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Pomological literature abounds with mention of graft combinations which involve more or less incompatibility of the parts destined to function as symbionts. In some cases there is complete failure to unite or to grow. In others, growth starts with some promise, but gradually diminishes and finally death follows. In still other cases growth is reasonably vigorous for an indefinite period and at least quasi-symbiotic relationship may continue until mechanical stress produces a fracture which reveals a faulty union. Botanical relationship is not an infallible basis for prediction, and experience seems to be the only safe guide, as to the success of a proposed combination. Through repeated trial some curious incompatibilities between varieties have become recognized, particularly in the stone fruits (15, 17).

Other less clearly defined cases of apparent varietal incompatibility occasionally appear. One man sets grafts of Rhode Island Greening and Northern Spy apples into adjacent trees of Oldenburg (Duchess); the Spy grafts make good unions, while the Greening unions are very unsatisfactory (Fig. 1) and forthwith he concludes that Greening is uncongenial with Oldenburg. In another orchard, grafts of many varieties on Kieffer (Fig. 2) seem all to afford evidence of incompatibility between the standard varieties of *Pyrus communis* and this particular hybrid with *P. serotina*. In other orchards, however, these same combinations appear perfectly congenial.

This diversity of behavior points to factors other than purely physiological as influencing the success of these particular—and, inferentially, many other—graft combinations. The present paper deals primarily with these cases of occasional, or false, uncongeniality; true uncongeniality is presented as a contrast to the occasional cases. As foundation for an understanding of these types of "unsuccessful" grafts, some consideration of wound healing and "normal" grafts seems advisable, even at the risk of repetition of facts already established, since much of the published information is rather inaccessible and fitting new observations into a collected whole seems more desirable than presenting them as fragments.

LITERATURE REVIEW

Graft Unions—Detailed study of wound healing and graft unions was obviously impossible prior to the invention of the microscope and for some time subsequently the lack of suitable technique for the preparation of material precluded close study. Even Duhamel seems to have based his study

(10) on observations made with no greater aid than that of a magnifying glass. Despite this limitation he was able to outline in a general way some of the processes involved; in particular, he stated that union occurred only in tissues formed subsequent to grafting and he noted the extensive development of callus tissue filling the vacancies incident to grafting and connecting stock and cion. There is, perhaps, some significance in his consideration of grafting immediately after his extensive discussion of wound healing, on

Fig. 1—A case suspected of uncongeniality. Rhode Island Greening on Oldenburg (Duchess). Other pictures of this specimen are shown in Figures 81 and 82.

which he reported experimental work, aimed principally to enable him to decide between the views of Malpighi and those of Grew on the formation of wood. Without a comprehension of cambium, his understanding of graft unions was naturally limited. De Candolle, with this comprehension, was better able to understand the nature of the union and to adduce reasons for his recommendation against the inclusion of wood in bark shields used in budding (3).

The next significant step in investigation of graft unions seems to have been taken by Goeppert (12), about a century after Duhamel. In 1841, he established the existence of a parenchymatous union between stock and cion, appearing to the naked eye as a "thin greenish stripe" and persisting, in the material he examined (interspecific grafts of Sorbus) throughout the first annual ring. Only in the second year was union completed through cambium continuity, and traces of union tissue persisted in tangential sections long after they had become indistinguishable in transverse. The parenchymatous connecting tissue he designated as "intermediary cell tissue," on account both of its nature and its position; this term covered a very wide

Fig. 2—A case suspected of uncongeniality. Winter Nelis on Kieffer. A section of the graft on the right is shown in Figure 78.

range of tissue variations. His work describes a number of kinds of unions, including the natural graft.

Other investigators contributed various items. Goeppert had considered parenchyma to arise from the xylem rays while others considered it to arise solely from the cambium; Sorauer (35) showed that parenchyma arising from any tissue capable of forming it could assist in establishing union and that, in budding, union is through parenchyma derived from the shield, from the wood surface of the stock and from the inside of the bark (cambium) of the stock. He also showed that in setting grafts actual contact of cambium layers is not essential; that it is, in practice, rarely achieved, but that contact of cambium-derived callus is important. In addition, he made (34) a useful classification of the various kinds of grafts into three groups, based on the method of establishing union; these are (a) the grafts in which union is established by surface contact, as in budding, (b) the grafts proper, in which contact is through union of callus proceeding from cut cambium edges and (c) an intermediate group, represented by bark grafts, in which union is established between a cut cambium edge and a meristematic surface. Accumulation of anatomical knowledge enabled Sorauer to avoid many mistakes his predecessors in this field had made.

Ohmann (29) divided the union processes into two stages, the secondary beginning when the cambiums have established union and vascular connection. In earlier stages, grouped as primary, he reported tracheids appearing in the callus, varying with species, age of cion and kind of graft, but apparently in proportion to the need. He observed considerable growth in cions before cambium contact was complete, indicating at least a fair amount of conduction through parenchymatous tissue. The callus tracheid-like cells in graft unions are less numerous in woody than in herbaceous plants, apparently because cambium union is established relatively earlier in the woody plants. Ohmann utilized gliding growth to explain the union of calli; when calli of completely uncongenial plants meet, he reported, periderm developing in the callus closes all communication between stock and cion. In line with most investigators, Ohmann found the cambium zone to be the origin of practically all callus growth assuming importance in graft unions. He was unable to observe actual union of cambium layers, but in one or two cases believed he could identify, through slightly different staining reactions, adjacent cells proceeding, one from the stock, the other from the cion. The union, he inferred, is not a straight line but more or less "zig-zag," with much interlocking. In grafts, though not in bud-unions, the primary wound tissue dies and becomes discolored after secondary union is established; he stated definitely that he had seen no evidence of reabsorption of any tissue. Ohmann noted the initial vascular parenchyma elements and considered their transverse course to be due, not to specific differences or to polarity influences but rather to mechanical influences, particularly the pressure induced by intrusion of callus between stock and cion, wedging them apart. On the much discussed question as to whether the cambium remains on the wood surface or goes with the bark, when it is raised, Ohmann decided that in the great preponderance of cases the cambium adheres to the bark and that, when it fails to do this, budding becomes unsuccessful. He reported that approach graft unions unite more rapidly when one of the symbionts is cut loose from its roots and he called attention to the fact that splice grafts in which a long diagonal cut (very acute angle) is employed heal no more readily than those with a short cut (wider angle), in the primary (parenchymatous) stage, but grow much more rapidly in the secondary stage because of the greater extent of callus in which more vascular connections can be formed. When this line is reduced to a minimum, by joining two square-cut ends, growth is very slow.

Herse (18), studying principally the splice graft, stated in great detail the processes involved in the establishment of graft unions in the apple. In addition he reported the changes occurring in the "original" tissues of stock and cion after grafting, such as wound-gum deposits, as mentioned later. Unlike other reports on graft unions, his goes into considerable detail on changes in the bark. Periderm formation generally cuts off the outer portions exposed in wounding, though in favorable cases callus growth proceeds and the cells derived from bast of cion and of stock may meet with no periderm intervening. He agrees with Massart that no important fundamental difference exists between wound cork and callus.

Herse was able to follow cambium growth from stock and cion and to observe its union, under favorable conditions, some ten or eleven weeks after the grafts were set. At this stage cambium elements were somewhat shorter than normal and were following a distinctly diagonal direction; under favorable conditions the cambium over the union zone shows a rather even course in August following grafting in March. The order of reappearance of wood elements in the wound zone is the same as in ordinary wounds. Conditions vary, however, normal relationships being restored much more rapidly near the middle of the diagonal cut used in splice grafting than at the upper or lower end, where disturbance was much greater. The first cambium products are often purely parenchymatous; next arise short, various-formed tracheae of various sizes which tend to form strands and tie stock and cion together. The wood parenchyma and vascular ray cells separate and the abnormal width of the vascular rays soon disappears. In the further stages of return to normal wood, the typical percentage relationships of the tissues is restored before the normal length of the elements is attained.

Defective unions caused by imperfect fitting of stock and cion, both in splice grafts and in the goat's foot graft, receive some attention from Herse. In particular, he directs attention to the dieback of the stock resulting from failure to establish contact at the rim of the stub. The most detailed accounts of union through shield buds are those of Sorauer and Ohmann.

The existence of protoplasmic ties between adjacent cells of different origin has been rather widely assumed. Vöchting, as cited by Herse (18), was able to establish the existence in beet grafts of corresponding pits in the walls of adjacent cells, one of which proceeded from the stock, the other from the cion. Strasburger (36) made similar observations in several interspecific grafts in herbaceous plants. Herse was unable, because of difficulties of a technical nature, to obtain definite evidence on this point in apple unions. The prevalent difficulty is the definite identification of individual cells at the union as proceeding from stock or from cion; J. W. Bailey (1) was unable to surmount this obstacle, but demonstrated protoplasmic continuity between cells unquestionably of cion origin, through those of doubtful origin to those unquestionably originating from the stock.

Waugh (42) reported the existence of parenchymatous tissue at the border between Clairgeau pear and quince stocks, a union which was mechanically weak and is generally recognized in European literature as distinctly uncongenial. He was unable to find evidence that faulty workmanship had any material effect in producing uncongenial unions, provided the cion once started to grow.

Proebsting (30) called attention to the initial success attending numerous interspecific grafts in Pyrus and the subsequent breakdown of cambium in this union; this is presented in greater detail on a subsequent page. In a paper read at the Nashville meeting of the American Society for Horticultural Science (1927) and subsequently published (31) he demonstrated the prevalence of parenchymatous tissue in the union zone of uncongenial grafts of Prunus, and the marked scarcity of conductive tissue in these areas.

Wounds—In the closely related matter of general wound reactions, independent of grafting but helpful to an understanding of the process, numerous reports are available. These deal with the tissues covering the wound, with the tissues adjacent to the wound, or with both.

The long series may, perhaps, be said to begin with the ingenious work of Duhamel (10), followed by that of Knight, Meyens, Hartig and Trecul (35). Most of these concern principally the tissues covering the wound area. On the other hand, de Vries (40, 41) investigated chiefly the reactions of tissues adjacent to wounds; so detailed and comprehensive was his work that subsequent investigation is almost necessarily based on it. Though he made no mention, in these papers, of graft unions, much of his findings can be applied very profitably to a study of these structures, aiding materially in interpretation of conditions found there.

De Vries divided the wood adjacent to wounds made by bark removal into five zones, based on distance from the wound in space or time, and showed distinct tissue characteristics for each; these range from the distant zone (2 to 7 cm.) in which cell length is unchanged and only direction and relative proportions of elements are altered, through various stages of increasingly shorter celled secondary wound wood to the isodiametric primary wound wood arising adjacent to the injured area immediately after the wounding. The extent and relative proportion of these varies with the type of wound (transverse, longitudinal, etc.). Predominantly longitudinal wounds, or the longitudinal edges of various wounds, occasion less disturbance than predominantly transverse wounds or the transverse edges of various wounds. In the wood covering the actual wound the same zones occur, though naturally they are less apparent in sections because of the very rounded nature of the surfaces on which they occur. Initial wound reactions were found to be the same on the upper and the lower edges of ring-wounds. Much of this work was done in *Caragana arborescens,* though its general applicability was determined in about 50 species of trees and shrubs.

Mäule (26), in the course of investigations amplifying Vöchting's work on polarity, studied the tissues covering the wound, which had been rather neglected by de Vries. In three-years-old twigs of *Abies cephalonica* (Loud.) he found conditions adjacent to the wound much as those described by de Vries; transitions are in some cases very abrupt; so sharp are they, in fact, that one cell may be tracheid above and wood parenchyma below. Mäule considered that, in dicotyledonous plants, wound wood proceeds only from cambium and its still undifferentiated derivatives, being thus more restricted than in conifers. Parenchymatous tissue develops much more freely in species richly supplied with vascular rays. He questioned the efficacy of tyloses as protectors of wounded wood and attributed greater potency in this respect to wound gum. Among factors determining the direction of the fibers in wood formed after wounding, Mäule considered polarity predominant, though naturally its effects are less obvious in wound healing than in Vöchting's transplantations. The formation of knurls is explained on this basis; they are noted to disappear as the wood resumes a definite unified longitudinal direction.

In 1914, Neeff (28) amplified and extended the work of de Vries on changes of orientation in tissues adjacent to wounds. Working principally on Tilia, but corroborating his findings with observations on several other trees, he cut off ("decapitated") the main shoot at various distances above an important lateral, and in serial tangential sections followed the changes in individual cambium elements and their woody derivatives; equally detailed study of the bast was not practicable, but the general agreement of changes in this tissue was established.

Reorientation of tissue on the decapitated trunk was found to begin first in the neighborhood of the lateral branch and to begin last on the side opposite this branch. Its rapidity varies with species and with other factors; the process is particularly rapid in plants making strong diameter growth, final readjustment being attained in many cases in one summer; the size proportion between the decapitated main shoot and the lateral is also influential, as is the distance of the decapitation point from the insertion of the lateral. In some cases, turning of 180° was observed. Changes extended to points 7 cm. below the insertion of the lateral.

As detailed by Neeff, the turning of cambium elements begins with transverse division, sometimes as many as seven cross walls developing in a single element. Thus divided, the part-cells are no longer to be distinguished from the vascular ray cells lying between them. This stage is like that presented below a transverse wound. The part-cells now lose their angular nature, becoming rounded, and they appear as individual units; while this development is proceeding there is more or less crowding, pushing and overlapping, the part-cells actually moving more or less and establishing contact with part-cells derived from other elements. Next, the individual part-cells become pointed again, the former cross and longitudinal walls moving in opposite directions and the pointing is now in the general direction of the lateral branch, but more or less influenced by adjacent cells. At this time more or less gliding growth occurs, and Neeff, like Vöchting, sees the effect of polarity at this stage. Elongation following the development of points compels the new elements to push between others, inducing another rather considerable rearrangement of part-cells of different origins; some push through the initials of the vascular rays. As size increase continues, numbers must obviously be reduced; this is accomplished by the pushing of scattered individual part-cells out of the rank of mother cells, outward or inward. With attainment of original size by the new elements, normal conditions are soon restored.

In general, the form and position of the wood and bast elements are determined in the cambium; most of the turning, consequently, occurs in this tissue. There are, however, some modifications. Woody elements partly differentiated at the time of wounding simply become parenchymatous, those which were cambium initials at the time of wounding are reoriented. After the new direction is established, vessels and tracheids appear, then shorter and finally longer fibers. In many cases, the author states, "it is surely possible that cells with completed, i. e., lignified, wall, still continue locally to grow in surface and length and that thus the independent growth of the elements occurs beyond the meristem."

Concerning ring wounds, Sorauer (35) gave an extensive list of earlier studies and added much from his own work. The work done by de Vries has already been mentioned. In recent years, Swarbrick (38) has studied these wounds, calling attention to the two-fold action of this process, in affecting, through wound gum deposits, upward, as well as downward, translocation. Swarbrick reports most of the callus covering these wounds to be derived, when the wounds are protected, from the phloem.

Wound Gum—Provision for wound closing in exposed tissues, more or less independent of the covering by new tissue, has been noted by numerous investigators. The most comprehensive work has been that of Herse (18). Reviewing in detail the work done by earlier investigators, he reported substantial agreement on the existence at the wound surface of cells which die rapidly without material modification, and below that a zone in which all wood elements, but particularly the vessels, are filled with a yellow or brown substance, designated as "wound gum." There was less agreement on the chemical nature of this substance, but substantial unanimity on its being a secretion from living plasma rather than a product of cell wall disintegration; starch was considered to play an important part in its formation. Divergent views had been advanced as to its origin, both in manner and in place. Protection of wounds by grafting wax, and like substances, was said to reduce the extent of gum formation.

Herse used, as the material for his studies, chiefly splice grafts of apples, in which, since gum formation was much reduced, he was able to study its progress very advantageously. He concluded that the basic substance originates in the parenchyma elements, diffuses to the other elements and is there deposited as gum and that its appearance as gum in the parenchyma elements is to be regarded only as a final and relatively rare stage. Its deposit in the vessels and tracheids is manifestly a protection against water loss and against fungus invasion. The prevalent closing of parenchyma cells in unprotected wood is through "the providing of the cell lumina with cork lamellae"; when secretions do appear in these elements they have a different appearance and present different chemical reactions. Rather similar processes are reported for the bast.

Recently Swarbrick (37, 38) has reported on the formation of wound gum in pruning wounds and under ring-wounds. In general his findings corroborate those already discussed; in addition he reports that these deposits are made only during certain months, regardless of the time at which the wounds were made. In contrast to that of de Vries, his work shows marked differences between adjacent tissues above and below ring-wounds.

Finally it may be said that no literature review on this subject, however brief, should omit mention of the excellent summary of regeneration processes furnished by Küster (22), in addition to his own work on callus formation.

WOUND HEALING IN THE APPLE

Meristematic Tissues—Wound healing is generally treated, in texts on anatomy, along with regeneration. An extensive literature, as summarized by Küster (22), abounds in cases showing regenerative properties of various tissues in various plants; in fact, Küster states (p. 77) that all organs and all kinds of tissue have this potentiality. If, however, regeneration is defined as the formation of new tissue by already differentiated cells, its role in the healing of ordinary wounds in apple and pear is but minor. It is true that no very extended search in graft unions is required to demonstrate regeneration in wood at the beginning of its second season. In the tongue graft, for example, a fissure in the cion above contact with the stock is likely to contain more or less callus formed by the pith and by the wood, primary and secondary. In poorly fitted cleft graft unions, the cion and the last-formed wood of the stock occasionally form so much tissue from their cut surfaces that it enters into the actual union. Developments of this sort are comparatively rare, however, and wound healing in the apple depends primarily and almost exclusively on the cambium and its as yet undifferentiated, or partly differentiated, derivatives.

Since the days of Palladius, occasional fruit growers have practiced slitting, longitudinally, the bark on "hide-bound" trees, to stimulate growth. Whether or not the tree as a whole grows more rapidly, there is a striking local response in enhanced wood growth, sometimes, though not invariably,

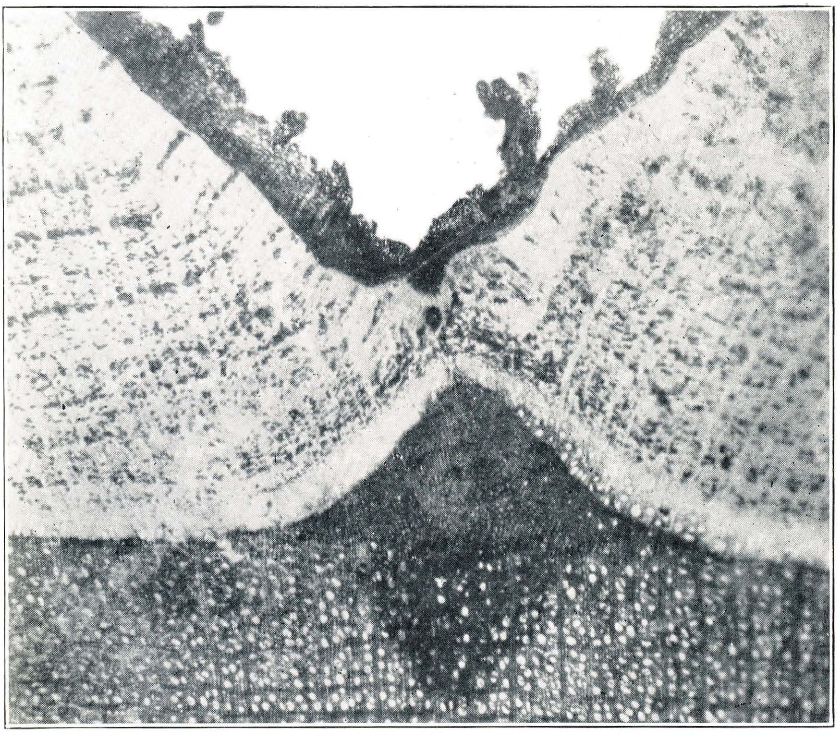


Fig. 3—Healing of a wound made by simple longitudinal slit through the bark, July 19; sectioned the following June. Wealthy apple. "Wound stimulus" shown by increased amount of wound wood formed by the cambium in neighborhood of cut. Wound gum deposit in old wood is also a wound effect. New periderm protecting bark is still another wound consequence.

taking the form shown in Figures 3 and 4. The wood formed immediately after the injury is composed of larger cells, parenchymatous in nature (Fig. 5), though most of the xylem rays preserve some measure of their identity (Fig. 4). In a short time, however, conditions return to normal. Apparently in these cases the cambium is the important factor in restoring union, since the cut surfaces of the bark suberized before union was established and the only bark continuity existing is in tissues formed subsequent to the injury.

The increased wood formation, incidentally, does not necessarily represent water-carrying capacity above that of the unwounded stem, because of the formation of wound gum thereby induced in the vessels laid down before the wound was made.

Whether the growth stimulation observed here results from release of pressure exerted by the bark, as contended by de Vries and denied by others, or whether it is the effect of a wound hormone, cannot be decided on the evidence available. Throughout the work here reported, pressure seems

Fig. 4—Enlarged detail of Figure 3. New wood principally parenchymatous, with some persistence of xylem rays. Vessels in old wood plugged by wound gum (darker portion).

to exert a very pronounced effect on the nature, as well as the extent, of new tissue formed. It may be proper to remark, since the point seems to have been overlooked in some rather controversial discussions, that pressure changes may affect the physical and chemical condition of the individual cell, and that affirmation of the one influence does not necessarily involve negation of the other. Moreover, these are not the only factors; numerous observations indicate that food and water supply play an important part in wound reactions. Nothing seen in this study furnishes clear evidence for

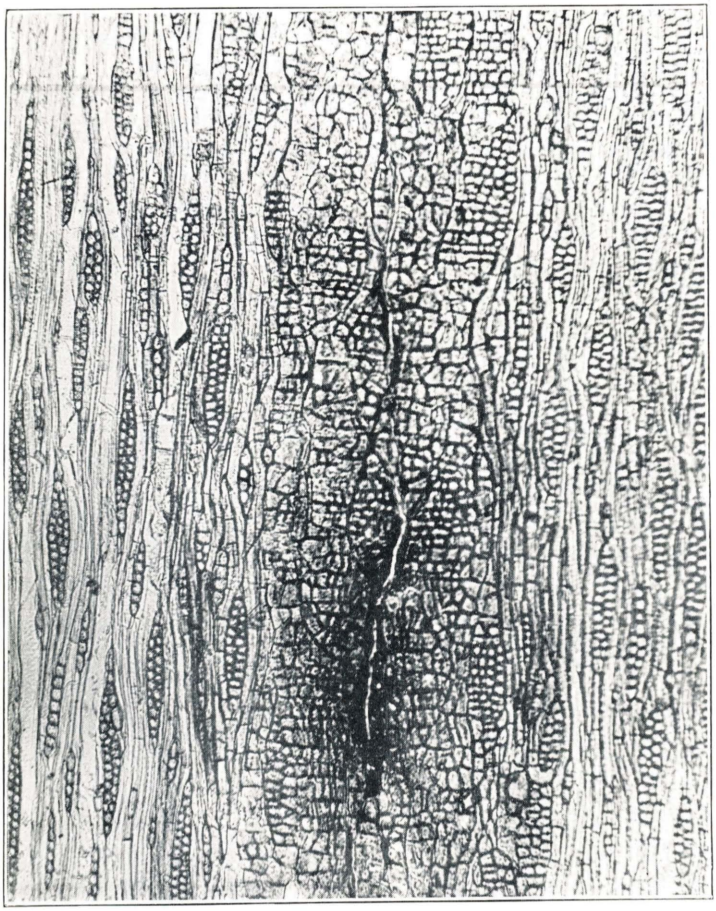


Fig. 5—Tangential view through wound similar to that shown in Figure 3. Parenchymatous tissue in center; almost normal tissues on sides.

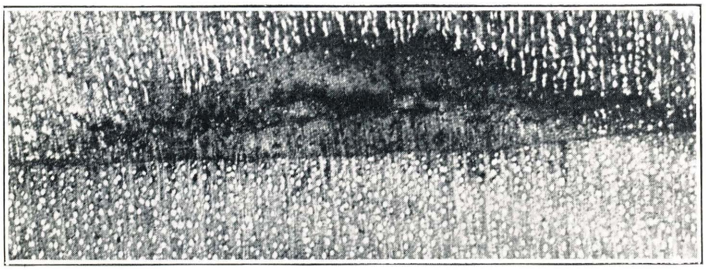


Fig. 6—Parenchymatous tissue filling cavity made by raising bark. Formed from bark and wood. The dark irregular horizontal lines separate the products of cambium and meristematic wood. Persistence and continuity of xylem rays rather marked.

or against polarity as a factor in healing wounds or in establishing graft unions; it is a hypothesis much more easily asserted than proved or disproved.

Meristematic properties are not confined, in apple and pear, to a single layer of cells. The plainest evidence of this fact is the success attending budding in these species. Whether the layer of cambium mother cells is considered to adhere to the bark when it is raised or to remain on the wood surface, new tissue is formed from both surfaces apparently with equal facility, at times when budding is done. In most cases observed, the tissue arising on the inside of the bark seems as completely parenchymatous as

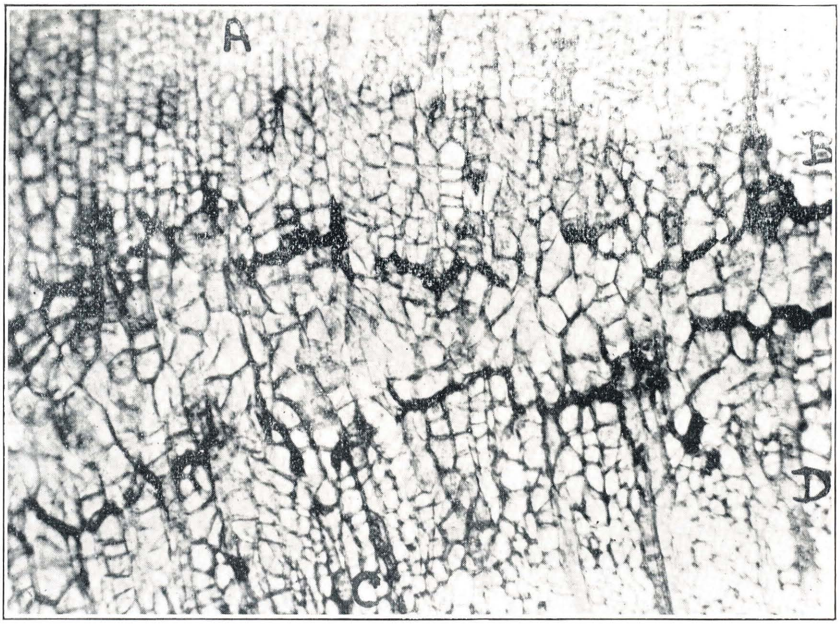


Fig. 7—A detail from the edge of a wound made by raising the bark for inserting a bud which does not appear in the picture. Lines from A to B and from C to D would mark the tissue formed before the wound was made; between them is parenchyma from bark and from wood. The irregular dark lines are presumed to be remnants of cells destroyed when the wound was made. Center of stem below lower edge.

that arising on the wood surface, which in the majority of cases retains some trace of the xylem rays (Fig. 6). DeVries and most other commentators, as cited by Herse, stated that the cambium, in such cases, remains attached to the bark, and this seems to be the case, though the statements de Vries adduced as evidence do not hold consistently in the material examined, which presents a diversity of conditions. Where the bark has been raised slightly without removal, as under the bark flaps at the edges of shield-bud insertions and bark grafts, there is often little difference in the parenchymatous product of bark and wood surfaces and in viewing small areas orientation is difficult without reference to the preparation as a whole. Ohmann used a thin brown line coursing through tissue of this sort as a mark of contact of the two calli; this, according to his explanation, is penetrated from one side or the other and the out-pouring tissue establishes the fusion of tissues. Herse, noting the presence of this line, considered it to be composed of remains of cells destroyed by the actual wounding, and that it does often mark the union, particularly in buds. Some preparations examined in the course of the present study show this line imbedded in callus which had not met another callus and in some two lines are present (Fig. 7). In many

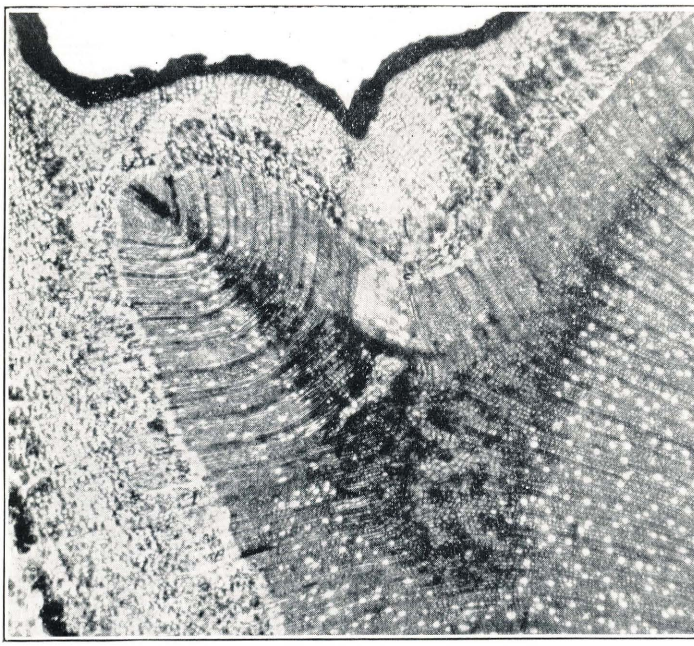


Fig. 8—The edge of a wound made for the insertion of a bud which did not take. Along the exposed wood surface (right) rapid restoration of nearby normal structure between August 1 and November 1. The "bush form" projection, at the left of center, rather common in bud unions, is a product of growth from the cambium attached to the bark. The light triangular spot in this structure is a fracture, produced by the tissues pressing up from the wood surface, and filled with parenchyma. This, too, is rather common.

cases, these remnants do not break the continuity of a cell series and it seems probable that they separate rather, on the inside, tissue formed by redivision of cells partly differentiated prior to wounding and of their derivatives, and, on the outside, mainly the tissue derived by redivision of cells which had penetrated the area of brown cells derived from the outer layer. In other words, these lines undoubtedly represent cell debris in some cases, but, in others, they appear to mark a temporary check in callus growth.

