A MACROSCOPIC AND MICROSCOPIC STUDY OF COMPARTMENTALIZATION AND WOUND CLOSURE AFTER MECHANICAL WOUNDING OF BLACK WALNUT TREES[1]

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ABSTRACT

Compartmentalization is a concept developed to explain tree response to injury. To study this concept, uniform mechanical wounds were made in fifty black walnut trees. Each tree was wounded at two different heights, 0.5 and 1.4 m, and at two different times, fall (November 1975) and spring (March 1976). The amount of wound closure was noted after one complete growing season, as were several macro- and microscopic characteristics of compartmentalization. Wound closure and compartmentalization were separate responses. Most of the wounds were closed after a single season's growth.

The eight trees with one or more open wounds were among the smallest and slowest growing trees in the study. This suggests a positive relationship between growth rate and wound closure, but statistically the relationship was not significant. Wood discoloration was the most prominent wound-related defect. Greater volumes of discolored wood were associated with fall wounds than with spring wounds. Similarly, fall and spring upper wounds were associated with larger volumes of discolored wood than their lower counterparts. Prior fertilizer treatments had no effect on wound closure or compartmentalization. The compartmentalization of wound-affected wood in black walnut agrees with the generalized model of compartmentalization of decay in trees (CODIT). The outer tangential and lateral compartment walls are the strongest, and the inner tangential and top and bottom compartment walls are the weakest and most easily overcome by invading microorganisms. The initial wood discoloration process did not appear to be associated with microorganism activity. Effective compartmentalization was positively correlated with growth rate. Some results of this study suggest that the relative ability to compartmentalize is under genetic control.

Keywords: *Juglans nigra*, wound response, discoloration, compartmentalization, anatomy, pathology.

INTRODUCTION

The economic importance of black walnut as a forest product does not require documentation. Wood discoloration, wood decay, and wood structural defects reduce the product quality. Association of these major wood defects with tree

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injuries has been documented in many tree species including black walnut (Shigo et al. 1978, 1979). Animals, environmental mishaps, and man, acting in a managerial role, can all be agents of tree injury. While injured secondary xylem cannot be healed and replaced by new tissue, trees have a mechanism to withstand such injuries by walling off or compartmentalizing the affected regions (Shigo and Hillis 1973; Shigo 1975, 1976). Since trees will encounter injuries as part of normal growth, it is necessary to consider wound closure and compartmentalization abilities of various trees as part of a comprehensive tree improvement program.

Recent research suggests that wound reaction in trees has two aspects, wound closure and compartmentalization (Shigo et al. 1977) and that wound closure is less significant with regard to wood defects than compartmentalization. Earlier research had shown wound closure to be correlated with current growth rate (Block 1941; Neely 1970). Data from wounding studies of *Populus* clones suggested that compartmentalization and accompanying wood discoloration was under genetic control (Shigo et al. 1977). While the compartmentalization of decay and discoloration in wood following prescribed wounding has been extensively studied in several hardwood species (see Shigo and Hillis 1973; Shigo 1976), similar information on black walnut is lacking.

Preliminary information on wound reaction in black walnut has come from the study of wood defects associated with pruned and nonpruned branch stubs (Shigo et al. 1978, 1979) and wound reactions in twigs (Armstrong et al. 1979; Armstrong and McGinnes 1979). These studies indicate that the mechanism of wound reaction in black walnut agrees with the generalized model of compartmentalization (CODIT) described for other trees (Shigo and Marx 1977). The formation of a barrier zone that limits decay and discoloration to the wood extant at the time of injury has been anatomically described in black walnut by Smith (1980). The barrier zone in walnut has been found to be the source of ring shakes (McGinnes 1975), a major wood defect of walnut (McGinnes 1968; McGinnes and Shigo 1975). Injury-associated discoloration and dark streaks in walnut are defects (Shigo et al. 1978; Shigo et al. 1979) since color and such color patterns have a direct bearing on the quality of the veneer produced (Maeglin and Nelson 1970; Phelps 1980).

The relationship between injury, wound response, and wood quality in black walnut indicates the need for further study. Similar aged, plantation-grown trees, experimentally wounded, would allow inter- and intra-tree comparisons of wound responses to be made. The objectives of this study are threefold: (1) to examine wound response in black walnut, in particular, wound closure and compartmentalization; (2) to document and characterize the pattern of wood compartmentalization and formation following mechanical wounding; (3) to examine the relationship between wound responses and the time and position of the wound, the growth rate, and prior fertilizer treatments.

METHODS AND MATERIALS

Fifty thirteen-year-old, plantation-grown black walnut trees, which had a known genetic background representing different seed source families, were selected for experimental wounding. These trees were designated for removal to thin the plantation. Each tree was wounded with a hand brace and bit at two different times and at two different heights, receiving four wounds in all. Fall and spring wounds were made in November 1975 and March 1976, respectively. At each time, wounds were located at 0.5 m and 1.4 m from the ground, abbreviated as L (lower) and U (upper) in text and tables. The bearing of the fall U wound was a random number of degrees from compass North. The location of the fall L wound was then located at +90° from the bearing of the fall U wound. The spring wounds were then located 180°, opposite the fall wounds. All wounds were 15 mm in diameter and 30 mm deep.

Twenty-four trees were selected for harvest and field dissection in December 1976, about 8½ months after the last wounding. The length and width of the column of discolored wood associated with each wound were measured. Column width was measured 2.5 cm above each wound. Accurate measurement of the column length required splitting many bolts. After macroscopic observations of discoloration were completed, the twenty-four trees were ranked in numerical order according to their ability to compartmentalize by summing the length of discoloration columns for all four wounds.

Trees that ranked high (1–8), average (9–16), and low (17–24) (Table 1) in their ability to compartmentalize were selected for detailed anatomical analysis. Specimens were prepared for microscopic observation by standard histological techniques. Sections were stained with hematoxylin and safranin. Selected sections and blocks were dehydrated, critical-point dried, and gold-coated for SEM observation. Sectioned material was examined from four locations around each wound: (1) 2.5 cm above wound site; (2) at the vertical limit of discoloration; (3) adjacent to wound, 1974 and 1975 increments extant at time of wounding; (4) adjacent to wound, 1976 increment formed subsequent to wounding. Locations 3 and 4 are indicated in Figs. 3–5.

DBH measurements were taken at time of first wounding and at time of harvest. The difference between these two diameters was the amount of growth during the 1976 season. The same plantation trees had previously (five years prior to present study) been used to study fertilizer treatments, indicated on Table 1.

