

WOUND CLOSURE RATES ON TREES

by Dan Neely

Abstract. The amount of trunk growth on ten species of plantation-grown trees differed among and between species. Wound closure rates on these trees correlated positively with trunk growth and varied between species and between years. More callus was produced around large wounds than around small wounds on the same tree. Callus growth at the periphery of the wound was greater than the radial growth of the stem. Closure rate on slow-growing trees within a species was greater per unit of radial growth than on the fast-growing trees. Significant variability in wound closure rates was found within a population, a finding that suggests that plant breeders may be able to select for plants with this attribute.

Key Words: callus, wound tissue, injury

Résumé. La croissance en diamètre de dix espèces d'arbres en plantation diffère parmi et entre les espèces. La vitesse de fermeture des blessures sur ces arbres était positivement corrélée avec la croissance en diamètre et variait entre les espèces et d'une année à l'autre. Plus de cal fut produit autour des grosses blessures qu'autour des petites sur un même arbre. La croissance du cal à la périphérie de la blessure fut plus grande que la croissance radiale de la tige. La vitesse de fermeture des blessures sur les arbres à croissance lente d'une espèce donnée fut plus élevée par unité de croissance radiale que sur les arbres à croissance rapide. Des variations significatives de la vitesse de fermeture des blessures furent observées dans la population, un résultat qui suggère que les producteurs d'arbres pourraient sélectionner des arbres pour cet attribut.

In annual plants and in the primary or immature secondary tissue of perennial plants, a periderm forms to seal wounds within a few days. In the woody tissues of perennial plants, however, there are insufficient parenchyma cells to initiate the formation of periderm. When wounded, these mature tissues heal by forming callus around the margin of the wound. The most frequent source of callus is the vascular cambium. As each annual ring is formed, the new layer of tissue assumes a position at right angles to the face of the wound. In this position, new tissue formed in the normal way extends the growing layer over the cut surface until opposite sides meet. Rings formed subsequently increasingly bury the wound (1).

Wounds damage trees directly and indirectly. When they are sufficiently wide, they interrupt or curtail the basipetal flow of food materials in the phloem; when they are sufficiently deep, they weaken the stem and make it susceptible to breakage (3). Wounds also serve as entry or in-

oculation sites for insects or disease organisms. Shigo and Marx (8) described the internal reactions of wood in their hypothesis on the compartmentalization of decay in trees (CODIT).

Closure of wounds on the stems of trees is associated with stem growth and has been correlated with the annual increase in stem diameter (6, 7). Martin and Sydnor (4) found differences in rates of wound closure between tree species. The present study was designed to establish more firmly the relationship between the production of callus and annual radial stem growth, to determine if tree species varied in rate of callus production, and to clarify if variability within a species was sufficiently consistent to encourage plant breeders to select for rapid-callus-producing clones.

Materials and Methods

The ten species used in this study were English elm (*Ulmus procera*), green ash (*Fraxinus pennsylvanica* var. *lanceolata*), hackberry (*Celtis occidentalis*), honeylocust (*Gloditsia triacanthos* var. *inermis*), littleleaf linden (*Tilia cordata*), Norway maple (*Acer platanoides*), pin oak (*Quercus palustris*), sycamore (*Platanus occidentalis*), tulip tree (*Liriodendron tulipifera*), and white birch (*Betula papyrifera*). The trees were growing in the Illinois Natural History Survey arboretum located 1 mile south of Urbana, Illinois. Species, year of planting, plant spacing, and size of tree when the study began in 1981 are given in Table 1.

The wounds inflicted on the trunks of the trees were ellipses with pointed ends and of two sizes: small, 25 mm wide by 50 mm tall, and large, 50 mm wide by 100 mm tall. A template was used to mark the wound margin, and curved and straight wood chisels were used to remove the bark and expose the wood. When bark adhered to the wood, the wood face was scraped clean.

Four wounds, two small and two large, were cut into the trunk of each of 20 trees of each species for 4 consecutive years, 1981-1984. Wounds were cut in the cardinal directions; large wounds were cut north and south in 1981 and 1983 and

east and west in 1982 and 1984. Within each year, wounds were at approximately the same height on the tree and within 0.5-2.0 m of the ground line. Cuts were made the week of 14 May 1981, 3 May 1982, 2 May 1983, and 16 April 1984. After the 4 years, each tree had been wounded 16 times.

Initial trunk diameter and subsequent diameter growth for 5 years were measured with a steel tape at a line painted on the trunk of each tree approximately 1 m above the ground. The initial measurement was made in April of 1981 (Table 1), and subsequent measurements were taken in late September or early October of 1981-1985.

Closure of wounds was determined annually through horizontal measurements at the greatest width of wood remaining exposed in late September or early October of 1981-1985. Since dieback can occur after wounding and since errors in wound preparation may be present, all wounds made in 1981 and 1983 were remeasured during the first week of May.

