PHLOEM POLARITY IN BARK REGENERATION [1]

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THE POLARITY of phloem transport is the basis for checking tree growth by inverting a ring of bark on the trunk of the tree (7). If a ring of bark is removed, turned upside down and held firmly against the xylem with a rubber band, it will reunite with the wood. The inverted ring of bark will continue to form xylem, but the growth is slow, due to the checking of phloem transport by the reversed polarity. The bark formed at the vertical seam of the inverted ring does, however, make normal growth, presumably due to its normal polarity. As a result the dwarfing effect of the inverted ring of bark is temporary, because normal phloem transport is soon established in the bark regenerated at the vertical seam.

In order to test the origin of the regenerated bark at the vertical seam of a ring of bark grafted on a woody stem we grafted a ring of bark from an apple tree with red wood and bark onto an apple tree with white wood and green bark. In the first experiment the ring of red bark was grafted in the normal position in early June. By the end of the growing season it was evident that the new wood formed beneath the ring of red bark was red, but that the wood formed at the vertical seam was white. Obviously the new wood and bark was derived from the regeneration of the underlying xylem elements rather than from the adjacent bark. The growth of xylem was essentially the same whether derived from the regenerated bark or from the ring of red bark, as is shown in FIGURE 1.

In the second experiment a ring of red bark was grafted, upside down, on a branch with white wood. The xylem formed under the red bark was red, but there was comparatively little wood formation under the ring of red bark as is shown in FIGURE 2. The wood formed at the vertical seam was white and made essentially normal growth. It is evident that the cambium regenerated at the vertical seam is derived from the underlying wood and not from the cambium of the adjacent bark. It is also evident that the growth of the xylem at the vertical seam is normal, regardless of the orientation of the adjacent bark. The growth of the xylem beneath the inverted ring of bark is, however, greatly suppressed, presumably because of the reversed polarity of the phloem.

The polarity of phloem regenerated from the surface of the xylem does not appear to be determined by the orientation of the adjacent cambium yet the adjacent cambium seems to play a role in the formation of new cambium. In *Hibiscus*, according to Sharples and Gunnery, the exposed wood, following removal of the bark, produces large thin walled cells derived from the ends of the medullary rays and smaller cells from meristematic cells which are normally destined to form xylem. If kept moist these cells form a parenchymatous cushion about a millimeter deep in two or

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three weeks. New cambium is then formed across the callus cushion, beginning where the callus is in contact with the cambium of the adjacent bark and "like a slowly closing diaphragm sweeps gradually inward until opposing edges meet. . ." (8). The cambium then produces new wood and bark.

According to Sharples and Gunnery both bark callus and wood callus are formed largely from medullary ray elements. Since the medullary rays are oriented across the long axis of the stem and pass from the xylem through the cambium to the phloem they would not be expected to be polarized in a vertical direction. How then does the phloem derived largely from medullary ray elements become normally polarized? Sharples and Gunnery observed that "new cambial elements do not appear except in close proximity to pre-existing cambial elements" yet the polarity of the resulting phloem cells do not appear to be influenced by the adjacent inverted cambium.

In order to further test the effect of adjacent cambial tissue on the orientation of regenerated phloem and xylem an experiment was designed based upon a technique described by Garner (1). Squares of bark a little more than an inch in diameter were removed from young apple trees with white wood, and replaced with squares of bark from apple trees with red wood. A smaller square of bark about a third of an inch in diameter was removed from the center of each of the red squares leaving the white wood exposed, surrounded on all sides by red bark. The grafts were covered with polyethylene film to keep the exposed wood moist, and the grafted bark was bound firmly with a rubber band until it was united with the wood.

The blocks of red bark were oriented in the normal position, upside down and laterally on the white wood. At the end of the growing season the grafts were removed and sectioned. As shown in FIGURE 3 the normally oriented graft made much more growth, both of the wood beneath the red bark and that from the regenerated cambium, than those in the inverted (FIG. 4) or transverse (FIG. 5) position. In all cases, however, the regenerated xylem was oriented in a vertical position, regardless of the orientation of the grafted square of red bark (FIG. 6). It is evident that the orientation of the cambium regenerated from the white wood is not determined by the orientation of the adjacent cambium.