Bolts from 15 trees were field-bagged in plastic and sampled for isolation of microorganisms. Two-hundred-seventy wood chips were removed from the discolored zone (see Results—Compartmentalization) of wound-affected wood and from the wound-containing section. Isolations were made on malt yeast agar plates and analyzed after a two-week incubation.

RESULTS

Wound closure

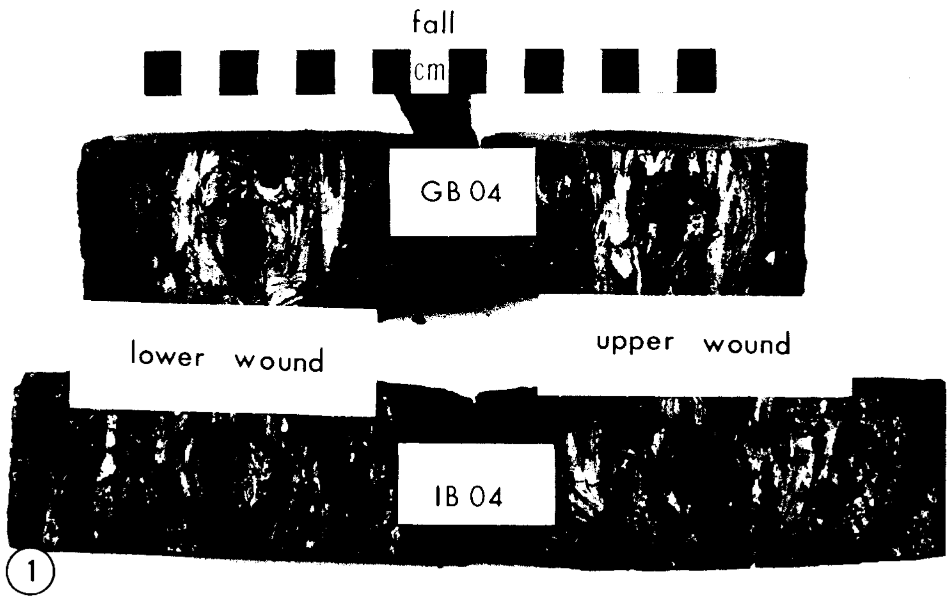
Sixteen of the twenty-four trees harvested had all four wounds closed at the time of harvest. None of the remaining eight trees had all four wounds open, and all open wounds showed some degree of closure. Three trees had three wounds open, one tree had two open wounds, and four trees had one open wound. The fifteen open wounds were distributed among the four possible wound sites as follows: fall U-6, fall L-3, spring U-3, spring L-3. Figures 1 and 2 show external views of fall and spring wound closure for two selected trees, GB-04 and IB-04[2]. Three of the four wounds in tree GB-04 were open, both fall wounds and upper

[2] USDA Forest Service plantation grid tree numbers.

TABLE 1. *Wood discoloration (column length and width), wound closure, tree size and fertilzer treatments.*

Tree ranking[a]	Wood discoloration										Number wounds open	Final DBH (cm)	1976 DBH increase (cm)	Fertilizer treatment
	Column length—cm					Column width—mm								
	Fall		Spring			Fall		Spring						
	U[c]	L[c]	U	L	Total[d]	U	L	U	L	Total[d]				
1 (IB-04)[b]	20	16	9	6	51	15	17	12	9	53	0	13.0	2.5	N
2 (IB-10)	37	19	11	8	75	16	17	13	10	56	0	15.5	2.4	NPK
3 (MB-10)	25	35	18	6	84	20	23	14	13	70	0	11.5	2.0	NPK
4 (MB-04)	55	29	9	9	102	17	17	12	11	57	3	7.5	1.3	N
5 (HH-04)	55	37	9	6	107	17	18	14	14	63	0	12.0	0.7	NPK
6 (LA-04)	36	56	13	9	114	20	18	14	12	64	2	10.0	0.6	NPK
7 (MA-10)	48	37	16	19	120	24	23	12	17	76	3	9.5	0.3	N
8 (IA-04)	51	43	13	15	122	18	17	11	3	49	1	8.5	0.4	NK
9 (LB-10)	46	65	8	8	127	21	22	10	11	64	0	12.5	1.7	NK
10 (FA-04)	66	35	27	10	138	18	17	14	15	64	0	10.9	0.6	NK
11 (GB-04)	75	43	12	8	138	18	23	14	13	68	3	8.5	0.6	Check
12 (FA-10)	66	35	22	14	139	30	22	20	15	87	0	12.6	1.5	N
13 (GA-10)	53	63	11	22	149	22	20	13	15	70	1	11.0	2.5	Check
14 (PA-04)	66	72	9	10	157	17	17	12	11	57	1	7.5	0.3	Check
15 (HH-10)	74	50	22	12	158	32	30	16	12	90	0	14.0	0.3	NPK
16 (EE-10)	70	52	25	16	163	23	24	15	15	77	0	8.5	0.5	Check
17 (JA-10)	66	49	28	23	166	27	21	15	15	78	0	10.0	1.1	NK
18 (NN-10)	94	39	14	19	166	18	20	18	15	71	0	10.0	0.9	N
19 (LA-10)	68	40	41	20	169	21	17	20	16	74	0	12.5	0.8	Check
20 (JB-10)	73	56	26	24	173	27	23	13	15	78	0	12.3	0.3	NPK
21 (FB-10)	78	63	17	16	174	19	17	13	12	61	0	13.0	0.8	NK
22 (IA-10)	62	65	24	29	180	20	22	14	10	66	0	10.5	1.0	NK
23 (GB-10)	74	44	51	11	180	23	20	19	17	79	1	10.0	0.3	NK
24 (KK-10)	127	86	35	24	272	25	27	17	15	84	0	11.5	0.5	Check
Mean	62	47	19	14	142	21	20	14	13	69		11.0	1.0	

[a] Based on total discoloration column length (column 5).
[b] USDA Forest Service plantation grid number.
[c] U, upper wound; L, lower wound.
[d] Total, sum of all 4 wounds.