Results

The growth in trunk diameter of the ten species of trees exceeded 8 mm/yr during 1981-1984 (Table 2). Growth in 1983 and 1984 was less than in 1981 and 1982 in ash, birch, honeylocust, maple, and tulip tree. These differences may have resulted from drought in June 1983 and July 1984 or from increasing competition between closely spaced plants. In addition, some birches were attacked by bronze birch borers in 1984. The honeylocust, linden, pin oak, and tulip trees averaged annual trunk diameter increases greater than 15 mm. These four species were in plots of widely spaced trees (Table 1).

First-year closure of wounds that were originally 50 mm wide was greater than that of wounds that were originally 25 mm wide in every year and on every species (Fig. 1) with the single exception of maple in 1982. The average increase in callus growth due to wound size ranged from 8% in maple to 27% in sycamore. Closure of wounds in 1983 and 1984 was substantially less than in 1981 and 1982 on birch, honeylocust, and tulip tree. The mean extent of closure on birch and honeylocust was less than one-half that on elm, maple, pin oak, and tulip tree. First year closure

was greater than diameter growth on all species except birch and honeylocust.

Many of the 50-mm wounds failed to close during the second year after affliction. On pin oak, most of the wounds closed in mid-season of the second year and were not subsequently measured. On ash, honeylocust, elm, maple, tulip tree, sycamore and hackberry, many wounds remained open throughout the second year. Data

Table 1. Species, year of planting, plant spacing, and diameter of test trees in April 1981.

Tree species	Year of planting	Plant spacing (m)	Diameter ¹ mean \pm s.e. (cm)
Littleleaf linden (<i>Tilia cordata</i>)	1972	4 \times 4	8.3 \pm 0.4
White birch (<i>Betula papyrifera</i>)	1966	2 \times 2	9.3 \pm 1.2
Norway maple (<i>Acer platanoides</i>)	1970	4 \times 4	9.1 \pm 0.2
Honeylocust (<i>Gleditsia triacanthos</i> var. <i>inermis</i>)	1970	4 \times 4	13.5 \pm 0.5
Pin oak (<i>Quercus palustris</i>)	1969	4 \times 4	13.7 \pm 0.5
Sycamore (<i>Platanus occidentalis</i>)	1962	2 \times 2	14.6 \pm 0.9
English elm (<i>Ulmus procera</i>)	1968	2 \times 2	15.2 \pm 0.8
Hackberry (<i>Celtis occidentalis</i>)	1962	2 \times 2	16.0 \pm 0.9
Green ash (<i>Fraxinus pennsylvanica</i> var. <i>lanceolata</i>)	1960	2 \times 2	18.9 \pm 1.2
Tulip tree (<i>Liriodendron tulipifera</i>)	1970	4 \times 4	19.0 \pm 0.6

¹Diameter at a marked height approximately 1 m above the ground

Table 2. Mean diameter growth at approximately 1 m height of ten species of trees wounded annually, 1981-1984. Average of 20 trees.

Tree species	Diameter growth (mm)				
	1981	1982	1983	1984	1981-1984
Oak	17.1	20.4	20.1	16.5	74.0
Tulip tree	25.5	19.4	15.1	11.2	72.2
Linden	14.4	16.8	14.8	14.9	60.8
Honeylocust	17.4	17.3	14.8	12.2	60.6
Maple	15.1	15.5	12.4	11.3	54.7
Sycamore	12.1	15.1	12.7	11.0	50.9
Elm	10.7	12.5	11.1	13.3	47.5
Birch	13.8	14.0	11.7	7.7	46.5
Hackberry	9.5	9.5	9.2	10.5	38.9
Ash	9.4	10.0	8.8	8.1	36.3