If it be assumed that growth is always centrifugal, then plainly the first cells laid down attached to the bark (after wounding) are as parenchymatous as those formed on the wood surface or even more so, and specialized tissue appears later, farther from the center. Sometimes, however, the inner (toward the center) edge of the parenchymatous bark-derived tissue shows some specialization, and the wood closest the phloem is regularly organized, while between them is parenchymatous tissue. This might possibly signify, still assuming centrifugal growth, that the first cells were laid down by the cambium before its cells divided longitudinally in response to the new conditions. It seems more plausible, however, that another cambium may be

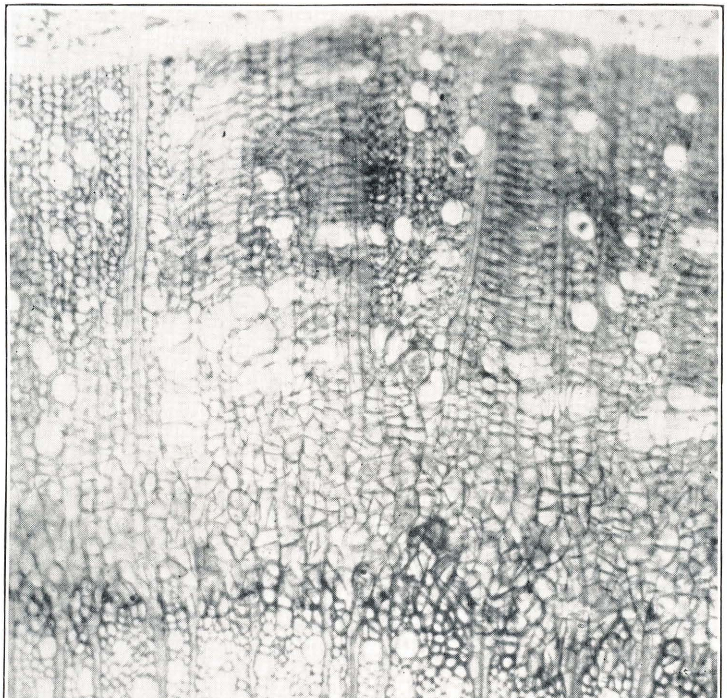


Fig. 9—An enlarged detail from Figure 10. Though both wood cells and xylem rays share in the formation of parenchyma, the xylem rays contribute more than their proportion.

formed, facing inward, and that, through the action of their wood products, the two are forced to grow in opposite directions. Indeed, an appearance of the sort presented by the bark flap in Figure 8 and noted by Ohmann could hardly be explained in any other way.

Type of Wound—The potential variability in response to simple wounds just indicated, is utilized by the tree in healing larger wounds presenting different conditions, both in surface exposed and in environment subsequent to wounding. When the meristematic surface of the wood is preserved intact, the healing process is quite different from that invoked to cover a surface on which the meristematic surface has been destroyed. Exposure to, or protection from, atmospheric influences affects the healing, whatever the nature of the wood surface. The vigor of the tree, likewise, has an undoubted influence.

If the meristematic surface exposed upon removal of the bark is uninjured, parenchymatous tissue develops rapidly, as already described. At this stage, atmospheric influences begin to play a part. Protected from drying and from infection, parenchyma develops rapidly and copiously. In this

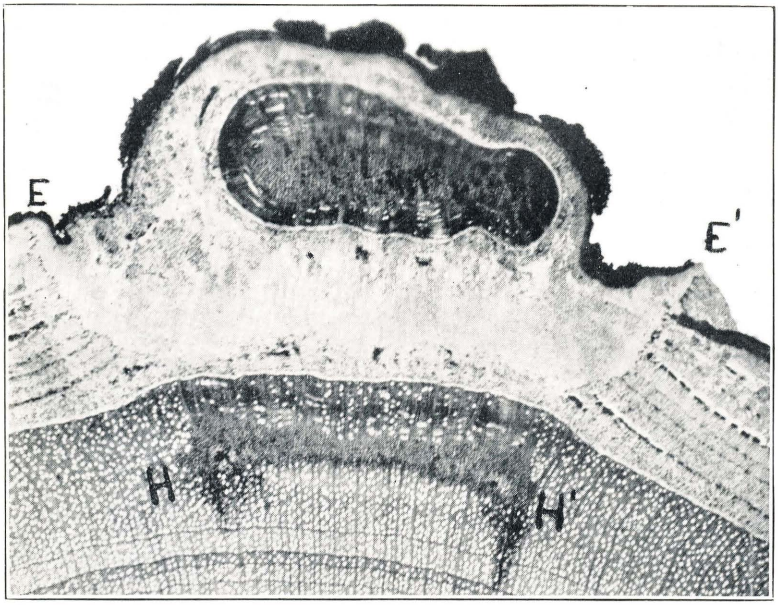


Fig. 10—A wound made in a Wealthy apple branch on July 19 as it appeared in the following winter. The bark was removed from H to H[1]; the wood surface uninjured except by the knife cuts at the edges, and the wound covered with adhesive tape. Wound gum where wood was injured; little or none elsewhere. Restoration of nearly normal wood was rapid. Abundant parenchyma formation from bark extending from E to E[1]; in this is a "wood island" (Rindenknoll) the product of an independent cambium formed in the cortical parenchyma. This, though not rare, is not normal.

formation, both xylem rays and undifferentiated wood elements appear to have a part (Fig. 9), presumably by very rapid transverse division. This process has been described in detail by Herse and by de Vries. The surface at this time is so uneven, in part because of more rapid development from the xylem rays, that it is difficult to conceive of a cambium laying this tissue down, and there is no readily recognized evidence of bark tissues. Herse reports finding indications of cell division in parenchymatous apple tissue, under similar circumstances. It seems probable, therefore, that, as has been demonstrated to occur under many conditions, a new cambium forms in the parenchyma and ultimately makes contact laterally with the advancing cambium of the wood at the side of the injured area (Fig. 10). This view is strengthened by the equal or even greater radial thickness of the area of organized vascular tissue in the middle of the wound; had cambium spread from the edges the condition would have been reversed. At the same time, the possibility of independent cambium formation in cortical parenchyma is illustrated by the "wood island" (rindenknoll) shown in the

Fig. 11—Tangential, enlarged, view through the new wood filling a wound similar to that shown in Figure 10. Through a ground work of parenchyma (the "primary" stage of de Vries), the first-formed tracheids and vessels course irregularly. This is the beginning of restoration of normal conditions.

figure. Vessels and fibers appear at first sporadically and coursing irregularly through the still parenchymatous ground tissue (Fig. 11). Their number increases rapidly and along with this increase comes a straightening of their courses, and normal tissue composition and structure may be restored in a comparatively short time; certainly, in small wounds, within two or three months. This process is essentially the same in small wounds, whether they are transverse or longitudinal.

Swarbrick reports the callus in protected small ring-wounds to come chiefly from pholem. Preparations made in September from protected ring-wounds made on July 19, 1927, indicate clearly that this parenchyma, as in the other cases, comes from the meristematic wound surface and the cambium at the wound edges (Fig. 30) and that the restoration process resembles that described for longitudinal wounds. Here, too, the wood island in the bark is evidence of independent cambium formation, but the greater amount of vascular tissue near the edges indicates cambium extension from the sides. Partial ring wounds of greater dimensions, whose wound surfaces have been "protected" by a coating of grafting wax, destroying the meristem on these surfaces, heal, for two or three years, much like corresponding longitudinal wounds, though the disturbance in direction is greater. In these, as in larger complete ring-wounds, the cambium plays the chief role. Other things equal, the upper edge of a ring-wound always forms callus much more abundantly, as all commentators agree, than the lower edge, and phloem activity is undoubtedly important in this process. If, however, two ring-wounds are made in close proximity, the upper edge of the lower wound grows but little, if any, more than the lower edge, while the upper edge of the upper wound grows most vigorously of all. This behavior would seem to indicate that the function of the phloem here is chiefly food conveyance to the cambium. This matter attains some importance in the healing of the stock in the pear-quince union, as is shown later. Despite the reorganization of the callus edge in ring wounds, its tenure of life is limited and unless it establishes contact in a few years, it dies, even before the stem above the ring. This dieback is more rapid in the bark than in the wood.

Environment—When the wood surface in the wounded area is injured, healing comes from the side, in the familiar manner known as overwalling. Environmental conditions play a great part in determining the quantitative tissue relationships involved in this process; indeed, the appearances presented by protected and unprotected wounds are superficially quite different (Figs. 12 and 13). Fundamentally, however, they show the same process.

In the protected wound, parenchymatous tissue fills the bulk of the gap. This of course proceeded from the cambium at the edges. In a short time the cambium began to extend laterally over the newly formed parenchyma (Fig. 14). The newest cambium thus formed gave off more parenchyma, while at the same time the first new cambium began to differentiate organized wood. The vigorous development of parenchyma from both sides of the wound soon brought the surfaces together but since there was no cambium present at the point of contact there was no union in the truest sense. This came only later, when the two cambium wings, advancing along the surface of the parenchymatous pad, joined (Fig. 12). There is no reason apparent why cambium may not differentiate independently in the parenchyma and establish union with the "old" cambium; but that in the present case, as in several others examined, the cambium covering was established by advance from the edges, is indicated by the notably thicker layer of organized wood near the edge of the wound. Understanding of this process is facilitated by consideration that the "old" cambium layer was not stationary during the period of wound healing, but advanced outward as ordinary diameter growth proceeded.

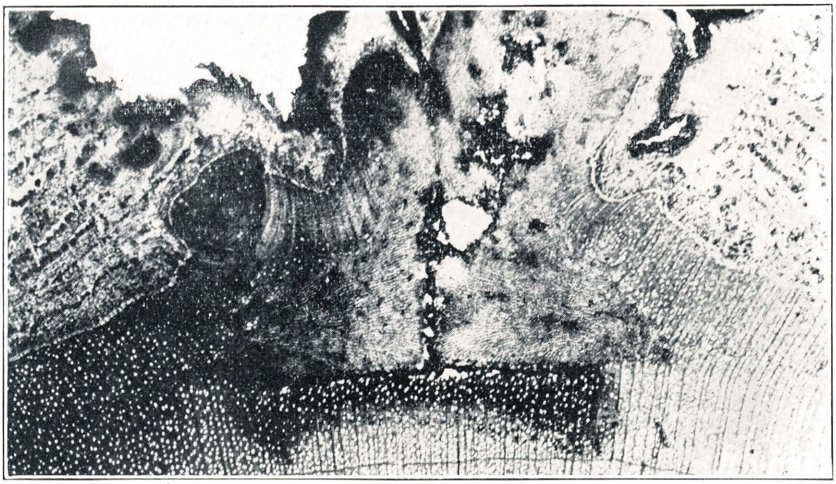


Fig. 12—A companion to Figure 13. These wounds, made July 19, stood about two inches apart on a branch of Wealthy apple. When the bark was removed the exposed wood surface was scraped in both cases; the wound shown in Figure 12 was covered with adhesive tape; the other was left unprotected. Sections cut in November following wounding. Figure 12 shows preponderance of parenchyma, with cambium creeping along its outer edge.

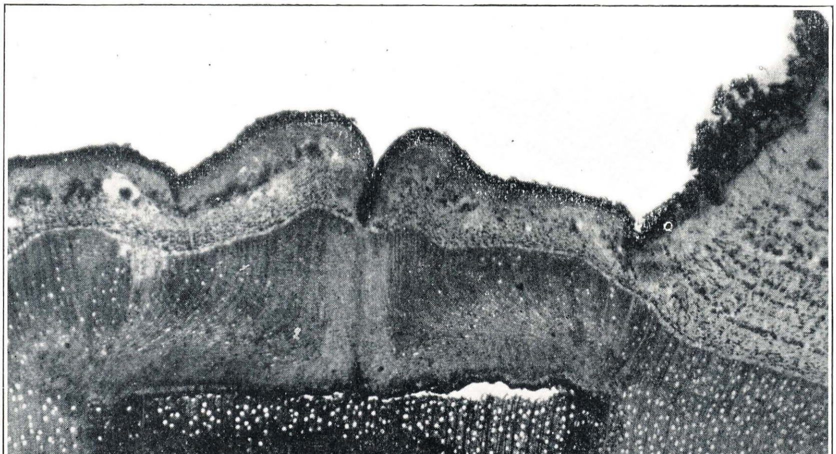


Fig. 13—(See legend for Fig. 12.) Parenchyma much reduced, differentiated tissue predominant. Xylem nearest wound surface died before wound gum could be formed.

Healing of the unprotected wound with injured wood surface, though at first glance quite different from that just described for the protected wound, actually varies from it only in the proportional relationship between parenchyma and organized wood. Growth is less rapid, and the cambium lateral extension across the wound and interstitial growth are relatively more rapid than differentiation from the cambium. Furthermore, little parenchymatous tissue is given off from any individual elements; more or less organization appears relatively early. As the callus advances across the wound, the pres-

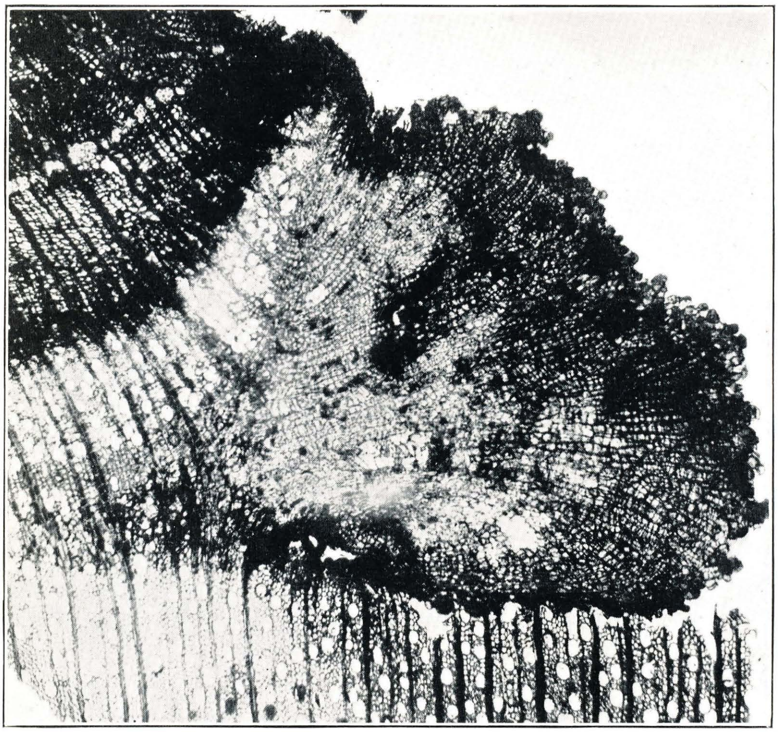


Fig. 14—An early stage of Fig. 12. Section, cut about August 15, through one edge of a protected wound like that shown in Figure 12, made on the same day, on the same branch. Parenchyma outstripping cambium.

sure of the bark already given off from the cambium holds the callus edge down, and only the presence of the wood surface prevents further bending of the type described and illustrated by Sorauer (35), who shows spiral formation of callus in trees with the center rotted away. The advancing callus (Fig. 15), then, has a narrow rim of parenchymatous tissue nearest the old wood, a zone of partly organized tissue and finally normal or nearly normal wood.

The zone of parenchyma on the lower side of the callus (i. e., adjoining the wound surface) is of rather varied composition. As the cambium edge advances, more or less of the cortex in front of it is pressed aside and rolled under. Along with it, however, is a varying amount of parenchymatous tissue laid down by the rather isodiametic cambium cells of the free edge. In other cases, however, the rolling under seems to originate from above, in the expansive force of cambium and some of the cambium edge is rolled under the callus and vascular elements are found occasionally on the inner side of the callus. Many of the overwalling calli examined seemed to have advanced at first with a free-hanging edge, pushing cortex ahead, leaving parenchyma behind, and rolling some cortical parenchyma underneath; later the rolling motion became more accentuated, and periderm, cortical

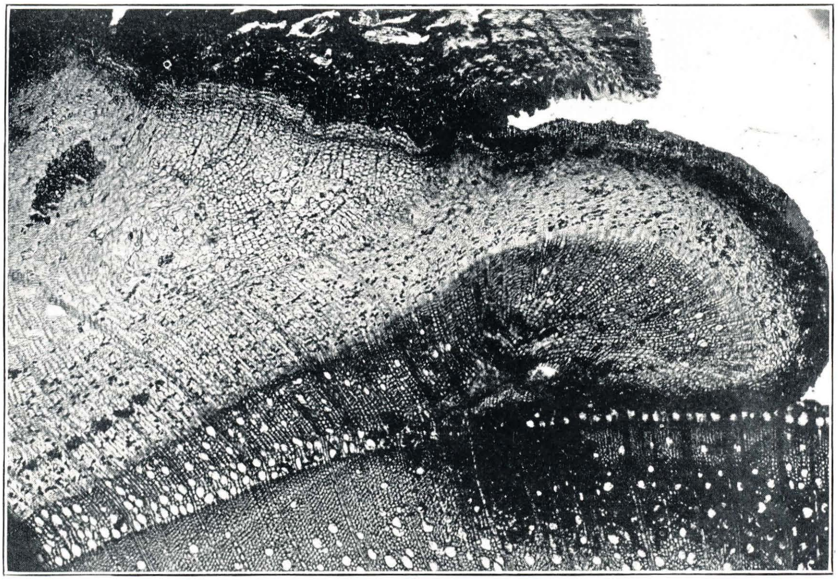


Fig. 15—Cambium outstripping parenchyma. The fan-like divergence of cell series from the edge of the wound indicates gliding growth in cambium, and the course of some series downward toward the old wood surface indicates the rolling nature of the advance. The backward pull exercised by the bark is shown by the abrupt turn of the vascular rays in the phloem region. Exposed wound, apple.

parenchyma and cambium were rolled under. This rolling motion may be traced by following the course of the xylem rays in Figure 15. In other cases, however, the initial stage of the process just described seems to have prevailed until union was accomplished (Fig. 13). The difference may possibly be explained by the relative rapidity of lateral extension and radial division in the cambium; indeed, the type represented in Figure 16 may be considered intermediate between the types represented by Figures 14 and 15.

The sequence of cell series in many preparations indicates that, in unprotected wounds, cambium covers the callus at a very early stage and that further development is chiefly interstitial, by the insertion of new cambium elements between those already formed. In other preparations, however, lateral extension clearly is considerable. This apparently occurs by lateral formation of parenchyma in which new cambium develops.

This statement of the origin and development of the callus lip differs widely, in some respects, from Sorauer's interpretation of a similar structure in the sweet cherry (35) in which "parenchyma of the inner bark" is given a more active role in covering and extending the wound edge than seems warranted by the preparations used in this study. These seem plainly to justify the interpretation of the new bark as a product of the laterally extending "new" cambium. Lateral extension of the cambium, however, is indicated in either explanation.

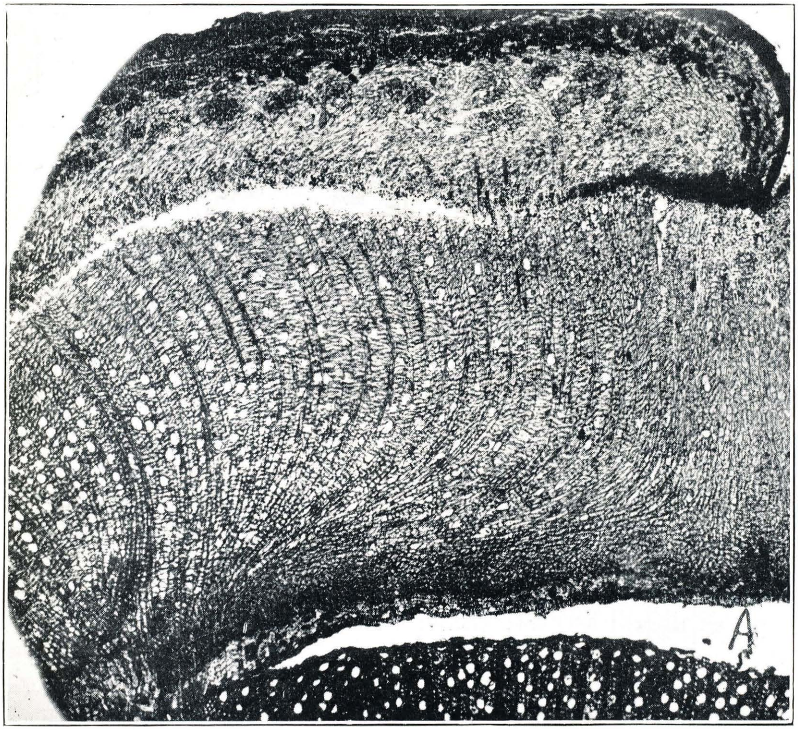


Fig. 16—Absence of rolling motion. One edge of a healed surface wound. Cambium lateral extension slow in proportion to cambium radial division; indicated by recurving of xylem rays. Parenchyma edge on lower surface of callus (with its own periderm) and parenchyma at union with callus from opposite edge (at A). Exposed wound, apple.

Establishment of Union—In small wounds, closing may occur and cambium continuity be established in one season; in larger wounds several years may elapse before the callus lips meet and several years more may pass before the cambium edges unite. The rapidity of this last process depends on the extent to which the opposing surfaces are suberized and on the pressure from within. Mäule, and as cited by Herse, others, have sug-

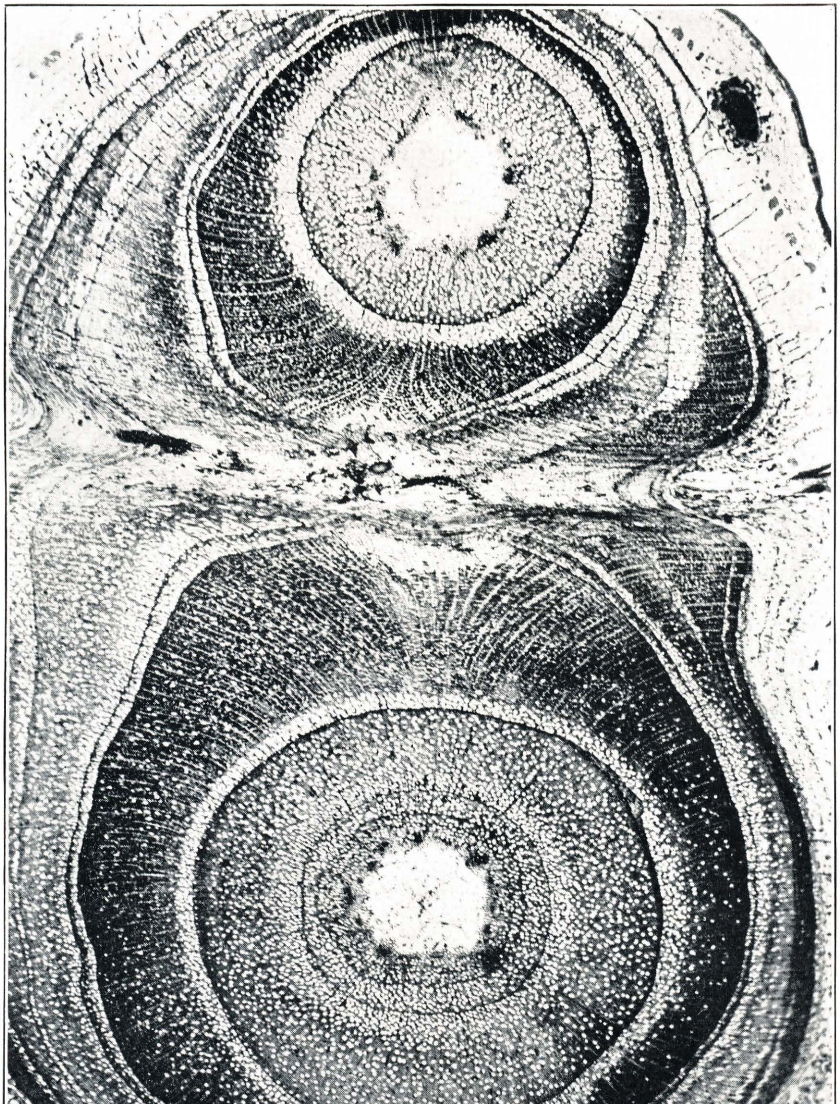


Fig. 17—A "natural graft," as formed in a live-brace, made by twisting together two shoots from opposite limbs in a young apple tree. The shoots were, therefore, growing in opposite directions. Bending of xylem rays, the first sign of contact, followed in two years by union of cambium of the two shoots into one continuous layer. Many sections of unions of this sort show decreased width in rings at zone of initial contact (Fig. 18); the increased width shown in this case probably signifies prior union in a contiguous area. Pressure at contact points not directly opposite and no inclusions in this area.

gested that cambium continuity is established in these cases by the solution and reabsorption of the intervening suberized cells; Herse regards the matter as unsettled. The material studied for this investigation suggests an interpretation in line with Herse's statement of analogous cases, and avoids the necessity of postulating an enzyme for dissolving the one plant product which seemingly resists solution most notably. It may perhaps be examined best in its most extreme manifestation, the natural graft, in which two twigs entirely enclosed in separate corky envelopes establish cambium continuity.

Figure 17 illustrates a "natural" graft, part of a live brace made by twisting together two shoots from separate limbs in a young apple tree. Incidentally, in most, if not all, cases examined, longitudinal growth was proceeding in opposite directions. Bending of the xylem rays, indicative of radial pressure and therefore of contact, begins with one shoot in its second annual ring and in the other in the fourth. The increase, rather than decrease, in the width of the annual ring at the time of initial contact, is probably a reaction to prior union at a near-by point, or possibly a reaction to the bending induced by twisting. It is by no means the prevailing condition; many sections from the same material show diminution of diameter growth at the point of contact and increase at either side. This occurs in the following year in the present case. It is clear that the zone of initial contact now consists of parenchyma, with occasional bark inclusions and that this parenchyma zone persists at the left, though it is replaced on the right by vascular tissue bridging the union zone transverse to the general course of the twigs.

There appears to be some diversity in the precise mode by which contact is established between the two cambiums. In the specimen represented by Figure 18, a rather early stage, separate wound periderms have formed, cutting off more or less cortex (lost in sectioning); with further expansion these bark edges are pushed aside, leaving the way clear for parenchyma and cambial extension at either end of the isolated bark area, which remains as an inclusion (Fig.19). These inclusions, noted by Mäule as unabsorbed remnants, are, as seen in the material studied here, almost invariably the spots of directly opposed impact, with no opportunity for shearing stresses to tear the bark. Once cambium continuity is established, the loose edges are joined by new phloem and only a fissure in the older portion of the bark denotes their original separate existence. Another method involves one point of union instead of two (Fig. 20). This depends principally on a second stimulus to wood formation, possibly influenced by union already accomplished elsewhere, piercing the non-expanding bark, establishing cambium continuity promptly and leaving little or no bark inclusion. Sometimes expansion occurs at points not directly opposite, resulting apparently in an actual tearing of the bark, followed by outpouring of cortical parenchyma, across which the cambium advances.

These natural graft unions may be considered to represent the processes by which union is established between overwalling calluses with well developed corky surfaces. In perhaps a majority of cases the initial meeting of the callus lips is denoted by a small remnant of suberized tissue close to the wound and perpendicular to it (Fig. 32). The force of the thrust is diverted outward, tearing and lifting the bark and permitting union through a common parenchymatous zone.

In large wounds, in which the callus lips do not meet for several years, the rather extensive development of suberized tissue prevents union for

Fig. 18—Early stage of natural graft union. Bark cut off by periderm formation. Preparation torn apart in sectioning.

some time, until the upward thrust, evident in Figure 22, tears the corky layers sufficiently to permit parenchymatous tissue to join. Sometimes this does not occur until the lips have been in contact several years. In comparatively rare cases, union through this parenchymatous tissue is broken (Fig. 22) by intrusion of tissue from more advanced contiguous callus in another plane or by growth advancing in radial direction imprisoning and cutting off areas of suberized tissue before they can be pushed out by growth from below.

In wounds in which the wood surface is uninjured, but left exposed to atmospheric influences, the response may be overwalling, or it may be very much like "regeneration"; often it is a combination of the two.