When the grafted bark is oriented in a normal position there is only a slight overgrowth of the normal tissue above the graft and a comparatively uniform growth of the grafted bark along its entire length as is shown in FIGURE 3. Such a uniform growth would be expected if normal phloem transport in the graft were soon established. However, when the grafted bark is oriented in an inverted or transverse position, there is considerable swelling of the normal tissue above the graft and differential growth in the grafted bark as is shown in FIGURES 4 and 5. The swelling above these grafts can be attributed to the blocking of normal phloem transport and the resulting accumulation of nutrients and hormones above the graft. The differential growth within the length of the graft can be attributed to the diffusion of nutrients and hormones accumulated above the graft. The diffusion must be slow because the growth of the inverted or transverse graft is greatly reduced, but the greater growth at the upper end of the grafted bark indicates that some nutrients are diffused into this tissue. This greater growth at the upper junction of the graft (A, Figs. 4 and 5) can not be attributed to growth stimulation by "wound hormones," because no such differential growth is found at the lower end of the graft union, either at the union between the abnormally oriented bark and the upper end of the regenerated bark (B, Figs. 4 and 5), or between the transverse or inverted bark and the lower union with the normal bark (D). There is, however, a secondary swelling at the junction of the lower end of the regenerated bark and the abnormally oriented bark (C). Apparently the diffusion of nutrients continues down the inverted or transverse bark to some extent and the nutrient sap passes freely into the regenerated bark, since the regenerated bark is normally polarized. But when it reaches the base of the regenerated bark it must then pass by diffusion into the inverted or transverse grafted bark and tends to accumulate and promote increased growth at the upper end of the abnormally oriented bark. The growth in this region is much less than at the upper junction of the graft because the nutrients have been greatly diminished by blocking of phloem transport in the upper part of the graft.

The inversion of a ring of bark on the trunk of the tree suppresses growth by checking phloem transport down the trunk of the tree and thus decreasing the flow of organic nutrients to the roots. The effect of the bark inversion is temporary, however, due to the regeneration of normally polarized phloem and xylem. If a single ring inversion is made, the normally polarized elements regenerated at the vertical seam grow so rapidly that the dwarfing effect of the inverted ring of bark is soon lost, especially in young vigorous trees. We have attempted to avoid this restoration of normal phloem transport by using two inversions with the vertical seams on the opposite side of the trunk of the tree. Restoration of normal transport is delayed, but not prevented, by this technique.

When a second inverted ring of bark is grafted directly above the first one, the growth of the tree is checked for several year. The descending sap moves down the phloem regenerated at the first vertical seam, but is checked by the second inverted ring of bark. There is, however, a lateral movement of the nutrient sap, particularly in the lower inverted ring of bark, so that eventually it makes contact with the regenerated phloem of the lower vertical seam on the opposite side of the trunk of the tree. This lateral diffusion of sap is followed by a lateral orientation of the new phloem and xylem. Eventually normal phloem transport is established down the regenerated phloem at the first vertical seam and then laterally across the lower end of the upper inversion, and the upper end of the lower inversion, to the regenerated phloem at the second vertical seam and then on down the stem.

When the two inversions are made with a ring of normal bark between them the nutrient sap descends the regenerated phloem at the vertical seam of the first inversion, but can pass by lateral diffusion across the ring of normal bark to the upper end of the regenerated phloem of the seam of the second inversion. The xylem and phloem of the normal ring of bark soon become oriented transversly at a downward angle to establish a continuity of normal phloem transport. Such a double bark inversion was made on a young poplar tree in June. At the end of the growing season the bark was removed to show how the xylem had grown at the vertical seams on opposite sides of the trunk and were connected by reoriented xylem

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DESCRIPTION OF FIGURES

FIGURE 1. Cross section of an apple branch with white wood on which was grafted, in June, a ring of bark from an apple tree with red wood. At the end of the growing season the sectioned stem showed that the red bark had produced a normal growth of red wood beneath it. The wood produced at the vertical seam was white, proving that this bark and wood was regenerated from the surface of the white wood and not from the adjacent red bark.

FIGURE 2. Cross section of a ring of red bark grafted in an inverted position on an apple stem with white wood. At the end of the growing season the inverted ring of bark had produced little red wood, due to the reversed polarity of the phloem. The regenerated white wood made normal growth, indicating that the phloem regenerated from the white wood was normally polarized.

FIGURE 3. Longitudinal sections of an apple stem with white wood on which had been grafted a square of red bark after removing a small square of bark from the center of the red bark. The wood developed under the red bark was red and that regenerated from the exposed white wood in the center was white. When the red bark is grafted in the normal position the growth of the underlying red wood and of the regenerated white wood in the center is essentially normal.

