels and vessel elements

The volume percentage of vessels, percentage of vessel multiples, vessel diameter, and vessel element length were significantly lower in wood block W (Table 3). The most obvious differences between wound-associated wood and the wood distal to the wound occurred the first year after wounding (Figs. 16A, 17, 18, 19A). Four years after wounding, vessel characteristics were still different from wood distal to the wound. Vessel volume (Fig. 16A) and vessel element length (Fig. 19A) became nearly that of the wood formed distal to the wound and before wounding, but percentage of vessel multiples (Fig. 17) and vessel diameter (Fig. 19A) did not show the same degree of return to normal.

Individual vessel elements were not only shorter than normal, but were often misshapen (Fig. 8), lacking the tubular shape typical of yellow-poplar. Perforation plates occasionally were unusual as well (Fig. 9).

Figures 10 and 11 show, respectively, normal and wound-associated wood. It is evident from these cross sections that the vessel elements are narrower than usual, and that pore multiples are less common in wood formed after wounding.

Fibers

Fiber length, as well as the vessel element length, was significantly shorter in the wound-associated wood (Table 3, Fig. 19B). But by four years after wounding

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FIG. 2. Cross section of normal wood of yellow-poplar. 35×.
FIG. 3. Cross section of wound-associated wood showing alternation of cell orientation. 35×.
FIG. 4. Wound-associated wood with groups of sclereids (arrow). 35×.
FIG. 5. Band of sclereids in wound-associated wood. 180×.
FIG. 6. Clump of sclereids in maceration. 180×.

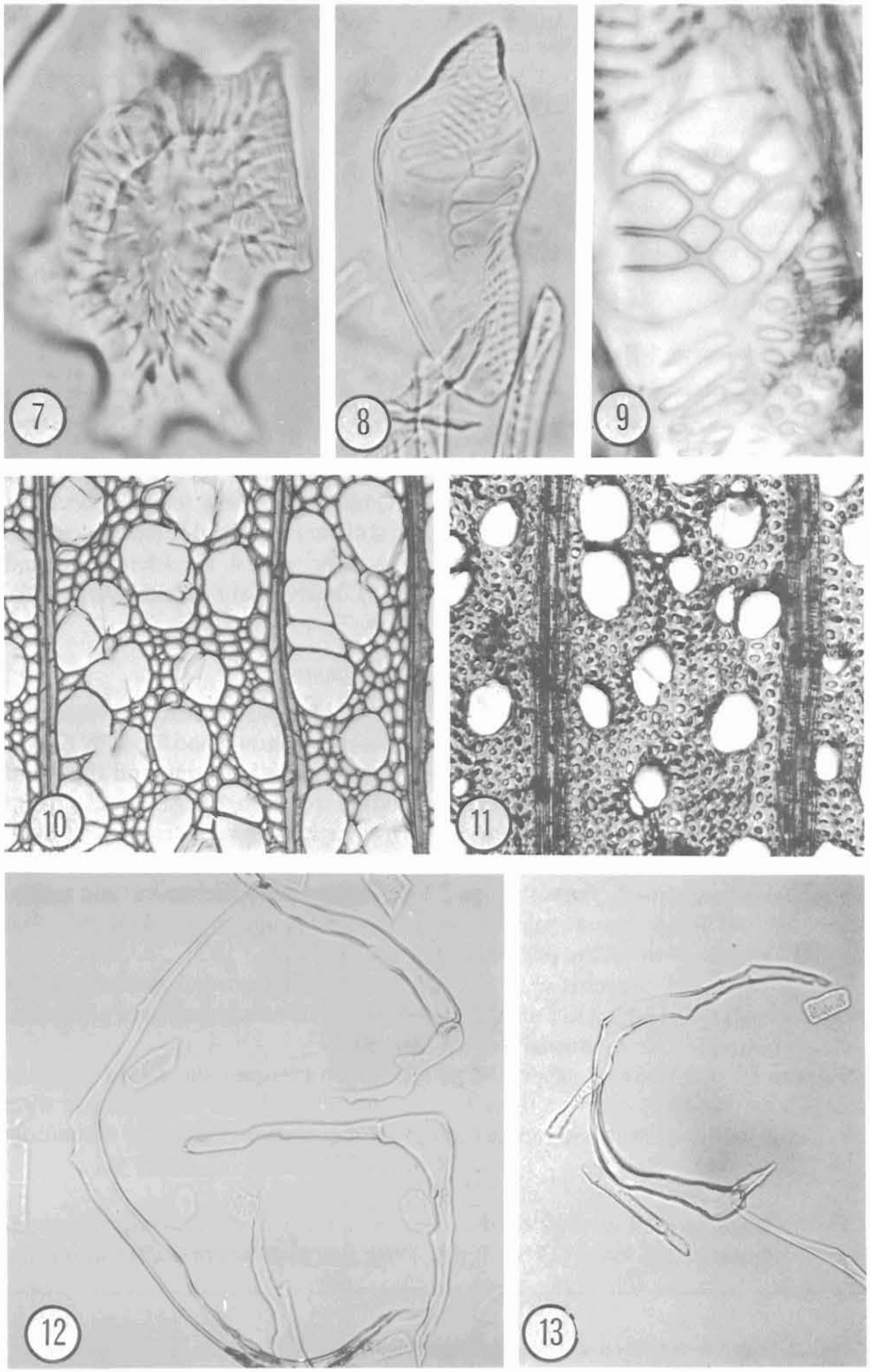
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TABLE 4. *Simple linear correlation of all wood properties with specific gravity and growth ring width.*

