How tree branches are attached to trunks

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The vascular cambium and the growth ring it produces are continuous from trunk to branch, but the cells formed by the cambium in the upper junction of branch and trunk are oriented at approximately right angles to the normal orientation in the trunk and branch. Branch tissues begin to develop before trunk tissues early in the growing season. Maturation of branch tissues proceeds basipetally. The branch xylem is oriented downward at the branch base and encircles it to form a collar. The collar tissues meet on the trunk below the branch. The branch collar is enveloped later in the growing season by a collar of trunk xylem. Xylem in the trunk collar meet above and below the branch. Conduction into and out of the branch follows the pathway of the branch collar. The branch is structurally attached to the trunk by a series of trunk collars that envelop the branch collars every growing season. When the trunk collar was injured or removed by branch pruning, the trunk xylem above and below the cut was rapidly and extensively infected and decay developed. When pruning cuts did not injure or remove the trunk collar, no infections developed in the trunk xylem. Dye movement and the patterns of spread of bacterial and fungal pathogens also suggested that there was no local direct conduction between trunk xylem above a branch and within a branch.

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Le cambium vasculaire et l'anneau de croissance qu'il produit s'étendent continuellement du tronc à la branche, mais les cellules issues du cambium dans la jonction supérieure de la branche et du tronc sont disposées approximativement à angle droit de l'orientation normale dans le tronc et la branche. Les tissus de la branche commencent leur développement avant ceux du tronc tôt dans la saison de croissance et la maturation des tissus de la branche se fait de manière basipète. Le xylème de la branche est orienté vers le bas à la base de la branche qu'il entoure pour former un collet. Les tissus du collet se rejoignent sur le tronc en deça de la branche. Plus tard dans la saison, le collet de la branche est enveloppé par un collet de xylème du tronc. Le regroupement du xylème du collet se fait en haut et en dessous de la branche. Le transport vers et hors de la branche suit la piste du collet de la branche. La branche est structuralement fixée au tronc par une série de collets de tronc qui enveloppent les collets de branches à chaque saison de croissance. Quand nous avons blessé ou enlevé par élagage le collet du tronc, une infection rapide et extensive du xylème du tronc au-dessus et au-dessous de la coupe a suivi et le dépérissement s'est développé. Lorsque l'élagage ne causa pas de blessure ou n'enleva pas le collet du tronc il n'y eut pas d'infections du xylème du tronc. Le mouvement de colorants et les patrons de la propagation des bactéries et des champignons pathogènes indiquent aussi qu'il n'y avait pas de transport direct local entre le xylème du tronc au-dessus d'une branche et à l'intérieur de celle-ci.

[Traduit par le journal]

Introduction

How large tree branches are attached to trunks has not been clearly described. Little information on the subject is given in Esau (1965), Büsgen and Münch (1929), Kozlowski (1971), Zimmermann and Brown (1980), and Zimmermann (1983). Eames and MacDaniels (1947) state "... the conducting tissues of branch and trunk may remain more or less distinct ..." and "... the branch is not 'tied to' the trunk on the upper side ..."

P. R. Larson and co-workers give detailed information on early tissue developments (Larson and Richards 1981; Richards and Larson 1981; Fisher and Larson 1983; Larson and Fisher 1983; Fisher et al. 1983). Böhlmann (1970*a*,1970*b*,1970*c*, 1970*d*,1970*e*) also gives details on early tissue developments at nodes of several tree species. Long reviews on branches and pruning by Mayer-Wegelin (1936) and Wegelius (1939) cite many papers on branch development, but the subject of branch attachment is not clearly discussed.

von Aufsess (1975, 1984) and Green et al. (1981) give details on the protection zone in the branch base. The zone contains phenol-based antimicrobial substances in deciduous hardwoods and terpene- or resin-based substances in conifers. Decay-causing microorganisms that invade dying and dead branches usually do not spread beyond the protection zone. The dead and decaying branches are then shed at the position of the protection zone (Shigo 1983, 1984).

During the course of many tree studies over the last 25 years, information has accumulated that helped to clarify how branches are attached to trunks (Shigo 1983). The information comes from dissections of over 12 000 mature trees. The information showed that the few discussions and diagrams of branch attachment in textbooks were not completely accurate. The commonly used diagram (Fig. 1) shows the xylem in the trunk above a branch connected directly with the branch (see Fig. 94 in Eames and MacDaniels 1947). Yet Eames and MacDaniels (1947) were some of the first investigators to question the conduction and attachment patterns at the branch–trunk junction.

The purpose of this paper is to clarify how tree branches are attached to trunks and to discuss how the attachment affects strength of the branch, patterns of conduction between trunk and branch, patterns of spread of pathogens, shedding, pruning, and stem form. Selected portions of many other studies are summarized to help present a clear explanation. Tree treatments such as pruning and topping and the patterns of spread of microorganisms associated with discolored and decayed wood help to show how the tissues are arranged at branch–trunk junctions.

Materials and methods

All wood samples analyzed and studied contained a branch–trunk junction. Samples were dissected through the medial longitudinal plane to expose the piths of branch and trunk. All wood surfaces were sanded or shaved smooth.

Tree species studied

The following trees were studied: red maple, *Acer rubrum* L.; sugar maple, *Acer saccharum* Marsh.; red oak, *Quercus rubra* L.; white oak, *Quercus alba* L.; paper birch, *Betula papyrifera* Marsh.; yellow birch, *Betula alleghaniensis* Britt.; grey birch, *Betula populifolia* Marsh.; American beech, *Fagus grandifolia* Ehrh.; American ash, *Fraxinus americana* L.; aspen, *Populus tremuloides* Michx.; black cherry, *Prunus serotina* Ehrh.; American elm, *Ulmus americana* L.; black walnut, *Juglans nigra* L.; white pine, *Pinus strobus* L.; red pine, *Pinus resinosa* Sol.; pitch pine, *Pinus rigida* Mill.; hemlock, *Tsuga canadensis* (L.) Carr.; balsam fir, *Abies balsamea* (L.) Mill.; red spruce, *Picea rubens* Sarg.; Norway spruce, *Picea abies* Karst.

Dissections of large trees

Longitudinal dissections through living, dying, and dead branches on more than 12 000 trees were made with a chain saw over a 25-year period to study patterns of discoloration and decay (Shigo 1983).

Dissections of small trees

Inner and outer bark was removed to expose the newly forming xylem from 30 small trunk sections that contained a branch, six each from white pine, red oak, elm, hemlock, and red maple. Each trunk section was 1−2 cm in diameter and 2−4 cm long and the branches on the trunk sections were 0.4−0.8 cm in diameter. The bark was removed in June at the time the earlywood was completing its development in all species and the large earlywood vessels of elms and oaks were seen clearly on the surface of the wood (Fig. 5).

Inner and outer bark was removed to expose the xylem from 15 oak branch−trunk sections in August. Five branch−trunk sections were the same size as those peeled in June and 10 additional sections had trunk diameters of 2−5 cm and branch diameters of 0.5−1.5 cm.

From the same species of trees, 30 additional trunk−branch samples of similar size as those cut in June were cut in a medial longitudinal plane through the piths of branch and trunk also in June and the cut surfaces were shaved smooth with a razor blade and examined under a dissecting microscope.