FIGURE 4. Same as above, but red bark inverted. The growth of the wood, both under the red bark and under the regenerated bark is greatly reduced, due to blocking of phloem transport by the reversed polarity of the phloem of the grafted red bark. There is evidence of diffusion of nutrient sap into the grafted tissue as indicated by greater growth of wood at the upper end of the graft.

FIGURE 5. Same as above, but with grafted bark oriented in a transverse position.

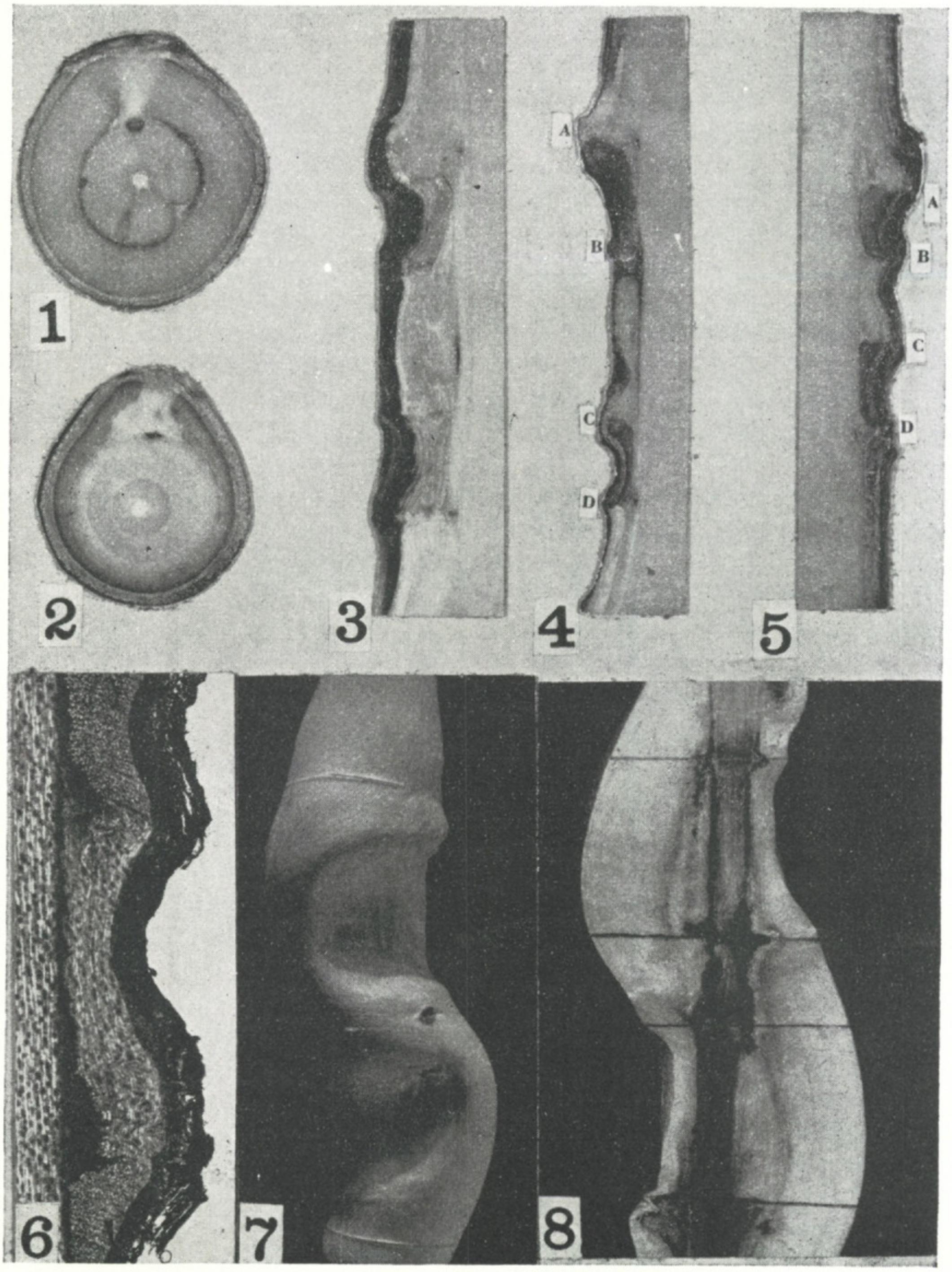
FIGURE 6. An enlarged section of the graft shown in FIG. 5. The red xylem is oriented transversely, but the xylem produced by the cambium from the tissue regenerated from the exposed white wood is normally oriented.