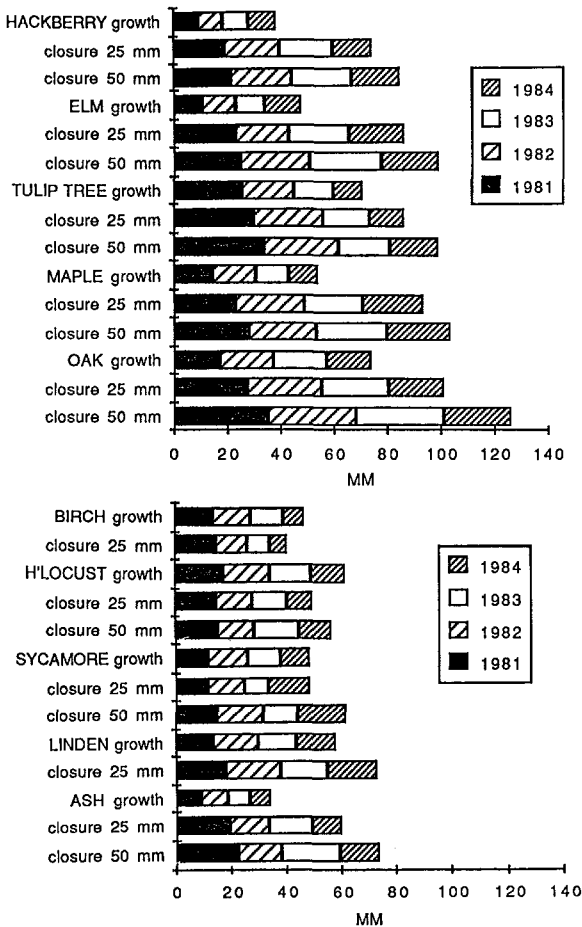


Fig. 1. Diameter trunk growth and first year closure of 50 and 25 mm wide wounds on ten species of trees (average from 20 trees).

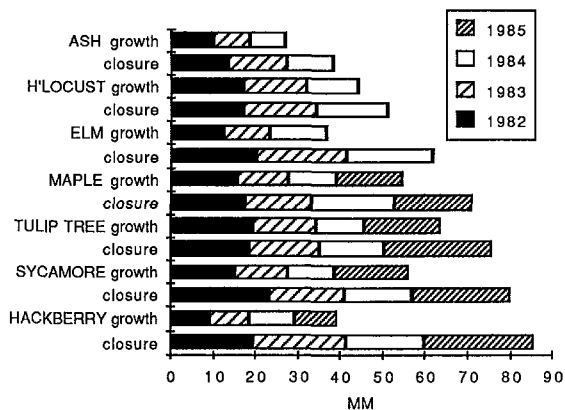


Fig. 2. Diameter trunk growth and second year closure of 50 mm wide wounds on seven species of trees (average of 12-20 trees).

collected the second year after wounding confirmed data collected the first year (Fig. 2).

Wound closure correlated linearly with growth in trunk diameter in both the first year and second year after wounding. The results of linear regression analyses to estimate closure using growth in trunk diameter as the independent variable for 25- and 50-mm elliptical wounds on the trunks of the ten species of trees studied are given in Table 3. Growth and closure were positively correlated; the slope for each year and for each wound size on all species was positive (with the exception of the 50-mm wounds on sycamore in 1983 and on ash in 1984). With the exception of the 50 mm wounds on ash in 1984, all of the Y intercepts were positive, a finding which taken in conjunction with a high correlation coefficient indicates that wound closure per unit of diameter growth is greatest for slow-growing trees.

Neither intraspecific nor interspecific growth was uniform, and growth also varied from year to year. As a result, comparisons of closure rates between species are difficult. Table 4 compares closure between species at increments of diameter growth within the range of data obtained in this study. Data are averages from 3 or more years and are based on the lines of regressions for those years. A significant difference in closure between species was found at increments of diameter growth of 6, 12, and 18 mm. Birch, honeylocust, and sycamore had the lowest closure rate per unit of diameter growth; elm, maple, and oak had the highest.

Wound closure rates for individual plants in a species propagated from seed are variable and this generality proved true in this study. Selection within a population for individual plants that exhibit rapid wound closure would, therefore, be a desirable practice. Trees with closure rates consistently greater than the standard deviation of the population are those most likely to be selected for additional study. The deviations from the lines of correlation for each wound size on each tree for each species for each of the 4 years were determined. The number of trees within a species with wound closure rates greater than the standard deviation of the population are shown in Table 5. The likelihood of finding trees within a species with rapid closure rates appears to be best in

honeylocust, pin oak, ash, and hackberry.

Discussion

Radial growth in tree stems results from three phases of cambial activity—division, enlargement, and differentiation. Each phase is regulated by a separate set of controls (9). All phases are modified by such environmental conditions as temperature and availability of moisture, but specific regulation is through the basipetal flow of products that are synthesized in the crown (leaves) of the plant, largely photosynthate and growth regulators (auxin, gibberellin, and inhibitors) (2, 5). The specific roles of individual components in influencing the thickening of the cambial sheath have yet to be determined, but both the amount and type of annual xylem increment as well as its distribution along the stems are influenced by the physiological activity of the crown in a predictable way (2). High correlations exist between cambial growth of trees and seasonal increase in leaf production, and these correlations vary among species (2).