Thirty branches ranging in diameter from 1 to 3 cm were pulled out of trunks that ranged in diameter from 2 to 4 cm on six each of red oak, elm, aspen, hemlock, and white pine. The torn wood samples were examined to determine the interlocking patterns of branch and trunk xylem. The samples were pulled apart slowly and the rupturing of the xylem indicated the arrangement of the xylem tissues. The branches came out of the trunk only when pulled downward.

Fifty trunk and branch samples, 10 each of birch, red maple, red oak, white pine, and hemlock, were split to show the configuration of the tissues at the trunk−branch junction. The trunks were 10−18 cm in diameter with living and dead branches ranging in diameter from 2 to 6 cm.

Fifty trunk and branch sections from several tree species were sliced into 0.5 cm thick discs at different angles to study the three-dimensional arrangements of the wood and bark tissues. Trunk diameters ranged from 5 to 20 cm and branch diameters ranged from 1 to 8 cm. Many other samples from several species were cut at different angles to help clarify the three-dimensional configuration of tissues at the branch−trunk junction.

All trunk and branch samples were alive, except some dead branches on living trunks that were studied after splitting, as noted above.

Pruning studies

Over an 8-year period, 1200 trees of the following 13 species ranging in diameter at 1.4 m above ground from 5 to 30 cm and ranging in age from 10 to 100 years were used in pruning experiments: red maple, beech, red oak, white oak, cherry, paper birch, yellow birch, grey birch, aspen, hemlock, white pine, pitch pine, and red pine. Each tree had living and dead branches cut (*i*) on the trunk side of the branch collar, thus removing the collar, and (*ii*) on the outer side of the collar, thus not removing or injuring the collar. A cut that removes the collar is called a flush cut (Shigo 1984). Most of the trees were felled from 1980 to 1984 and the pruning wounds were dissected through the medial longitudinal plane, thus exposing the piths of the inner branch core and trunk.

Living branches 1−3 cm in diameter were cut leaving 30 cm long stubs on an additional 50 trees of red oak and red maple. After 4, 12, 24, and 36 months, the trees were felled and dissected to examine visually the position and degree of development of the phenol-based chemical protection boundary within the base of the branch.

The central trunks at the top of 50 red maple, paper birch, cherry, and red oak trees were cut. The trunks that were cut ranged from 4 to 20 cm in diameter and they were cut at a position directly above a living branch of 2−4 cm diameter. The trees were dissected after 1, 2, and 3 years to examine the patterns of spread of microorganisms associated with the discolored and decayed wood.

Tree-disease studies

To determine the patterns of spread of *Ceratocystis ulmi* (Buism.) C. Moreau, the cause of Dutch elm disease in American elm, *Ulmus americana* L., more than 100 branch−trunk samples of elm were dissected through the medial longitudinal plane and examined. The stem or trunk diameters ranged from 5 to 30 cm and the branch diameters ranged from 1 to 8 cm.

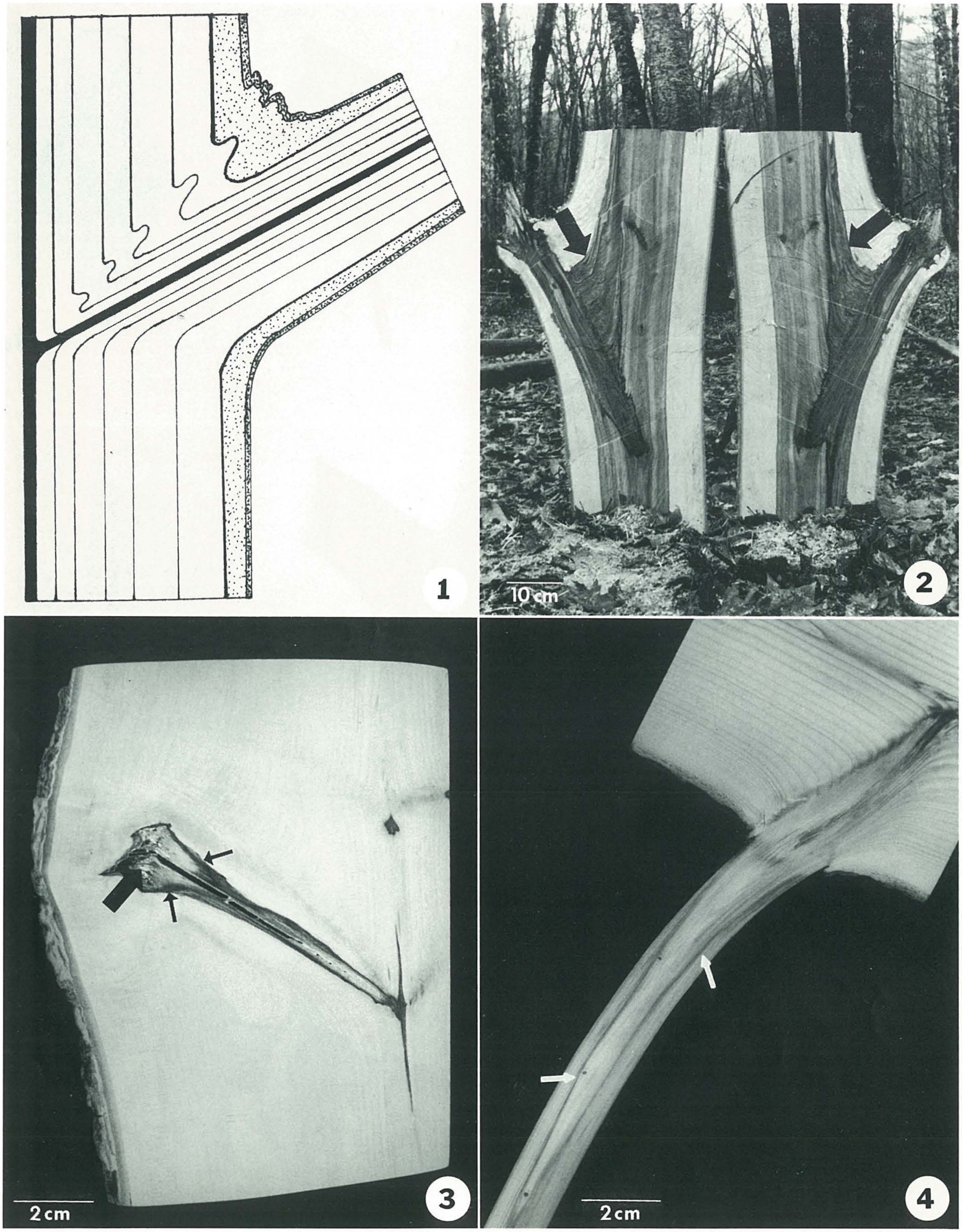
To determine the patterns of spread of *Erwinia amylovora* (Burr.) Winsl., the cause of fire blight, more than 50 branch−trunk sections of pear, *Pyrus communis* L., were dissected through the medial longitudinal plane and examined. The trunk diameters ranged from 2 to 14 cm and the branch diameters from 1 to 5 cm. All samples were sanded smooth to reveal details of the wood.