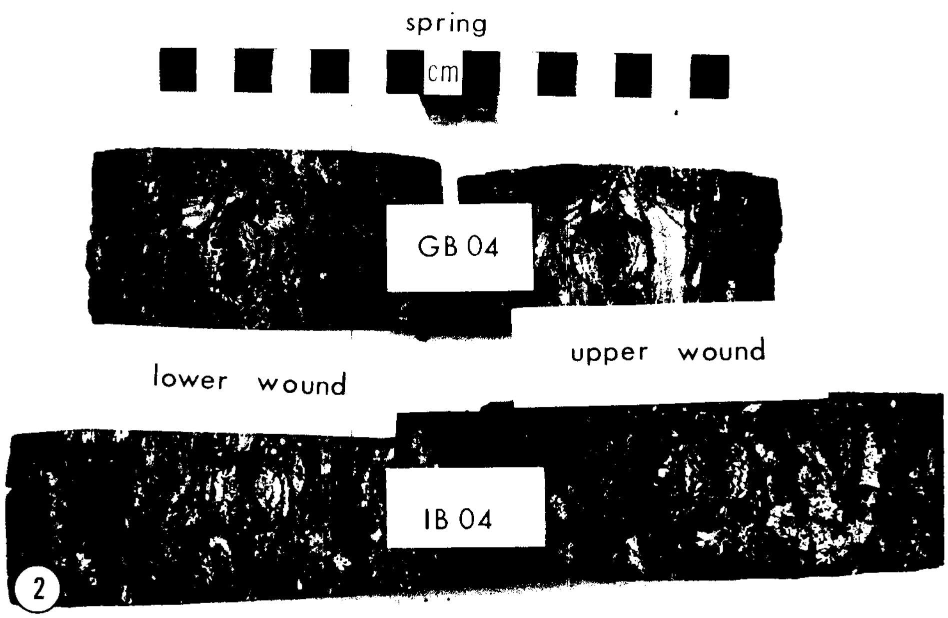


FIG. 1. Upper and lower fall (Nov.) wounds of trees GB-04 and IB-04, ranked 11 and 1, respectively (Table 1). Note the vertical furrow produced by the lateral closure of the wound plugs and the open wounds of GB-04.

FIG. 2. Upper and lower spring (March) wounds of trees GB-04 and IB-04, ranked 11 and 1, respectively (Table 1). Only the upper spring wound of GB-04 was still open at the time of harvest.

spring wound, while all wounds in IB-04 were closed. Figures 4 and 5 show open wounds in cross section, and Fig. 3 shows complete wound closure.

The tissue forming the wound plug was derived from the vascular cambium adjacent to the wound. There was cambial zone dieback immediately adjacent to the wound (Fig. 6, small arrow) causing a separation that extended 1–2 mm laterally and 2–4 mm vertically from the margin of the wound.

Cells in the disrupted cambial zone, cambial initials and immature cambial derivatives, and phloem parenchyma cells formed a callus, which gradually aligned with the intact cambium forming parenchymatous derivatives (tail of small arrow, Fig. 6). Numerous anticlinal longitudinal divisions increased the number of derivative files that expanded laterally into the wound opening. The wound plug tissue formed a vertical furrow externally and internally (Figs. 1–3) as laterally expanding tissues met forming a complete wound plug. Distally the wound plug cambium formed parenchymatous derivatives. A cork cambium differentiated in the distal regions of this tissue, producing a limited amount of periderm that covered the wound plug internally and externally (Figs. 3 and 4). No callus tissue was formed on the internal surfaces of the wounds.

Wound closure was anatomically complete when the continuity of the vascular cambium was reestablished following lateral contact of the wound plug tissue (Fig. 3). Cambial activity and the production of xylem derivatives displaced the external parenchymatous and corky tissues in the central region of the wound plug. New cambial initials were differentiated from the intervening parenchyma. Wound plugs were formed and wound closure was completed prior to complete anatomical closure.

The eight trees with open wounds had no statistical correlation with their compartmentalization rankings, which were 4, 6, 7, 8, 11, 13, 14 and 23 (Table 1). There was no statistical correlation between wound closure and increase in diameter following wounding, although six of the eight trees with open wounds were among the eleven trees with the smallest diameter increase following wounding—less than .63 cm (Table 1). Similarly, seven of the eight trees with open wounds were among the ten smallest trees (DBH) in the study (Table 1).

Compartmentalization—macroscopic

A zone of dark, discolored wood, sharply contrasting to the light-colored normal sapwood, was associated with each wound. Generally, the discoloration formed a column extending vertically above and below each wound. While the

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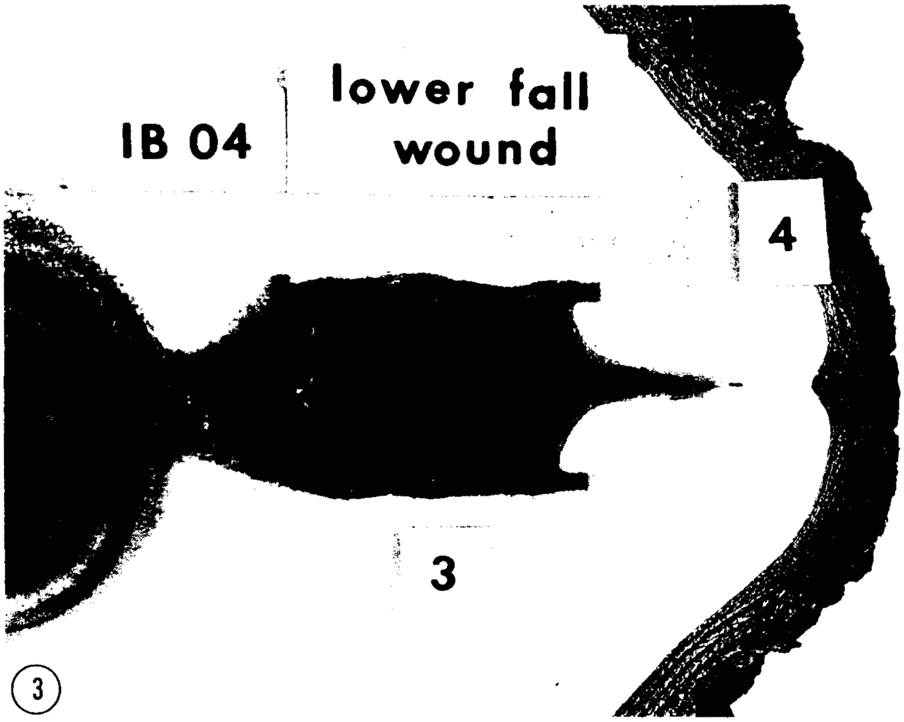
FIG. 3. Cross section through a representative wound showing complete anatomical closure. Note the discrete boundary of the discolored wood lateral to the wound. All wood to the right of the wound was formed in the 1976 growing season. Areas designated 3 and 4 in this and Figs. 4 and 5 were anatomically examined in detail. The wound is 15 mm wide.