	Specific gravity	Growth ring width
Growth ring width	0.05 ns	1.00
Specific gravity	1.00	−0.05 ns
Vessel diameter	−0.73**	−0.15 ns
Vessel multiple percentage	0.39**	0.22 ns
Vessel element length	−0.62**	−0.45**
Vessel volume	−0.56**	−0.40**
Fiber volume	0.29 ns	0.22 ns
Ray parenchyma volume	0.54**	0.36**
Ray density	0.53**	0.30**
Fiber length	−0.42**	−0.55*

* = significant at 0.05 probability level.
** = significant at 0.01 probability level.
ns = not significant.

(1981 wood), fiber length was comparable to the fiber length of wood formed prior to wounding (wood block B). Figures 12 and 13 show macerations of the wood adjacent to the wound and illustrate that the fiber shape was deformed in such wood. Bent and forked fibers were common.

Ray parenchyma

Ray density and volume of ray parenchyma were significantly greater in wood block W than in wood blocks A and B (Table 3, Fig. 16B). An increase in ray width and size of individual ray parenchyma cells, as well as the increase in ray density, apparently contributed to the increase in ray volume. The cross sections of Figs. 10 (normal wood) and 11 (wound-associated wood), and the tangential sections of Figs. 14 (normal wood) and 15 (wound-associated wood) show that ray height and width are increased and that individual ray cells are larger in diameter and have thicker walls. The maximum ray density (number per mm) occurred the first year after wounding, but the maximum ray volume occurred the second year after wounding.

Specific gravity and growth ring width

The alteration of cell proportions and dimensions was reflected in the specific gravity of each wood block. The highest specific gravity occurred in wood block W and was significantly different from wood blocks A and B (Table 3). Throughout the four-year period following wounding, the specific gravity of wood block W was greater than wood block A (Fig. 20) and was not rapidly approaching normal.

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FIG. 7. Individual sclereid from wound-associated wood. 800×.

FIG. 8. Individual vessel element from wound-associated wood. Note lack of tube-shape characteristic of normal wood. 400×.

FIG. 9. Abnormal perforation plate in vessel element from wound-associated wood, perforation plate appears more foraminate than scalariform. 800×.

FIG. 10. Normal yellow-poplar wood, cross section. 180×.

FIG. 11. Wood formed one year after wound. 180×.