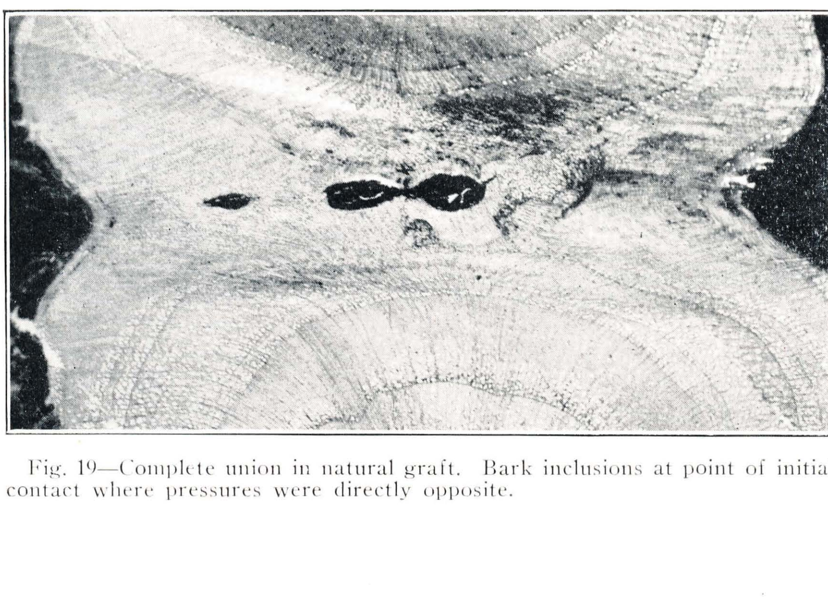


Fig. 19—Complete union in natural graft. Bark inclusions at point of initial contact where pressures were directly opposite.

Vigor—The rate of covering of wounds is obviously related to vigor of growth. The wound shown in Figure 23 healed in the period between July 19, when the wound was made, and the end of the growing season. Reference to the successive annual rings in the stem, where the width of the annual ring has varied inversely with the size of the fruit crop, and principally in the late summer wood, indicates plainly that a similar wound made on the same date in the previous year would not have been covered over in the same length of time.

Vascular Bridges—Tangential sections of wounds like those described, besides confirming the observations made on transverse sections, show in addition that the course of the first-formed wood elements in the overwalling tissue is very irregular, undulating more or less in all directions but assuming gradually a general longitudinal trend; later-formed elements deviate less.

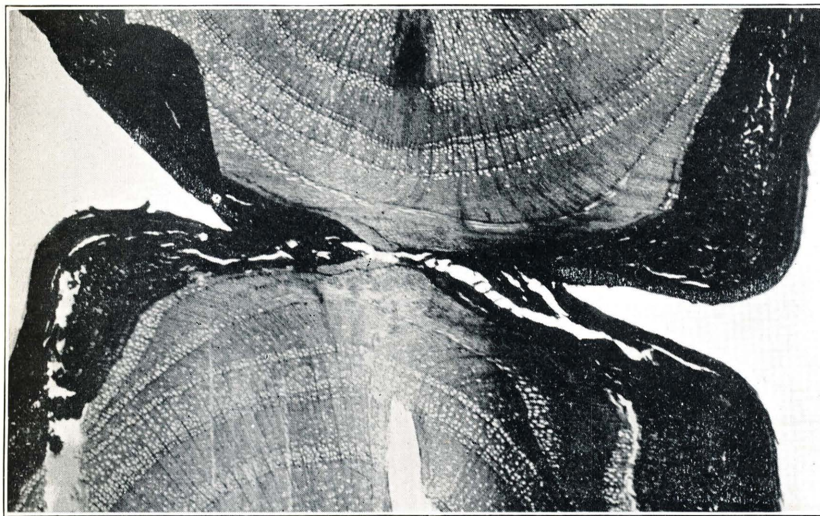


Fig. 20—Initial contact in a natural graft by bark perforation at one point.

Parenchymatous tissue is at first the most abundant (Fig. 11), fibers coursing singly through it. Later it is much reduced and the appearance presented is predominantly of fibers (Fig. 24). The parenchyma which faces the callus lips persists for a considerable time after contact is established, forming a well defined belt running longitudinally along the wholly covered wound surface, bounded on either side by rather regular strands of tracheids, with here and there a short chain of short vessels. Sooner or later, in the first year of contact or perhaps not until the third or fourth, isolated tracheids leave the ranks of the bounding organized tissue and wander rather irregularly through the parenchyma. More and more of this occurs, proceeding ordinarily from both edges; later several associated vagrants follow this wandering course and then one of these groups and finally numbers of them cross the parenchyma entirely (Fig. 25). The large belt of parenchyma, which may be regarded as an aggregate ray, according to Jeffrey, though as seen in transverse sections the cells appear isodiametric, is thus cut into smaller rays. As the bridging proceeds, the number of these rays increases and their size decreases. From bridge to bridge new connections develop, taking therefore a less oblique course and the rays are cut vertically as well as more transversely. Thus the parenchymatous zone gradually disappears, the last trace observable tangentially being a more or less undulatory course of the fibers and ultimately even this gradually straightens out.

Fig. 21—Union of callus healing by overwalling a surface wound (which was below the lower edge of this section) in apple. Same forces evident as in natural graft union, i. e., inclusion (black area in lower center) where pressure squarely opposed, with shearing strain where pressures were lateral, rupturing corky tissues sufficiently to permit union of parenchyma (immediately above bark inclusion), which is the prevailing union throughout the first year.

This process, it may be pointed out, is essentially the making of a graft union, and the description just given needs only a supplement to make it applicable to conditions occurring in cases coming under the more usual acceptance of the term. It may be added that there is no regular sharp line of demarcation running from end to end of the union. There is at first a buffer zone of parenchyma in which the tissues preserve more or less individuality, according to their origin, but in which there is also a certain

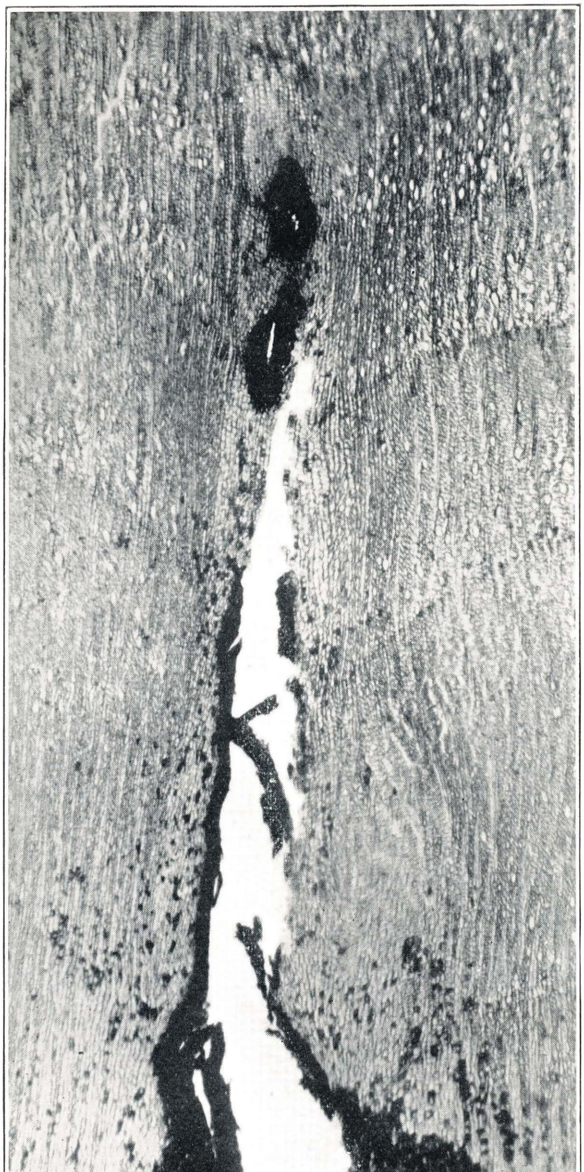


Fig. 22—Union of overwalling callus covering a large wound and meeting with heavy cork layers intervening. Part of the cork was lost in sectioning. First union through parenchyma was broken twice (by bark inclusions in upper portion of picture) before union of vascular tissue was established.

amount of invasion from the one side into the other. Into this zone reach fiber strands from both sides for various distances. Some join the fibers from the opposite sides somewhere in the parenchymatous zone, while others reach clear across this zone before establishing contact. If the parenchymatous zone is broad, the area over which contact is occurring is correspondingly broad; if it is narrow the zone of contact is correspondingly narrow and it may even zig-zag across a vertical line connecting single xylem rays. This conception is in line with Waugh's statement (42) of the line of union in grafts.

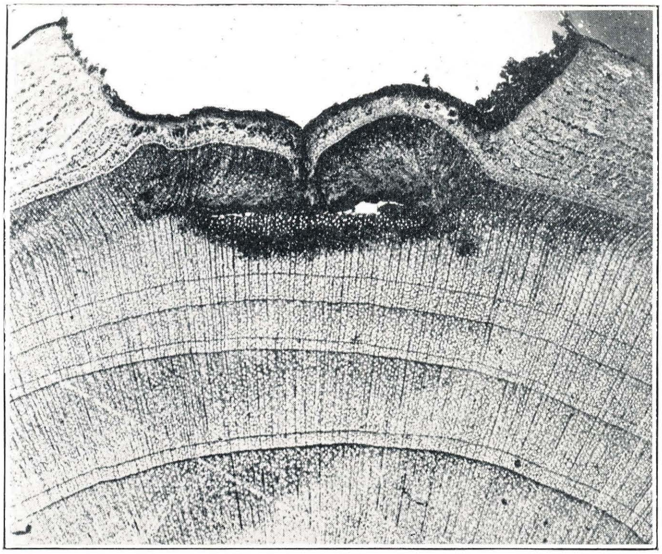


Fig. 23—A wound similar to that shown in Figure 13. Wound made July 19, 1927, covered before winter. The width of the annual ring of 1926—less than that formed subsequent to wounding in 1927—indicates that a wound made on the same date in the previous year probably would not have been covered in the same season. The alternation in width of annual ring is inverse to size of crop on this tree.

Orientation Changes—Consideration of wound healing is not complete without recognition of the changes occurring in tissues adjacent to the wounded area. The mechanics of change of direction of tissue arrangement have been outlined by de Vries and described in considerable detail by Neeff, whose statements have been reported already. To them may be added a note to the effect that many radial sections of tissues adjacent to amputation wounds show a downward displacement, particularly in the xylem rays. Otherwise their findings seem in general to be corroborated for the apple, except perhaps in regard to time required. The promptness with which readjustments of direction, varying with the shape of the wound, are made, is striking, but the persistence of the transition changes seems greater than Neeff observed in his material. No attempt was made in this study to evaluate the several factors which might conceivably be operative in determining the direction of readjustment. De Vries, whose investigations led him to believe that bark pressure was the factor determining tissue organization, stated definitely that no difference existed in tissue formation above and below a ring-wound; Neeff, contending that all readjustments were made with primary reference to polarity, does not mention

Fig. 24—Tangential view of longitudinal surface wound similar to that shown in Figure 10. A somewhat more advanced stage of surface healing than that shown in Figure 11 and at a lower magnification. Longitudinal trend of vascular elements more pronounced, particularly at edges. Parenchymatous ground tissue still abundant, but increasingly cut off by vascular elements, which have established connections across the wound.

any difference. The study here reported, though too limited to warrant definite statement, showed, in the material examined, a rather consistently, though not always notably, greater amount of parenchymatous tissue relative to vascular above a ring-wound—partial or complete—than below it. As to vascular direction, however, the observations made could be explained as well on one basis as another, although it may perhaps be pertinent to mention here that "bridge" grafts which have grown three years with contact only at the upper end seem entirely normal in wood structure and there appears to be no reason why supply of elaborated foods or the transpiration stream should not have been the chief influence in these readjustments, as readily as polarity.

Aside from possible effects of polarity, the transpiration stream seems to be the determining influence, since in numerous wounds, of one kind or another, reorientation is affected by the establishment of parenchymatous union, before cambium or phloem union is established.

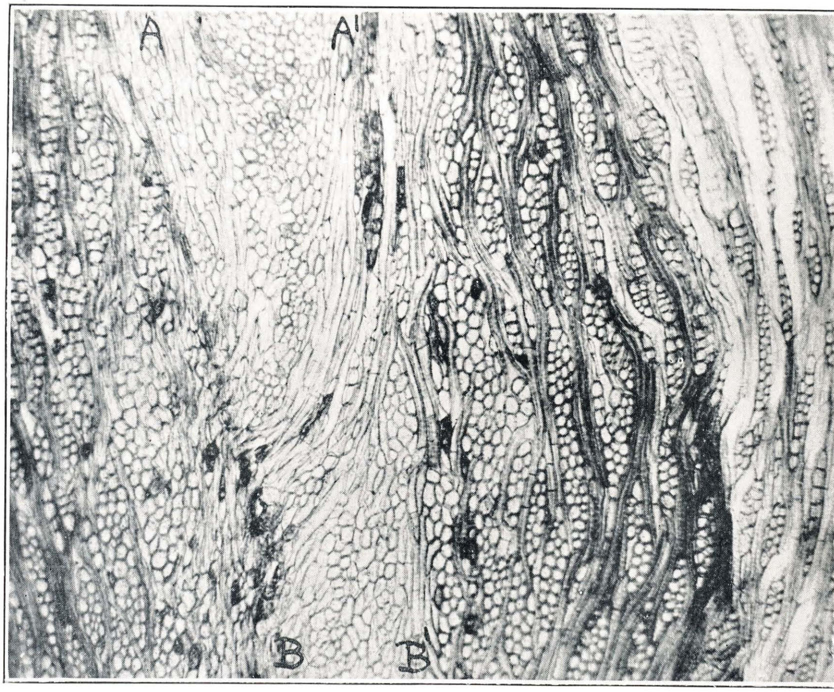


Fig. 25—Tangential view of healed pruning wound, showing, near the center, initial vascular bridging of parenchymatous zone (A-A^1, B-B^1). Overwalling tissue at sides.

In general the changes in tissues adjacent to longitudinal wounds may be described in this way: close to the edge of a narrow longitudinal wound there is a very marked increase in the size of the xylem rays, particularly in their tangential diameter. This disturbance is greatest at the edge of the wound, decreases with distance from it and virtually disappears at a distance of one cm., or even much less, from the wound edge.

Secondary Wound Wood—This stage, in the healing of actually wounded areas, follows the parenchymatous (primary) stage, and is called "secondary wound wood" by de Vries. In these adjacent areas, however, no primary stage could be detected, though de Vries insists that it is always present, even if in very much reduced form. Along the greater extent of the longitudinal edge, growth direction is not changed and normal conditions are quickly restored, except for the disturbance at the immediate edge of the wound, where the development of the callus still occasions some irregularities.

At the end of these longitudinal wounds there is at first a virtual disappearance of vascular tissue (the "primary wound wood" stage) but very soon this tissue reappears, coursing rather irregularly, with some of it ending blindly, but most of it tending to right or to left around the wound. Bending at the corners of the wound seems to be easily accomplished. With

Fig. 26—Late "primary" wound stage. Tangential view of tissue adjacent to ring-wound. Almost entirely parenchymatous, but occasional vessels coursing through it. Dieback has set in at numerous spots, especially in lower right corner.

the greater number of strands converging at the corners there is, in rather broad wounds, a considerable piling of vascular tissues at these points, easily seen with the naked eye.

In ring-wounds the disturbances in adjacent tissues above and below are of much the same nature, but more intensified, and they extend to a greater distance from the wound edge. Near the wound, vascular tissue disappears almost altogether for a time (Fig. 26) and for some distance back from the wound it is still much reduced in amount (Fig. 27). Deposits of undetermined nature, but resembling starch, are very abundant near the wound in wood formed subsequent to the injury, but become less common farther back (Fig. 28). In complete ring-wounds, when vascular tissue finally reappears it tends to course along the wound edges, at right angles to its previous direction, and the covering of these wounds is principally by longitudinal overwalling transverse to the stem, i. e., with cambium initials arranged at right angles to their usual direction. However, the connection of the advancing callus with the tissues farther back is maintained chiefly by longitudinally coursing strands. There is, then, in a healing wound of this kind, at first, a belt of transverse tissue, above which (radially outside) is a belt of longitudinal tissue (Fig. 29). If the ring does not extend entirely around the branch, all tissue reorganization is done with reference to the

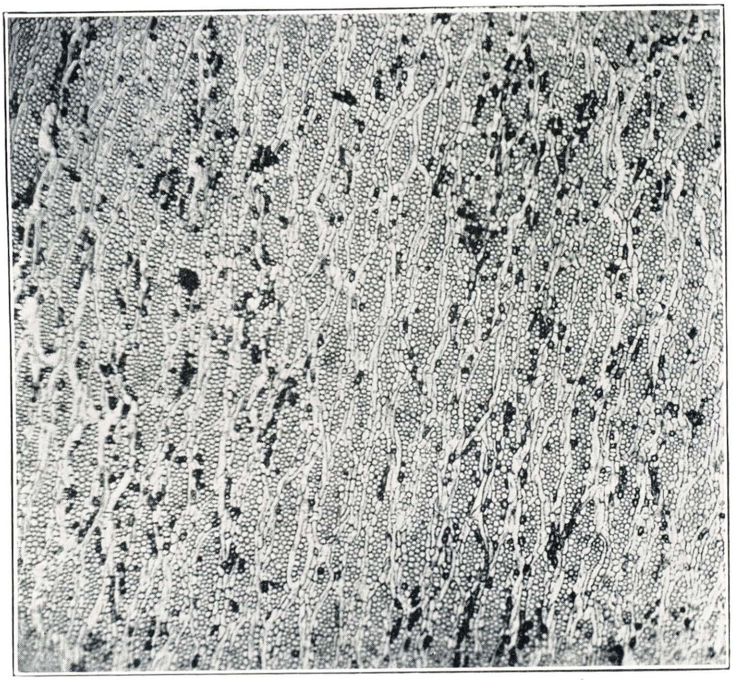


Fig. 27—Tangential view about 2.5 cm. back from tissue shown in Figure 26. Parenchymatous tissue divided apparently into aggregate rays. Vessels less conspicuous. Magnification same as for Figure 26.

bark bridge, definite strands are more promptly established, there is less wavering in direction, and the accumulation of vascular tissue at the corners of the bridge is even greater than in the longitudinal wound. If this wound, though not complete, still embraces a considerable fraction of the circumference, there is likely to be a "dead" spot at the middle of the edges, where the initial response, parenchyma formation, proceeds well enough, apparently from locally stored foods, but further developments into the vascular condition are much retarded or entirely lacking. This seems to indicate that the parenchyma is a strictly local response and that the vascular tissue is laid down with reference to general conditions. These permanently parenchymatous areas may be overlaid gradually from the sides, by invasion which is chiefly by lateral extension, or they may die and subsequently be walled over. It may possibly be significant that in these extensive transverse wounds any slight projection of the wound edge immediately becomes the focal point toward which the new vascular tissues converge.

A T-shaped wound (Fig. 31) offers special interest, since it is a combi-

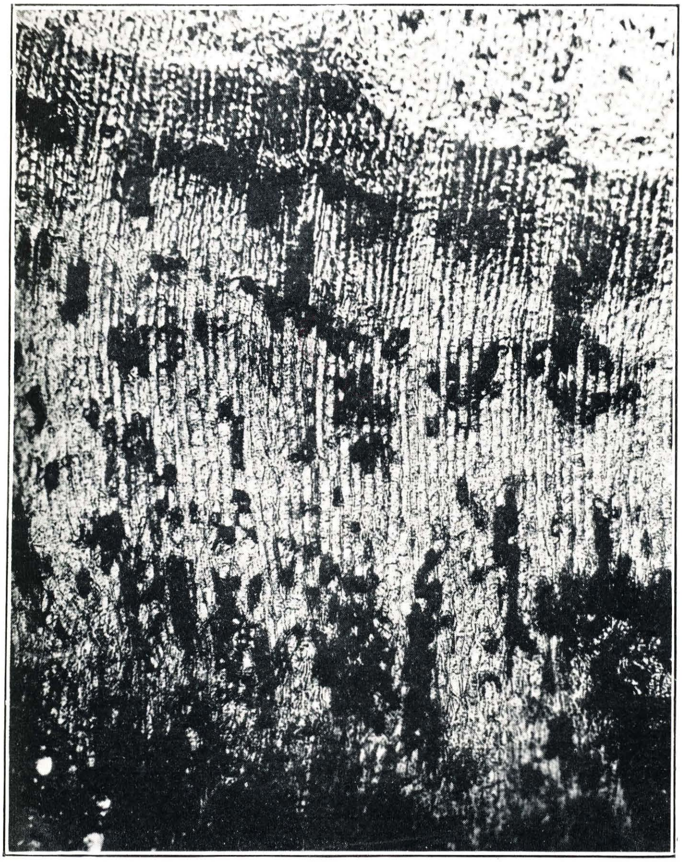


Fig. 28—Transverse view of area located similarly to that shown in Figure 27. Almost wholly vascular ray tissue. The dark-staining cells appear to be packed with granular deposit, possibly starch.

nation of longitudinal and transverse wounds and further since it has a general resemblance to the injury in the stock produced by cleft grafting. Here the general trend of reaction is similar to that set up by the transverse wound. Close under the transverse (horizontal) bar of the T, the vascular rearrangement is virtually at right angles to that existing prior to the wounding except close to the right angle, where the tissue is parenchymatous. Along the longitudinal (vertical) edge, rearrangement in direction is very quickly established; with a transverse wound of 2.5 cm. length, there is more or less realignment of vascular tissue along the vertical bar for nearly 2 cm. Vascular tissue, then, diverges downward (or converges upward) from (or to) the ends of the horizontal bar, tending to proceed in a straight line to its appropriate position on the vertical bar. The strands bend somewhat toward the right angle between the horizontal and the vertical bars, but the straight-line diagonal tendency is very pronounced. This type of rearrangement has a very important bearing on the establishment of some kinds of graft unions, as explained later.

The rearrangement of tissues in the inverted T- (⊥)-shaped wound is roughly as though a T-wound were viewed in inverted position, i. e., the vascular direction of the new tissues along the vertical bar is downward and outward toward the end of the horizontal bar.

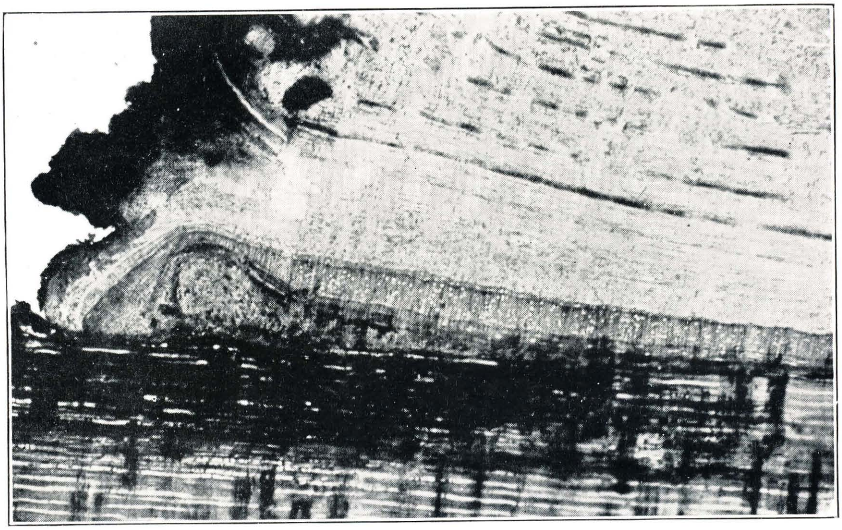


Fig. 29—Radial view near corner of lower edge of square unprotected wound. The wood formed first after wounding is parenchymatous. Later, a definite trend around the wound corner was established and the vessels in the newest annual ring are directed at right angles to those in the wood formed before the wounding.

Wounds occurring more or less frequently in the ordinary routine of orchard work fall into two classes, one in which the wood surface is exposed (as when a branch or trunk is "barked" by a wagon or tillage implement) and those in which the wood is cut transversely (pruning wounds).

Large Surface Wounds—Wounds in which large amounts of wood surface are exposed are but modifications of the simple longitudinal wound. Under very favorable conditions these may heal by regeneration of cambium and bark directly on the wood surface; under unfavorable conditions the slower process of overwalling is invoked. Actually many wounds represent a combination of the two processes; regeneration occurs where conditions are favorable and from the areas thus covered overwalling covers the remainder (Fig. 32).

Amputation Wounds—Amputation wounds, made when a lateral branch is removed, differ from the ordinary longitudinal surface wounds chiefly in the fact that the wood surface exposed is cut transversely and also in the fact that a stub of wood is left protruding. Even when the branch is cut absolutely flush with the surface of the bark there remains a stub of wood projecting from the stem cylinder for a distance equal to the thickness of the bark. Overwalling callus must surmount this before it can cover the wound surface; consequently healing of this sort of wound is, other things equal, slower than healing of a simple surface wound. Under favorable conditions a slight growth of callus advances at once from adjacent tissues for a slight distance over the wound. This parenchymatous growth is apparently produced without much reference to polarity, transpiration stream, sieve tube arrangement, or to the general balance. Vascular elements of one sort or another occasionally appear, but often they are isolated and generally they are without definite arrangement. Extensive covering must await the overwalling callus which, in large wounds, forms in definite relation to the rest of the tree and by lateral growth extends up the side of the stub and across its top (Fig. 33). If the bark is loosened in the removal of the limb, the initial parenchymatous callus is likely to form

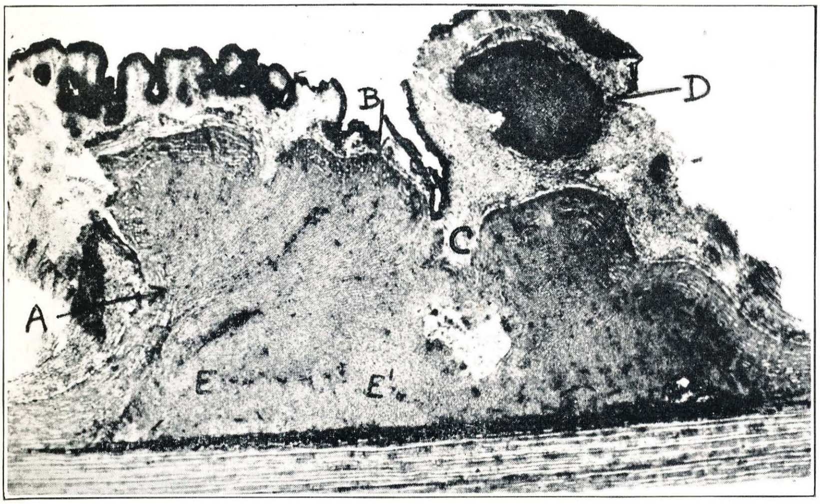


Fig. 30—An approximately radial view of a parenchymatous callus covering a ring wound about 0.6 cm. wide; made July 19; healed in same season. Wood surface uninjured; wound protected with adhesive tape. Parenchyma developed on wood surface, though the latter died subsequently; the outer line of this parenchyma is indicated by the broken dark lines (E-E[1]) similar to those shown in Figure 7. The balance of the parenchyma was developed from the cambium advancing from the wound edges. This parenchyma developed rapidly enough to outstrip cambium extension and in turn it developed a cambium of its own, as at B. The cell series from A to B are clear. This happening is analogous to that shown in Figure 8. At C the two calli met and an inclusion of new bark is plain. A wood island (D) in the new bark. Much of old bark torn away in sectioning. Upper edge of wound at left.

along the side or at the base of the stub, instead of at the edge of the cut and healing is correspondingly delayed. In any case, however, overwalling of this circular wound is accomplished by processes fundamentally the same as those involved in healing the longitudinal wound. There is the same transverse division of cambial cells, emergence of new points with changed polarity, elongation in the new direction, with, of course, corresponding changes in the cambium derivatives. That the healing is less rapid than it

Fig. 31—New tissue formed subsequent to wounding, at the right of the vertical bar and below the horizontal bar, of a T-shaped wound, made in spring. Pronounced diagonal tendency. Compare with Figures 44 and 82.

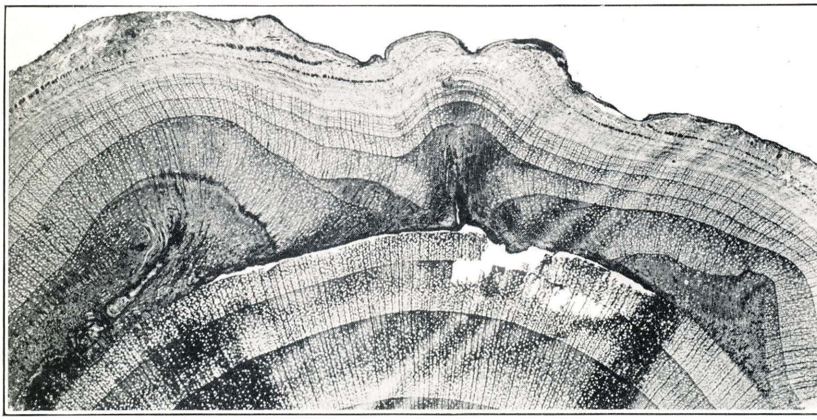


Fig. 32—Healing of surface wound on apple limb. Surface healing at edges; balance by overwalling. The diagonal light bands are due to uneven thickness of section.

is in the simple wound is due principally to the mechanical obstacle presented by the stub; once the callus edge has well surmounted this, its growth becomes more rapid and follows the same course as in the simple wound. Healing proceeds not only from the sides of the wound, but also, to some extent, from the basal end and particularly from the apical end. This, how-

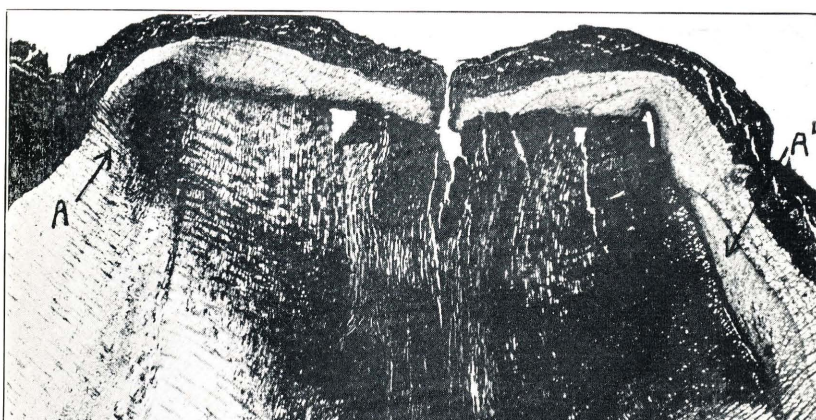


Fig. 33—Healing of pruning wound, not quite complete. Parenchymatous beginning at A and A¹. Four seasons' growth since wound made. Wound gum in branch stump.

ever, proceeds by lateral extension, and in a section transverse to the main branch the elements formed from above or below are cut longitudinally.