The portions of the tree-disease studies given here are from more extensive studies designed to determine patterns of compartmentalization of pathogens (Shigo 1983). We know that pathogens do not spread freely in trees but follow orderly patterns that are in part determined by the anatomy of the tree.

Dye experiments

Thirty 30 cm long small trunk samples that contained a living branch of red oak and red maple were used in dye experiments. The trunks were 1−2 cm in diameter and the branches were 0.3−0.8 cm in diameter. The trunk samples were cut in the field and immediately brought into the laboratory and cut again into 8- to 10-cm lengths; branches were cut into 3- to 4-cm lengths. A cup, made by encircling the cut branch or trunk with tape, had 2 mL of toluidine blue O dye poured into it. When color first became visible on the bottom of the trunks, the entire trunk and branch sample was washed to remove all dye from the cup. The samples were split longitudinally through the pith and some were cut in transverse sections to show the patterns of

FIG. 1. Diagram of branch−trunk junction that appears in many textbooks. The diagram shows the growth rings in the trunk above the branch continuing into the branch. At the plane of the diagram, it is difficult to understand how xylem elements in the growth rings below the branch connect with elements in the trunk above the branch. Furthermore, the diagram implies a conduction continuous from trunk tissues above a branch to the branch. The tissue arrangements below the branch are correct for the medial longitudinal view shown, but the tissue arrangements are not correct when the longitudinal plane is not directly through the piths of branch and trunk. FIG. 2. Dissection of a paper birch shows that the discolored and decayed wood associated with the large branch stub was confined to the trunk wood present at the time the branch died. When large columns of discolored or decayed wood spread downward into the trunk below a branch, the infection may spread into the collar tissues that circle the branch. The discolored and decayed wood may then spread slightly above the branch (arrows). FIG. 3. Dissection of a well-compartmentalized branch core in a yellow birch. The small pocket of decay at the distal end of the dead branch (large arrow) was confined by the protection zone that forms in branches (small arrows). Trees that have such strong protection zones will have sound trunk wood from cambium to pith. FIG. 4. Dissection of a hemlock shows the resin-soaked cone of wood that developed within the living branch (arrows). The resin-soaked wood is resistant to infection and the trunk is protected against invasion by pathogens. The resin-soaked cones stall shedding of the branches and when the branch does break, it does so at the distal position of the resin-soaked cone.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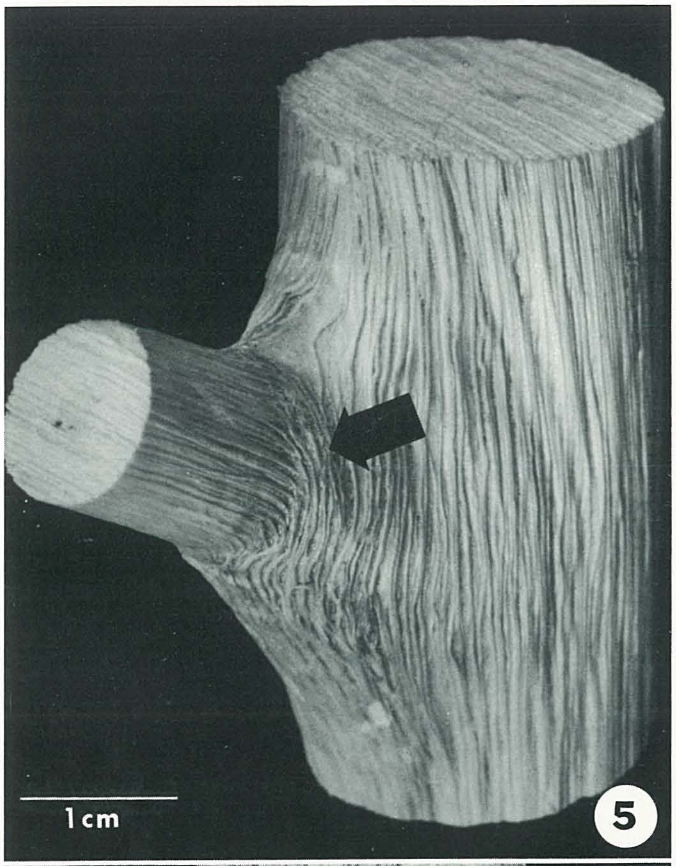
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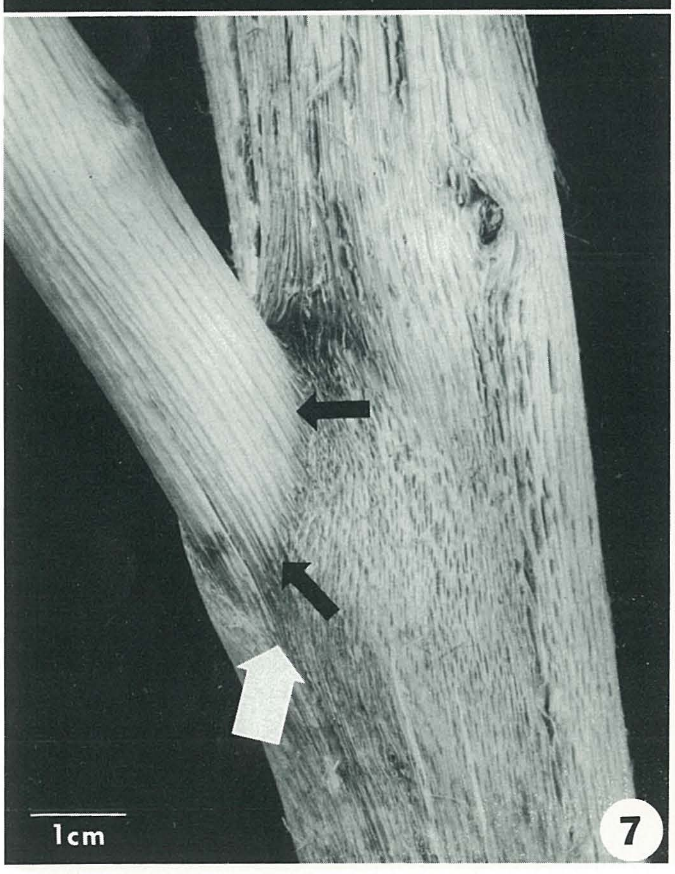
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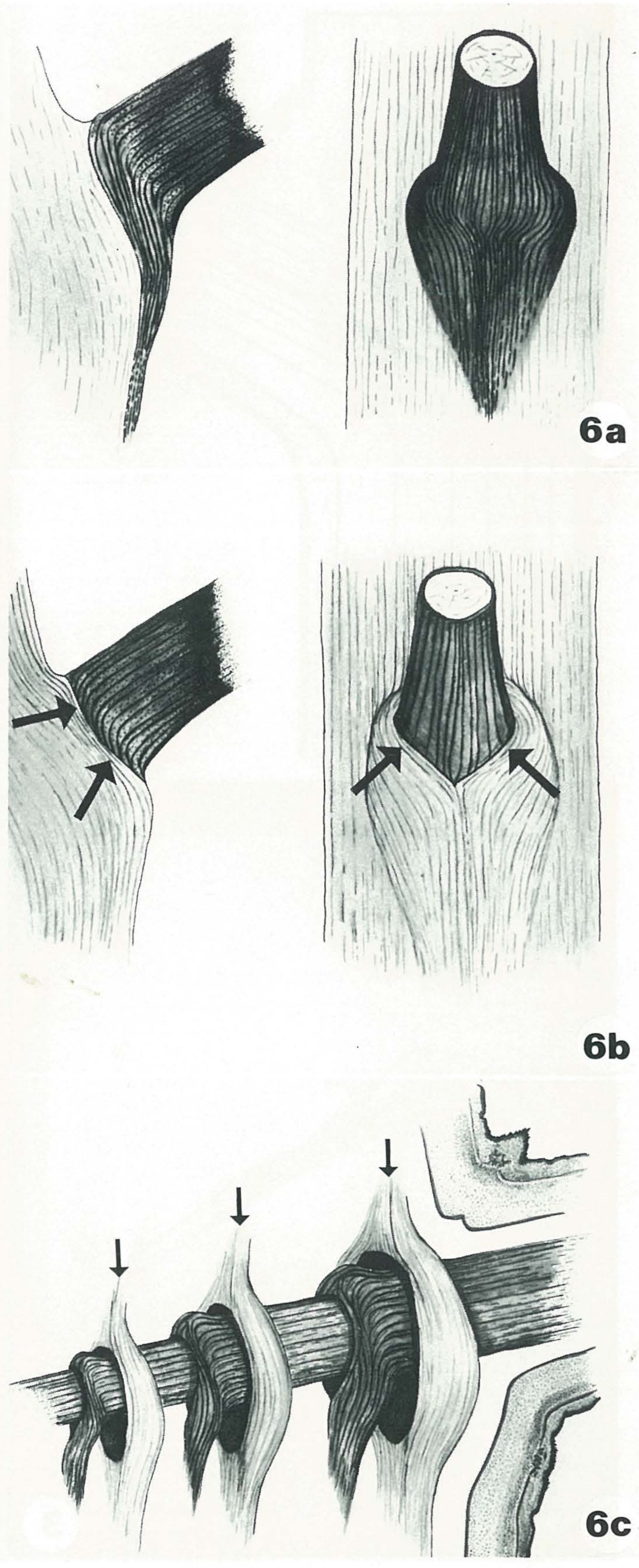
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dye. Some samples were debarked to show the patterns of dye on the surface of the wood and inner bark. The bases of 10 samples were placed in a reservoir of dye and a vacuum was applied to the upper portion of the trunk or branch until periodic examination showed the presence of dye at the top of the trunk or branch. The samples were then washed and split longitudinally through the pith.