FIG. 4. Cross section through a partially closed upper spring wound. Periderm and phloem of the wound plug are continuous with the normal stem tissues. In this smaller diameter tree, 8.5 cm DBH, the wound penetrated into the heartwood. Arrowheads correspond to those in Fig. 6, a microscopic view of area 3. The wound is 15 mm wide.

FIG. 5. Cross section through a partially closed upper fall wound, the compliment of the wound shown in Fig. 4. Wound plug tissues show some mortality (arrows). The wound is 15 mm wide.


IB 04
lower fall
wound
4
3
3


GB 04
upper spring
wound
4
3
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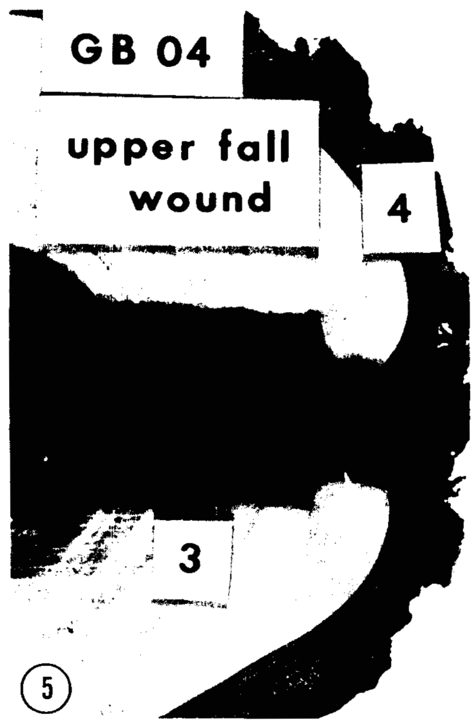
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lateral extent of the discoloration was rather limited, about as wide or slightly wider than the width of the wound at the point of measurement 2.5 cm above the wound, the vertical discoloration column of each wound varied from as little as 6 cm to as much as 127 cm (Table 1).

The length of the discoloration column for fall wounds (U + L) was highly correlated with those from spring wounds (U + L) ($r = +0.55$, $P < 0.01$). The length of the discoloration column for upper (U) wounds (fall and spring) was highly correlated with those from lower (L) wounds (fall and spring) ($r = +0.57$, $P < 0.01$). Since trees with shorter or longer columns of discolored wood tended to have shorter or longer columns of discoloration associated with all four wounds, the lengths of columns of discolored wood for all four wounds in each tree were summed, and the total was used to arrange the twenty-four study trees in a numerical ranking (Table 1).

The data by tree and the mean data (Table 1) show that the lengths of discoloration from fall wounds were significantly greater ($P < 0.05$) than those from spring wounds, and usually accounted for approximately 75% of the total discoloration. Upper wounds (fall and spring) had significantly longer columns of discolored wood ($P < 0.05$) than the lower wounds. The total length of the column of discoloration was highly correlated to the total width of the column ($r = +0.58$, $P < 0.01$).

There were seven pairs of genetically related trees among the twenty-four trees studied. All trees that were planted in each plantation column, indicated by the identification letters (Table 1, column 1), were progeny of a single seed tree. These trees are at least half-siblings (¼ genetic relatedness), and perhaps full siblings (½ genetic relatedness); but since the trees were open-pollinated, there is no way to determine this precisely. The members of the IB, MB, and FA pairs had very similar discoloration rankings, 1 and 2, 3 and 4, 10 and 12, respectively (Table 1). In the other four pairs, GB, HH, IA, LA, the row 04 tree ranked higher than the row 10 tree (Table 1). In all four pairs, the row 10 tree had a total discoloration column approximately 1.5 times as long as its (half) sibling from row 04. As a general trend, row 10 trees ranked lower (average rank = 15.1) than the row 04 trees (average rank = 7.4) (Table 1). The difference between row 04 and row 10 trees may be related in some unexplained way to the transplanting of the row 10 trees that took place at the time of the fertilizer study, five years prior to the present study.

There was no significant difference between fertilizer treatments and between treatments and controls with regard to either final DBH or DBH increase in 1976. The mean length of the discoloration column was greatest for the unfertilized

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FIG. 6. Transverse section of area 3 from wound shown in Fig. 4. Arrowheads indicate a portion of the lateral wound edge; cf. Fig. 4 for orientation. Lateral boundary of discolored wood and the lateral compartmental wall are delimited by ray and axial parenchyma with dark-colored contents and vessels containing tyloses (squares). Small arrow indicates area where cambium was torn at the time of wounding. Bar equal 1 mm.

FIG. 7. Tangential section of area 3 showing lateral boundary of discolored wood (black arrows). A small portion of the wound margin is at the upper right. White arrow indicates vessel containing tyloses. Bar equals 1 mm.