Decapitation Wounds—A wound made by decapitating a branch, cutting it back to a side limb, is essentially but a special case of the amputation wound. It differs from this in that the wound is larger in proportion to the bulk of tree above it—a matter which may affect rapidity of healing. It differs, too, in that the tissue readjustments on the side opposite the remaining branch may be more radical. Just to what degree cambium cells will turn has not been determined from the material examined. Neeff re-

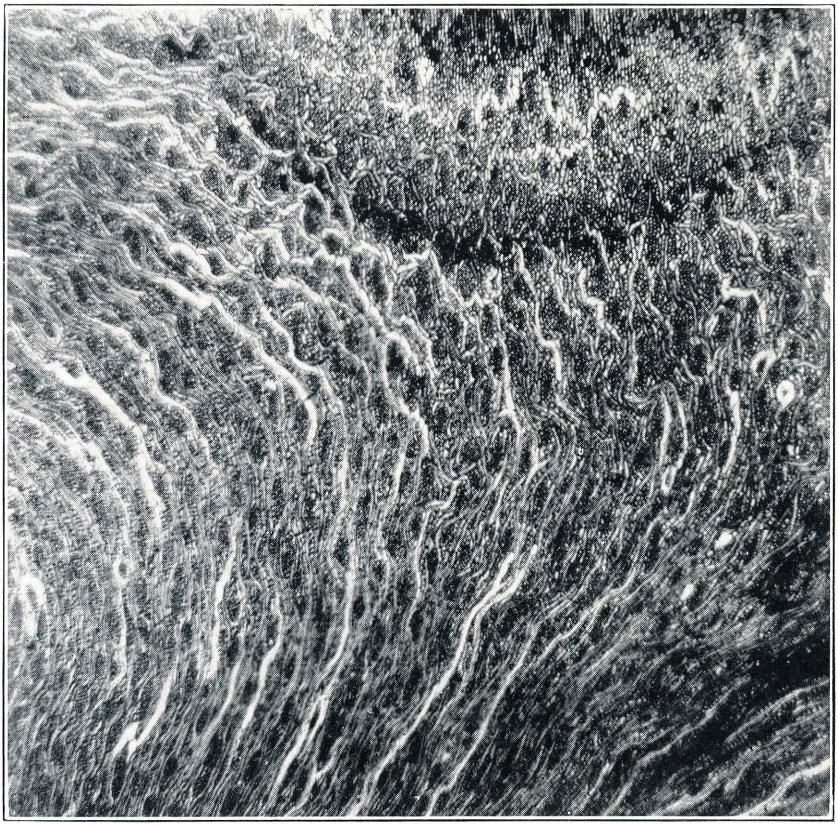


Fig. 34—Reaction in tissue adjacent to pruning wound in Baldwin apple. Tangential view of main branch, opposite a lateral which has become the leader by amputation of main branch. The section passes through two annual layers, the division being marked by the dark circular zone near the top. At the extreme upper edge appears wood formed before the wound, now well filled with wound gum. Immediately below is characteristic secondary wound wood, with little definite trend of vascular elements. The remainder is tissue formed in the second year. Here the rearrangement of vascular elements in the direction of the new leader is better established, but the vascular rays in general have preserved thir original orientation. Slower reorientation than that reported by Neeff for Tilia. This is the process invoked when cions are set in large stubs in grafting.

ports cases in which cells close to the side branch have turned 180°, but he states specifically that turning of this sort was not widespread, and the common horticultural practice of making decapitation cuts at an angle more or less parallel with the axis of the side branch sanctions the view that radical turning in tissues at some distance from the side branch cannot be extensive. That turning occurs, however, is plain enough (Figs. 34 and 35). Again the cambium cells virtually disappear into an almost homogeneous mass of parenchyma, out of which they emerge with new orientation. At the same time new vessels appear, cutting across the stem almost exactly transverse to the former direction, coursing irregularly but with a definite trend toward the new leading branch. Again the callus roll forms, more

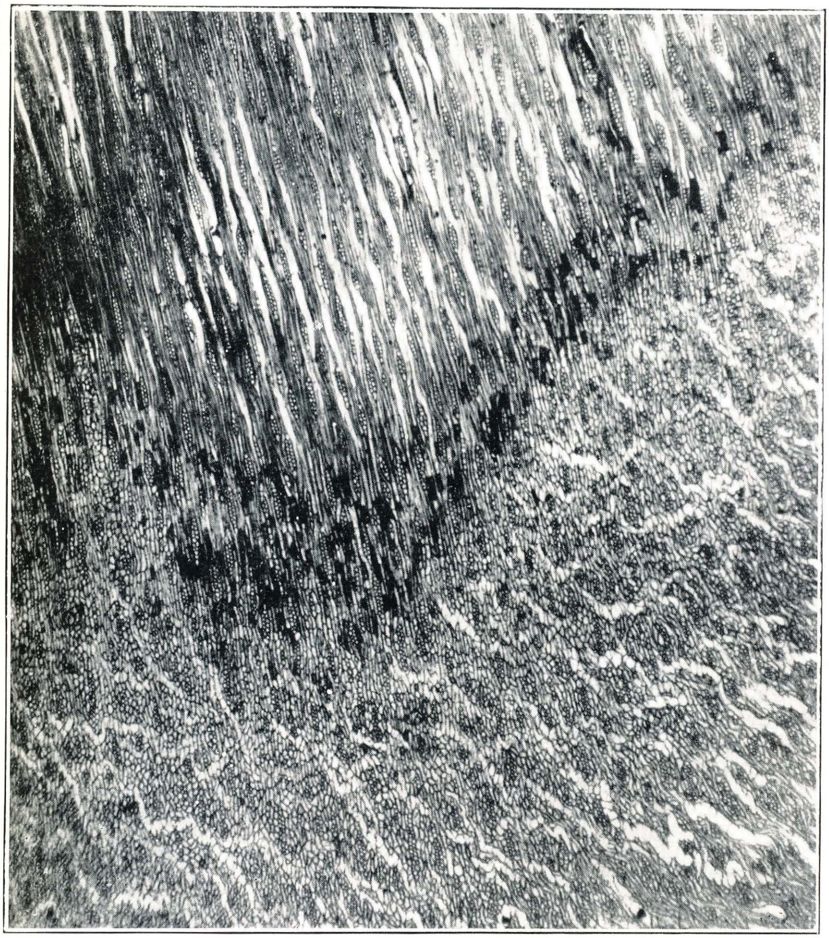


Fig. 35—The first season after amputation, with reorientation toward new leader. This was the condition at 90 degrees from the new leader. The upper portion of the section shows arrangement before the pruning was done; some wound gum appears. Careful inspection shows the vascular rays intact and unchanged, in the midst of goundwork of parenchyma. Formation of new vessels results from recombination of sub-divided cambium cells.

or less transverse to the old stem but approximately longitudinal to the new stem, which is a composite of the old main stem and the new leader. With the new direction established, healing goes on as before, by lateral extension, with perhaps a delayed start where the bark was loosened, retarded at some point by mechanical obstruction, or favored at some point by proximity to source of carbohydrate supply; a radial section through a callus does not show all vessels cut transversely. Growth from the upper edge is likely to

Fig. 36—Radial view of amputation wound, at approximately 90 degrees from leader. The wood formed before pruning and the parenchyma formed immediately after, as primary wound wood are dead. The new wood formed is almost at right angles to the old, though the rays have turned less. The apparent downward course of the rays is due in part to the section cutting them somewhat transversely, but there is very often, in wounds of this sort, an actual downward trend to these rays. The callus covering the wound by overwalling was blocked at its front by callus proceeding downward from the rim adjacent to the new leader. The irregular manner of its growth is attested by the alternation of bands cut longitudinally and those cut transversely. A successful grafted stub heals in this manner.

be more rapid and to proceed along the arc of the circle as well as toward its center (Fig. 36) and growth on the side opposite the new leader is much slower (Fig. 37). In Figure 36, where the section is very nearly radial to the new growth, the xylem rays show, as they generally do in similar cases, a slight downward trend. This may be considered as due to bark tension, since the same deflection of rays from the wound edge appears in longitudinal

Fig. 37—Approximately radial view of wound shown in Figure 36, but from the side directly opposite the new leader. Growth much less vigorous and overwalling has not even reached the rim of the stub. Higher magnification than Figure 36.

wounds (Fig. 23). This, plainly, is not indicative of the course of the vascular tissue, which converges toward the new leader, whether it must go downward, horizontally or upward.

All in all, if it be imagined that an amputation wound is made at a point where the main stem bends markedly, the picture presented is virtually the same as that found in the decapitation wound.

A decapitation wound is, then, so far as healing is concerned, essentially the same thing as the amputation wound which, in turn, is only a somewhat complicated surface wound. The healing involved in all is essentially the same. The particular interest attached to the decapitation wound arises from the fact that the cleft grafted stub is virtually a decapitation wound case.

Wounds in General—This sketch of wound healing in the apple and pear, though by no means exhaustive, illustrates amply their adaptability to various conditions. Wounds of various kinds, under various environmental conditions, are healed through the very variability which, paradoxically, enables the plants to follow one general plan and attain one end. The readi-

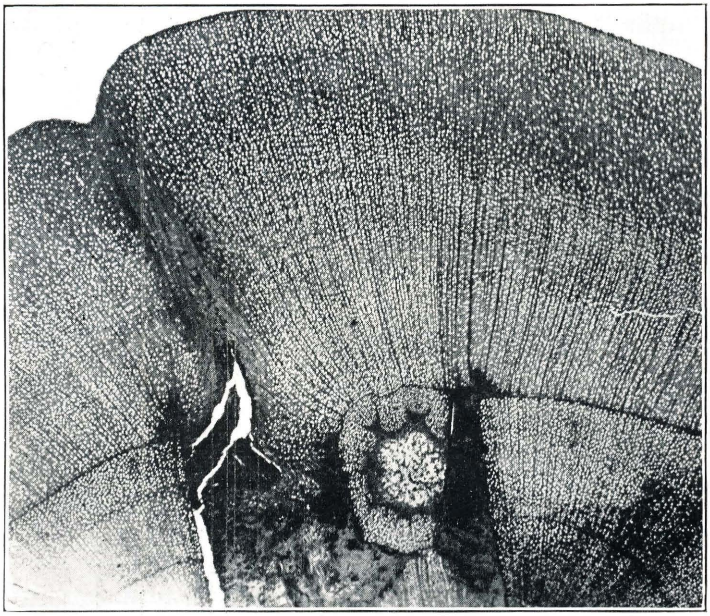


Fig. 38—This figure and the next represent an average "successful" cleft graft, in a rather small stub (apple). This section, cut close enough to the top of the stub to include wound gum (lower right), shows the difference in union tissue arising from differences in the space to be bridged. On the right, normal conditions quickly established; on the left, not altogether normal at the end of the year.

ness of transformation of cambium to parenchyma and of formation of cambium in parenchyma is perhaps the key to this adaptability, along with the richness of formation and comparative self-sufficiency of parenchyma. The effect of pressure is important. Other matters seem to be more or less incidental and symptomatic of varied conditions under which the essential processes work. Distinction between the fundamental and the incidental in unions of tissue where incompatability is eliminated can be applied profitably to appraisal of tissue variations in grafts involving unions of tissue from different individuals.

UNIONS KNOWN TO BE CONGENIAL

Grafting is essentially the removal of a piece of plant tissue to a new location, generally, but not necessarily, on another plant, and placing it so that wound healing may ensue. Since the cion is limited in its capacity for independent life, this healing process must be comparatively rapid. Prompt healing is secured by placing the cion in such position that its cambium is close to that of the stock and there is no obstruction to the union of tissues. Almost at once—Herse says even before general cambial activity begins—in both stock and cion typical reactions set in, very much the same as in ordinary longitudinal wounds. From the cut edge of the cambium of the stock, parenchymatous cells develop rapidly, pushing outward radially and tangentially, and meet a similar outpouring of parenchymatous cells from the cambium of the cion. If these tissues meet squarely, the course of further

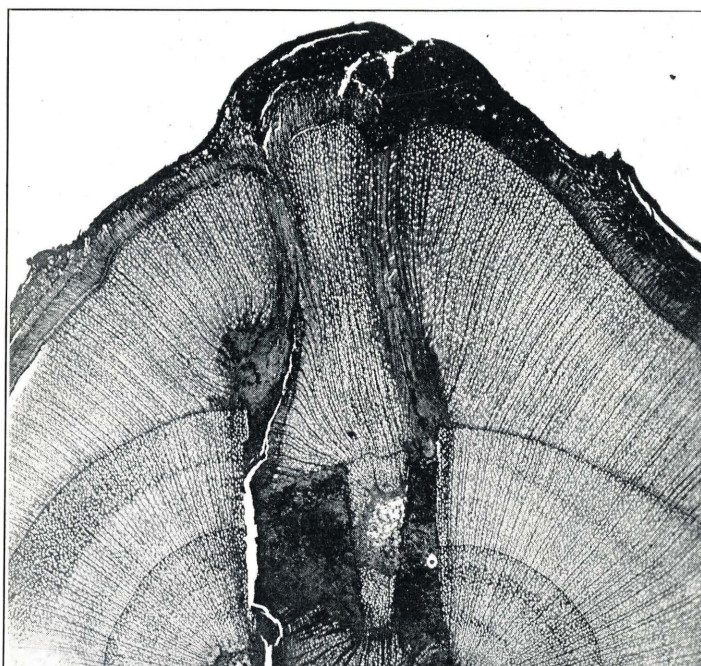


Fig. 39—Lower level than section shown in Figure 38, as indicated by difference in size of cion. On the right the space between stock and cion is as in Figure 38, but improper alignment increases the distance between cambium edges, with resultant persistence of parenchymatous union zone. The decreased width of the cleft brings cambium edges closer on the left than in Figure 38 and, despite the formation of bark on the cion before uniting, the union is, on the whole, as good as that shown at the left in Figure 38.

development is diverted to a more nearly radial direction. Some of the parenchymatous tissue pushes into the space between stock and cion (into the cleft in cleft grafting) where it becomes a negligible factor, for a time at least, except as it functions temporarily for water conduction. The tissue pushing radially outward, however, becomes the zone of union.

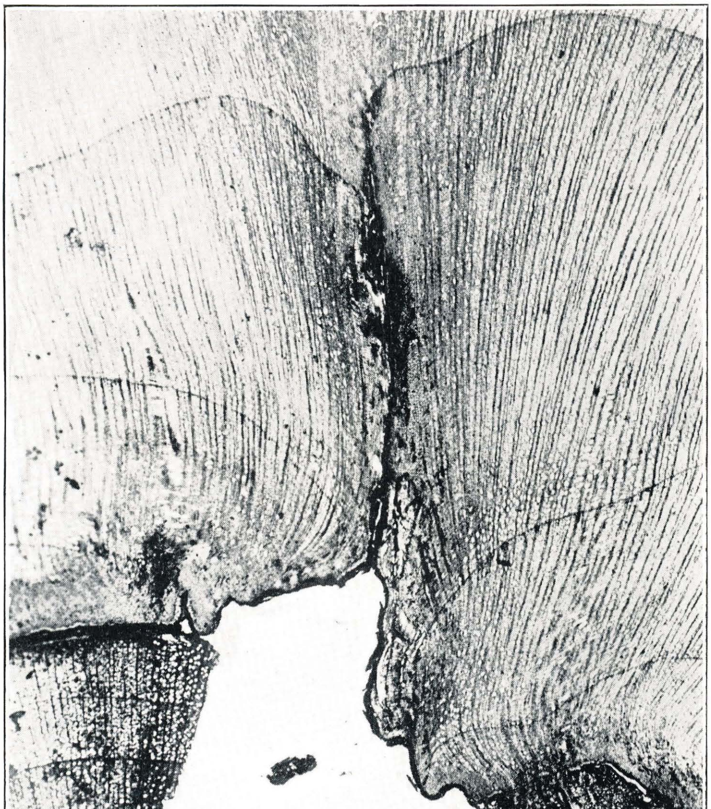


Fig. 40—A cleft graft in which no cion was set in one end of the cleft. Lower center is callus pushing through the cleft from the cion. Overwalling calli of the stock met in the third year, but corky surface (black line in center) and insufficient pressure prevented union until fourth year. More or less parenchyma at callus edges at all times. However, congeniality cannot be a factor here.

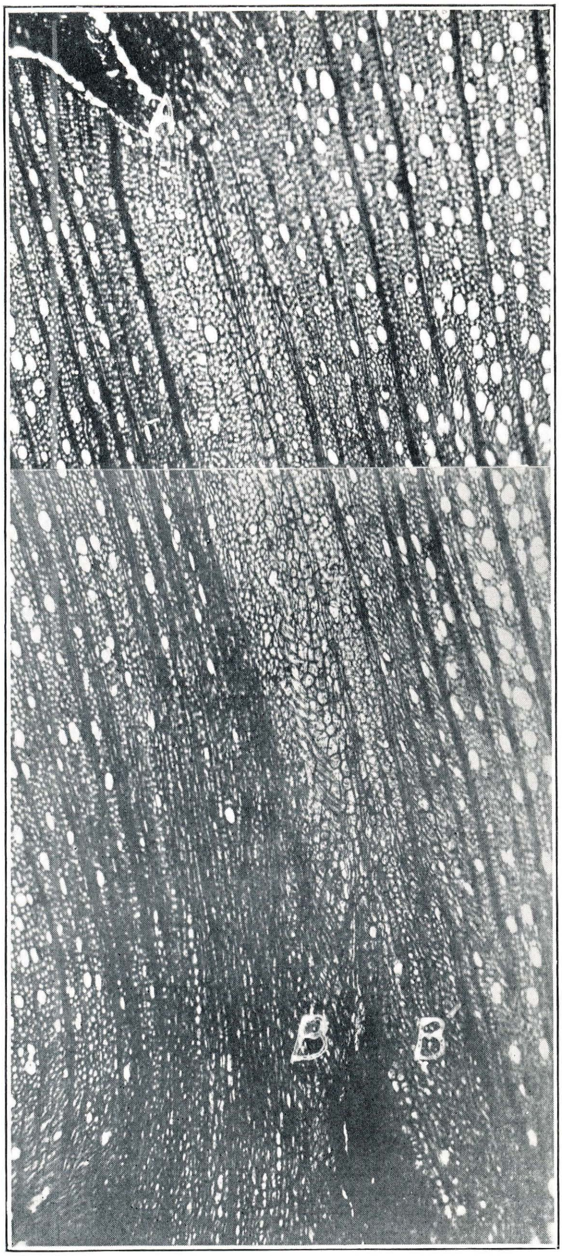
The Parenchymatous Zone—It will be recalled that, in healing of wounds, union occurs first in a zone of parenchymatous tissue which becomes gradually cut up by tracheids, vessels and fibers and finally disappears. The same procedure is followed in the healing of artificial graft unions. If the fit of stock and cion is particularly close, the zone is very limited in extent and quickly disappears (Fig. 38). In a large proportion of grafts, however, it may be traced for some distance, particularly in cases in which the cambium layers have not been well matched (Figs. 38 and 39). This is one of the conditions producing the "greenish" zone noted by Goeppert, as marking to the unaided eye the line of union.

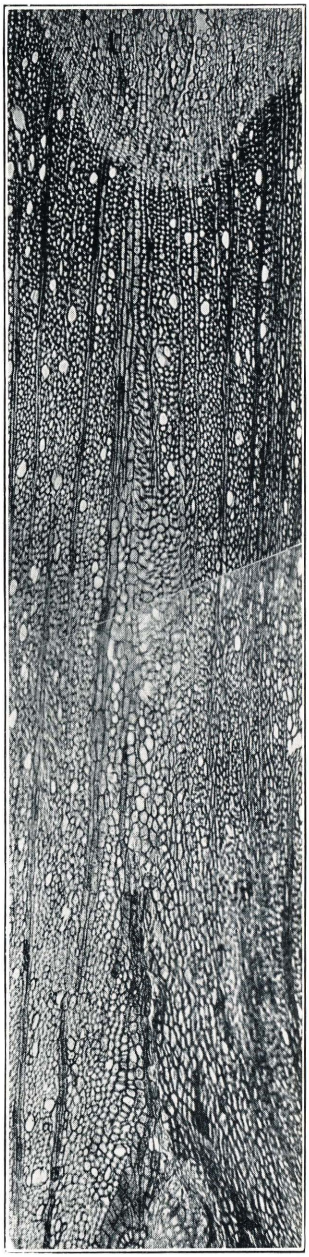
With no cion in the way, the two wound edges of the stock would extend tangentially, partly by more or less of radial expansion and partly by the regular overwalling process (Fig. 40). With the cion intervening, this process is limited in realization by the presence of cion tissue with its own expansion propensities; nevertheless the tendency is always present. The zone of parenchymatous tissue is therefore subjected to no little pressure and it is subject to invasion by occasional strands from stock and from cion. Cambium union apparently takes place with the cambium cells still isodiametric, as they have been shown to be in the neighborhood of all wounds, and parenchymatous tissue is still the result of its activities. This appears to be the prevalent conditions in unions of splice grafts, as described by Herse. As in other cases, however, tangential (lateral) pressure ultimately sets in and the cambium products increasingly assume normal character. The parenchymatous zone does not bear striking resemblance to vascular ray tissue at the outset, but it increasingly assumes that appearance, and, indeed, the last distinguishable remnant of it is sometimes an aggregate ray of greater width than the adjacent rays, double in a region of uniseriate and triple in a region of bi-seriate rays.

This process may be traced very readily in Figures 41, 42, 43, which represent two magnifications of the same or neighboring sections. Preparations showing higher levels of the union presented a much smoother union on one side (Fig. 38) due to better placing of the cion and to its larger size, leaving less space between stock and cion. The views shown here represent conditions where the union was not formed immediately, as appears in Figure 39. The cion obviously had time for some little expansion on the left in a tangential direction before it received a check from meeting the callus from the stock. Here growth came to a definite stop, after turning radially inward in the direction of slighter pressure, and the first ray to succeed in making its way outward can be traced to its origin well away from the cut edge of the cion. Before this could happen, the bark had to be torn apart, as in the natural graft.

The callus from the stock shows, in turn, the effect of pressure from the cion. Apparently it was extending tangentially (laterally) across the cleft, when it met the new growth from the cion and was pushed outward, producing a rough approximation to the "bush" appearance already noted (Fig. 8). The tangential impulse continued, however, and finally produced union, through the parenchymatous zone, with the cion.

Initial Effect of Cion on Stock—The presence of the cion makes one important difference between the initial healing of a simple wound and that of the graft. If, as has been shown, a T-shaped piece of bark is removed from a branch, the first definite vascular trend to be established in tissues





Figs. 41 and 42—These present details of union in series shown in Figures 38 and 39. In Figure 41 the tissues of stock and cion appear to join in a common vascular ray A to BB[1]; in Figure 42 the union is at the right of the ray. In both the preponderance of wood parenchyma cells and the scarcity of vessels, in the union zone, are clear. These pictures are reductions of large pictures, taken in sections and matched.

along the upright (longitudinal) bar of the T is in the general direction of the ends of the horizontal (transverse) bar of the T. With a cion inserted in the cleft, however, the trend is upward in the opposite transverse direction, i. e., toward the cion. This is essentially the same as that shown in a somewhat advanced stage in Figure 44. In general, however, it would

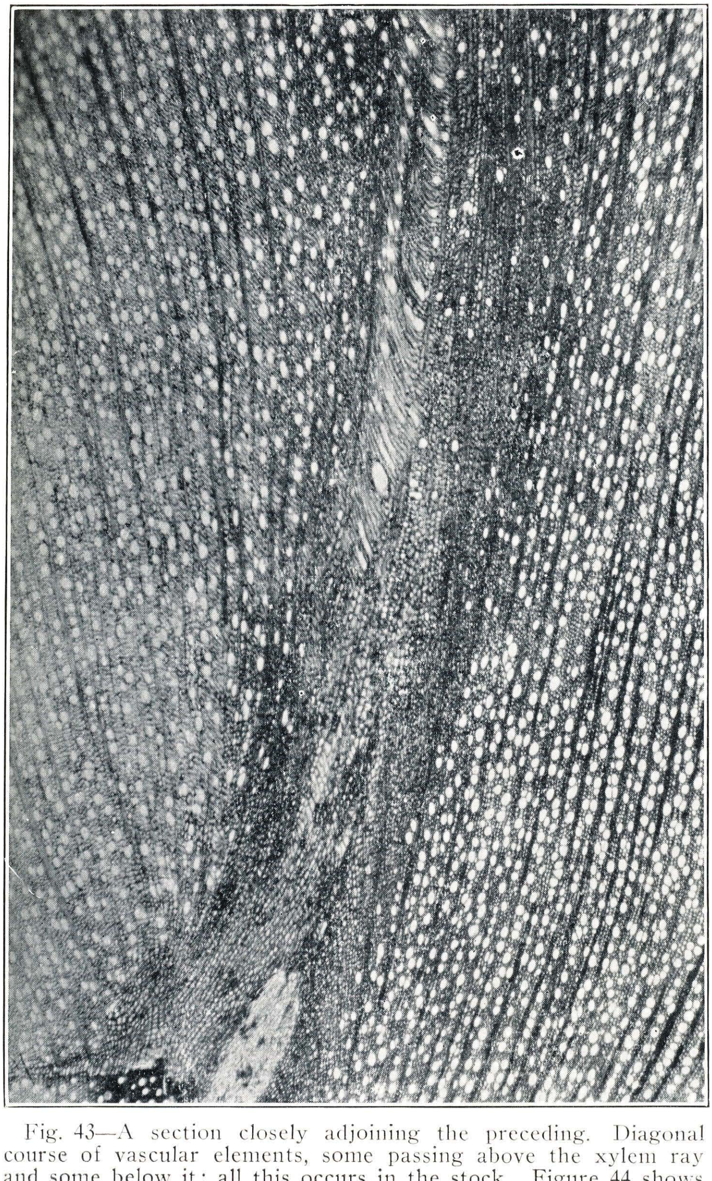


Fig. 43—A section closely adjoining the preceding. Diagonal course of vascular elements, some passing above the xylem ray and some below it; all this occurs in the stock. Figure 44 shows the same condition, viewed in another plane.

appear that the cion itself is the more active agent in actual bridging of the parenchymatous zone and the peculiar turning of the vascular elements of the stock is affected in some degree by the continuity of the parenchyma connecting stock and cion; certainly the turning begins with no connection between stock and cion other than parenchymatous. This coincides with observations on numerous specimens of wounds, indicating that in reorientation of tissues the transpiration stream—or polarity—is the decisive factor in direction determination.

Variations in Union—Differences in detail of healing, depending partly on closeness of fit and partly on conditions at adjoining points, appear

Fig. 44—A cleft grafted stock after the cion was pulled out. The cion influence is evident in the changed orientation of tissue, in contrast with that shown in Figure 31.

in the series shown in Figures 45, 46, 47, 48, 49. These pictures were all taken from the same graft, Figures 45, 46 and 49 being taken at one side of the cion and Figures 47 and 48 at the other. Union was established quickly at the rim of the stock on both sides and very readily along the right side; in fact it had reached the stages shown in these pictures before there was any vascular connection on the left except at the rim. In Figures 45 and 46 the callus from the stock had extended so far that the xylem rays are cut almost radially. Figure 45 shows the union of parenchymatous outgrowths, forming a continuous parenchymatous zone; Figure 46 shows an early stage of cutting of this into rays by vascular strands from the cion, before vascular bridges are established. In this particular specimen, vascular union was established first at the rim of the stock, then at the base of the cion and later at an intermediate point (Fig. 47). Other bridges followed, but most of the final union was established by expansion of the first-established, rather than by continued formation of new, bridges. From this point on, development followed the course indicated by Figures 47 and 48 and in the second year after grafting the only trace by which the location of the union could be determined was a poorly defined series of very small knurls.