FIG. 12. Fibers from wood adjacent to wound. 180×.

FIG. 13. Fibers from wood adjacent to wound. 180×.

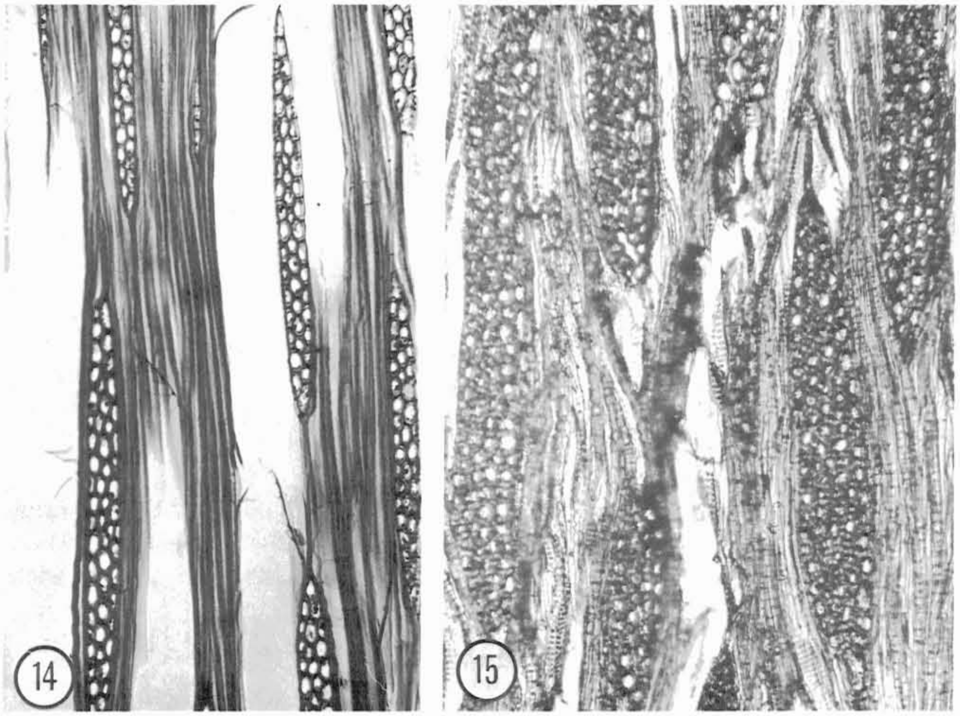

FIG. 14. Tangential section of normal wood. 180×.

FIG. 15. Tangential section of wound-associated wood. Note wider rays and thickened ray cell walls. 180×.

Vessel diameter, vessel element length, proportion of vessels and ray parenchyma and ray density were strongly correlated with specific gravity (Table 4). The correlation of specific gravity with the proportion of fibers and growth ring width was not as strong as the correlation with vessel diameter and ray volume. No doubt, an increase in ray cell-wall thickness (Figs. 14, 15) also contributed to increased specific gravity of wound-associated wood.

Growth ring width was not statistically significantly different among the wood blocks (Table 3). Fiber length was significantly greater in wood block A than in wood block B, a fact that can be attributed to the increase in fusiform initial length that occurs as the cambium ages. Growth ring width was most strongly correlated with fiber length (Table 4).

DISCUSSION

Yellow-poplar trees isolate all wounded tissue by utilizing simultaneous biochemical and anatomical defense mechanisms. Unique and highly fungitoxic chemicals are found in discolored wound-associated sapwood of yellow-poplar (Hsu 1976), and a barrier zone forms to prevent the spread of microorganisms into wood formed after wounding (Shortle and Cowling 1978). In this study, it was found that wood produced radial to the wound and after wounding (wood block W) had cells with abnormal dimensions and had different cellular proportions than wood formed away from the wound both before and after wounding.

The abnormal wound-associated wood was most obvious in the first year after wounding, but the wood formed in subsequent years was also abnormal.