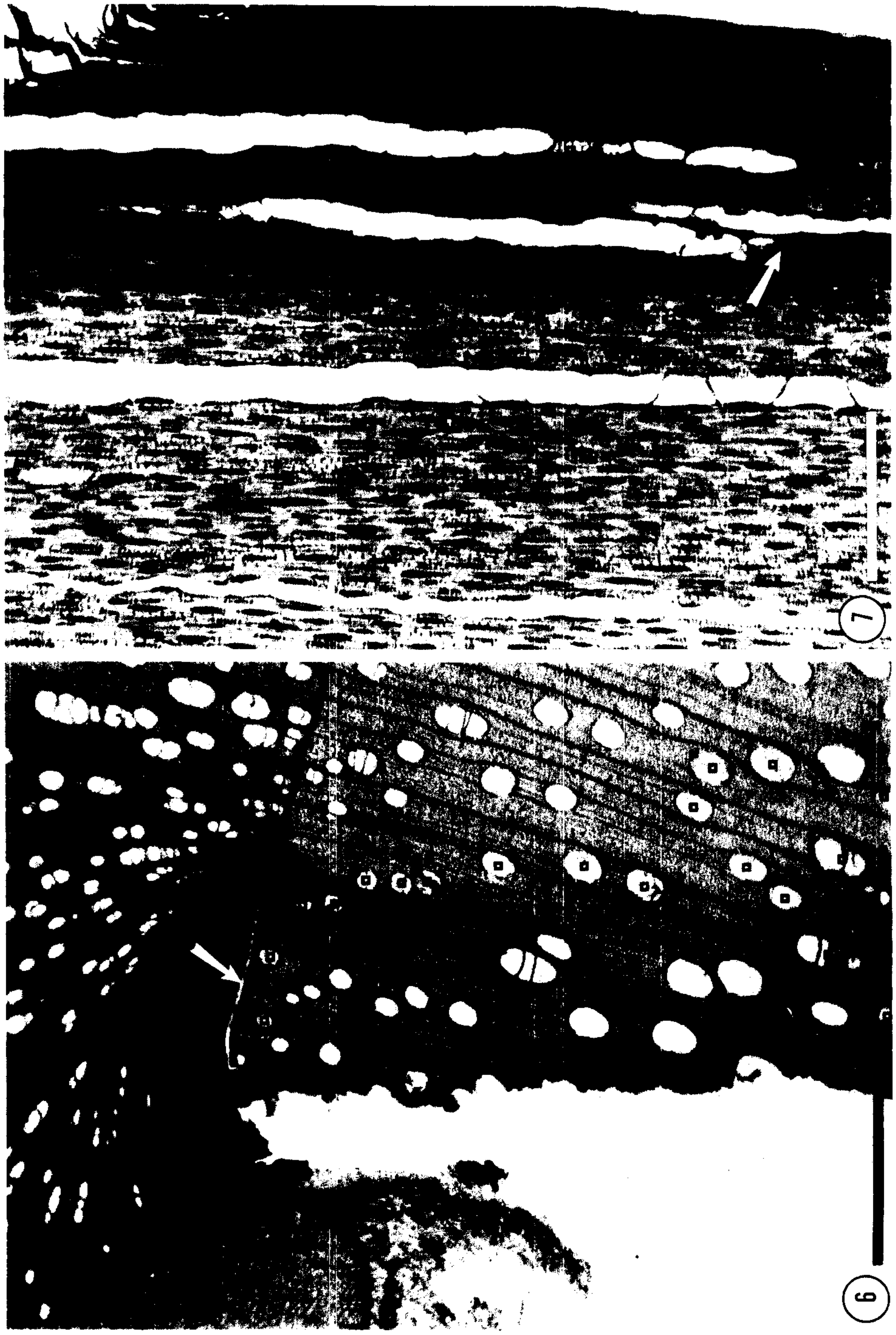
7
6

TABLE 2. *Mean total lengths of the discoloration columns by fertilizer treatments.*

Fertilizer treatment	Mean total length (cm)
N	115[a]
NPK	119
NK	155
Check	175

[a] No significant differences between mean values joined by vertical lines. Least Significant Differences (LSD) = 47.4 cm for mean total lengths of the discoloration columns.

trees (Table 2). Both the N and NPK treatments had significantly shorter discoloration columns than the control trees. However, tree 24 had a discoloration column 50% longer than tree 23, and seems to be solely responsible for the statistical significance. The mean discoloration length for the other five control trees was 156 cm. There was no significant correlation between total width of the discoloration column or 1976 increase in DBH and the various fertilizer treatments.

The final DBH of the trees was not correlated with any variable; however, the 1976 increase in DBH, which followed the wounding, was highly correlated to the total discoloration column length ($r = -0.58$, $P < 0.01$). Cambial activity was greatest in the immediate vicinity of the wounds with up to two times as much wood production adjacent to the wounds (Figs. 3–5) compared to areas 90° away from the wound site.

Compartmentalization—microscopic

The lateral margins of the discolored wood associated with each wound were very discrete both macroscopically and microscopically (cf. Figs. 4 and 6, white arrowheads indicate orientation, and Fig. 7). The axial and radial (ray) parenchyma of the discolored wood had darkly-colored cell contents (Figs. 6, 7). Most of the vessels at or just beyond the lateral margin of the discoloration were plugged by tyloses (Figs. 6, 7, 8). The vertical extent of the discolored wood was both macro- and microscopically rather diffuse (Figs. 11, 12), marked by dark parenchyma cell contents and tylosed vessels over a broad area. The radial extent of the discoloration was very discrete at the 1975–1976 increment boundary, but was more diffuse inwardly (Fig. 3). The wounds in the largest trees penetrated to the inner regions of the sapwood (Fig. 11), but in smaller trees the wounds penetrated the heartwood (Figs. 4, 5, 12) so that inner portions of the discolored wood were difficult to distinguish from normal heartwood.

The wounds affected wood in at least three sapwood increments in all trees, 1973–1975. The heartwood-sapwood boundary was located in the 1971 and 1972 increments in all the study trees. In radial longitudinal sections, the discoloration

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FIG. 8. Cross section of 1975 increment 5 cm below wound. Discolored wood is to the left of the arrows, normal colored to the right. Vessels containing tyloses form a radial band a little to the left and right of the arrows. Many of the vessels in the discolored region have crusty contents. Bar equals 1 mm.