The dye experiments using gravity flow and vacuum procedures were used to give a rough view of conduction patterns between trunk and branch. It was understood that dye movement alone is a poor indicator of actual conduction pathways in living trees. But, the results were intended to be used as an adjunct to the information gained from other experiments and observations.

Results

Dissections of large trees

Discolored and decayed wood in trunks associated with dead branches was confined to wood in the dead branch and the trunk wood present at the time the branches died, indicating that the branch wood within the trunk was separate from the trunk wood (Fig. 2). Dissections of enclosed branch cores often revealed a small pocket of decayed wood at the distal end of the branch core in hardwoods and again, the microorganisms did not spread into surrounding trunk tissues, suggesting that there was an anatomical separation between branch wood and trunk wood (Fig. 3). The decayed wood was confined to the tip or outer portion of the enclosed core wood of the branch. Similar patterns of decayed wood in branch cores was described by von Aufsess (1975) and Green et al. (1981). In conifers, dissections showed that the inner branch core wood had been impregnated with resin while the branch was still alive. Again, similar patterns were described by von Aufsess (1984). In hemlock and white pine, the resin-soaked wood in the branch core wood developed centripetally to the trunk pith and outward into the living branch to 20–40 cm beyond the trunk (Fig. 4). When such branches broke, they did so where the core of resin-soaked wood in the branch ended.

Dissections of small trees

Removal of bark from oak and elm in June after the large earlywood vessels had completed their growth, revealed clearly the arrangement of the vessels (Fig. 5). The orientation of the vessels at the branch base bend sharply at approximately right angles to the vessels in the branch. The vessels formed a swollen collar about the branch base. The branch vessels did not continue from the branch onto trunk tissues to the sides and above the branch (Fig. 5). There was a branch gap devoid of vessels at the upper junction of branch and trunk (Fig. 5). In June samples, a narrow strip of branch vessels that turned abruptly at the branch base, came together on that portion of the trunk directly below the branch (Figs. 5 and 6*a*). But, trunk and branch samples peeled in August showed that the trunk xylem to the sides and above and below the branch had enveloped the branch xylem that had formed early in the growing season (Figs. 7 and 6*b*). The later-developing trunk xylem buried the earlier-formed xylem (Fig. 6*b*). A collar of branch tissues formed first about the base of the branch and later the branch collar was enveloped by a collar of trunk tissues (Fig. 7). Such an arrangement resulted in a "ball and socket" union (Figs. 7 and 6*c*).