The characteristics of the wound-associated wood are similar to those described for other hardwoods. The proportion of vessels and vessel multiples, vessel diameter and vessel element length decreased in the wound-associated wood of yellow-poplar. A similar decrease in proportion of vessels, vessel diameter, and vessel element length occurs in *Acer, Betula,* and *Fagus* (Mulhern et al. 1979; Bauch et al. 1980; Rademacher et al. 1984). Vessel elements are shorter than normal in black walnut (*Juglans nigra* L.) (Smith 1980) and sweetgum (*Liquidambar styraciflua* L.) (Moore 1978). Unlike any other species, vessel diameter increased in fall-wounded black walnut (Smith 1980).

The decrease in vessel diameter and percentage of vessels in wound-associated wood would reduce water conductivity, since the hydraulic conductivity of capillaries is proportional to the fourth power of the radius of the capillary (Zimmermann and Millburn 1982). It was demonstrated that lateral conductivity of dye through the barrier zone of red maple (*Acer rubrum* L.) is slower than through normal xylem (Mulhern et al. 1979). The decrease in longitudinal and lateral conductivity would serve to inhibit the spread of microorganisms.

Ray density and the proportion of ray parenchyma are greater in wound-associated wood than in normal wood of yellow-poplar as is true for species of *Fagus, Betula,* and *Acer* (Rademacher et al. 1984). In yellow-poplar, the proportion of ray cells increases with increasing ray density ($r = 0.38$), but this correlation accounts for only 14% of the variation between ray density and ray cell proportion. Rays in the wound-associated wood are not only more numerous, but have more and larger ray parenchyma cells than in normal wood. An increase in the number of ray cells has been observed in the barrier zones of *Acer* spp. and *Betula* spp. (Sharon 1973; Bauch et al. 1980). Neither Smith (1980) nor Moore (1978) observed an alteration of ray size or volume in black walnut and sweetgum, respectively, but they did observe a marked increase in axial parenchyma. It could be that if a tree is capable of producing large amounts of axial parenchyma and/or traumatic gum canals (sweetgum), ray characteristics will not change.

Ray parenchyma cells are responsible for the synthesis of various fungitoxic chemicals (Shortle 1979) and are the source of tyloses and gum deposits in vessels (Chattaway 1947). An increase in the number of ray parenchyma cells and in ray density would result in an increased number of vessel to ray parenchyma cell contacts. Increased vessel to ray parenchyma cell contact would enhance the transport of fungitoxic compounds and gums into vessels, preventing the spread of microorganisms into the wood formed after wounding.

The proportion of fibers was similar in wound-associated wood and normal wood, so the increase of specific gravity in wound-associated wood must be the result of the decrease of vessel volume and an increase in ray density and the proportion of thick-walled ray parenchyma cells. The presence of thick-walled scleroid cells and hot water soluble phenols, which were not extracted, also could have contributed to the increase in specific gravity of wound-associated wood.

The change in cell orientation of wound-associated wood indicates that the vascular cambium's normal organization has been altered. The change in cell proportions, the shortened cell lengths, and the presence of sclereids indicate a change in the patterns of cellular differentiation. Sclereids of course, are not a