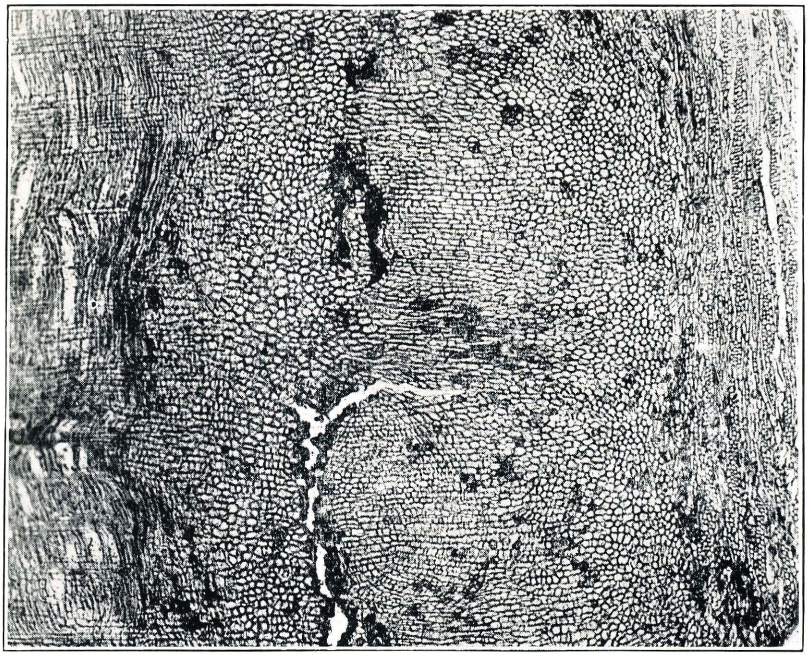


Fig. 45—This and the three succeeding figures form a series of tangential views of the parenchymatous wound zone in a cleft graft. They are from substantially the same sections, the first two being taken from one side of the cion where the wound zone is wide and the last two from the other side of the cion where the fit was closer and union established more quickly. In the first two the cion is at the right; in the third and fourth it is at the left. In the first two an overwalling callus has developed on the stock, as shown by the radial cutting of the xylem rays. Figure 45 depicts the initial stage of contact, purely parenchymatous.

The greater the space to be bridged, the greater is the tendency of the vascular bridges toward horizontal circumferential growth. A transverse view of a region where this is occurring is shown in Fig. 43. Here the vascular bridge crosses above one ray for a space, and then below it. It should be added, however, that this condition is not confined to graft unions but may occur, apparently, wherever radical changes in growth direction are occurring.

Union of Bark—Union of bark between stock and cion usually presents little difficulty. Sometimes, just as in wound unions, there is growth of parenchymatous nature from the cortical regions, establishing a union between stock and cion. Whether this is established or not, new bark is formed as soon as the cambium layers unite; for a time the tissue is more or less parenchymatous as is the tissue inside the cambium, but phloem formation seems to begin concurrently with the appearance of vascular xylem at the point of union.

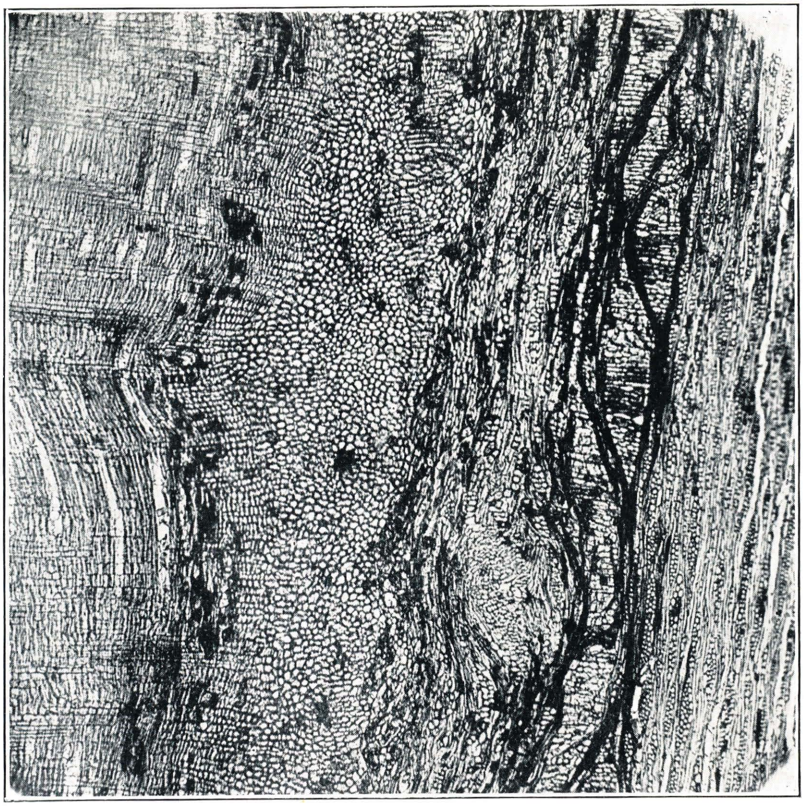


Fig. 46—Tracheids cutting through parenchyma, mostly from cion (at right). Cion presents appearance of secondary wound wood, resembling Figure 27.

Covering of Stub—Another very important detail of graft unions, the covering over of the stub of the stock, is discussed on a later page. This is principally a matter of growth relations, essentially quite distinct from matters of congeniality. So far as concerns union by grafting, in congenial plant material, it is virtually the same process as that by which an amputation wound is finally healed. With slight exceptions, nothing has been observed in the one that has not been observed in the other.

Shield Bud Unions—The union accomplished by shield budding varies with the amount of wood taken with the shield. When any considerable amount of wood is present, as in chip-budding or even in some shield bud insertions, the union may be regarded as a graft. This condition is presented by the inlay graft described on a later page. As to unions with no wood in the shield, previous published accounts, and the preparations examined in this study, agree in presenting the union as established through

Fig. 47—Vascular bridges established and some crossing between bridges, the initial stage of restoration of longitudinal coursing. Parenchyma being rapidly cut into aggregate rays. Some vessels in vascular bridge. Cion at left.

parenchyma given off from stock meristematic xylem and shield cambium. The width of this zone varies widely, apparently in accord with the force with which the shield is pressed against the stock; the parenchyma has every appearance of the normally formed wound reaction tissue already described. Following union by parenchyma, normal xylem may or may not be formed by the shield cambium in the same season.

Beyond—in a lateral sense—the edge of the inserted shield, typical wound reaction xylem forms on the stock, parenchymatous under the corners of the raised bark flaps, well organized near the shield. This unites so smoothly with the shield that the line of union is not always obvious and the unwary may easily consider the union to be along the tissues growing from the bark-flap, when in reality it is often some distance inside. In other words, wound reaction xylem of the type shown in Figure 10 may push up from the wood surface of the stock, between the bark flap and the shield. An

Fig. 48—More advanced stage. Knurls developing. Cion at left.

extreme case of this growth is shown in Figures 8 and 50, which depict a stock on which the shield failed to unite.

The prominence of parenchyma in the cases described seems to be greater than that found by Proebsting (31) in unions of *Prunus domestica* on *P. cerasifera*. His statement that "the cambium cells of the scion have formed medullary rays cells if they were in contact with ray cells, and xylem elements if they were in contact with xylem elements" seems to imply the absence of parenchymatous tissue at the union. No apple or pear material examined in these studies showed union without more or less parenchyma intervening. Parenchyma plainly cannot be regarded as *per se* a symbol of uncongeniality in the pear and the apple, since it occurred in grafts which had made excellent subsequent growth and in wounds made by lifting the bark, which involved no question of congeniality. This does not mean, however, that unusual amounts of parenchyma may not be present in bud unions that are not wholly congenial.

Correspondence of ray cells on stock and cion in bud unions is apparent

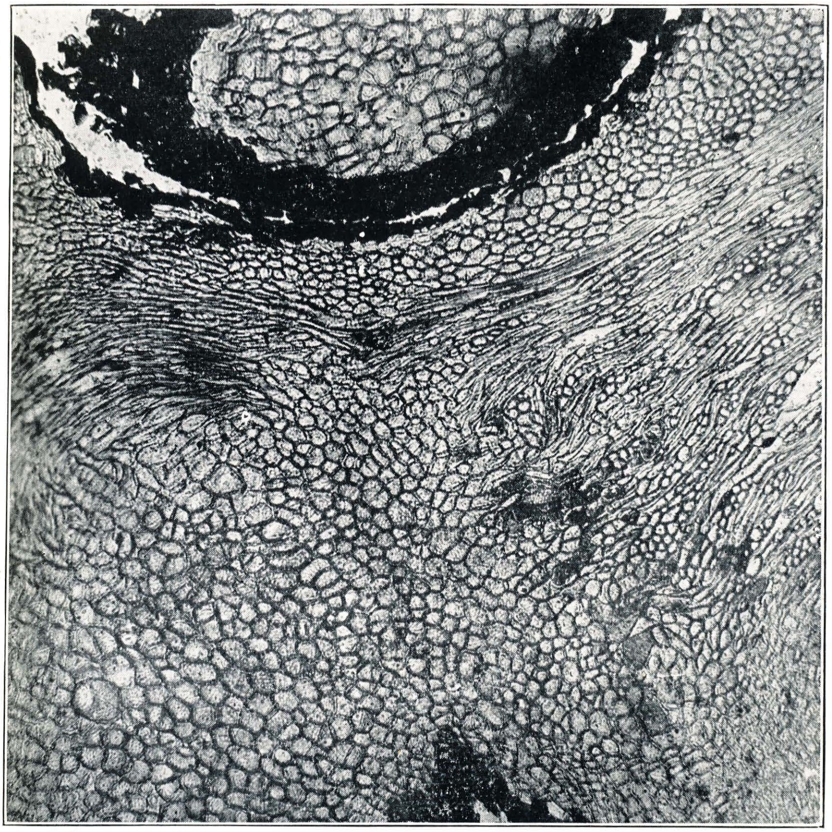


Fig. 49—First vascular connection between stock and cion. Cion on right. Higher magnification of a stage somewhat succeeding that shown in Figure 45.

frequently, but by no means constantly. Though the cases of such correspondence may exceed the frequency established by rigid mathematical calculation of the laws of chance, it must not be overlooked that parenchyma develops more rapidly from the ray cells, and expands as it develops, so that it occupies the most advanced position in, and an undue proportion of, the callus surface (Fig. 9). The chance of ray parenchyma meeting ray parenchyma is therefore great. It is, then, but natural that a considerable number of rays should exhibit some continuity, even though in the ma-

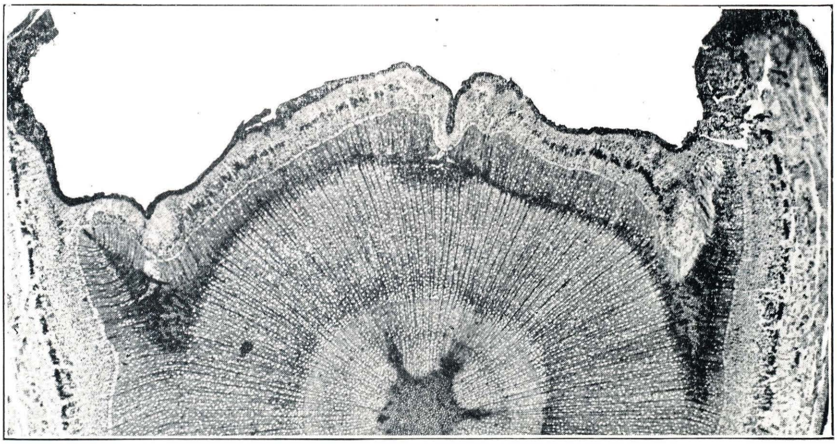


Fig. 50—Pear stock on which an inserted shield bud failed to unite, and all tissue shown is derived from the surface of the stock. Ray continuity is virtually perfect here.

jority of cases it is not a straight line continuity, and though the bending which maintains it is not always in the same direction, as would be the case in tissue developing under lateral tension. Ray continuity is naturally more abundant, or more obvious, in unions in which parenchyma development is slight, but it appears to be no more significant than that, in the apple and the pear.

Graft Unions in General—In general, perhaps the most striking and significant—for purposes of the present discussion—characteristic of a "normal" graft union, as it is of wound unions, is the variability of methods

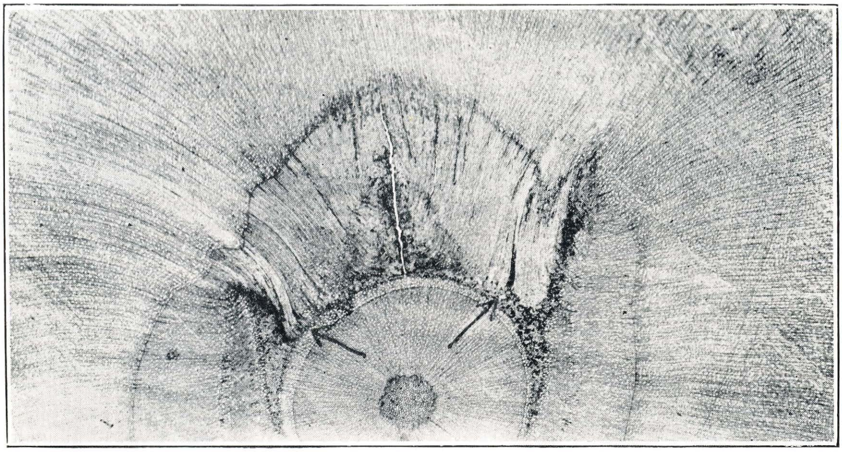


Fig. 51—Bud union of apple on apple, from first grade nursery stock. Union is well within the bark flaps, at points indicated by arrows on figure. This is the common condition.

by which the same ultimate end—union—is accomplished. Since graft unions are more uniformly protected from atmospheric influences than wounds and since the surfaces are more uniformly prepared for union in grafts than in wounds, the chief sources of variation are somewhat different. In graft unions the exactness of fit between stock and cion is the chief factor underlying variation in union processes. Within limits, the difficulties and disturbances arising from poor fit are gradually overcome. Whether some fits can be both good enough to permit the cion to grow and poor enough to prevent restoration of normal conditions, is still to be discussed. First, however, cases of admittedly uncongenial grafts claim consideration.

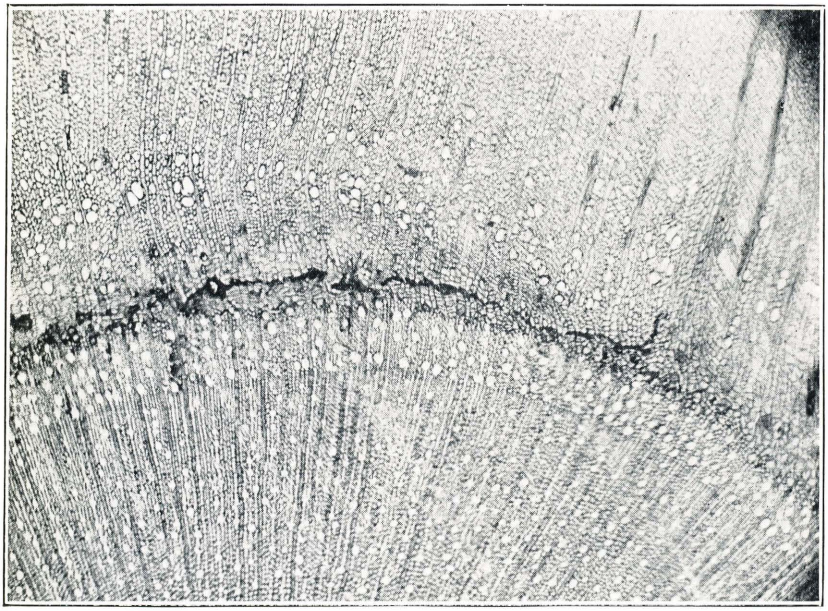


Fig. 52—A detail from Figure 51, showing development of parenchyma, even in a most successful union.

UNIONS KNOWN TO BE UNCONGENIAL

Between a study of graft unions known to be uncongenial and a study of graft unions where congeniality is plainly not a factor, some light should be thrown on cases where uncongeniality is suspected.

Proebsting (30) has reported on uncongeniality as observed in one-year-old nursery trees involving numerous interspecific grafts of Pyrus. His statement is to the effect that in the weak unions there is a double layer of bark with corky tissue of indeterminate origin between them, the bark being in each case characteristic of the species. The layer of bark "extends nearly to the point at which the cambium layers * * * were placed in contact at the time the graft was made * * *. It would appear that soon after growth had started, the region of the cambium which lay at the line of union ceased to function. As growth continued above and below, a layer of bark was laid down by the cambiums of both stock and scion. The result is a formation closely resembling in its final condition that described by MacDaniels in narrow crotches. The layer of bark pinched between the xylem on either side forms a line of mechanical weakness. It is doubtful whether such a union would survive the second season, when a larger leaf surface would provide a greater resistance to wind movement and place a greater strain on the union."

This statement provides characteristics sufficient for identification of uncongeniality, but since the cases which occasioned this present study have

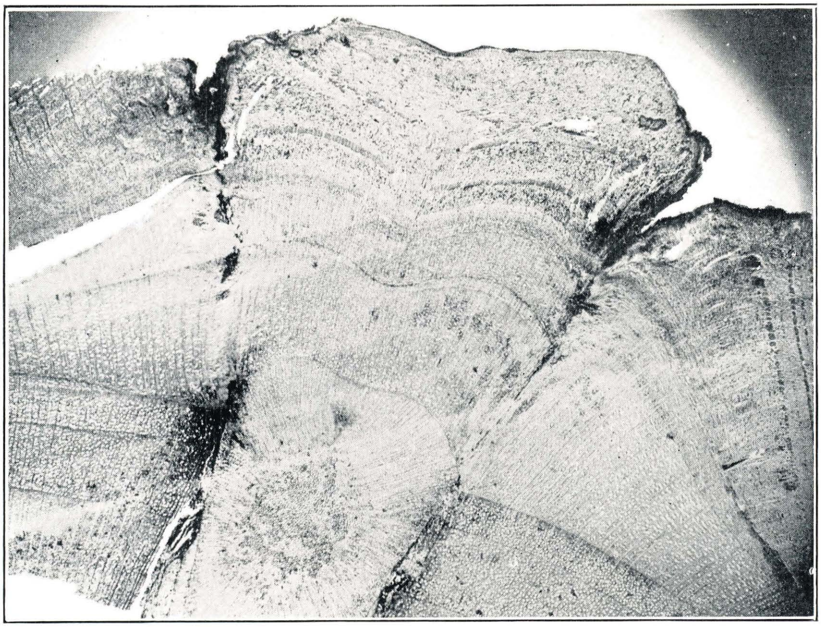


Fig. 53—Cleft graft, pear on apple. Third season after grafting. Union established and broken several times.

persisted for several years it seems desirable to set forth conditions in grafts which, though admittedly uncongenial, live for an indefinite term of years.

Pear On Apple

Gross Appearance—The graft of pear on apple used in this study was of Bartlett upon Tolman Sweet, a variety which has been reported occasionally as a better stock for pears than most apple varieties. The cions were set in branches about one and one-half inches wide, in a tree about 35 years old. Of cions set in eight or ten stubs, only one grew; this made 19 inches of growth the first year, about one inch in the second and when cut, in June, 1927, it had completed its growth for the year at about one-half inch. In the third season it had blossomed, but set no fruit; whether it would have survived to the next season is questionable. Externally it presented no evidence of difference from other grafts, aside from the marked decrease in vigor.

Fig. 54—Pear (lower left) on apple (lower right). Vascular bridge established very early, but inordinate number of cells have deposits of one kind or another. Breakdown visible at top.

General Internal Conditions—Internally this union (Fig. 53) presented marked differences from that of apple on apple (Figs. 38 and 39). Instead of starting poorly and becoming better, it started well and became worse, as Proebsting (30) has reported of other uncongenial combinations. At various levels it presented strikingly different appearances, but these variations in detail seem throughout to be but varied manifestations of the same

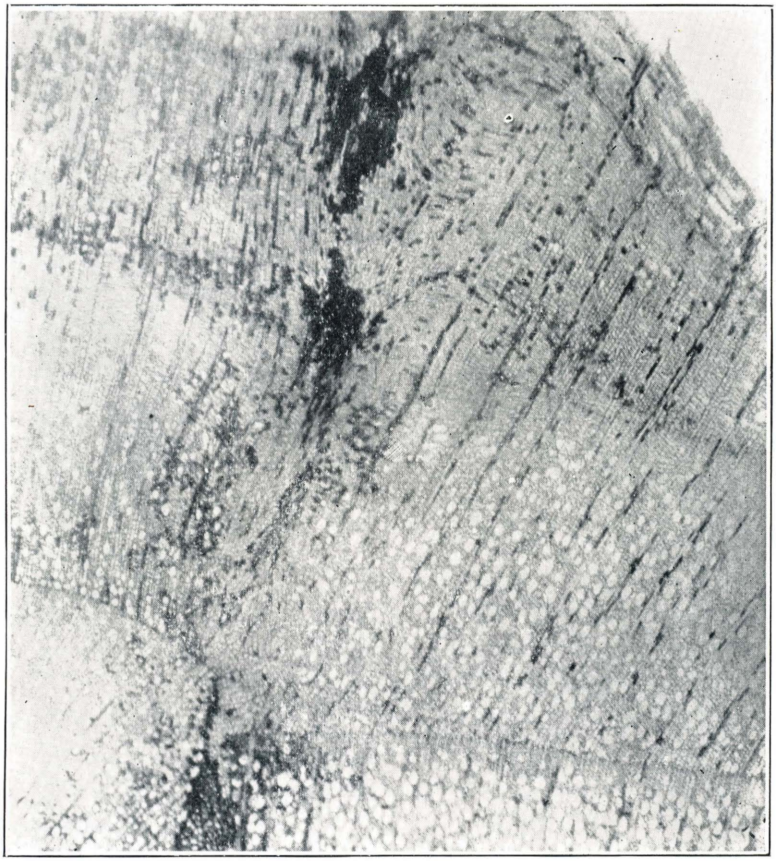


Fig. 55—Cleft graft, pear (left) on apple. Disturbance as shown by deposits extends to some distance from union line. Union entirely parenchymatous, both in first and second years.

underlying tendency. A quasi-union, varying from formation of parenchymatous zone to establishment of vascular bridge (Fig. 54) occurred soon after growth started. In one form or another, this persists to the end of the first year. In the parenchymal unions growth lags behind that on either side. This is, however, not in itself a symptom of uncongeniality, since it occurs in ordinary grafts and even in normal wood of red oak, where the contour of the annual ring is markedly depressed by the slow growth of the large wood rays (20). The difference between uncongenial and congenial grafts is not the slow growth at the union, but in a condition developing after most or all of the growth for the year is completed, or sometimes possibly not until spring. In congenial unions, growth resumes in the following spring in the depressed area and with the gradual narrowing of the parenchymal area the annual ring presents a uniform contour. In the pear-apple graft, normal growth ordinarily does not resume at

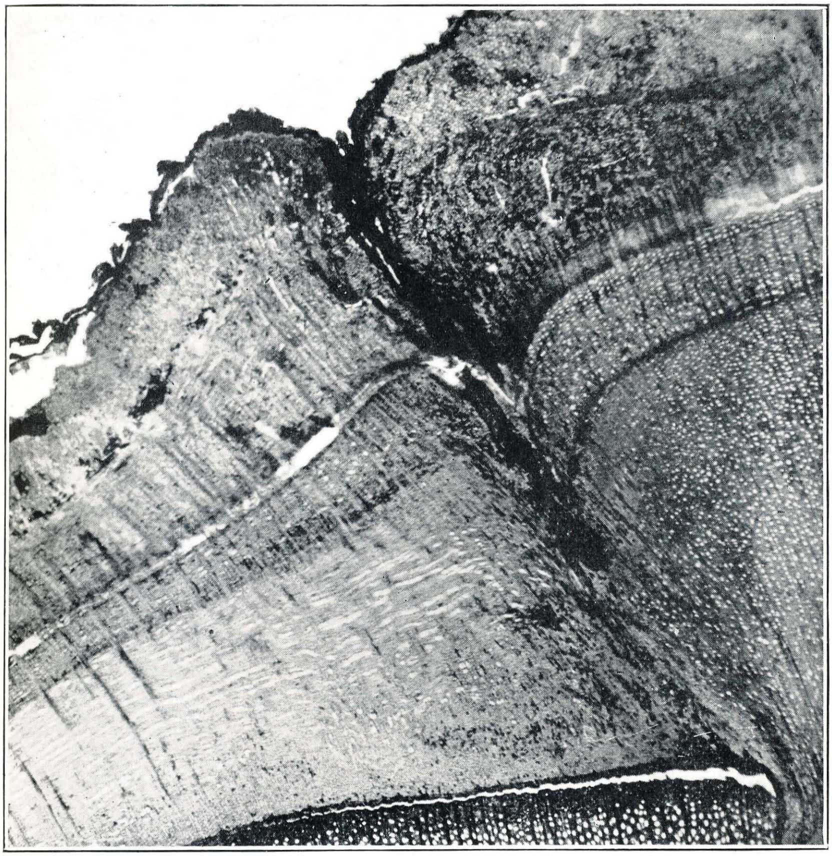


Fig. 56—Pear (right) on apple, near the top of the stub, as shown by the transverse course of the vessels in the stock. No connection between stock and cion after first year. In this case the inclusion is clearly bark. No connection in bark between stock and cion at any time.

the union but at either side. Either before or after this failure, probably afterward, some of the tissue at the union, both parenchymatous and vascular, dies. This happens even in comparatively well established unions (Figs. 58 and 59). The new tissue is invariably parenchymatous and in some cases presents essentially a new graft union; in others even the parenchymatous union is of short duration. Vasular bridges are very rare in the second annual ring and most preparations show no connection whatever (Fig. 56). Henceforth the picture presented by this union is that of two masses of tissue growing side by side, but with virtually no connection except through older annual rings. At the edge, each bears striking resemblance

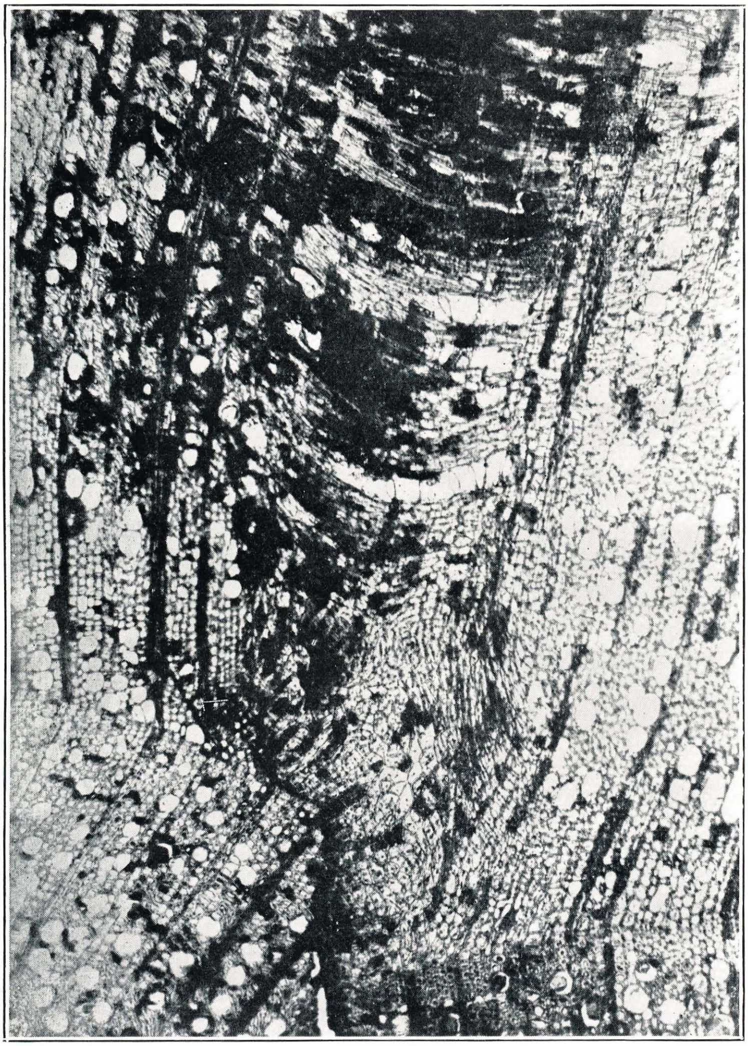


Fig. 57—Pear (left) on apple. Vascular connection well established, but much impaired by deposits, apparently of wound gum.

to overwalling callus advancing over a wound surface (Fig. 15) leaving some cortical and some wound parenchyma along its edge. The zone of parenchymatous cells is generally wider on the apple side of the union than on the pear. This, of course, is another way of stating that the organized wood comes closer to the union in the pear than it does in the apple; whether the condition is inherent in the two materials or is due to their relative positions, cannot be stated. In many places two triple plates of suberized, cortical and wood parenchyma tissue, are left between the cion and stock as they advance. In other places the inclusions are composed of parenchyma

Fig. 58—Pear (right) on apple. Vascular connection established in first year. Much of this subsequently involved in wound gum deposit. Wood of next year largely parenchymatous, as in the neighborhood of wound; no vascular connection after first year.

only, pinched out as such tissues are in ordinary wound unions, notably in the natural graft. They differ, however, in that they occur after union has reached a more advanced stage than thas been observed accompanying pinching out in wounds.

First Year—Conditions in the wound zone in the first annual ring present some peculiarities. Strands of large short vessels sometimes appear strikingly early in the season (Fig. 57). In all cases where vascular bridges were established, they tend markedly toward a position transverse to the diameter, in strong contrast to the prevalent condition in apple grafts presenting the same alignment of cambium in stock and cion.