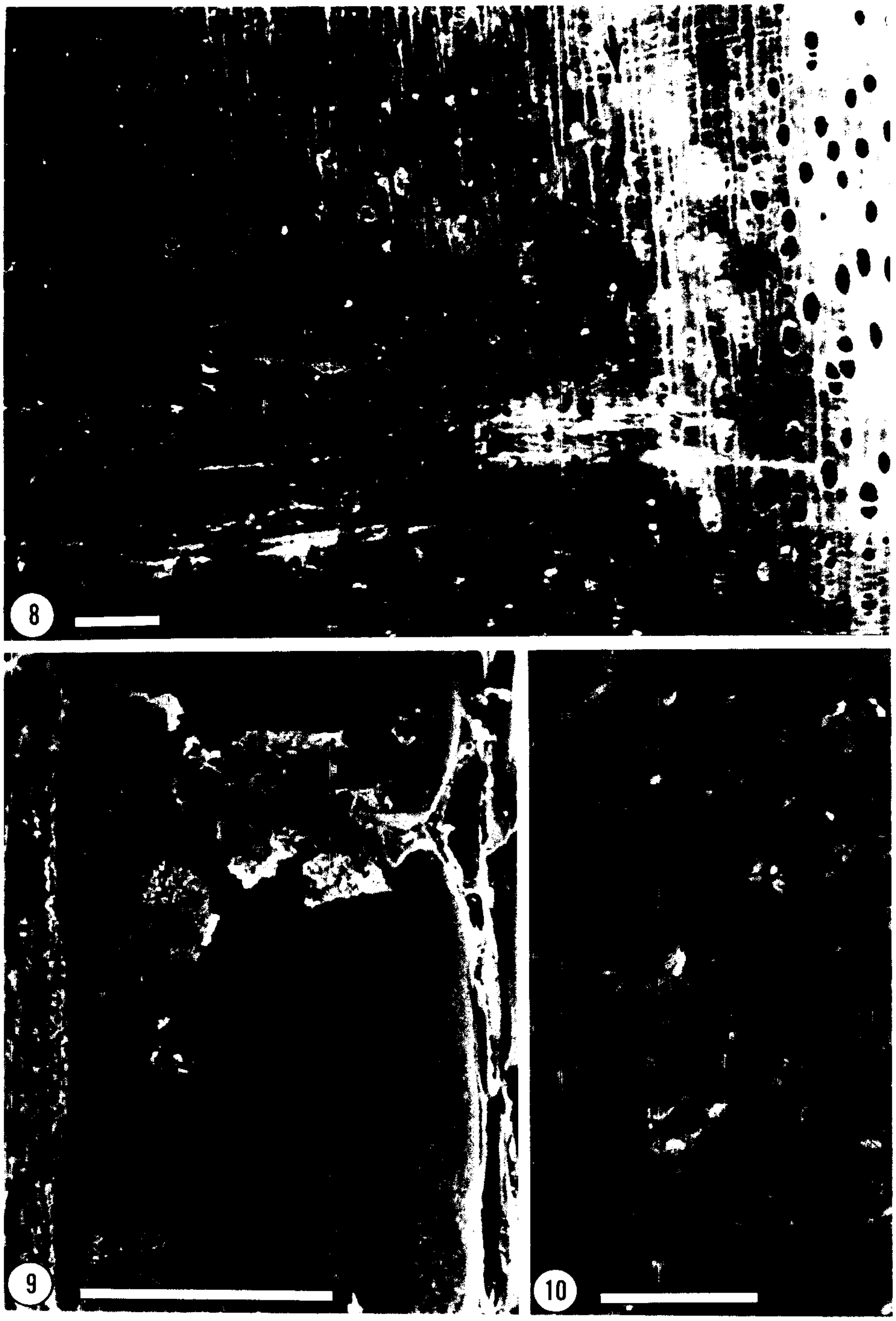

FIG. 9. SEM of longitudinally sectioned vessel from the left central portion of Fig. 8 showing a crusty deposit on the margin of the simple perforation and the lateral wall pits. Bar equals 100 μm.

FIG. 10. SEM detail of vessel wall in Fig. 9 showing a variety of bacterial cells. Bar equals 10 μm.

showed a very regular pattern, with the discoloration increasing in length in each progressively older sapwood increment, so that the discoloration column in the 1975 increment was always shorter than the portion in the 1974 increment, and similarly, the portion in the 1973 increment was usually the longest (Fig. 11). Within any single increment the vertical extent of the discoloration column was greater in the earlywood than in the latewood.

Microorganisms

Many of the vessels in the discolored wood of the 1974 and 1975 increments, particularly larger diameter earlywood vessels, contained golden or brown-colored, crusty deposits. In several trees such vessels extended vertically beyond the limits of the discolored wood and appeared as dark-brown or golden streaks in contrast to the light-colored sapwood (Figs. 11, 12). These vessels were not tylosed in the vicinity of the wound, while vessels immediately adjacent to the discolored wood were almost completly tylosed (Fig. 8).

Figure 9 shows a portion of a vessel and the crusty deposits on the vessel perforation and adjacent vessel wall pits. Scanning electron microscopy revealed that the crusty deposits were composed of numerous bacterial cells in an unidentified amorphous substance (Fig. 10). Most of the vessels without tyloses that were vertically aligned with the wound contained bacteria. No fungal hyphae were observed in specimens studied by SEM. Little bacterial invasion of vessels was observed in discolored wood in the 1972 increment, where most of the vessels contained tyloses at the time of harvest.

Bacteria and microorganisms were isolated from all fifteen trees sampled. Bacteria were isolated from 83% of the discolored-wood and wound-section chips. Sixty-four percent of the chips yielded microaerophyll type bacteria. Seventy-five percent of the wound-section chips yielded Myxomycetes, and Hymenomycetes were isolated from two trees. There were no qualitative or quantitative differences in microorganisms isolated from fall and spring, or upper and lower wounds.

In non-wound-affected wood, there were three increments in which the vessels were essentially free of tyloses at the time of harvest. In the 1973 increment 10–40% of the vessels contained tyloses, particularly the larger diameter earlywood vessels. The 1972 increment was at or near the heartwood-sapwood boundary, and almost all the vessels contained tyloses. Other vessels containing tyloses were clearly associated with the wounds.

DISCUSSION

Wound responses in black walnut are consistent with responses described for other species. The response to mechanically inflicted wounds can be separated into two components, wound closure and compartmentalization. The lack of correlation between the black walnut trees' relative success with wound closure and wound compartmentalization suggests that these responses are separate. This agrees with recent findings on *Populus* (Shigo et al. 1977).

The great majority of the trees in this study were able to close the mechanically inflicted wounds in a single season. While wound closure has been related to growth rate in many studies (Block 1941; Neely 1970), there was no statistically significant correlation between either final DBH or 1976 increase in DBH and