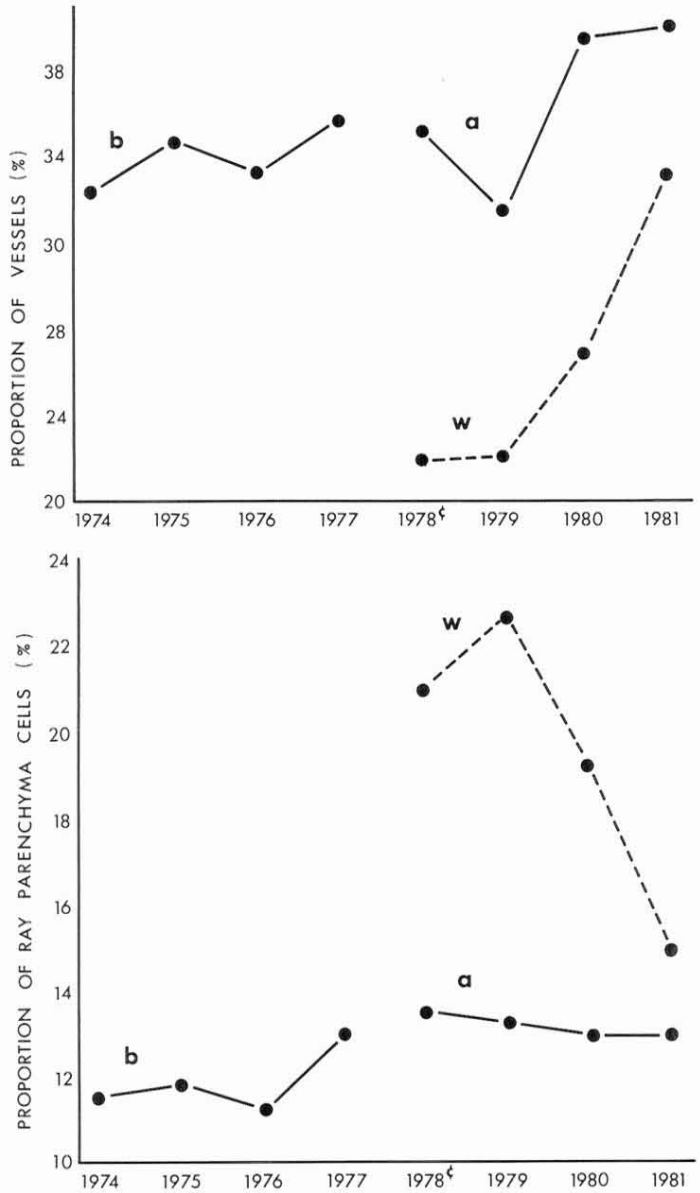

FIG. 16. Changes in tissue volume percentages. A. Vessel volume. B. Ray parenchyma volume. w = wood formed after wounding and radial to the wound hole, b = wood formed *before* wounding and away from the wound area, a = wood formed *after* wounding and away from the wound area. May 1978 = time of wounding.

normal component of wood; they occur in yellow-poplar bark, but they are rare (Nanko and Côté 1980). When a tree is wounded and the continuity of the vascular cambium is destroyed, the greatest production of abnormal cells would be expected the first year after wounding, since the wound hole must be sealed and the continuity of the vascular cambium reestablished. As the vascular cambium is restored in the wound area, normal xylem cell differentiation processes could grad-

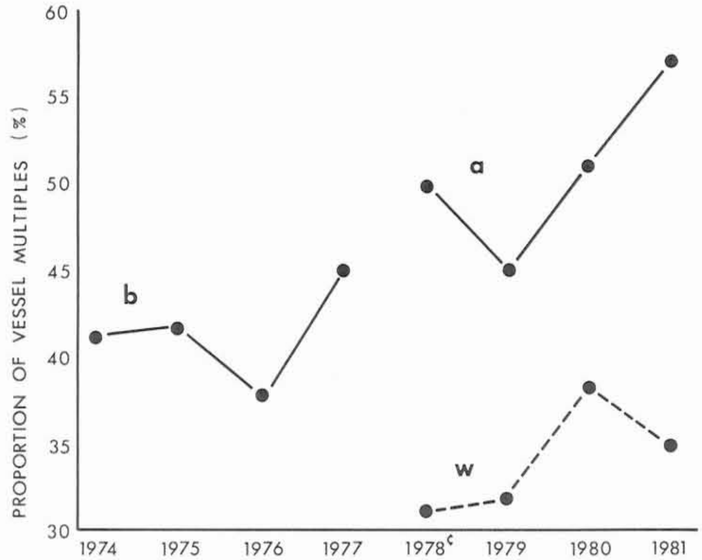

FIG. 17. Changes in percentage of vessel multiples. w = wood formed after wounding and radial to the wound hole, b = wood formed *before* wounding and away from the wound area, a = wood formed *after* wounding and away from the wound area. May 1978 = time of wounding.

ually resume, thus allowing for the eventual formation of normal xylem cells. It would be difficult to state that all anatomical characteristics of "barrier zones" are specific adaptations for protection, rather than the by-product of the cambium reestablishing itself.