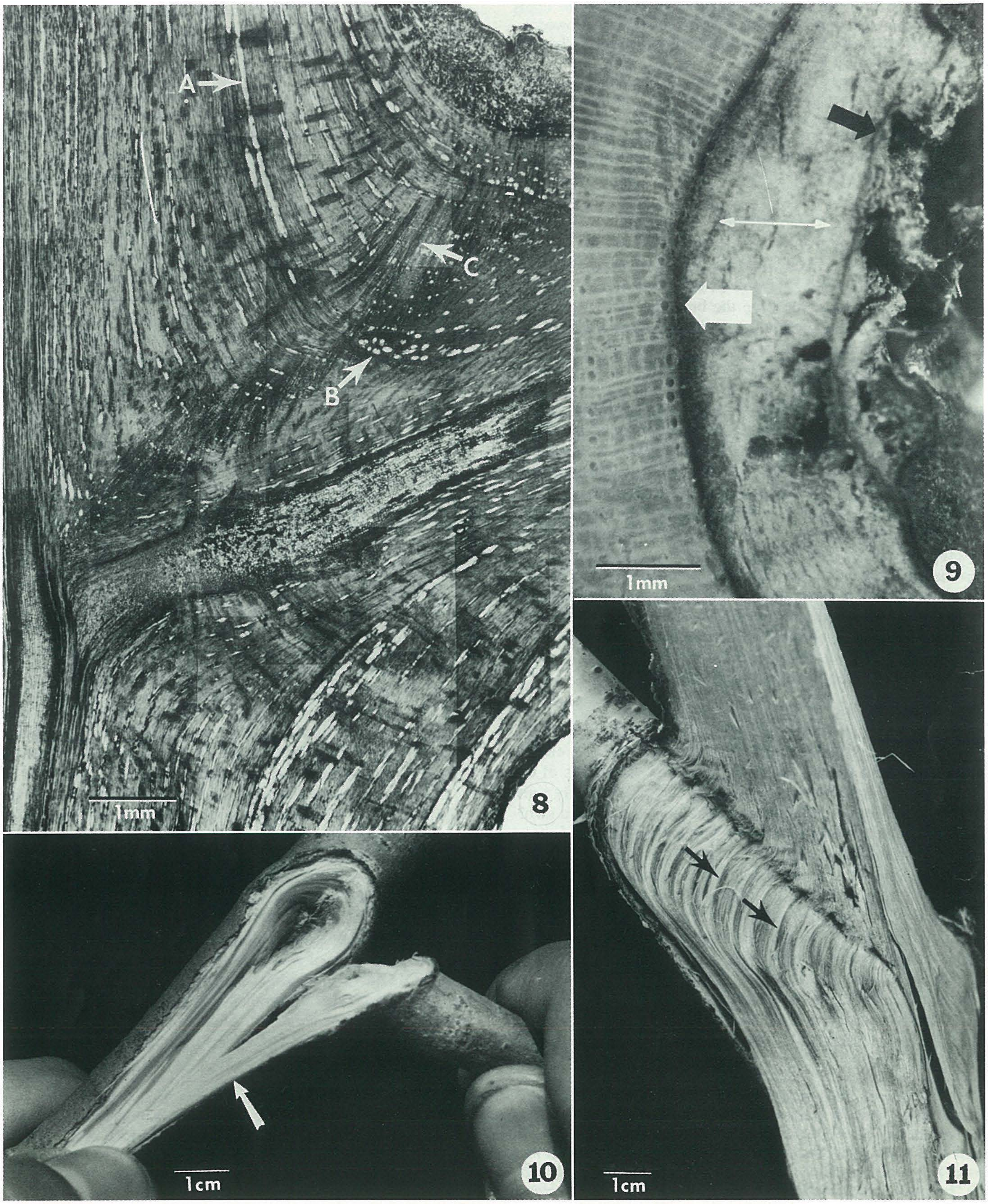
Longitudinal medial dissections through the piths of small trunk and branch samples showed vessels in longitudinal sections in the trunk and branch, but the vessels and other xylem cells in the branch crotch appeared as they would in a transverse section (Figs. 8 and 9). The vessels in the crotch were crosscut and the vascular rays were also oriented at approximately right angles to the trunk axis (Figs. 8 and 9). The change in direction of the rays appeared as upward sweeping tissues when viewed in a longitudinal section (Fig. 8). In medial longitudinal sections, the growth ring was continuous between trunk and branch. Longitudinal dissections through the zone of compacted xylem at the branch–trunk junction showed the continuation of the growth ring from branch to trunk. The zone of compacted xylem formed where the expanding cylinder of the trunk met the expanding cylinder of the branch at the upper inner side of the branch–trunk junction. Böhlmann (1970*a*) refers to this zone as a disturbed zone.

Branches that were pulled slowly out of the trees showed the "ball and socket" pattern of the trunk and branch tissues (Fig. 10). There was a weak connection between branch and trunk above the branch within the crotch. When the branch was pulled downward, the first separation between branch and trunk started within the branch crotch. It was very difficult to pull out a branch by pulling upward.

In some samples, small cracks, separations, or splits had occurred in the crotch and to the sides of the junction where the trunk and branch tissues met and turned abruptly downward. The cracks separated the trunk cambium from the branch cambium within the branch crotch. As the two separated cambia continued to develop, they folded inward within the branch crotch. When such samples were pulled apart, the bark from the trunk cambium and the bark from the branch cambium now occupied the position normally occupied by the compacted xylem. When bark separates a branch from the trunk within the crotch, the arrangement is called included bark.

Larger samples of trunk–branch junctions that were first split partially by a knife or axe and then pulled apart slowly by hand in August showed that the trunk tissues formed a collar about the earlier-formed collar of branch tissues. The downward bending of the branch tissues at the branch base resulted in a swollen branch collar. The collar of trunk tissues formed over this swollen area later in the season (Fig. 6*c*). After several growing seasons in all trees studied, a pattern of ribs or high and low bands of wood developed by this repeated process (Fig. 11). Only a small strip of wood directly below the branch was connected with the branch when the branch was pulled away from the trunk (Fig. 10). This small strip of wood was the bottom of the branch collar (Fig. 6*a*). Upward conduction from

FIG. 5. A small trunk section of red oak shows the arrangement of large spring vessels. The bark was peeled from the sample in June. The vessels turned abruptly at the branch base to form a branch collar (arrow). The vessels in the branch collar came together on the trunk beneath the branch. FIG. 6. Diagrammatic view of branch attachment. (*a*) Branch tissues develop first and form a collar about the base of the branch (dark lines). (*b*) Trunk tissues (arrows) later form a collar about the branch collar. The trunk collar tissues do not always meet to form a tight union below the branch. A gap in the trunk collar below the branch is common on older branches. (*c*) If the growth rings were pulled apart, the "ball and socket" arrangement of the trunk collars over the branch collars can be seen. Arrows show the trunk collars for each growth ring. FIG. 7. A red oak sample debarked in August. The collar of trunk wood enveloped the collar of branch wood that formed in June. Compare this figure with Fig. 5. Black arrows show where the trunk collar enveloped the branch collar. A white arrow shows where the trunk collar may not close completely, especially on older, larger branches.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the trunk into the branch would follow this strip of wood.

Pruning studies

Pruning cuts that injured or removed the ring of swollen tissues about the branch base resulted in rapid and extensive trunk infections above and below the cut, thus indicating that trunk tissues were injured. Pruning cuts that did not injure the swollen collar tissues did not result in trunk infection (Fig. 12). Pruning cuts that injured or removed (flush cut) the swollen collar did result in larger ribs of trunk callus because the trunk was wounded. These pruning patterns were similar on more than 1000 branch pruning wounds dissected over an 8-year period.

Dissections of cut leaders of trunks showed that the microorganisms that infected the cut trunk seldom spread from the trunk wood into the branch that became the new leader trunk (Fig. 13). The pathogens acted as anatomical markers.

When the trunks and long stubs were split through the pith, protective boundaries of phenol-based materials similar to those described by Green et al. (1981) were found at the branch bases (Figs. 14 and 15). The protective boundary formed between the inner tissues of the dying branch and the still-living trunk tissues (Fig. 15). In all trees studied, a circular swollen ring of trunk tissues formed about the base of the branch. This experiment showed that there was a separation between trunk and branch tissues and that the trunk tissues grow around and envelop the base of the branch. Therefore, to understand the arrangement of tissues at the branch–trunk junction, it is absolutely essential to study the tissue arrangements over a period of time, because what may appear as primarily branch tissue in spring, is enveloped by trunk tissue later.

After living branches were cut, or after they died, the trunk tissues below the branch decreased their growth rates for 5 to 10 years (Fig. 16). The decreased growth rate of the tissues often resulted in a sunken area below the branch. The sunken areas extended from 5 to 20 cm below the branches. When the branch was alive, the combined growth of branch wood below the branch and later trunk wood that enveloped the branch wood together made up the girth of the trunk below the branch. After branch death, only the trunk tissues were involved in the girth.

Tree-disease studies

Ceratocystis ulmi spread downward in branches of American elms, but not laterally across the crotch to other branches adjacent to the infected branch (Fig. 17). In some cases, the fungi did spread downward from branches into the trunk below the branch, but when the fungi did, they were confined within the trunk tissues that were connected directly to the infected branch.