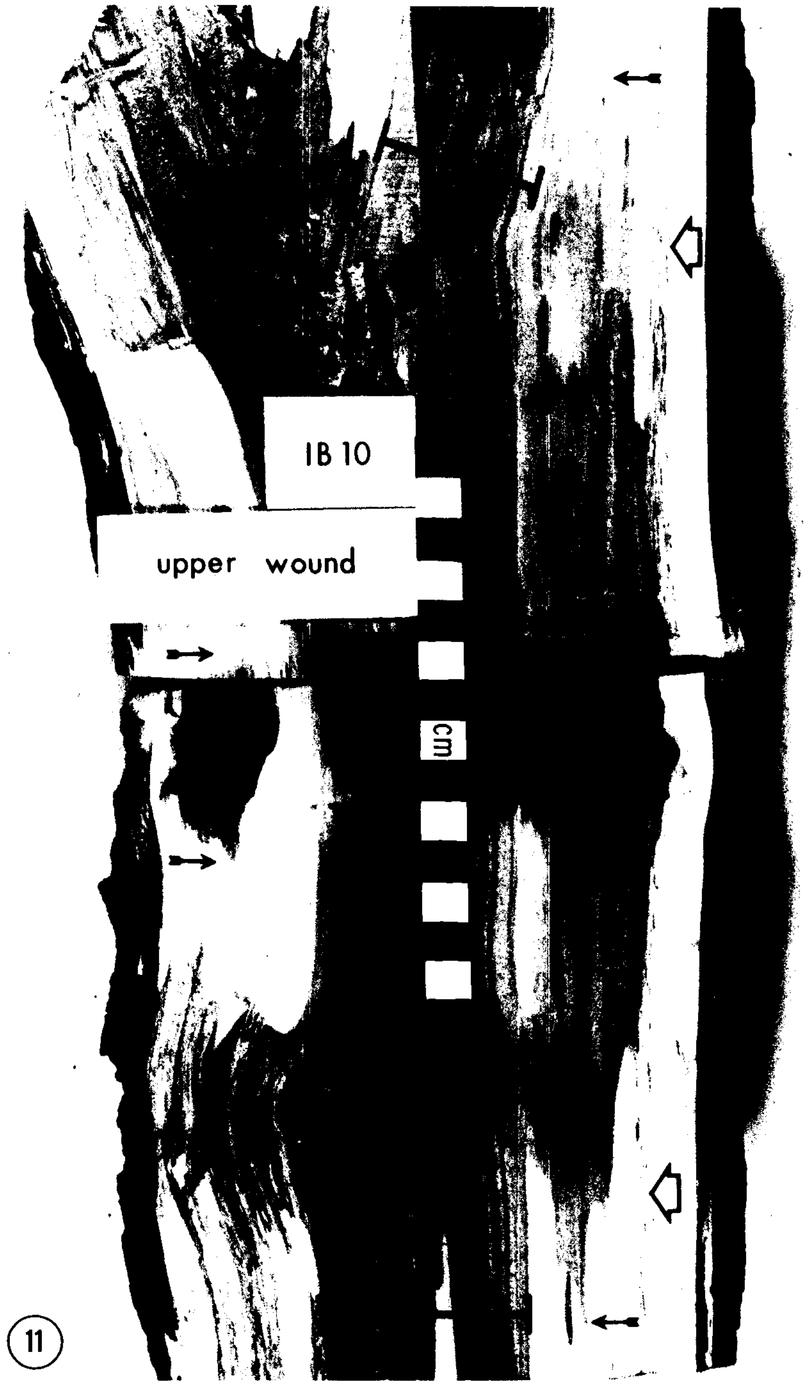

FIG. 11. Longitudinal section through upper wounds of the number 2 ranked tree. The spring wound is on the left, fall on the right. Black arrows indicate the approximate vertical limits of the discoloration. Radial limits of the normal heartwood are indicated by brackets. Note the dark streaking vertically exceeding the discoloration of the fall wound (open arrows).

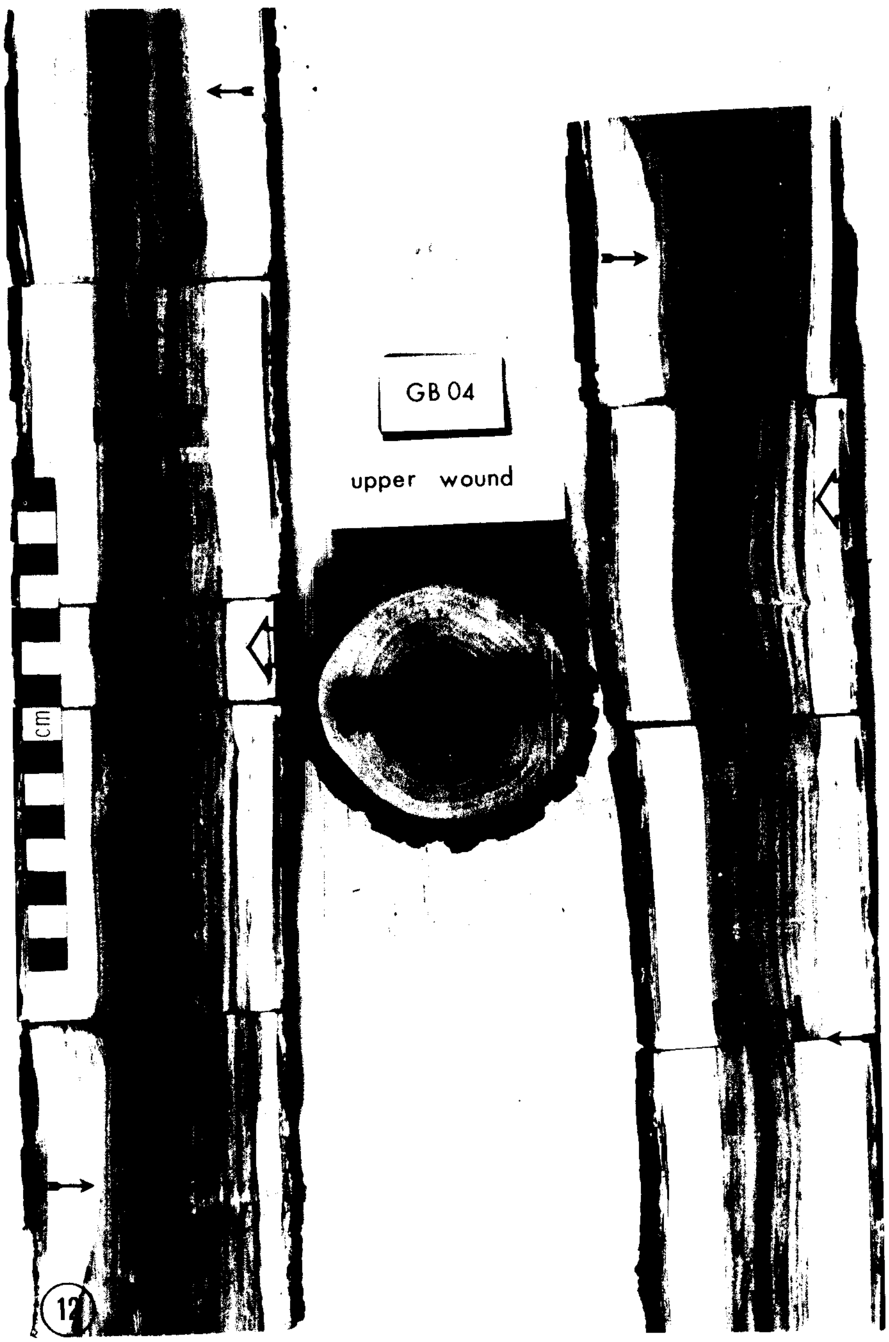

FIG. 12. Longitudinal sections showing the vertical extent of discoloration (black arrows) associated with the upper wounds of the number 11 ranked tree. The spring wound is on the left, fall on the right. The wounds are in the 5-cm-thick bolt seen in cross section to show the width of the discoloration columns. Basipetal sections are arranged bottom to top on the left, acropetal sections top to bottom on the right. Note the dark streaking vertically exceeding the discoloration of the fall wound (open arrows).

successful wound closure. However, most of the trees with open wounds were among the smallest, slowest growing trees in the study. This suggests a positive relationship between growth rate and wound closure, which would generally be expected since wound closure is essentially a growth phenomenon. Neither growth rate nor wound closure was related to the previous fertilizer treatments, indicating that all effects of the fertilizer treatments were prior to this study. Time of wounding, fall or spring, and wound position, U or L, had no affect on wound closure. A 15-mm-diameter wound can be considered relatively small since most of the trees studied completed wound closure during a single season's growth. Larger wounds may be required to demonstrate to a greater extent varying abilities of wound closure.