CONCLUSIONS

The changes in wood structure in response to wounding observed in yellow-poplar match the general pattern of changes observed in maple, beech, and birch:

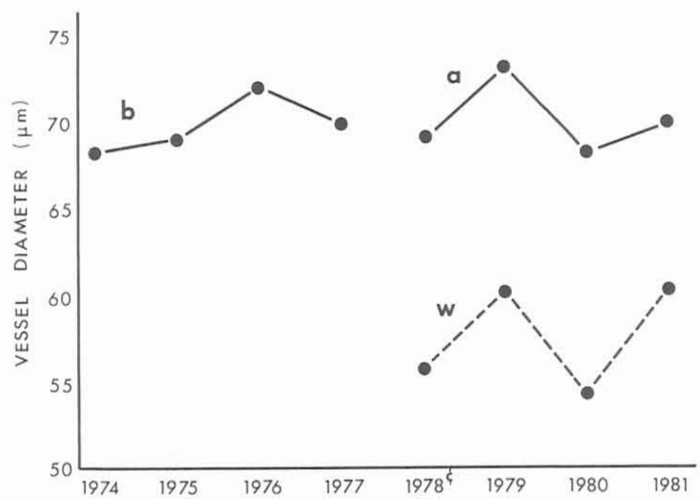

FIG. 18. Change in vessel diameter. w = wood formed after wounding and radial to the wound hole, b = wood formed *before* wounding and away from the wound area, a = wood formed *after* wounding and away from the wound area. May 1978 = time of wounding.