In a similar way, *Erwinia amylovora* spread downward in trunks of pear trees, but not from the trunk into branches that were growing rapidly at the time the infection reached the branch (Fig. 18). *Erwinia amylovora*, like *C. ulmi*, did not grow through the zone of compacted xylem within the branch–trunk junction.

Dye experiments

Dye infiltrated into the upper cut end of branches moved downward into the small trunks, but not upward into trunk xylem above the branch, and the dye did not move radially across the zone of compacted xylem tissues within the branch–trunk junction. Dye infiltrated into the upper cut end of the small trunk samples, but did not move up into branches (Fig. 19). Dye "pulled" upward by vacuum moved in the same patterns: when the vacuum was on the trunk, the dye stayed within the trunk tissues associated with the trunk, and when the vacuum was applied to the branch, the dye did not move into those tissues associated with the trunk. Similar patterns were shown on the peeled samples. Samples that were cut in transverse sections showed that the dye followed the tissue patterns shown in Fig. 6.

Changes in bark

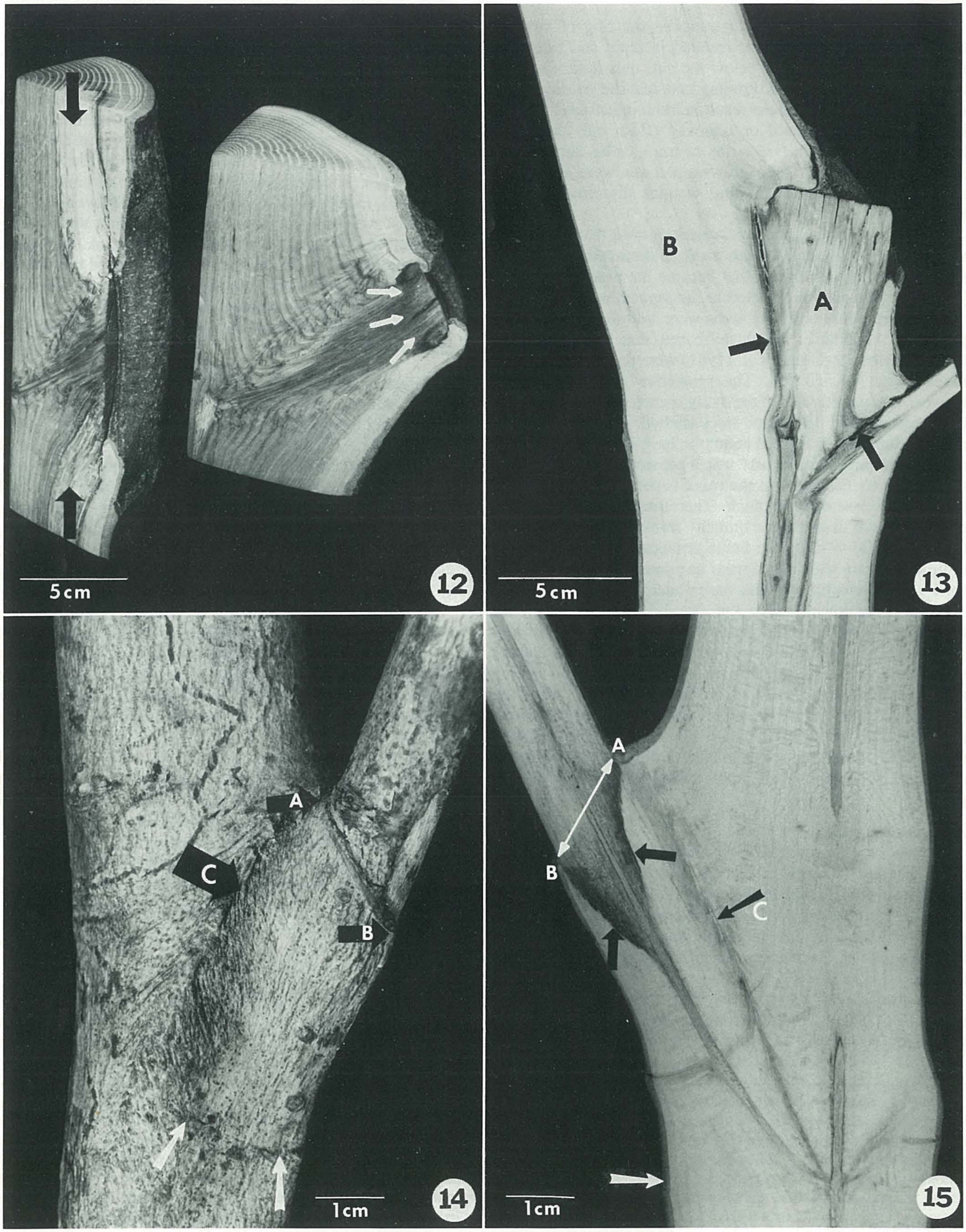
The phloem was continuous from branch to trunk (Figs. 8 and 9), but the phellogen was very wrinkled within the branch crotch. At the time of earlywood formation in June, the phellogen was broken and exposed to the air in places (Fig. 9). Disrupted plates of phellem were formed within the crotch at this time. The phloem and periderm were greatly thickened within the crotch. As the diameter of the trunk and branch increased, the thickened layers of bark that formed in the crotch were "pushed" to the sides of the branch onto the trunk to form a bark ridge, the branch bark ridge (Fig. 14). The ridge has also been called a Chinese beard. After developing for several years, the angle of the bark ridge was approximately the angle of the branch core wood that was located within the trunk (Figs. 14 and 15). The branch bark ridge forms in the crotch and is maintained at this site on the expanding trunk below and to the sides of the branch on most trees, so long as the branch is alive.

Another series of bark ridges form on the trunk below a branch. They are obvious on young branches and on trees that have smooth bark, such as aspen. When branches begin to develop on a small trunk, a swollen ring of bark encircles the base of the branch where the expanding branch bark meets the expanding trunk bark. The upper portion of the bark ring is the beginning of the branch bark ridge and the lower portion of the bark ring is maintained on the bark of the trunk below the branch (Fig. 14).

Discussion

The results help to clarify and expand the information given by Eames and MacDaniels (1947). The results are in agreement with those of P. R. Larson and co-workers (Larson