Wood discoloration was the most prominent aspect of the compartmentalization of wound-affected tissue. While wood discoloration was the most easily observed and easily documented aspect of compartmentalization, discoloration was accompanied by other changes to both the wood extant at the time of wounding and the wood formed subsequent to wounding. The wood discoloration was highly coordinated with other anatomical changes and, therefore, was a good indicator of the relative volume of the wound-affected tissue. More importantly, the uniformity of the discoloration associated with the four wounds in each tree indicates that the tree, more than external factors, is regulating the extent of the wound-affected tissue.

The discolored wood was characterized by dark contents in the ray and axial parenchyma. Dehydration, cell death, depletion of nutrients and deposition of darkly colored compounds in parenchyma cells have all been found to be associated with the process of wood discoloration (Shigo and Hillis 1973). Since there was no evidence of decay observed and the discoloration was not necessarily associated with the presence of microorganisms, this initial stage of discoloration could be considered abiotic, the general result of oxidative chemical reactions and the formation of phenols and other compounds (Gagnon 1967; Sucoff et al. 1967). The larger volume of discolored wood associated with the fall wounds can be attributed to a longer environmental exposure prior to the onset of physiological activity. This agrees with the conclusions of Smith (1980) based on the study of abnormal wood formation following wounding in these same walnut trees. Fall and spring upper wounds produced larger volumes of discolored wood than their lower counterparts, perhaps the result of differences in environmental exposure and/or dessication at the two wound heights. Positional differences in tree physiology may also play some role.

The discoloration in the wood extant at the time of wounding was accompanied primarily by tyloses formation in vessels. The lateral compartmental walls were very discrete. Tyloses were formed in nearly all vessels immediately adjacent to the discolored wood (Figs. 6 and 8). The inner compartmental walls and the top and bottom compartmental walls were more diffuse. In almost all cases, the wound penetrated near the heartwood-sapwood boundary if not into the heartwood. The normal discoloration and tyloses formation associated with heartwood formation and the lack of physiologically active cells combined to make the inner compartmental wall macro- and microscopically indistinct. The vertical extent of the discolored wood was associated with a diffuse array of vessels containing tyloses. The presence of microorganisms in vessels greatly exceeding the vertical limits of the discolored wood indicated that the top and bottom compartmental walls were either very weak or incompletely formed. The absence of bacteria in vessels of older increments suggested that normal tyloses formation associated with the cessation of conduction formed a barrier to the movement of microorganisms.

The outer tangential compartmental wall was very distinct and coincided with the 1975–1976 increment boundary. This compartmental wall was formed by tissue formed subsequent to wounding and was characterized by parenchyma cells with darkly colored contents and a zone of abnormal wood. The formation of abnormal wood after wounding was studied in detail by Smith (1980). The abnormal wood was the anatomical manifestation of a barrier zone that reduces centripetal movement of decay organisms (Smith 1980). The barrier zone corresponds to wall 4 of the model of compartmentalization of decay in trees (CODIT) (Shigo and Marx 1977). While abnormal wood zones have been associated with ring-shake defects (McGinnes 1975), the abnormal wood zones around these wounds were rather limited (Smith 1980) and would not be a probable source of severe defect. This was supported by the observation that air-dried specimens in the lab did not develop ring-shakes.

The compartmentalization of wound-affected tissue in black walnut agrees with the generalized model of compartmentalization of decay in trees (Shigo 1975, 1976). The outer tangential and lateral compartment walls are the strongest, and the inner tangential and top and bottom compartment walls are the weakest and most easily overcome by invading microorganisms. These are called walls 4, 3, 2 and 1 in order of decreasing strength (Shigo 1975, 1976). Walls 2 and 1 in black walnut were the most diffuse. The presence of microorganisms in vessels beyond the vertical limits of discolored wood confirmed the weakness of wall number 1 and questions the validity of using discoloration to determine the position of wall 1 and to measure relative success in compartmentalizing.

The negative correlation between the 1976 increase in DBH and total length of the discoloration suggested that rapid growth rate, and therefore, tree vitality, has a pronounced effect of compartmentalization. This does not suggest genetic control of compartmentalization as did the study by Shigo et al. (1977) on *Populus*. However, tree growth rate would have a genetic as well as an environmental component and could be selected.

While trees that had previously received NPK and N fertilizer treatments had significantly shorter discoloration columns, trees that had received NK were not significantly different from the controls (Table 2). Since tree 24 was responsible for the difference between NPK and N treated trees and control trees and since there was no statistical correlation between DBH or 1976 DBH increase, it is doubtful that the previous fertilizer treatments had any influence on the results of this wounding study. If growth rate is positively related to successful compartmentalization and wound closure, fertilizer application might reduce defects from pruning.

Ring-shake and discoloration are both wound-related defects that degrade walnut quality. The results of this study, and other studies of walnut wound reactions (Smith 1980; Shigo et al. 1978) indicate that other managerial practices can reduce wound-related defects. Spring pruning of young branches to produce a clear bole would reduce both ring-shake and discoloration. Other recommendations have been made based on pruning studies of black walnut (Clark 1955; Shigo et al. 1978).

The question of genetic control of compartmentalization in black walnut cannot be answered directly from the results of this study; however, the similar reactions of the seven half-sibling tree pairs are highly suggestive that the ability to compartmentalize is genetically controlled. When wood quality is the ultimate goal of a tree improvement program, it would be important to incorporate information about relative abilities to compartmentalize wound defect. However, this study should demonstrate the difficulty of obtaining that information. Numerous intrinsic and extrinsic variables had to be considered and evaluated, and while it would have been better to eliminate or reduce the numer of extrinsic variables, this was not possible, even in the relatively controlled context of a plantation.

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