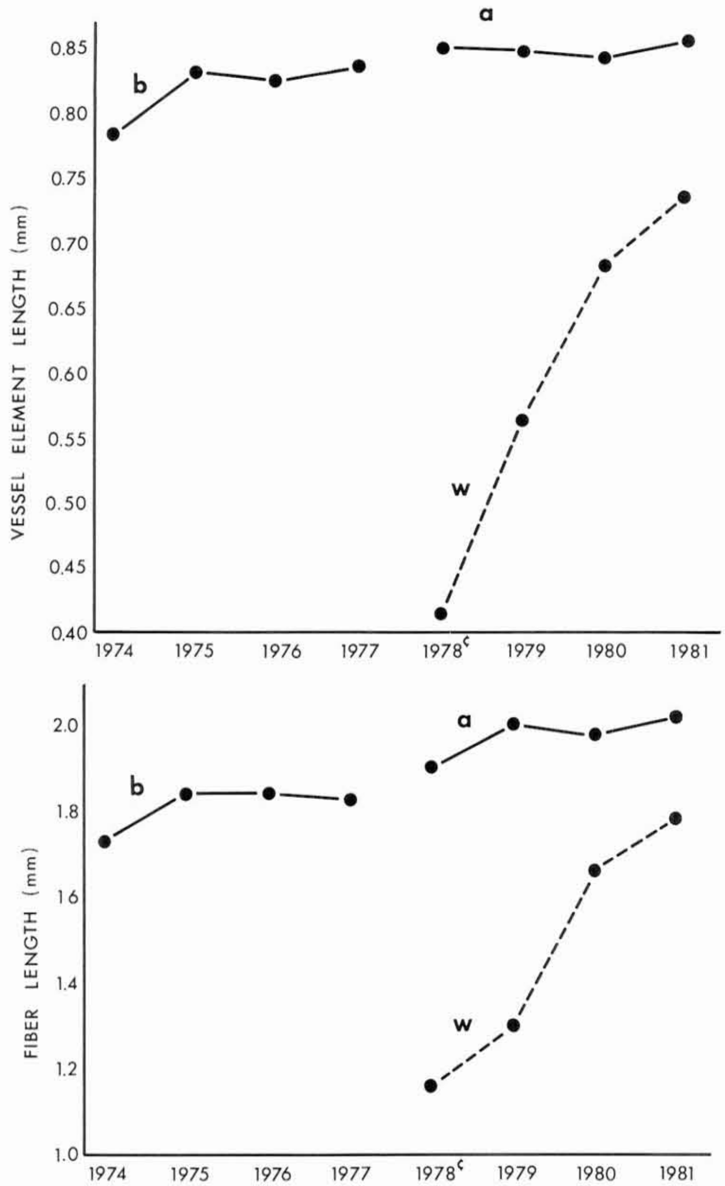

FIG. 19. Changes in cell length. A. Vessel element length. B. Fiber length. w = wood formed after wounding and radial to the wound hole, b = wood formed *before* wounding and away from the wound area, a = wood formed *after* wounding and away from the wound area. May 1978 = time of wounding.

more ray parenchyma, fewer smaller vessels, shortened cell lengths, disoriented axial tissues. There are differences in detail. It is likely that different trees with different structural patterns will exhibit some variation in wound response. In yellow-poplar, the proportion of fibers was lower in the wood formed for two years after wounding, while fiber volume was unchanged in the other species. Also, in maple and birch (Bauch et al. 1980) "there was a remarkable increase in connecting vessels (vessel grouping)," while in yellow-poplar there was a marked

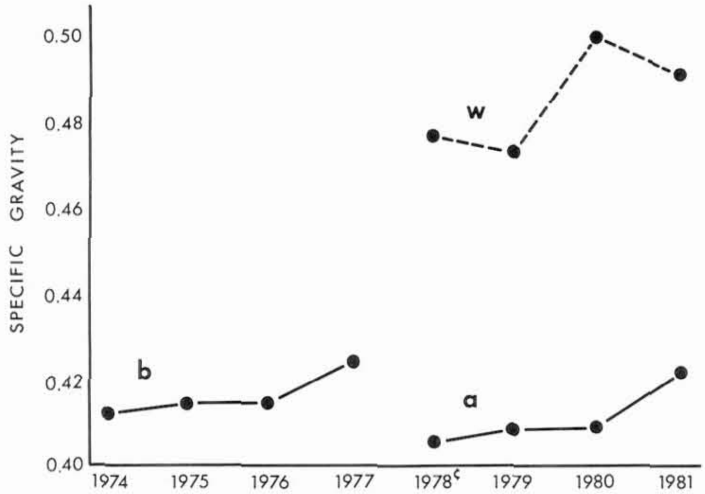

FIG. 20. Changes in specific gravity. w = wood formed after wounding and radial to the wound hole, b = wood formed *before* wounding and away from the wound area, a = wood formed *after* wounding and away from the wound area. May 1978 = time of wounding.

decrease in vessel multiples. A decrease in vessel grouping could be interpreted as being adaptive, as the fewer the vessel connections, the more difficult for pathogens to move from one vessel to another and to spread through the tree.

This study of *Liriodendron tulipifera* has shown that wood formed after wounding has distinctive characteristics. With increasing distance from the wound area, wood anatomical features of the wound-associated wood grade back into normal wood, although four years after wounding, the wood still had not returned to normal.

The extent of discoloration and decay associated with wounding are of concern, but it is also important, in terms of wood quality, to consider how rapidly a tree resumes production of normal wood. Figures 16–20 clearly show that different characteristics return to normal at different rates. The studies of maple, birch, and beech examined the wood formed for only two years after wounding. In maple and birch it was suggested that "it may take several years before the tissue is similar to that formed before wounding" (Bauch et al. 1980). Beech may recover more rapidly for it "formed normal-sized vessels after two years" (Rademacher et al. 1984). Ultimately, in tree improvement programs, it might be well to look for trees that not only are effective in compartmentalizing wounds, but that also are quick to resume production of normal wood.

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