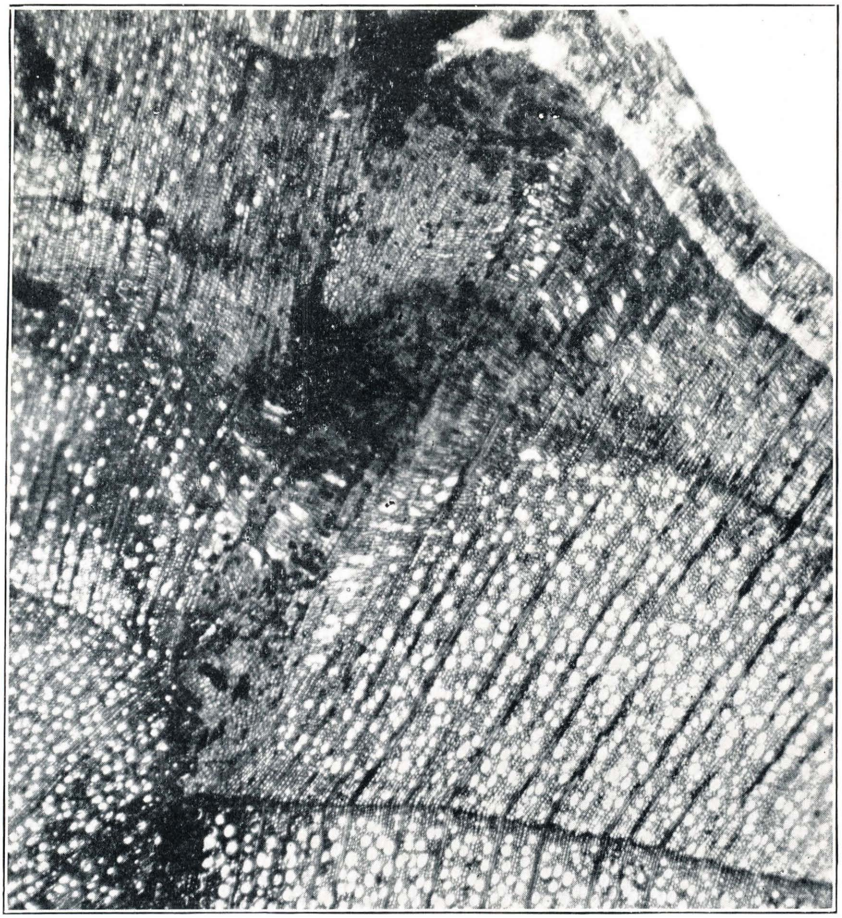


Fig. 59—Pear (left) on apple. Much like Figure 58, except that union resumed in second year, but only parenchymatous, in contrast to vascular stage attained in first year.

Tissue Modifications—Another striking contrast to the congenial graft lies in the great number of cells, both parenchymatous and vascular, containing precipitates, apparently of various kinds. These cells occur not only in the immediate neighborhood of the union but at considerable distances from it. Similar appearances are sometimes presented near wounds which have not healed readily and they are to be regarded, not as producing the uncongeniality, but rather as produced by it. Wound gum occurred in these unions, but has been found in apple tissues where grafting or wounding in the ordinary sense, was not a factor, as, for example, in three-year-old galls. The junior author has found wound gum in black walnut in wood formed after grafts were set, apparently without any question of uncongeniality being involved. It would seem, therefore, that, under some circumstances wound gum may be, as well as a wound reaction, a symptom of surfeit or of starvation, consequent upon disturbance of the normal transpiration stream.

Xylem rays are frequently the scene of much disturbance, the deposit generally having a granular appearance. Parenchymatous cells, singly and in groups, likewise are affected, in some cases suggesting starch accumulation, in others suberization and death, though the cell still appears to have preserved its normal contour. No microchemical studies were attempted with this tissue and nothing further can be said about it other than that it seems to differ in degree rather than in kind from tissue in the neighborhood of wounds which are not healing readily and it seems to be an effect rather than a cause of other disturbance.

In general it may be said that the cion tissues not in close proximity to the wound have a rather striking resemblance to tissue at some distance above a ring wound. At spots the rays are merely increased in diameter; at other spots the number of rays is rather considerably increased.

Bark—The statement of cambium behavior renders almost superfluous the report that bark continuity is extremely rare at any stage. In one or two preparations there was some union in bark between stock and cion, but it had occurred in the cortex shortly after the initial grafting and in no case in this pear-apple union was anything approaching phloem continuity observed.

Pear On Quince

In the union of pear on quince, various degrees of congeniality and uncongeniality are commonly recognized in the practice of double-working, which utilizes a congenial variety to make contact with the quince and to serve in turn as stock for the uncongenial variety whose fruit is desired. Double-working of this sort is often practiced in growing dwarf Bartlett pears; many trees of this variety, however, are worked directly on the quince.

Gross Appearance—Material for this study was taken from Bartlett, budded directly on quince of unknown origin. The use of budded material does not preclude comparison with grafted, since, after the initial union, further development is essentially the same in grafted and in budded material. The trees were eight or nine years old from the bud; they had been transplanted once after the initial planting in the orchard and had stood in the latest position two or three years previous to the time of study. They averaged about five feet in height and from an inch to an inch and a quarter in diameter at a point two inches above the union, which was at or slightly above the surface of the ground.

The tangential longitudinal view presented in Figure 60, showing conditions near the center, gives something of a perspective of these unions. A transverse perspective of any of the unions examined (Fig. 61), reveals conditions strikingly like that reported for pear on apple. The line of union be-

Fig. 60—Pear (left) on quince (right). Tangential view at right angles to plane of insertion. Good and poor union. Occasional vascular bridges across stretches of poor union.

tween stock and cion is marked by the same series of dark spots, broken at first, but tending later to form a continuous line of separation. As compared with the pear-apple combination, the pear-quince union is, on the whole, distinctly better, year for year. This is in accord with general field experience.

Adjacent Tissues—More detailed examination shows distinctly less of deposits of various sorts in the tissues adjacent to the union, or in the union zone itself, than in the pear-apple union, though they are not altogether lacking. What discoloration does appear is chiefly in the xylem rays; the

Fig. 61—Pear (above) budded on quince. Considerable difficulty in initial union. At left, vascular union in first, second, and seventh years; at right in first and second years only. Bark inclusions in later years. Dieback in stock has reached beyond the level of this section, which was cut at the level of the inserted pear bud. Slow healing of stock by overwalling. In most sections no continuity between cion and stock in any part of bark. Points of initial union marked by arrows.

parenchymatous zone is relatively free through most of the width of the annual ring. One striking modification of adjacent tissues is the enlargement of the rays, which become tri-or multi-seriate, as in the neighborhood of wounds or in girdled twigs. Vessels are much more evenly distributed throughout the width of the annual ring than in normal pear or quince tissue. These modifications of structure, without apparent breaking down, seem more pronounced than in the pear-apple union.

Later Stages—In general it may be said that union proceeds through the parenchymatous zone stage into the transverse bridge stage but after the first year it apparently does not proceed far beyond this, and that the cion is constantly offering union and the stock often declining it, as in the pear-apple combination. In detail, however, much variation occurs.

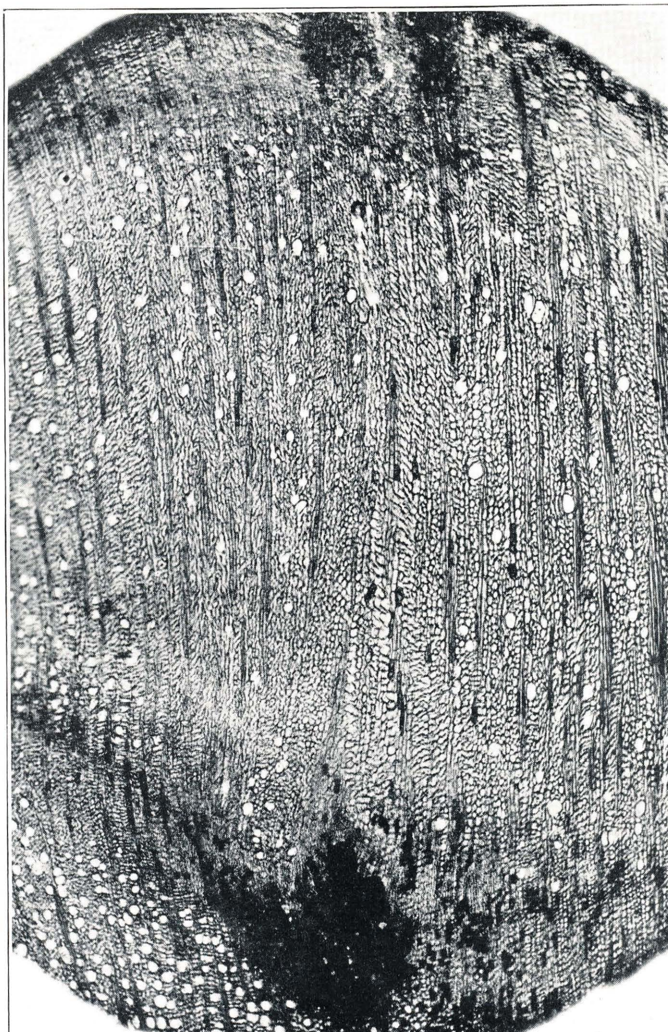


Fig. 62—Pear on quince. Typical new graft union after first breakdown of cambium (shown at lower edge). Second breakdown above.

There is very pronounced difference between conditions in the early years of association and those prevailing later. The transition is, however, not uniform; in one section the same annual ring may have a fairly good union on one side and none at all on the other.

Initial Stages—The initial union between the meristematic surfaces of the inserted shield and the stock is apparently accomplished with less facility than in ordinary shield-bud unions, such as pear on pear (Fig. 61). The lack of ready union between parenchymas is manifested in an unusual development of this tissue, in some cases pushing the bud some distance from the original surface of the stock. Indeed, in some preparations there is apparently no union of parenchyma surfaces inside the shield and union is accomplished solely by graft unions at the edges of the shield, as in chip-budding. Since successful bud unions seem to depend on the filling of the cavity under the bud itself by parenchyma from the stock, this refractoriness may account for the reported failure of buds of certain varieties of pears to

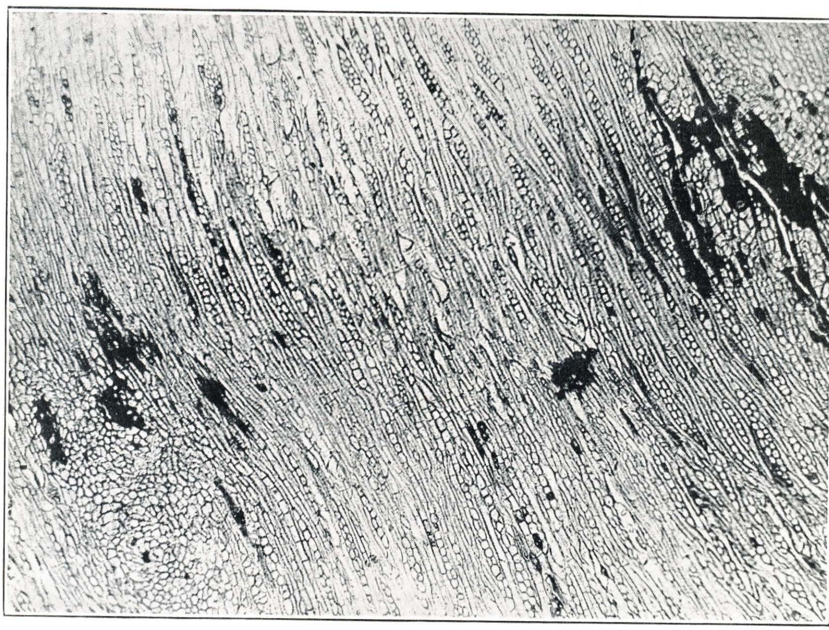


Fig. 63—Rather typical vascular bridge. The dark spots (upper right and lower left) mark location of union. Union zone approximately on a line connecting these. Pear above; quince below. Tangential section.

push out when inserted on quince, even though the shield "unites" with the stock and it suggests that chip-budding might be more successful in these cases than shield-budding. This initial evidence of uncongeniality, it should be emphasized, involves parenchymatous tissue, where length of cambium elements—sometimes suggested as a factor in uncongeniality—would hardly be important. Whether this condition would prevail in buds set at seasons outside the ordinary—late summer—might become a point of interest. Discussion of the bud union is renewed on another page.

First Year—Growth is generally best in the season after the bud is inserted. The parenchymatous zone of union is often much reduced, sometimes even to a single aggregate ray; in these cases it is distinguishable chiefly

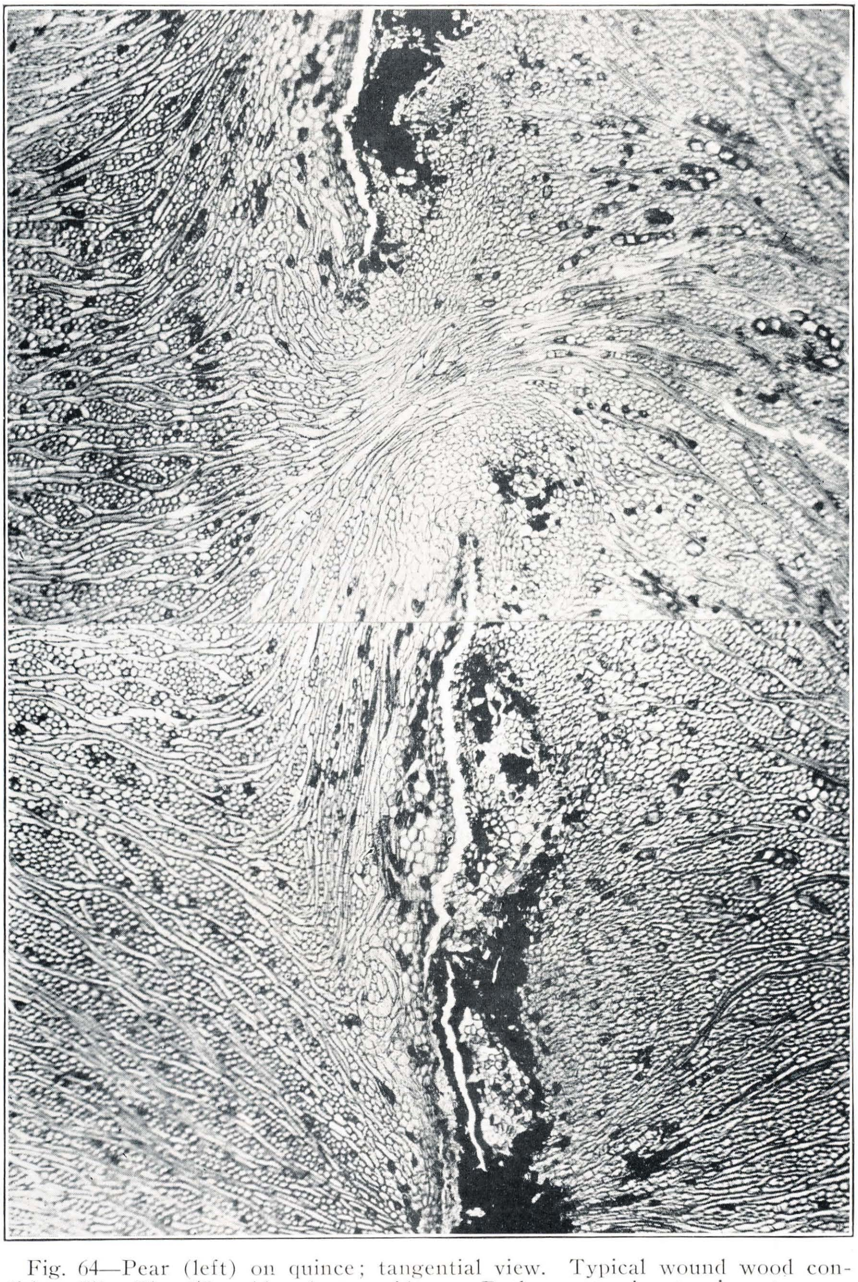


Fig. 64—Pear (left) on quince; tangential view. Typical wound wood condition (like Fig. 27). Abundant periderm. Rather extensive turnings to connect with vascular bridge. (Photograph taken in sections and reduced.)

by the small size or absence of xylem rays for a short distance on either side of the larger ray and it may even become a zone of fiber-tracheids, but have a singular paucity of vessels (Fig. 62). In other words, good unions are all but completed and at the outer edge are to be marked chiefly by the

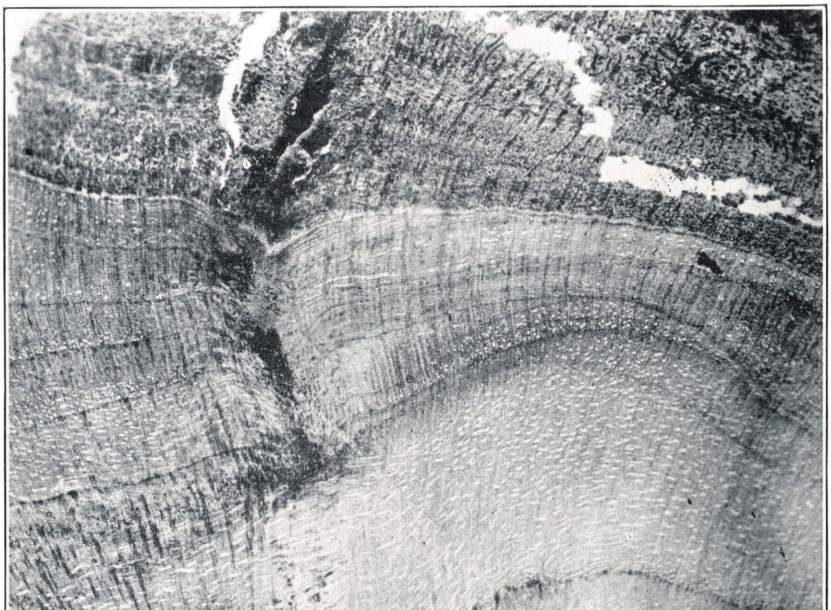


Fig. 65—Pear (left) on quince (right). Union has been established five times and broken four. A fifth break appears to impend. Phloem connection at present. Xylem formation is proceeding in pear without connection with xylem in quince. This xylem will soon become plugged with wound gum (See Fig. 68).

indentation produced by somewhat slower growth, as is the case in many perfectly congenial unions.

This happy condition is not universal, even in this first year, but it is decidedly preponderant. Nevertheless, just as the virtual establishment of the union in the first year is the prevalent occurrence, the breaking of the union in the second year is equally prevalent. Generalizing again, it may be said that this first breaking-down is but temporary. Instead of more or less definitely organized tissue continuing growth at the point where it ceased in the autumn, the union is marked by a small spot of discolored parenchyma. Beyond this is other, but normal, parenchyma, converging from either side, and forming a new graft union, identical with the initial stages of a congenial cleft graft union.

The discolored parenchyma is rather variable in appearance, but shows no evidence of having been subjected to any particular mechanical influences. Such signs of compression as it exhibits may be attributed to the growth of the surrounding parenchyma; the cells clearly were not crushed. Generally they appear black and absolutely opaque, in unstained or in stained specimens. In addition to this parenchyma, the underlying tissues formed the previous year are often discolored for some distance.

During the second season of growth, union is generally very good. Figure 63, a tangential view in one of the early-formed rings, shows a union which seems to lack continuity only in regard to vessels and even this apparent lack may be due to the irregular course followed. The union line runs in a general direction from one area of broken-down tissue to the other, possibly slightly above them and sagging somewhat between them. Xylem rays are often uniseriate in quince and wider in pear, but this character is too variable under wound conditions to be acceptable as an identifying mark and the exact border cannot be established. Figure 64 shows another well established union, in which vessels predominate for a time.

Re-Grafting—For a variable period, union is established in early summer and broken in late fall or early spring (Figs. 65 and 62). In fact, the graft union, as it appears in the specimens examined, is virtually a series of separate graft unions, with an occasional continuance of unbroken union for two or three years, or failure for an equal period. Even more notably than in the initial years, there seems more effort toward establishment of union emanating from the pear than from the quince. Though there is much variation, it seems safe to make a general statement that pear tissue near the union, but not at it, resembles girdled tissue above the wounded areas, while quince tissue in corresponding position resembles the primary or secondary wound wood found just below an ordinary decapitation wound (or close to ring-wounds).

Unions Become Poorer—In the annual rings formed in later years, however, a considerable change develops. There is a general, though not pronounced, tendency for the two associates to contract growth along the union line, resulting in somewhat wider space between them. As they continue to grow radially, the edges thus formed facing each other develop bark and become more or less like callus edges of wounds. Further growth occasionally cuts off areas of bark beyond which temporary unions may form, producing inclusions of distinctly suberized nature. Union at this stage is almost wholly by transverse bridges, proportionately small and comparatively short lived. About this there is much variability; some sections

Fig. 66—A section transverse to the tree, but radial at the point of union because of the horizontal nature of the union tissue. Growth proceeded from below upward. Breakdown in center, after vascular union.

Fig. 67—Pear (right) on quince (left). Bark intervening between stock and cion. Phloem continuity broken. Some bark contact in cortical region, apparently established in first year or two, when vascular connection existed.

show no union after the second year (Fig. 67), while others from the same specimen show union in the seventh (Fig. 65). The presence of the double layer of incurved bark is not to be considered the cause of failure to maintain the union; in the natural graft, bark and cork in far greater quantities than presented here, were penetrated. The absence of internal pressure,

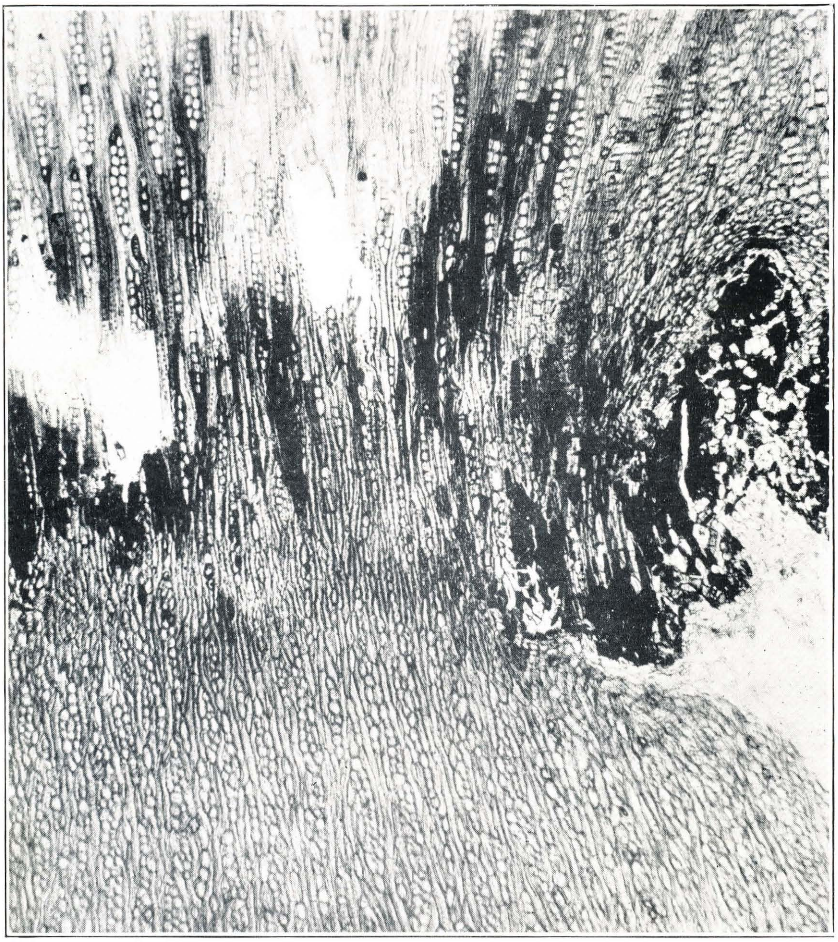


Fig. 68—Union by vascular bridge is breaking down. Faster growth of pear (above) has produced xylem which is continuous with phloem of quince (below) (see Fig. 70). Wound gum deposits in pear wood. Periderm forming along edge of phloem on right.

possibly a reflection of declining vigor, permits the bark to be an obstacle. This behavior may account for the rather general experience that dwarf trees are short lived in infertile soils; with high fertility regrafting may occur more readily.

Associated Conditions—The failure of the transverse bridges, the second stage, it will be recalled, in the ordinary graft union, to progress to the third stage, or even to maintain their own existence, may be a two-fold matter or a two-fold manifestation of the same influence. Available evidence on this is by no means conclusive and only conjecture, based on observation, can be offered, though detailed inquiry may well yield definite results. Obviously, the comparative scarcity of transverse bridges, and the absence of parenchymatous tissue between them, preclude the bridging between bridges that characterizes successful grafts. This, however, need not be an insuperable difficulty, since similar bridges in grafts of apple on apple have pivoted

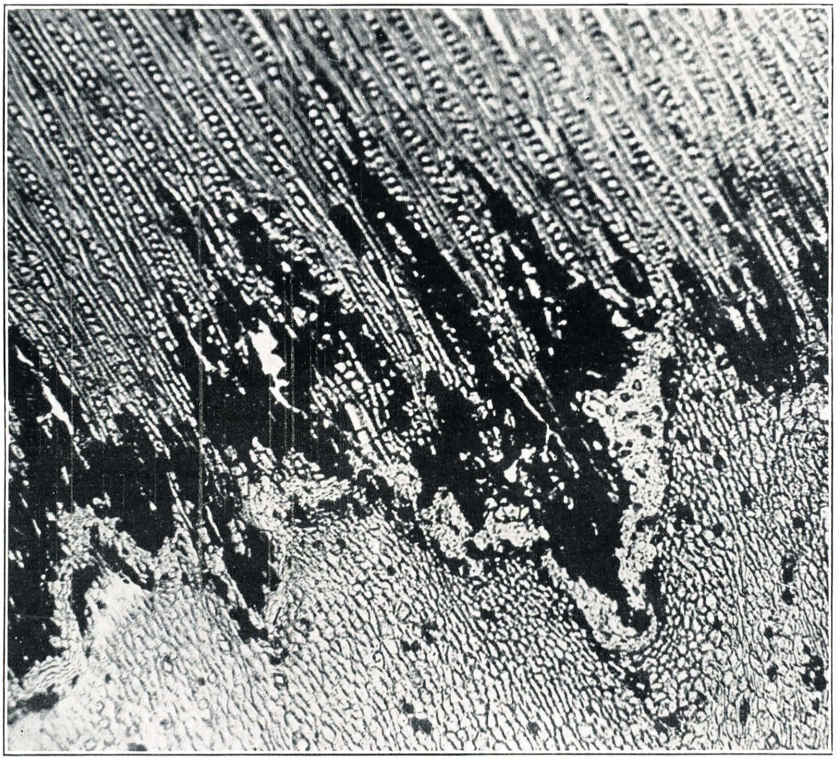


Fig. 69—More advanced stage than Figure 68. Parenchyma and periderm in quince. Wound gum in pear tissue.

successfully, filling in, above on the cion, below on the stock, and assuming finally a longitudinal direction. This the transverse bridge in the pear-quince union fails to do. Its failure to maintain itself seems to be due to uneven growth, either in fall or in spring, probably in the fall.

Some sections, transverse to the tree, but virtually radial to the bridge, show four or five rows of pear cells, apparently fiber tracheids, projecting like a pile of cord wood, with no quince xylem to connect with them (Fig. 70). This break would be repaired quickly in apple on apple or pear on pear; in the present case it is the beginning of break down. Figures 68 and 69, tangential views of the same occurrence, illustrate the beginning of wound gum formation in pear tissue consequent upon this failure. This uneven growth need not necessarily be regarded as a simple matter of seasonal activity or inactivity of cambium. It may reflect a seasonal or nutritional or specific differentiation in products of cambium activity. Dau-

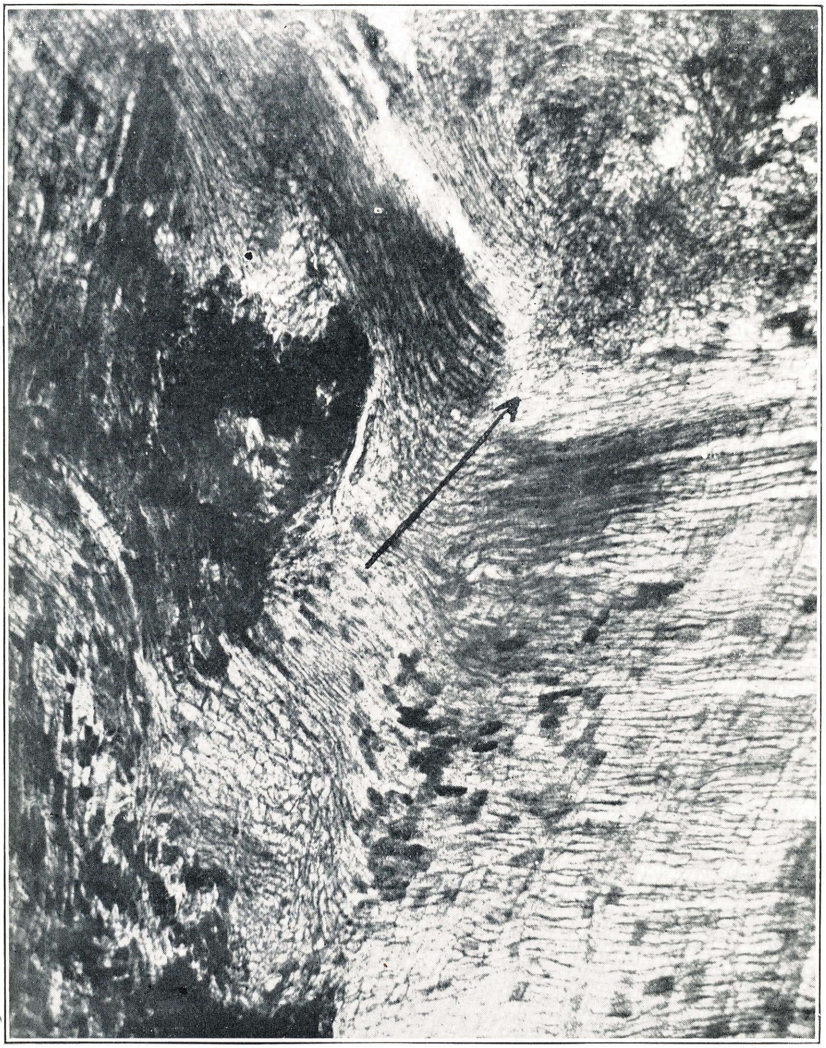


Fig. 70—"Radial" Section. Pear (left) on quince (right). Failure of connection in xylem of stock and cion. Xylem of pear is continuous with a wholly distinct tissue, apparently phloem, of the quince (marked by arrow). The cloudy area in the bark immediately above this union is apparently crushed pear phloem. This points to a difference in period of cambium activity or a relative difference in cambium products as causing the break which is developing. Figure 68 shows the same stage tangentially; Figure 69 shows a somewhat more advanced stage.

phiné (8) records, in *Artemisia vulgaris*, a differential production of xylem and phloem which may be interpreted as associated with the nutrition of the cambium in the rhizome. In Figure 70 and in Figure 68 there is no apparent present break in continuity between the xylem of the pear and the unidentified but probably phloem tissue of the quince. Though there is little specific information available on the point, it would seem altogether possible that cambium may produce xylem or phloem in differing quanities at various seasons and that these periods do not synchronize in the pear and the quince, and that, specifically, the pear cambium is forming xylem at a time when the quince cambium is forming phloem. For a time these two tissues might interlock, but the cambium continuity would be broken, and the presence of the quince phloem would preclude its re-establishment. In the locally almost radial preparation depicted in Figure 70 there is only the very slightest deviation from straight line continuity between the xylem and the probable phloem; this is a slight bending inward of the phloem elements as they join the xylem. This would indicate that the xylem has not pushed up through the phloem; on the other hand the pear phloem is plainly crushed at the union line.