FIG. 8. Longitudinal medial section through the branch–trunk junction of an American elm shows the longitudinal view of the vessels in the trunk (A) and a transverse view of vessels (B) and vascular rays (C) at the branch–trunk junction. The vessels and rays at the junction are oriented at approximately right angles to the tissues elsewhere in the trunk and branch. Note that the pith of the branch and the pith of the trunk meet, but do not connect. FIG. 9. A closer longitudinal medial view of a sample through a branch–trunk junction of an American elm made in a region similar to C in Fig. 8. The vessels and rays are cut transversely. The phloem (thin, white arrow) is greatly thickened and the phellogen (black arrow) is almost exposed to the atmosphere. The position of the phellogen makes it a possible infection court for pathogens. The cambium is shown by a thick, white arrow. FIG. 10. A small branch of an aspen pulled out of the trunk shows the tissues structurally associated with the branch and trunk. The thin strip of tissues directly below the branch are connected to the branch (arrow). FIG. 11. A split section of a paper birch shows the curvature of trunk tissues about the branch core wood. Note the ribs or bands of high and low wood (arrows). The low bands are branch collars and the high bands are trunk collars.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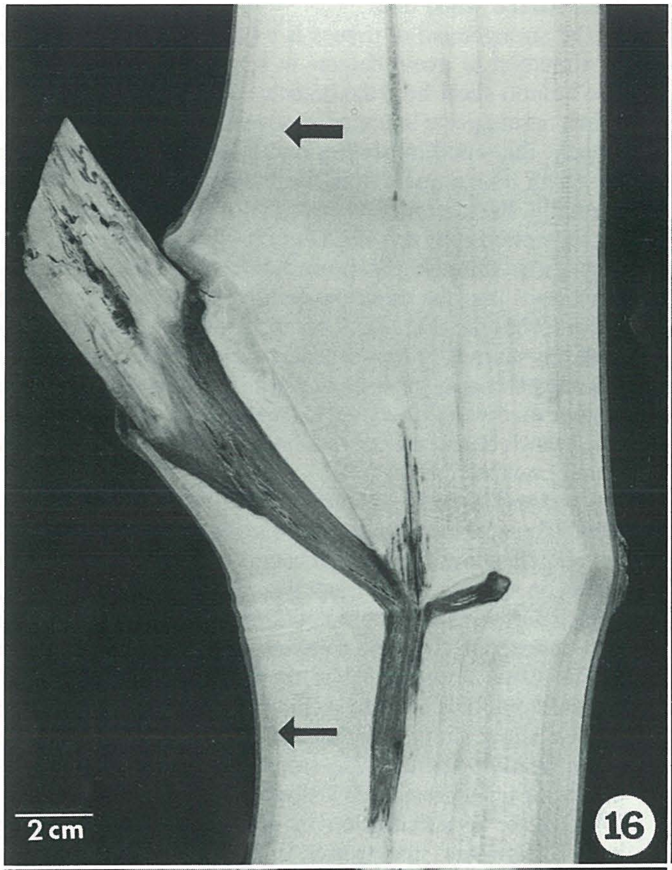
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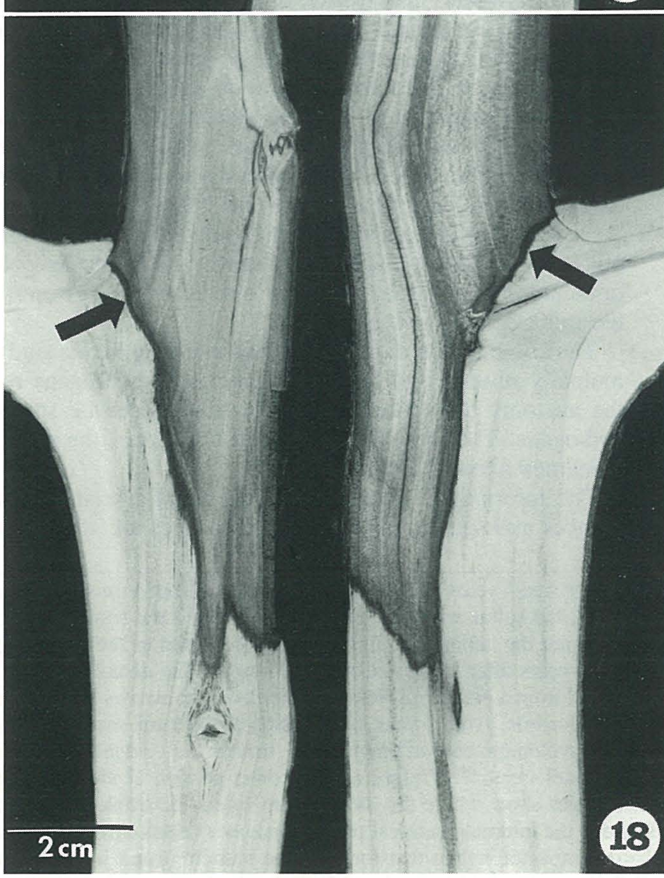
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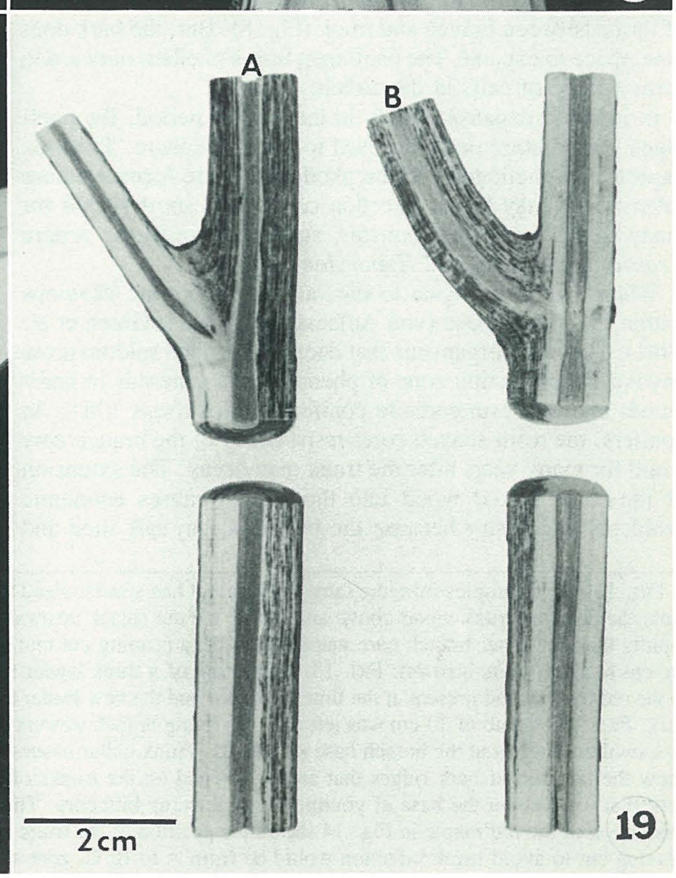
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and Richards 1981; Richards and Larson 1981; Fisher and Larson 1983; Larson and Fisher 1983; Fisher et al. 1983) and Böhlmann (1970*a*,1970*b*,1970*c*,1970*d*,1970*e*) and serve to expand their information, especially as the information relates to tree pathology, tree treatments such as pruning and topping, and to older tissues.

Branch tissues develop basipetally (Larson and Richards 1981; Richards and Larson 1981). Results given here show that xylem tissues turn abruptly downward from the longitudinal direction of the branch to the direction of the trunk axis at the position on the branch base where the branch is still circular. Böhlmann (1970*a*,1970*b*,1970*c*,1970*d*,1970*e*) gives a similar description of some tissues in developing young branches. The rhythm of branch tissues developing a basal collar first in the spring and then having the trunk tissues envelop this collar later in the growing season results in a unique tissue arrangement that accounts for the great strength and resiliency of branches. The arrangement of tissues helps to explain why there is no direct xylem conduction from trunk tissues above a branch into the branch (Figs. 6*a* and 6*c*).

The expanding cambium of the trunk annually overtakes the newly formed tissues of the branch at the branch base and below the branch on the trunk (Fig. 7). It is not possible to have the orientation of cells on the xylem side of the cambium different from the orientation on the phloem side. Therefore, the phloem must also be turned in a similar way to the xylem.