Trees have an inherent capacity to regenerate lost or damaged parts. Parenchyma cells in the various secondary tissues, especially those of the cambial zone and its derivatives, proliferate rapidly. Ray and vertical parenchyma cells in the phloem regenerate more rapidly than do those in the xylem by de-differentiating to become meristematic. The pattern of healing on stems depends on where the separation occurred, the time of wounding and on which tissues were ex-

posed to the environment. When the separation leaves the vascular cambium attached to the xylem and the exposed surface is kept moist by covering it with foil, plastic, or the removed bark, a relatively uniform wound callus rapidly forms across the entire surface of wood (10). Occasionally, relatively rapid and uniform formation of callus will occur even when the cambium is attached to the removed phloem if sufficient proliferating ray cells are present in the xylem. When the newly

Table 3. Formulas for the lines of regression between trunk diameter growth (x axis) and wound closure (y axis) on wounds of two sizes on ten species of trees. Average from 20 trees over 4 consecutive years.

<i>Tree species</i>	<i>Wound width</i>	<i>Slope</i>	<i>Intercept Y</i>	<i>Coefficient (R)</i>
Ash	25	0.37	12.5	0.38
	50	0.33	17.2	0.19
Maple	25	0.72	14.3	0.52
	50	1.04	13.9	0.55
Linden	25	0.60	10.6	0.55
Oak	25	0.41	17.9	0.59
	50	0.68	24.3	0.59
Birch	25	0.79	1.3	0.67
Honeylocust	25	0.53	5.4	0.63
	50	0.79	3.5	0.72
Hackberry	25	0.41	16.1	0.75
	50	0.60	16.3	0.73
Sycamore	25	0.64	6.1	0.79
	50	0.75	9.1	0.74
Tulip tree	25	0.78	8.3	0.84
	50	0.89	9.7	0.84
Elm	25	0.76	12.8	0.94
	50	0.94	14.0	0.90

Table 4. Wound closure at given increments of diameter growth (average 1981-1984)

<i>Tree species</i>	<i>Wounds 25 mm wide</i>			<i>Wounds 50 mm wide</i>		
	<i>Diameter growth increment (mm)</i>			<i>Diameter growth increment (mm)</i>		
	6	12	18	6	12	18
Birch	4.9	10.0	12.6	---	---	---
Honeylocust	---	11.0	13.8	---	11.6	15.6
Sycamore	9.2	12.3	15.4	12.5	15.8	19.2
Ash	14.7	16.8	19.0	18.7	20.2	21.7
Linden	---	17.3	20.7	---	---	---
Tulip tree	---	17.7	22.3	---	20.2	25.5
Hackberry	17.3	19.8	22.3	19.5	23.2	26.8
Elm	17.2	21.6	26.1	19.6	25.2	30.8
Maple	---	22.4	26.4	---	24.9	30.4
Oak	---	22.5	24.8	---	27.6	31.6

exposed parenchyma cells of the xylem remain uncovered and die of desiccation or when they are mature and have lost the potential to regenerate, the pattern of closure is different. Under these conditions, the callus originates in the existing cambium around the outer periphery of the wound, and the newly formed cambium forms adjacent to and in continuity with the existing undisturbed cambium (10). With yearly centripetal growth, the callus completely covers the exposed xylem.

Table 5. Range of deviations from the mean of wounds 25 and 50 mm wide in 4 years (1981-1984) from 20 trees of ten species.

<i>Tree species</i>	<i>Deviation Range (20 trees)</i>	<i>Number of trees (of 20) > s.d.</i>
Birch	32.0 - 67.3	1
Tulip tree	8.8 - 85.6	1
Linden	17.7 - 75.9	2
Maple	22.0 - 86.5	2
Elm	32.9 - 75.3	2
Sycamore	22.0 - 86.5	2
Honeylocust	7.5 - 70.1	3
Oak	17.9 - 72.5	3
Ash	14.7 - 91.6	3
Hackberry	28.3 - 76.1	4

The mechanism that regulates growth of meristematic tissue at the periphery of a wound versus the growth on the same plant a short distance from the wound has not been established and may be physiological, anatomical, or genetic. This study suggests that this mechanism varies among tree species. Because all growth uses the photosynthate produced by the leaves as an energy source and building material (9), the amount of thickening probably relates to the distribution of photosynthate. Wounds can be considered partial girdles, and Kozlowski (2) observed stimulated cambial growth above stem girdles and inhibited cambial growth below them.

Wounds can also be viewed as obstructions in the phloem pipeline (9). Mass flow of photosynthate around the obstruction and through the narrower channels would be more rapid than that above or below the obstruction. Sway causes redistribution of cambial activity in the tree stem (9). In a similar manner, wounds may serve as sinks that utilize more photosynthate than would normally be used. Differences in anatomical structures among tree species as related to wound closure have yet to be studied. This study supports the hypothesis that growth across the wound face occurs at a rate more rapid than that of the vascular cambium and that the increase is proportionately greater on slow-growing trees.

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*Plant Pathologist
Illinois Natural History Survey
607 East Peabody Drive
Champaign, Illinois 61820*