As a supplementary, though less supported and perhaps less likely, factor, it seems plausible that the two failures in the transverse bridge have some influence in the failure of cambium continuity. These two manoeuvres, pivoting and stretching across a slight gap, both easily accomplished in other unions, require a notable amount of gliding growth in the cambium. The union through the parenchymatous zone, which was rather well accomplished, does not require a great amount of gliding growth by the two cambiums in unison. Nowhere, in the specimens examined, was there any indication of considerable gliding growth executed by the two jointly; on the other hand, wherever it was called for to any great extent, continuity was broken. Either, alone, is obviously capable of it; jointly they appear to fail. It is true that more or less gliding growth is necessary to establish union such as that shown in Figs. 63 and 64, but this may be gliding growth of cambium derivatives, and distinct from gliding growth of the cambium.

Actual demonstration of failure in gliding growth is not claimed here and reasons for failure must await more detailed explanation of its normal occurrence in uniform tissue. The suggestion of an action "something akin to enzymic action" (11) may point to the difficulty.

Bark—After this account of cambium failures, it is almost superfluous to comment on the general failure of bark continuity. Occasional bridges occur (Fig. 67), sometimes in cortical regions and occasionally in the phloem region, but they are, if anything, even rarer than they are in the wood.

UNCONGENIAL UNIONS IN GENERAL

Considering both the pear-apple and the pear-quince unions as types of uncongeniality in the pome fruits, it may be said that their most striking pecularity is not their failure to unite but their failure to stay united. It seems significant that they exhibit abundant union of the type shown by wounds and by congenial grafts until the point of apparent cambial continuity is reached. In the first stages of association, while reserves are presumably abundant, they grow side by side, with cambium edges suspended, forming parenchymatous tissue. Whether the vascular bridges represent true cambium unions or whether they represent union of cambium derivatives cannot be stated. It seems, however, so far as the material examined permits any opinion, that true cambial continuity is rare; certainly it is of short duration.

Possible Causes—Alternative and necessarily tentative explanations have been offered in previous pages for the failure of cambium continuity on the basis of inability of the associated cambiums to work unitedly in gliding growth or of seasonal variations in cambium activity and its products. Others have been advanced from time to time.

Difference in normal size of cambium elements may conceivably be a factor, though this assumption would not be necessary to explain failure of gliding growth and difference might not prevent union. The behavior of unions not yet completed suggests that instead of resulting in complete breakdown, unequal length of cambium elements might produce a permanently parenchymatous wound zone, such as Eames and MacDaniels (11) report in uncongenial combinations of apple on one of the so-called Paradise stocks.

Wide differences in periods of vegetation have been suggested as a factor and reports made of supposed uncongeniality in apple varieties differing widely in this respect. Distinction should be observed between the period of vernation and the period of cambium activity. Such observations as are pertinent fail to link uncongeniality with wide differences in vernation or of elongating growth. Five-years-old unions between a very early blossom-apple stock and the latest blossoming material available—a seedling—used as cion, give no external sign of uncongeniality and are growing vigorously. The vernation differences between these are wider than those between pear and quince or Kieffer and *P. communis.* Some of the material used in this study, Rhode Island Greening on Oldenburg, is taken from an orchard where grafts of Northern Spy, the latest blossoming of the varieties common in Michigan, make entirely congenial unions with Oldenburg, the earliest blossoming. These instances, to be sure, are in cases in which the cion is late-starting and the stock early; specific evidence based on the reverse condition is not at hand, but in view of the great number of Northern Spy trees which were topworked many years ago to other and necessarily earlier blossoming varieties, the absence of reports of uncongeniality is itself significant.

Differences in vigor or amount of growth can hardly be the basic influence, since wide differences of this sort in grafts of apple on apple fail to produce any evidence of uncongeniality such as those described here.

There is always a temptation to attribute cases of this sort to chemical incompatibilities and some of the observations recorded here seem to lend some plausibility to this as a factor. In particular an apparently inordinate amount of failure of parenchyma union at the contact of stock and shield, where the pear bud is inserted, seems to point in this direction. The comparatively small number of these unions examined precludes establishment of this as a general occurrence, but a wide range of bud unions examined, including numerous kinds of fruits, failed to disclose conditions like those found in pear on quince. Carrière (4) reported that several varieties of pear give much trouble in budding on quince, stating that the buds do not start even though the shield unites; he even stated that better results are secured in these cases by cleft grafting than by budding. This view did not meet with universal acceptance at the time, but has received rather striking confirmation in recent work on plums in England (15). Difficulty in budding the quince is not wholly imaginary. In the figure shown (Fig. 61) there was, at the level depicted, almost no parenchymatous union. The shield was virtually held in by the grafting of the overwalling edges. In this case grafting worked better than budding, and cambium union of a sort was better than union through parenchymatous tissue. This condition is not universal, but if it should prove to be more than occasional, it would indicate that something else beside cambium interlocking is at fault.

Conjecture, almost wholly without evidence, may be of questionable propriety, but it at least illustrates the nature of the action conceived as possible. The microscope preparations indicate that the influence, if it exists, is more or less seasonal. It might conceivably be due to a substance occurring only at certain times, at certain places, under certain conditions, secreted by one of the associates and poisonous to the other or, having been secreted, accumulated because of inability to pass into the other associate and thus becoming toxic. For a definite hypothesis, perhaps the most obvious suggestion would be a cyanogen compound.

As reported by Guignard (14), cyanophoric glucosides occur in some of the Rosaceae and not in others, they do not diffuse across the graft union and in plants in which they occur they are markedly seasonal and localized, generally increasing as the growing season advances, being generally more abundant in leaves and branches, decreasing toward the root, where they may even be absent. Czapek (7) cites reports that in leaves amygdalin is localized in parenchyma, while the enzyme, emulsin, seems to be confined to portions of the conductive tissue; in some plants Prulaurasin is present in cambium and young wood but not in old. These, obviously, would be the tissues immediately involved in budding. Guignard made no definite statements as to the nature of the unions in the various grafts on which he reported, but his measurements and descriptions suggest that some, at least, of them may be uncongenial and have the same lack of bark continuity reported here, which might make the cyanophoric glucoside differences he reports either cause or effect—or both. This conjecture of poisonous effect could, apparently, be rather easily tested by microscopic examination of some of the unions studied chemically by Guignard. At present it can be advanced only as entirely speculative, with realization that cyanophoric glucosides have been found only very sparingly in pear and with ready admission that much of the evidence points equally in other directions. Without the behavior of the parenchyma in the initial pear-quince union and the marked antagonism between pear and apple, it would have scant plausibility. It may, however, not be inconsistent with failure in gliding growth and might explain the disturbance of the action "akin to enzymic" which seems necessary for gliding growth.

In short, the observations available do not wholly support any one of the explanations advanced as to the cause of the break in cambium which plainly occurs. It seems possible that careful investigation might eliminate some factors or that it might show more than one to be operative.

Bark—Most of the present discussion has concerned the woody cylinder, because the record of a period of years is more easily read there than in the bark. Actually, however, in these uncongenial unions the breakdown in the bark seems more consistent, more complete and perhaps more important than that in the wood. The disturbance of the transpiration stream in the xylem is undoubtedly considerable, but whether it is as extensive as the interruption of the phloem is questionable. Indeed it is difficult to conceive how the quince roots, dependent wholly on the pear top for their elaborated foods, are supplied at all except by round-about diffusion along the xylem rays and intervening tissues.

In the pear-apple combination, where breakdown is more complete, even this channel must be seriously diminished. This of course is bound to have a girdling effect on the stub below the graft and it may become a question whether the cion, with its transpiration stream shut off by the gradual senescence of the existing vascular connections, would die before the stock, shut off from phloem connection with the cion, died. The common experience with grafts of pear on apple, as reflected in horticultural literature, is that they grow well for a time, bear fruit and die. There are cases of pear grafts on apple flourishing indefinitely, in some cases for 20 years, but there is a significant lack of cases of flourishing apple trees wholly top-worked to pear. Reports of young apple seedlings top-worked to pear indicate that the cion strikes root or the tree dies. If the graft was made near the base of a side branch, it is conceivable that the stub might receive foods from the main branch and the pear-apple graft persist for many years, as girdled limbs sometimes do. Of course, too, there may be various degrees of uncongeniality between pear and apple. A case possibly analogous is presented in the union of peach on an American plum, as reported many years ago by Arthur Bryant, a nurseryman of Illinois. He could, he stated (19), make the peach grow on this plum stock, if he allowed some plum branches to remain; if these were removed, the tree died.

Incidentally it should be stated that these findings do not tally completely with the description sometimes given of uncongenial grafts which break apart at the point of union. It is sometimes said of them in substance that the wood did not unite and they were "held together only by the bark." In several cases of this sort examined by the senior author, including an unknown variety of apple on the so-called Paradise, bark inclusions were clearly evident well within the union, and stock and cion were actually held apart by the bark.

In a budded tree the stub of the stock presents an ordinary decapitation wound and heals by the process already described for wounds of this sort. In the dwarf pear, however, healing of the stub by overwalling callus was very slow (Fig. 61), and was accompanied by dieback on the "off" side of the stock, extending sometimes to a point opposite the insertion of the pear bud; this would in itself retard the longitudinal healing of the wound and the bending of the stem at the point of union was still very marked after nine years. Though wholly within the boundaries of quince tissue, this dieback must ultimately have considerable effect on the strength of the whole union. This condition may be attributed to the girdling action of the failure in bark connection.

Uncongeniality and Dwarfing—Uncongeniality is clearly not the universal cause or attendant of dwarfing. It seems plain, however, that uncongeniality which breaks continuity of bark must retard the growth of the stock and secondarily, as well as primarily, the growth of the cion. The dwarf Bartlett tree is apparently perpetually self-semi-girdled and the quince root, as well as the pear top, seems distinctly dwarfed, at least for some years. Sahut (32), with apparently no intimate knowledge of anatomical conditions at the union of pear on quince, considered the chief difficulty to be in the downward movement, rather than in the transpiration stream, and likened these dwarf trees to girdled trees, with the root system suffering in consequence. Dwarf pear trees look and behave differently from trees on standard roots which have been stunted by poor soil or lack of water. A stunted quince tree, in comparison with normal or vigorous trees, has, at the end of winter, less carbohydrate reserves in the top and more in the roots (24). On the other hand, the top of a dwarf pear tree is consistently higher in these materials than the top of a standard of the same variety (23). No comparison of quince roots under pear and under quince tops is available, but quince roots are consistently lower in carbohydrate reserve than pear (24). A stock which is itself poor in carbohydrates, then, produces an increase in the carbohydrate supply of the top; this seems to indicate an effect similar to girdling.

Some pear varieties are recognized as growing more vigorously on quince than others, but available evidence drawn from observation does not permit any decision concerning an association of vigor with congeniality. De Liron d'Airoles (25) recognized two groups of pear varieties which should not be worked directly on quince: (*a*) particularly vigorous varieties, because of the large swellings at the point of union, and (*b*) varieties which are particularly weak growers, because the trees so constituted die. These weak varieties, he stated, grow more vigorously when double-worked on a vigorous variety. In England, John Scott (33) seems to have held similar views. Decaisne (9), discussing double-working in pears, stated that the intermediate must make a good union with the quince and be vigorous. Carrière (5), on this same subject, specified certain varieties as taking well on quince or pear, but growing slowly and needing a short intermediary—as Curé—to make them fruitful. On the basis of experimental evidence Grubb (13) has recently reported " * * * the variety used as intermediate in double-working has a distinct influence on the vigour of the second cion * * * this influence of the intermediate on vigour is not always directly correlated with the vigour of the variety used as intermediate." Grubb offers no explanation of these differences, and, with the opinions quoted, they may be tentatively considered manifestations either of the collar influence reported by Knight (21) and by Swarbrick and Roberts (39) or of the effect of bark interruptions. On the other hand, Bussard and Duval (2) state that vigorous growth of a weak variety on a vigorous intermediary is secured in certain cases and not in others. According to their view, the intermediary must have foliage of its own, if it is to stimulate the final cion. They state explicitly that without this foliage a stimulatory effect could be explained only by better unions, but that "nothing justifies such a theory; the varieties having little vigour on the quince have little vigour on seedling pear and among these, those with weak wood * * * unite perfectly with the quince; the varieties which form a swelling at the union are those with coarse wood; they are at times rather vigorous."

Uncongeniality and Swelling at Union—Most of the comments available indicate that degree of uncongeniality has been measured by the size of the swelling at the union. The pear-apple graft examined in this study, though plainly more uncongenial than the pear-quince combination, gave little or no external evidence, at the union, of uncongeniality, and had produced no swelling; it appeared, exteriorly, more "congenial" than the pear-quince union. It seems quite logical that greater uncongeniality, producing less growth, should result in smaller tissue accumulation at the union. In other words, so long as there is uncongeniality, its external evidence in accumulation at the union will be greater in the more vigorous trees and will decrease as vigor decreases (as uncongeniality increases). Girdling certainly results in a larger callus in a vigorous than in a weak growing tree.

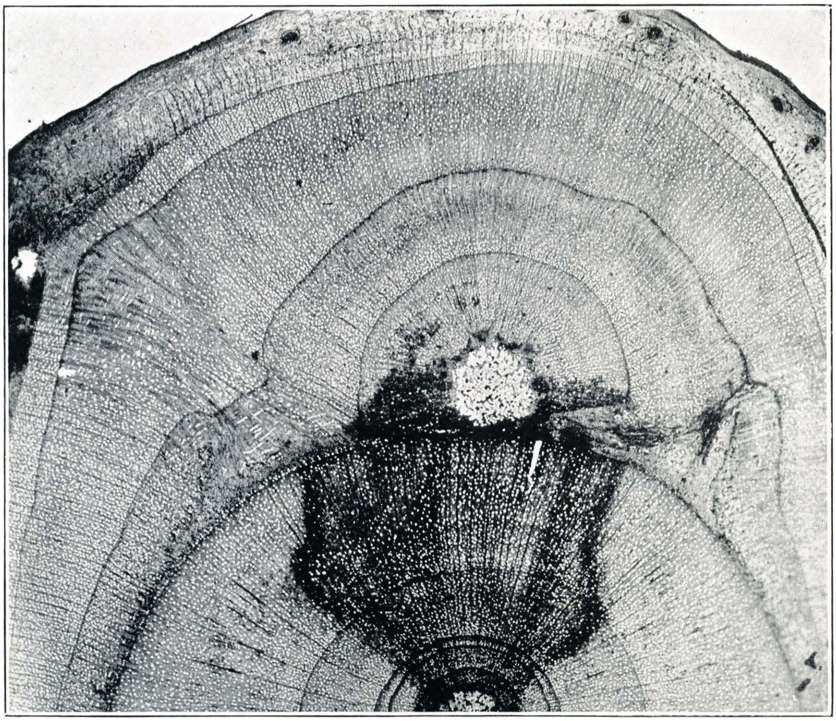


Fig. 71—"Normal" inlay bark graft. Dieback in wood exposed in grafting. Retarded union on right, but normal in second year.

A rather congenial combination might, conceivably, grow vigorously and produce a top large enough to break off easily and the combination be therefore rated as highly uncongenial.

Establishment of this view would plainly alter the significance of many observations, including some of those just quoted. This must, however, await much close investigation.

General Remarks—The emphasis given the discontinuity of the bark should not obscure the very real break in the channels of the transpiration stream. It is not without significance that dwarf pears, though they may grow well in shallow soils, are generally reputed to be more exacting than standards as to soil fertility, and probably as to soil moisture. Under the best conditions, however, unless they develop cion roots they are still dwarfs.

Regardless of the cause and effect of the uncongenial unions, their identification marks are plain. Essentially the chief manifestation is the break in the cambium; the parenchymatous zone and the regrafting are incidental. Disturbances in tissue direction and extensive development of parenchyma are characteristic of all graft unions or even of wounds. Reduction of vascular tissue in proportion to parenchymatous is a typical wound reaction. In a wound or in a "normal" graft, once cambium union is established it is not broken; therein is the difference between the congenial and the uncongenial graft.

Fig. 72—Section of a defective inlay bark graft. Lack of pressure permitted callus from cion to penetrate between cion and stock. Original stock completely dead at this level. To accommodate stretching of cion from stock more or less longitudinal reorientation at union zone.

UNIONS SUSPECTED OF UNCONGENIALITY

With conditions established for unions where congeniality is plainly not a factor and for some in which it is generally conceded to exist, the ground is prepared for consideration of the suspected cases which occasioned this study.

Inlay Graft—A simple and rather obvious case is presented by an inlay bark graft of a solid red strain of Northern Spy on Longfield. Alone, this graft presents many of the characteristics commonly reported for uncongeniality. The presence of numerous other grafts—bark and cleft—of this same combination, showing no symptoms of any irregularity, suggested that faulty workmanship in setting the graft or accidental displacement subsequent to the grafting, led to this con-

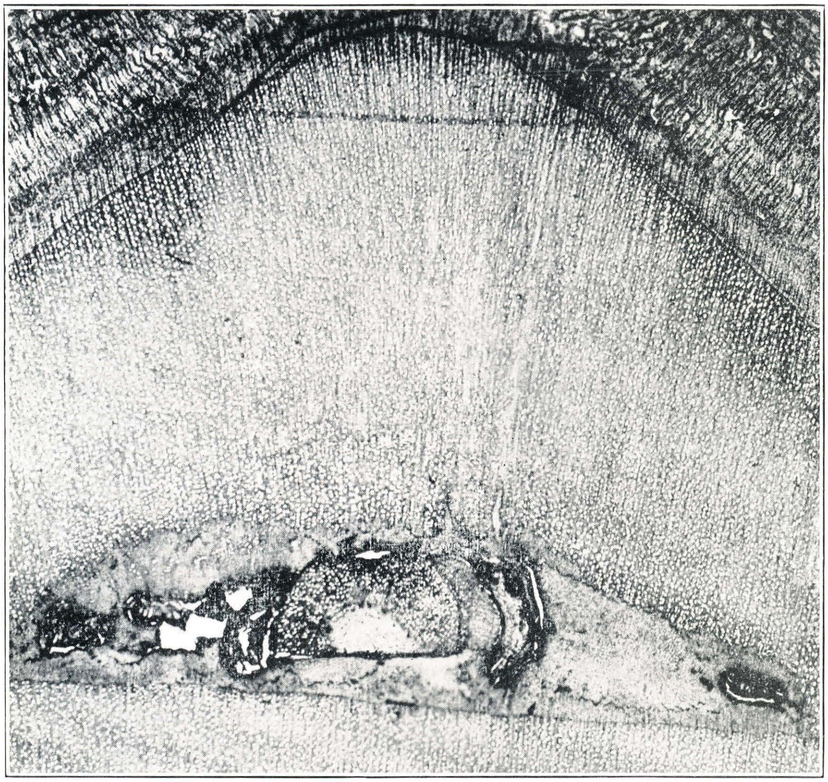


Fig. 73—Graft under the bark. Stock outside and inside of cion. Union with parenchyma of stock, both on wood outer surface and original bark inner surface. No connection with phloem of stock. A graft with no more union than this could not survive long; this condition could come about through setting cion very deep below rim.

dition. This proved actually to be the case. Figure 71 shows union established in a normal graft of the same combination; Figure 72 presents a section through the lower portion of the faulty graft, at a point where the union was best. This type of graft is theoretically intermediate between budding and grafting (in the narrower sense of the term) in that union is supposedly established between overwalling callus from the cion and surface callus from the stock. Actually, in a rather considerable number of cases examined, overwalling is the predominant factor. Whatever the precise method by which healing is secured, pressure is obviously important in preventing a pushing apart of stock and cion with consequent failure of the two calli to connect. This is apparently what happened in the case under consideration, the cion callus on the right becoming directed inward and establishing connection with the callus on the left. With no connection with

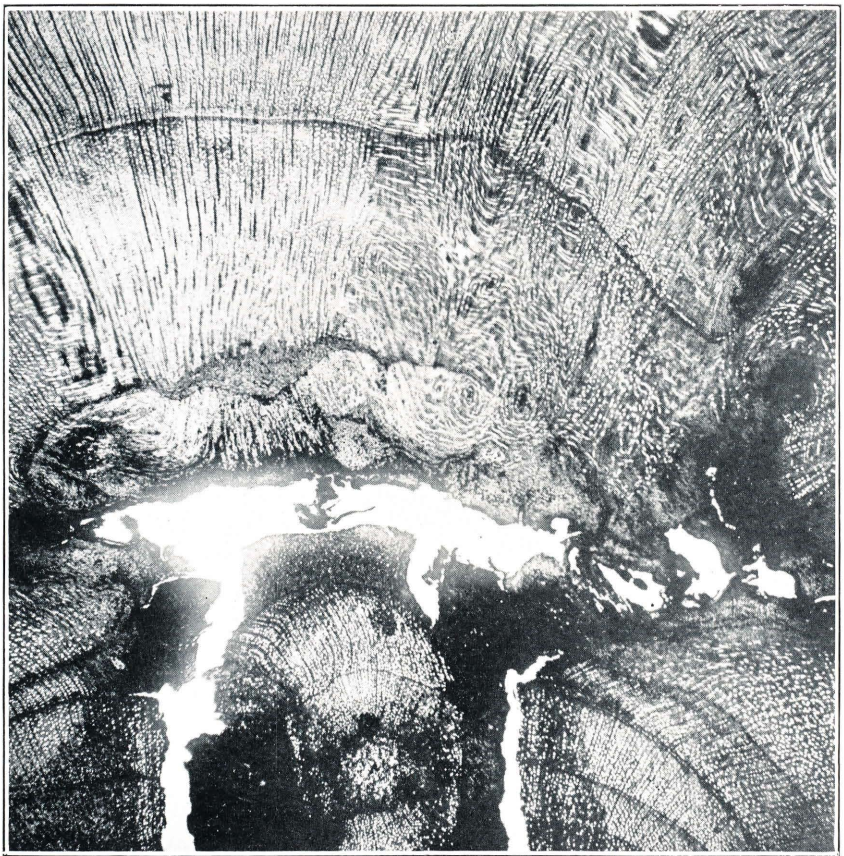


Fig. 74—A cleft-graft union presenting a marked swelling. This was due to the disturbance incident to growing around string used to bind the stock. String was found in the vacant space in the section. These disturbances are clearly not confined to the union zones.

the cion, the portion of the stock on the right became in effect a projecting stub and died back, as do projecting stubs everywhere.

Incidentally it may be remarked that this failure to unite at the top is very common in inlay bark grafts because of the difficulty in securing pressure at the rim of the stock. Added to the fact that grafts of this sort cannot be set until the bark begins to slip, a time when spraying begins to press, this difficulty makes the inlay bark graft less useful in the orchard than the cleft graft, at least until the bark slips so freely as to make the cleft graft troublesome, because of the irregular splitting of the bark.

Under the Bark—It may be pointed out also, at this point, that grafting "under the bark" presents possibilities of untoward development.

Fig. 75—The beginning of a gall due to the failure of cion to connect with stock at point where stock had died back. The gall is merely overwalling callus which cannot establish connection with stock because of intervening bark and absence of sufficient pressure to tear it. Union in cleft perfectly congenial.

Figure 73 is taken from a bridge graft which is, obviously, a special case of a bark graft. Union was established on three of the four cut cambium edges, but no phloem connection with the stock is apparent. Unless, therefore, this can be secured near the end of the union, where the bark is raised most, the durability of the cion is questionable. This condition is likely to occur only when the cion is set so deep that its cut surfaces are buried deep inside the bark, and its own bark interferes with union near the top of the stub, either with the wood surface or with the raised bark. In many cases there is the possibility that it may interpolate some of its own tissue with that of the stock and thus secure its connection with the phloem. The ultimate development of a graft of this sort might easily be conceived to be rather involved and this may account for some of the bizarre appearances occasionally presented by bridge grafts.

Fig. 76—This was intended to be a cleft graft, as shown by the trim of the cion and the fissure in the stock. Apparently the cion was set in the bark and the overwalling callus of the stock pushed it outward before union was established. Xylem from the narrow side of the cion has shared in this union. The cion must have been supplied by conduction through the cortex for some time before vascular connection was established. The cion was set parallel with the stock and union well established along whole surface. The stock was alive to the top of the stub. This case contrasts with the tilted cions shown subsequently, which were fastened definitely in place, by initial growth after grafts set. Compare with Fig. 77.

Swelling at Union—Another graft showed a large swelling, though apparently all tissues at the point of union were alive and growth was proceeding well. The cion in this case was Daru grafted three years on McIntosh, which had been planted two years at the time of grafting. An adjoining tree of the same varietal composition had a normally smooth union. Examination showed (Fig. 74) that the disturbance in this case was due to failure to remove string which had been used to tie the stub at the time of grafting; portions of the string were found upon sectioning. Above and below, the growing tissues had flowed around the string and reunited, but the disturbance occasioned in this readjustment had persisted and normal longitudinal direction was being re-established slowly. The trouble, however, consisted entirely in this confused condition; there was no appearance of the sort found in the pear-apple or pear-quince graft.

The gall depicted in Figure 75 resulted from failure of union, in a manner which had no relation to congeniality. This was another graft

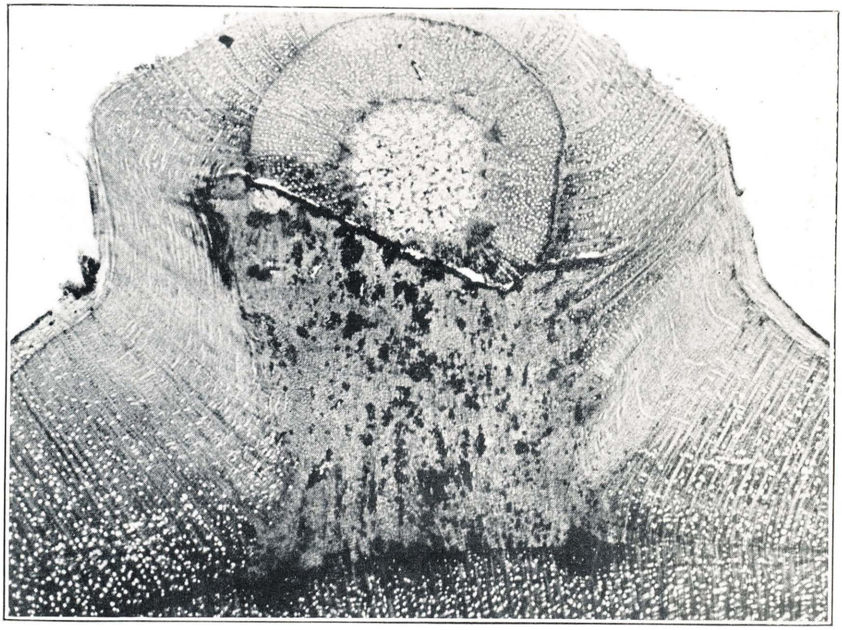


Fig. 77—An inlay bridge graft in which the cion, at this level, was not pressed close against stock. As this was a protected wound, parenchyma developed freely on the wood surface, and the cambium developed along its edge, as in Figure 12, except that it connected above with the cion, instead of bridging the gap. Xylem elements cut longitudinally at union, as in Figue 76.

of a red strain of Northern Spy on Longfield, a combination which has given only two suspicious unions in a great number of cases. The stock was small and only a single cion was set in it. This made a good union, barring a slight disturbance resulting from too long retention of the string tie. Union between the two edges of the stock on the side opposite the cion was established to a point near the top. When, therefore, the expanding cion pushed "backward" through the cleft and, encountering the united live tissue below from within, failed to unite with it, growth of the cion was diverted upward and poured out through the top of the cleft and over the adjacent rim. Since the tissues at these points were dead, there was no union, and growth continued to advance down over the bark of the stock, much the same as has been demonstrated in the case of the swelling on the projecting lower end of a cion whip grafted on a root. Similar swellings have been observed in old saddle grafts and are in no way to be regarded as symptoms of uncongeniality. Though this gall was but three years old, the first formed wood was markedly discolored and many of the vessels were plugged with wound gum.