FIGURE 7. Orientation of xylem of a poplar stem at end of growing season after making a double bark inversion in June. The two bark inversions, with their vertical seams on opposite sides of the stem, were separated by a ring of normal bark. The regenerated bark at the vertical seam was normally polarized, permitting normal phloem transport. The nutrient sap descended the phloem of the upper regenerated bark at the seam, diffused laterally across the ring of normal bark and down the normally polarized seam of the lower inverted ring of bark. The lateral diffusion of the sap across the normal ring of bark was followed by a reorientation of phloem and xylem, establishing normal phloem transport and normal xylem growth by the end of the season.

FIGURE 8. Longitudinal section of a poplar stem following a double bark inversion as described for FIG. 7. Note greatly restricted growth of xylem beneath the inverted rings of bark, due to reversed phloem polarity.

across the stem under the normal ring of bark between the two inversions (FIG. 7). A longitudinal section of a poplar stem subjected to the same type of double bark inversion is shown in FIGURE 8.

The regeneration of new bark from exposed wood and the reorientation of the xylem and phloem has long been known. Thomas Andrew Knight in 1807 (3) referred to the work of Henri Louis Duhamel done more than



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fifty years earlier. If a piece of bark is removed from a tree and the exposed wood is kept moist, "a glareous fluid exudes from the surface of the alburnum; this fluid appears to change into a pulpous mass, which subsequently becomes organized into cellular matter. . .". A more modern and detailed description of this process was described by Sharples and Gunnery in 1933 (8).

Knight was also aware of the origin of new wood formed beneath a strip of grafted bark. In 1808 he wrote as follows: "Having procured, by grafting, several trees of a variety of apple and crab tree, the woods of which are distinguishable from each other by their colours, I took off, early in the spring, portions of bark of equal length, from branches of equal size, and I transposed these pieces of bark, inclosing a part of the stem of the apple with a covering of bark from the crab tree, which extended quite around it and applying the bark of the apple tree to the stem of the crab in the same manner. . . . A vital union soon took place between the transposed pieces of bark and the alburnum . . . and in the autumn it appeared evident that a layer of alburnum had been, in every instance, formed beneath the transposed pieces of bark." (4).

The reorientation of newly generated xylem and phloem was also observed by Knight (3). He found that the new vessels "may be made, by appropriate management, to traverse the new cellular substance in almost any direction," by controlling the direction of flow of the nutrient sap. In 1862 Hartig (2) described the reorientation of the xylem in the new wood developed above a spiral deletion of a strip of bark. These and other experiments, which show that the direction of flow of the nutrient sap controls the orientation of the newly formed xylem and phloem, have been described more recently, and in more detail, by MacDaniels and Curtis (6). The vessels gradually become reoriented so that they are parallel with the spiral.

SUMMARY

The inversion of a ring of bark on the trunk of a tree results in checking phloem transport to the roots and dwarfing the tree. The effect is not permanent because the new bark regenerated at the vertical seam is normally polarized and permits normal phloem transport. By grafting a ring of bark from an apple tree with red wood on a tree with white wood, it has been shown that the new bark and wood regenerated at the vertical seam of the grafted ring of bark is derived from the underlying wood and not from the adjacent bark.

A double bark inversion, with the vertical seams on the opposite sides of the trunk, increases the duration of the dwarfing effect, but the lateral diffusion of nutrient sap soon results in a lateral orientation of the new xylem and phloem, to bridge the normally polarized tissues regenerated at the seams of the two inverted rings of bark.

The nutrient sap may diffuse laterally or vertically if normal phloem transport is checked.

If a strip of bark is removed from a tree, the exposed wood, if kept moist, will regenerate new bark and wood. It is shown that the new cambium is oriented in the long axis of the stem, regardless of the orientation of the surrounding grafted bark.

The general conception of the regeneration of new growth from exposed wood, and the control of the orientation of xylem and phloem by the direction of flow of nutrients, dates back to the work of Knight early in the 19th century. These ideas, supplemented by more detailed analyses in later years, are of value in designing experiments dealing with the practical problems of controlling tree growth.

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