The trunk and branch vascular cambia expand as two cylinders joined at different angles at their bases. The cylinders abut at the crotch and the cell orientations of each are changed in this region. The developing xylem tissues in the crotch have little space to occupy and they are compacted to form the hard zone of tissue between branch and trunk (Fig. 8). But, the bark does have space to expand. The phellogen forms phellem outward to form a ridge of cells in the crotch.

In its rapid expansion early in the growth period, the phellogen may rupture or be exposed to the atmosphere. Then the unprotected phellogen and the phellem that are formed before suberization may be an infection court for a short period for many canker-causing organisms, such as those in the genera *Nectria*, *Cytospora*, and *Hypoxylon*.

When a branch begins to die, a protection zone develops within the branch base (von Aufsess 1975, 1984; Green et al. 1981). The microorganisms that decay the branch seldom grow beyond the protection zone of phenol-based materials in hardwoods and the resin cores in conifers (von Aufsess 1984). In conifers, the resin-soaked cores resist decay of the branch core wood for many years after the trunk may decay. The extension of the resin-soaked wood into the branch causes economic problems in forestry because the branches may not shed and when they do, they break 20–50 cm from the trunk, where the resin-soaked wood ends.

The arrangement of tissues is a key factor affecting pruning as a method to avoid defects in trunks. Pruning experiments also help to show how the branch–trunk tissues are arranged. When pruning cuts injure or remove the collar tissues about the branch, the wood-inhabiting microorganisms rapidly infected the trunk above and below the branch. When branches shed normally, the microorganisms usually grow to the boundary of the protection zone and stop (Fig. 3) (Shigo 1983, 1984). When they grow through the protection zone, they usually grow downward into the trunk tissues that were present at the time the branches die (Fig. 2). A reversal of this arrangement is seen with the removal of tops of leader trunks (Fig. 13). The microorganisms usually grow downward into the trunk tissues below the cut that were in connection with the original trunk leader. The branch below the cut that becomes the new trunk leader is usually not infected.

The same patterns of spread were seen with *C. ulmi* in elm (Fig. 17) and *E. amylovora* in pear (Fig. 18). It appears that if the branch below an infection begins to grow rapidly before the pathogen spreads to the trunk where the branch is located, the branch will remain free of infection because there is no conduction connection from the trunk above a branch to the branch.

The tissue arrangement at the branch–trunk junction also affects stem form because as branches wane and die, the trunk tissues below the branch that are connected to the branch also begin to wane and die. The trunk tissues that continue to live below the dead branch grow slower for several years (Fig. 16). Thus, there is a reduction in growth rate below the dying branch; however, the growth of the trunk above the branch continues at its normal rate. Such a process results in a more cylindrical-shaped trunk when many branches die at approximately the same time and position on a trunk.

The dye experiments and the spread patterns of *C. ulmi* and *E. amylovora* indicate that there is little or no conduction directly from the tissues above a branch into the branch. Water and essential elements move upward into the branch through the xylem strip below the branch. Conduction downward in the phloem presumably follows the same pattern as the phloem turns abruptly at the branch base and continues downward on the trunk below the branch.

The combination of pathology and anatomy in this study are mutually reinforcing. Patterns of spread of pathogens reflect the anatomy of the tree, which in turn affects the spread of pathogens. The more that is learned about one, the more that is learned about the other.

The information given here comes from a relatively small number and species of trees. As more trees are studied, vari-

FIG. 12. Two samples from the same red oak that had similar-sized branches pruned 5 years ago. At left, a pruning cut that removed the collar. Note the decayed trunk wood above and below the cut (black arrows), although the callus was large. The fungi infected the trunk wood more rapidly than the inner branch core wood. At right, a pruning cut that did not injure the collar. The infection was confined to the outer edge of the cut branch (white arrows). FIG. 13. Dissection of a trunk leader stub (A) 4 years after being cut on a red maple. The decay was confined to the old trunk wood present at the time of the cut and the new leader that formed from a branch (B) was not infected. The arrows show included bark. FIG. 14. A stub of 30 cm was left after the living branch was cut on this red maple. After 1 year, the position of the trunk tissue was shown as a swollen ring about the branch base (A and B). Trunk collar tissues usually envelop the base of branches; C, branch bark ridge. White arrows show the position of bark ridges that are maintained on the trunks of smooth-bark trees. The ridges are the lower portion of swollen rings of bark that form about the base of young, newly forming branches. The bark ridges show where the branch pith meets the trunk pith. FIG. 15. Dissection of the red maple in Fig. 14 shows the position of the trunk collar and the internal chemical protection zones (black arrows). A proper pruning cut to avoid trunk infection would be from A to B; C, zone of hard compacted xylem that forms at the branch–trunk junction. When cracks form at position A, the cambium of the living branch and trunk at that position fold inward and included bark forms where compacted xylem normally forms along the zone shown by C. The large white arrow (bottom) shows the position of the lower bark ridge shown in Fig. 14. The center position of the bark ridge indicates the position of the internal junction of the piths of the branch and trunk.

ations in the patterns shown here will surely be found. The purpose of this study was to change our direction in looking at a simple but important part of tree biology.

The arrangement of tissues at the branch–trunk junction is complex; however, there is order. The cambium and growth rings are continuous; yet the cell orientation within the growth ring at the crotch turn abruptly to form collars about the base of the branch. When an injury or crack in the crotch occurs, included bark forms (Fig. 13), indicating that the cell arrangements are, at least, potentially discontinuous. The conducting xylem elements between branch and trunk are not continuous except for the thin strip below the branch; yet the way that the branch collar, which is made up of branch tissues early in the season and later trunk tissues, envelops the branch base results in a structurally and functionally unified arrangement. The tissue arrangements give the branch unique properties for strength and resiliency; yet when the branch dies, a protection zone forms that walls off the branch and sets a boundary between decayed wood of the branch and sound wood on the inner side of the zone, thus facilitating shedding. Therefore, in a sense, tree branches are not really "tied to" the trunk, but attached by a series of trunk collars that annually envelop the branch collars.

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FIG. 16. Dissection of a trunk on a red maple 7 years after a branch was cut leaving a stub. The arrows show the size of the trunk at the time the branch was cut. The trunk tissues connected to the branch beneath the branch decreased their growth rate after the branch was cut. The stem directly beneath the branch was constricted, while the stem above the branch continued to grow at the same rate as it did before the branch was cut. FIG. 17. Dissection of an American elm infected by *Ceratocystis ulmi*. The branch at left was infected and the fungus did not spread into the branch at right. The infection did not spread into the zone of compacted xylem (arrows). FIG. 18. Dissection of a pear stem infected by *Erwinia amylovora*. The bacterium did not spread through the zone of compacted xylem into the rapidly growing branch (arrows). FIG. 19. Dissection of red maple trunks after dye was applied to the upper cut surface of a trunk (A) on one sample (left) and to the upper cut surface of the branch (B) on another sample (right). The dye did not move from trunk to branch (left) or from branch to trunk xylem above the branch (right). The thin strip of wood devoid of dye beneath the branch on the sample at left shows that the trunk collar did not close completely about the branch collar and the trunk wood directly connected to the branch.