Kieffer Stocks—A cleft graft of pear, probably Clairgeau, on Kieffer, furnished a distinct swelling, of a type quite different from those just discussed and suggesting a poorly fitted bark graft, except that the stock was in good condition to the top, which was healing over. A section of this graft, presented in Figure 76, illustrates the conditions found. The shape of the cion and the cleft in the stock indicate that the operator intended to set a cleft graft; the callus from the stock flowing into the cleft indicates that the cion was set in the bark rather than in the wood and that the callus actually wedged it outward, aided in no small measure by the growth from the cion itself. The cion stood out at the same distance from the original woody cylinder of the stock for the whole extent of the contact surface. In this it differs from some types to be described presently. The cion shown in Figure 38, typical of the normal cleft graft, occupies perhaps about 10 degrees of the total circumference; in the present union over 100 degrees of the cion's stem is developing. The change of direction in the fibers, transverse on the outer portion, and longitudinal for some little distance on the sides, indicates that there was some distance to be covered in establishing and maintaining union. It bears a rather striking resemblance to Figure 77, which depicts the union of a cion set in an inlay bridge and not pressed firmly against the trunk at the point where later the section was cut. In this case parenchymatous tissue developed on the surface of the trunk and the over-walling callus developed along the outer edge of the parenchyma and ultimately connected with the callus advancing from the cion. Examination of the series of sections taken through the whole union showed no point where the cion was not separated from the stock by a considerable amount of parenchyma, despite its being fastened with a brad, and indicates that the cion was actually pushed outward for some distance and that the change in direction of the fibers was an accommodation to this movement. This, then, would explain the condition found in the pear graft.

Grafts on Kieffer have special interest, since there is more or less opinion to the effect that Kieffer is uncongenial to many or all varieties of *Pyrus communis*, though this view is by no means universal (6). One orchard furnished numerous examples of poor unions, representing perhaps ten or twelve standard commercial varieties which had been topworked, four years previously, into Kieffers then about five years old. The occurrence was so widespread and practically without exception that it would have been accepted as evidence of uncongeniality were it not that good unions of the same varieties had been observed elsewhere and were in fact to be found in grafts set subsequently in these same trees. Figure 2 represents a typical, not an extreme, case. This happens to involve Winter Nelis as the cion variety, but similar conditions prevailed in all others. Coincident with grafting, the orchard was seeded down to alfalfa, but the cions have consistently made very vigorous growth, though the stocks have been, as most topworked stocks are, somewhat dwarfed by excessive removal of ungrafted branches.

Figure 78 illustrates the condition found universally in these unions. Growth tensions apparently had caused some fissures to develop in various places and wide areas had assumed a dark brown coloration, of quite different character from the isolated spots in the pear-apple and pear-quince combinations, but rather similar to that occurring in the

Fig. 78—Transverse section of union of Winter Nelis on Kieffer shown in Figure 2. Almost the whole area shown in the section was impregnated with brownish stain and the dark spots appearing in this picture are quite different from those appearing in pear-apple and pear-quince unions. Bark unions were good. Sections cut at lower levels showed cion in proper alignment with stock and there the union was normal. Here the cion was out of alignment and the disturbance in the course of the xylem of the stock, similar to those in Figures 76 and 77, is due to the distance to be covered in establishing and maintaining union. Actually, the tissue appearing longitudinal here, has a slightly downward trend as it approaches the cion. In a well fitted graft, tissue in similar position has a sharp upward trend and is cut transversely (Fig. 38).

gall on apple. Despite this complication it is plain that the line of union has not suffered any breakdown. The striking difference from typical congenial or uncongenial grafts is the marked change in direction of fiber course marking the line of union. This is found in less extensive development near the top of the stock in ordinary grafts, but the appearance here far transcends anything observed elsewhere except in the inlay bridge graft (Fig. 77) which was set too far out to make normal contact; at this level the section is almost a duplicate of the inlay graft. The position of the original cion, as it appears in series

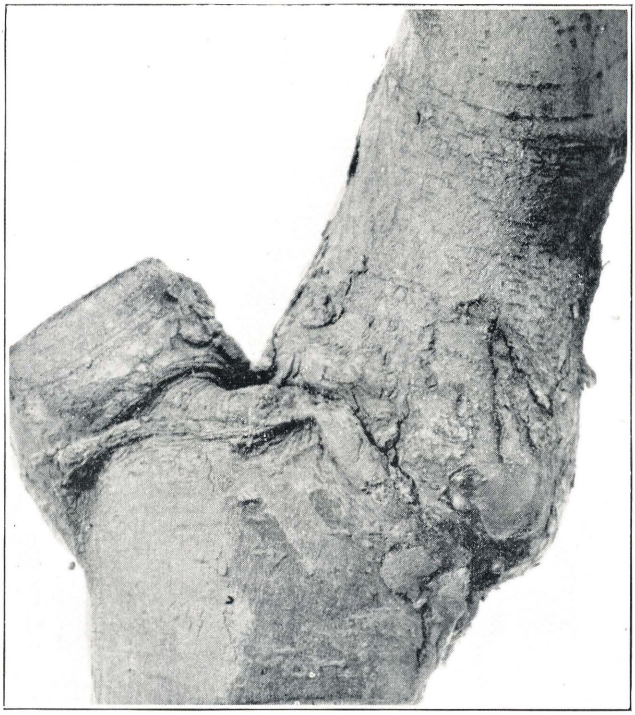


Fig. 79—Rhode Island Greening, cleft-grafted on Oldenburg (Duchess). Swelling on outer side of cion (at right); apparent break in bark near rim of stock.

of sections of a number of these grafts, shows that the cions were set at a tilt, the lower portion being in approximately correct position, the upper portion projecting as much or even more than indicated in Figure 78.

The great portion of cambium on the cion—fully one-third of the circumference—which participates in the formation of new tissue, coupled with its advanced position in respect to diameter growth, gives the cion derivatives opportunity of expanding and occupying an inordinate amount of the expanding circumference. In effect, instead of one circumference expanding with the center of the stock as center, the condition in ordinary grafts, diameter growth here is proceeding from two distinct centers, one at the center of the original stock and another just outside its rim. This would tend to produce compression on the tissue derived from the stock and indeed traces of compression are apparent in the bending of the xylem rays, but not at the union. The inordinate diameter growth of the cion clearly outstripped that

Fig. 80—The same, with bark removed and some of cion dissected away to center. Cion had been tilted and no contact established at top of stock. Gradual encircling by cion covered the area in which no contact had been established. Overwalling callus on rim of stock very poorly developed.

of the stock and literally kept the stock tissues "stretching" to maintain connection.

Bark inclusions were found in some cases; not, however, at the point of union (Fig. 88). They were caused by the bending of stock fibers backward on themselves in effort to maintain connection with the cion, an accentuation of the condition visible at the left of Figure 78. Near the top of the stock the inclusion apparently divided stock and cion;

this is explained in a later page. Nowhere did the bark show the discontinuity prevalent in uncongenial grafts.

Apple on Apple—The whole complex of confused fiber direction cannot be presented adequately by sections alone, since these fail to show direction. Gross photographs, reproduced in Figures 79 and 80, representing a graft of Rhode Island Greening on Duchess, and in Figures 81 and 82, the same combination—depicted before bark removal by

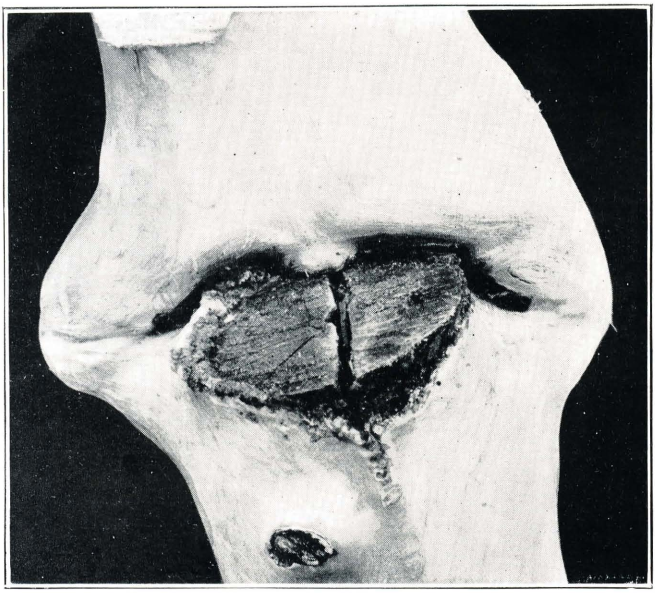


Fig. 81—Rhode Island Greening on Oldenburg. This figure and the next present the union shown in Figure 1, but with the bark removed. They are at angles of 180 degrees and 90 degrees, respectively, from the point of view used in figure 1. In this figure appears a suggestion of the processes by which bark inclusion came about through the growth of cion over stock without any union at the rim to pull the callus into overwalling of the stub.

Figure 1—indicate conditions very similar to those in the pear. These pictures show, to the most ordinary inspection, that the stubs are not healing properly; therein is the clue to the principal difficulty in this whole group of pear and apple grafts.

Figure 83 shows a pear graft, set at a later time in these same trees, which was shown by dissection to have established union between stock and cion on the left and to have failed in this on the right. The cut shows a greater development of callus, continuous with the cion, along the rim of the stub at the left; at the right the callus is smaller and is not continuous with the cion, which is merely growing over it. At the time of examination this callus was dead. Figures 84 and 85 represent in greater detail the conditions in the stock on the left and the right respectively; unfortunately they were not cut in the same relative plane, but, as they are, they show the differences plainly enough. Where

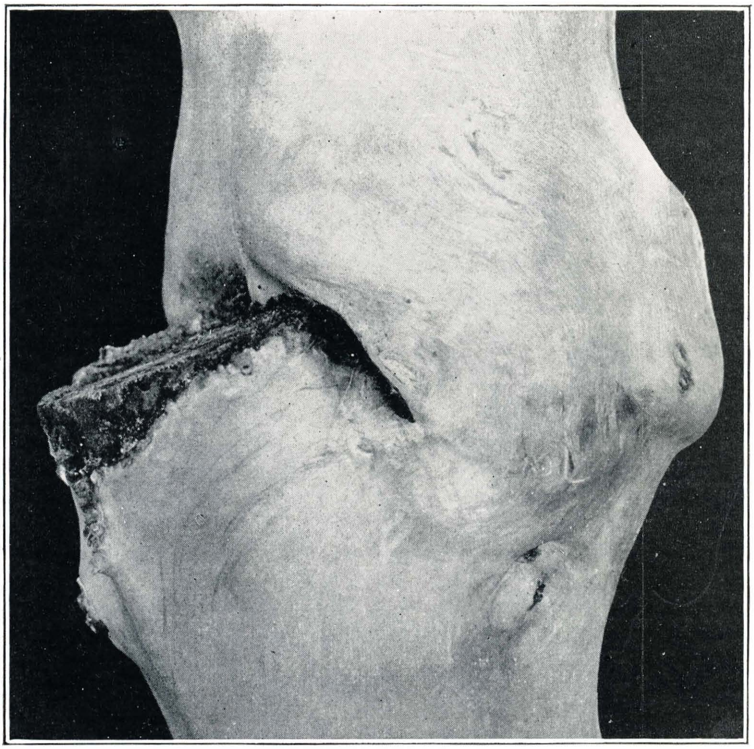


Fig. 82—The top of the stub shows turning away from the rim of the stock, and the gradual folding of the cion over this rim by growth from below rather than from above. Compare with Figures 31 and 44.

union was established between cion and stock at the top of the stub, the fiber direction at the top changed completely (Fig. 84) and from this an overwalling callus has rolled up laterally over the rim of the stub, as already detailed for the healing of amputation and decapitation wounds. On the other side, where contact was established only about one-fourth of an inch below the rim, the initial wound reaction pushed a small unorganized callus up over the rim, but no new wood formed nearby; the cambium died, and the bark along with it. As a result the initial callus died.

Figure 86, depicting a more advanced stage of healing in a well made graft, illustrates the importance of contact at the top of the stub in hastening the covering of the cut surface. In fact, the cleft graft is but a special case of the decapitation wound, with a very small branch above. Setting the cion so that it is not in contact at the top of the stub is like cutting back to a small side branch and leaving a stub. The difference in the growth of the two callus lips on the wound shown in Figure 87 illustrates the comparative slowness of overwalling which must surmount the rim and it indicates the advantage of having cambium contact at the top of the stub. Failure to secure this alignment, characteristic of the unions under present consideration, forces growth away from the stub rather than over it, in marked contrast to the condition shown in Figure 86.

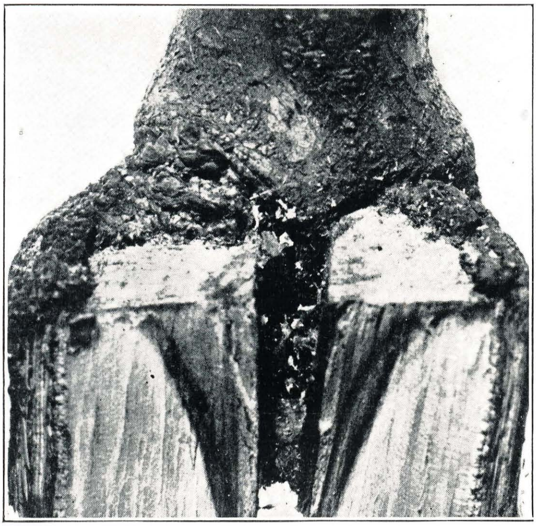


Fig. 83—*P. communis* on Kieffer. This is a more recent graft than the others. On the left, overwalling of the stock is already well under way, by tissue continuous with the cion. On the right, contact between stock and cion was not established at the rim; the slight overwalling callus formed on the stock as primary wound response has died and the cion is advancing by rolling over this dead tissue. On the left, a normal union developing; on the right, a partial approach to the condition shown in Figure 82 is impending.

In brief, then, these graft unions present at once two distinct types of wound reaction. At the lower end of the cion, where alignment was correct, the fiber course was normal, just as in a normal graft (Fig. 44). Microscope preparations showed no deviation from normal. Above the point of initial union with the cion, the stock tissue readjustment as-

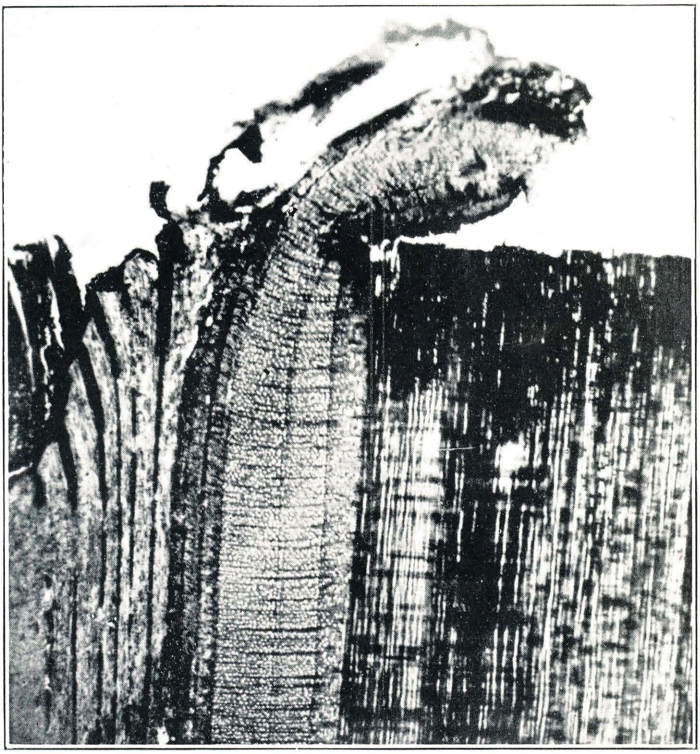


Fig. 84—A radial section from the left of the stock shown in the preceding figure. The turning of the conductive system from longitudinal to transverse coincides with the time of grafting. Overwalling callus connecting with the cion and growing as the cion grows. This condition is analogous to the healing of the amputation wound as shown in Figure 36.

sumed the direction normal to a T-wound, as shown in Figure 31, and the tissues appearing in Figure 78 are trending generally downward, instead of upward (Fig. 82). The whole effect is to throw growth away from the rim of the stock and to concentrate at the point of actual contact all the expansion of stock, as well as cion, which normally spreads over the stub (Fig. 81). This, therefore, is the cause of the swelling and of the failure to heal over the stub and is undoubtedly the basis of many reports of "occasional" uncongeniality.

These imperfect unions which resemble uncongenial grafts in enough

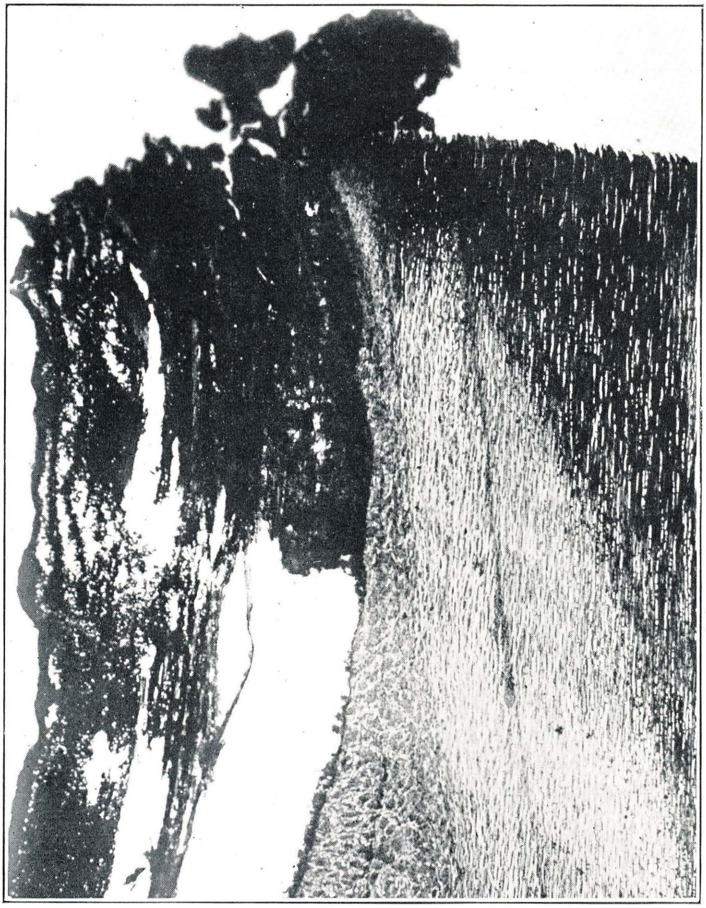


Fig. 85—A semi-radial, semi-tangential section from the right of the stock shown in Figure 83, but reversed for better contrast with Figure 84. Instead of callus extension over the rim, here is dieback along the side. Instead of orderly arrangement of new xylem leading to cion, secondary wound wood persists, indicating lack of orientation.

points to be confused with them rather easily, having even apparent breaking of the bark (Fig. 79) are to be regarded as consequences of two mechanical irregularities: (*a*) failure to establish union at the top

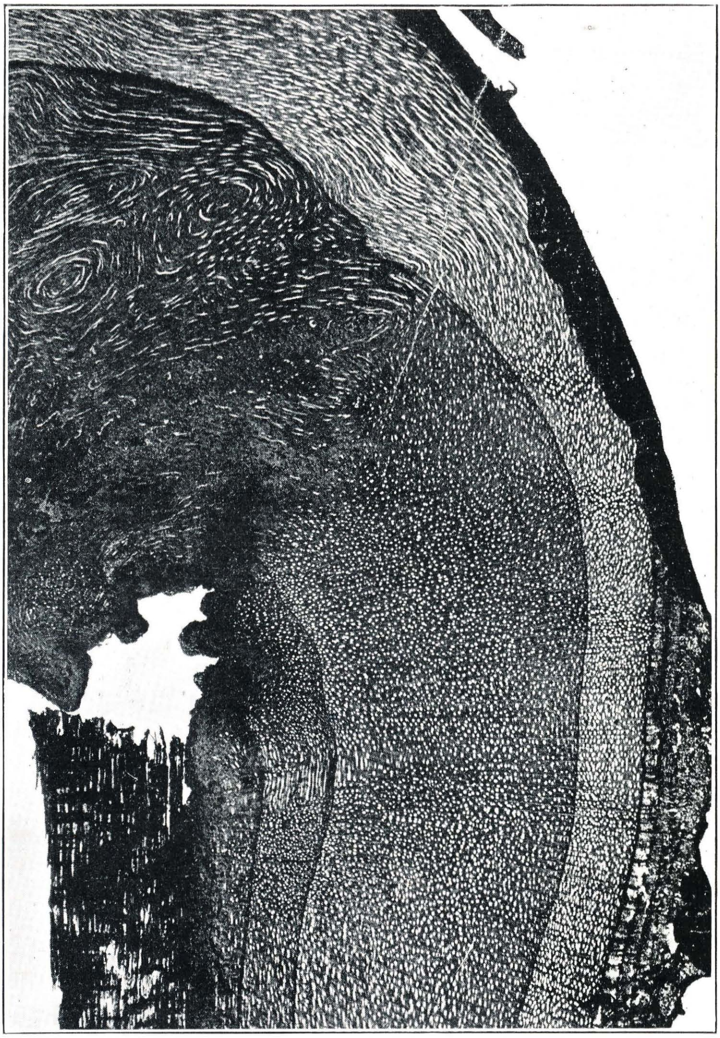


Fig. 86—Radial view showing overwalling of top of cleft-grafted stub in normal union. Union between stock and cion corresponds roughly with transition from transversely cut tissue to that cut longitudinally. At this plane the callus, including cion tissue, covered the stub.

of the stock and (*b*) the position of the cion outside the circumference of the cambium of the stock. These are not the same thing. Cions may be set in correct alignment but so deep in the stock that their bark prevents contact at the top of the stock; these result in failure to cover the stub, which dies back, but they have not, in the few cases observed, caused the marked confusion at the side that is presented in the cases just described.

The fact that Northern Spy cions set by the operator who set the

Fig. 87—Growth from adventitious bud on callus lip has stimulated growth of lip on that side. This illustrates the handicap of the callus which must surmount a rim, whether in a wound or in a graft, with its source of supply below that rim.

Rhode Island Greening cions, at the same time, in the same block of the same variety, showed no difficulty in establishing union, may be attributed to the difference in the source of the cions. The Spy cions were taken from young trees and were large; the Rhode Island Greening cions were cut from old trees and were below normal size. Under these circumstances an operator might readily, though unconsciously, slant them somewhat more, to ensure cambial contact, or with the same slant, set them somewhat too deep and thus fail to secure contact at the top. Herse reports that weak cions are slow in initiating growth and fail to do their share in establishing union. In the case under consideration this laggard tendency would still further lower the upper edge of the union, thereby enhancing the downward trend of vascular tissue on the upper end of the stock, increasing the "piling up."

Fig. 88—Another Rhode Island Greening on Ruchess. Cion on right expanding so as to include bark of stock, but making perfect union below. On the left, another symptom of uncongeniality, the breaking of cion at point of failure to unite. This, however, is due to downward growth of stock tissue which should have united with cion and grown upward. This is the result of tilting cions and virtually making a semi-side graft and at the same time forcing a downward reorientation of the stock above the union, by cutting off the top.

General Observations—Though there is no ground in this study for considering Kieffer to make uncongenial unions, it may still be a refractory stock, likely to produce defective unions. Pears in general seem to give more trouble of this sort than apples (16); Kieffer may be an accentuated case. It is quite possible that they do not make the readjustments of tissue necessary to smooth healing of graft unions as readily as apple; on this basis a pear stock might make defective union with its own cions. Casual comparison of microscope preparations of bark from several varieties of pear indicates that Kieffer has a greater amount of sclerenchymatous tissue, which always seems to furnish an avenue for dieback influences. On large stubs the bark not within close proximity to the cion appears to die back in the pear more than in the apple and this tendency is particularly pronounced in Kieffer. This variety may in a purely mechanical way justify the general reputation it has acquired as a stock, when it is not handled properly. There is, however, abundant evidence in many orchards that it can be made to establish good unions with standard varieties, as there is also that Rhode Island Greening unites well with Oldenburg, if the cions are set properly.

Tilting of cions does not in itself bring about the conditions described here. Some perfectly good unions have been established with tilted cions; in these cases, however, correct alignment was established at the top of the stock and the cion pivoted inward below that point, so that the only contact was at the top. A union of this sort should heal without serious difficulty. Tilting does, however, introduce an element of uncertainty. It is just as easy, if not easier, to establish contact at the rim with a straight as with a tilted cion; this being the case, there is no reason for, and some reason against, tilting the cion. Even with the best effort at exact fit, deviation is great enough.

NEW DEFINITION NEEDED

Finally, assembling the plain evidence from the pear-apple, the pear-quince and the mechanically defective unions, attention may be directed to its broader implication. Horticultural and botanical literature dealing with grafts teems with statements and inferences predicated on the assumption that a swelling at the union retards conductive processes of one sort or another, that it is *per se* an obstacle and an accompaniment, if not the cause, of uncongeniality. In the material here described, the most uncongenial union produced no swelling whatever and the greatest swelling found is due to mechanical difficulties rather than physiological incompatibilities. The magnitude of these swellings corresponds with the growth made by the cion; where conduction, as indicated by growth, is best, the swelling is greatest. The relationship between swelling at the union and congeniality is negative, rather than positive, in this series. New consideration of old opinions based on what now appears to be an unreliable index of congeniality may well alter many conceptions of the relationship between stock and cion.

SUMMARY

1. Defective grafts of apple on apple and of various varieties of pear on Kieffer were examined for evidence of uncongeniality.

2. To establish criteria by which uncongeniality could be determined, wounds, successful grafts and grafts generally accepted as uncongenial were examined.

3. In wounds, where congeniality is assured, considerable variations were found in the details of the processes by which healing is established. These variations are induced by differences in the nature of the wound surface, of the environment, and of the vigor of the tree. Fundamentally, however, the variations are but adjustments which permit the basic process to go on under a wide range of conditions. This basic process is cambium activity.

4. Final healing, i. e., the establishment of cambium continuity over a wound, is accomplished across a zone of parenchymatous tissue, which is sometimes a product of the morphologically inner side of the cambium and sometimes—where healing is slow—across cortical parenchyma. In any case, pressure is an important agent in furthering union, securing it, in many cases, through fissures in the cork envelope.

5. Healing of decapitation wounds is a special case of the amputation wound which in turn is but a special case of the surface longitudinal wound. The necessary readjustments in tissue orientation in apple seem to require a longer period than those reported for certain other woody plants. The decapitation wound is of special interest because of its similarity to the wound made in the stock for cleft grafting.

6. Union by grafting repeats the processes observed in healing of wounds under rather favorable circumstances. The width and duration of the parenchymatous zone, the primary wound stage, varies chiefly with the distance between the cambium edges of stock and cion. Even grafts with rather poor fitting of cambium edges may gradually make good unions—if the cions live long enough.

7. Budding differs from grafting in that the primary union is between the surface of the cambium on the shield and the meristematic wood surface of the stock. Even in successful bud unions of apple and pear there is more or less parenchyma intervening between stock and cion. This type of primary union is not, however, essential, since graft union may occur at the edges of the shield, as in chip budding. All bud unions involve more or less union by grafting.

8. Uncongenial grafts, as represented by pear on apple and pear on quince, differ from congenial grafts principally in failure to maintain cambium continuity. The break in the cambium comes apparently at the end of the growing season; re-grafting often occurs but becomes less common with advancing years. As stock and cion expand, the cambium failure leaves a zone of parenchymatous, sometimes suberized, tissue between them. Both the transpiration channels and the phloem become generally discontinuous.

9. The cases of dwarfing here considered seem to be associated with

phloem discontinuity. The effect is, apparently, reciprocal. The stock is dwarfed and in turn dwarfs the top.

10. The more uncongenial graft, pear on apple, produced no swelling at the union and had none of the external appearances generally associated with uncongeniality.

11. Defective unions of apple on apple and pear on Kieffer were found to be produced by faults in setting of the grafts.

12. In inlay grafts lack of pressure between stock and cion may jeopardize the ultimate healing of the union.

13. Contact between cambiums of stock and cion at the top of the stub is essential to proper healing of graft unions. Tilting of cions, preventing contact at the rim, gave rise to tissue changes which retarded covering of the stub, producing considerable swelling at the union, and produced the general appearance often considered to characterize uncongenial unions. Internally, however, there was no evidence of tissue break-down such as characterizes the uncongenial unions, and these unions are not regarded as uncongenial.

14. In the various unions, the most uncongenial produced no swelling and the greatest swelling occured in grafts which are not uncongenial. Within the latter group the swellings were greatest in the specimens which were most vigorous. This seems to indicate that the swelling is not *per se* an important obstruction to transpiration or translocation, that it is not *per se* a sign of uncongeniality and that much horticultural thought founded on assumption of connection between uncongeniality and swelling at the union may be modified by re-examination without this dubious premise.

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