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Anatomical and Histological Examinations of the Union of Scion and Stock in Grafts of Scots pine (*Pinus silvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.)

Anatomisk och histologisk undersökning av sammanväxningen mellan ympkvist och underlag hos ympar av tall och gran

Резюме на русском языке

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I. Introduction

Grafting as a method in forest tree breeding was introduced by SYRACH LARSEN in Denmark in 1936 (see SYRACH LARSEN 1947). In Sweden experiments were started in 1940 (STEFANSSON 1952) and during the last decade, grafting has been used increasingly in Swedish forestry. Every year about one hundred thousand Scots pine and Norway spruce grafts are made. The main object is to propagate selected trees, so called plus trees, for planting in seed orchards where high quality seed is to be produced, *cf. e.g.* ANDERSSON & JANSSON (1952) and ANDERSSON (1960, 1962). A great many factors of importance for the result of grafting still remain unknown. The present investigation was instituted because it was presumed that some factors of importance were to be found in the process of union of the scion and the stock. The number of successful graft unions in Scots pine is generally superior to that of Norway spruce. It was felt desirable, therefore, that the histological pattern of union in both of the species should be examined, so as to enable conclusions to be drawn as to the best method of grafting.

II. Literature review

The literature on the growth processes in graft junctions is extensive. Among the woody species the fruit trees have attracted most interest. Many investigations have also been carried out in regard to herbaceous plants, primarily the *Solanaceae*. It is only in the last decade that a few investigations have been devoted specially to grafts of conifers.

It has been my intention to give a clear survey of earlier findings on the process of union in grafts of other species, as a background to the following description of the process of union in grafts of pine and spruce.

The history of grafting from primeval times has been reviewed by VÖCHTING (1892). BRADFORD & SITTON (1929) presented a full summary of the literature published up to that time, and KRENKE (1933) referred to a great many papers in his comprehensive discussion of various stages of union.

The possibilities of successfully transferring a part of one plant individual to another, of getting it to unite and continue its growth, have long been known. The earliest information was found in a paper by PSEUDO-HIPPOCRATES about 424 B.C. He, and later on THEOPHRASTUS, pointed out that the scion retains its specific character. Although living on the supply of nutrients from the stock to begin with, the scion, he said, gradually develops roots which penetrate through the stock, and thus provide for its nourishment. THEOPHRASTUS stated that union is most easily established when the components are as equal as possible. Up to the end of the 17th century his successors described a great number of the most fantastic graft combinations (VÖCHTING). DE LA QUINTINYE (1690) finally refuted these absurd statements by defining the kind of stock feasible for various kinds of fruit trees.

DUHAMEL DU MONCEAU (1758) was the first to attempt a histological investigation of graft unions. Three weeks after grafting, he noticed formations of the kind we now know under the name of callus: "substance tendre herbacée et comme grenue". He also found that union developed only between newly formed tissues of this kind.

During the first part of the 19th century reports on graft unions were published by *i.a.* TURPIN (1831), DE CANDOLLE (1832) and TREVIRANUS (1838). In time the functioning of the cambium came to be gradually understood and thus also the nature of the union. TREVIRANUS, however, submitted there was union of the graft components only in the rind.

HANSTEIN (1865) was of the opinion that all new growth was to be traced back to the activity of the cambium. GÖPPERT's investigations on grafting were published in 1874, but as early as in 1841 in a paper on the healing of wounded spruce stems, he had given some views on the graft union. The first year he found in some grafts of *Sorbus* a macroscopial green stripe between the graft components, which in the second year was embedded in a continuous ring of wood. The tissues established in the first year and then embedded between wood surfaces he called "intermediäres Zellgewebe". In the publication of 1874 the process of union was described as follows: "Auf der vertikalen Fläche des Mutterstammes, wenn sie von der des Pfröpflings eng umgeschlossen wird, entwickelt sich jenes wie ich nun fand deutlich von den Markstrahlen ausgehendes *Parenchymgewebe, welches mit dem des Pfröpflings in Verbindung tritt* und so unter Begünstigung möglichst vollkommen Abschlusses von der Atmosphäre der Vereinigung nebst der bald zu erwähnenden Cambialschicht bewirkt".

GÖPPERT stated further that the healing tissues soon become difficult to detect after neatly performed bud grafting, and after grafting with vertical cuts. They never vanish however. After oblique cuts such as in splice grafts, or when the grafting has been done less carefully according to the methods previously mentioned, the tissues soon wither. In old grafted stems the tissues can always be observed as a dark stripe in the wood.

In the following year SORAUER (1875) published an article that contradicted GÖPPERT in certain details. His views are described more elaborately in his "Handbuch der Pflanzenkrankheiten" (2.—5. edition, 1884—1924). He stated that in various types of grafts there is a slight difference in the healing process of herbs and herbaceous parts of ligniferous plants on the one hand, and of branches with a fully developed wood cylinder on the other. "Im ersteren

Falle nehmen häufig an der Bilding der 'Kittschicht' mehr Gewebe teil als im letzteren Falle, bei welchem es sich vorzugsweise um eine von der Kambiumzone (bisweilen auch noch von der Markkrone) ausgehende Gewebemasse handelt, welche sich in den Zwischenraum zwischen Edelreis und Wildling hineinzwängen oder, bildlich genommen, die Fugen zwischen den beiden aneinaderliegenden Teilen ausgiessen muss" (4. edition p. 829). "Kittschicht" is SORAUER's expression for GÖPPERT's "intermediäres Gewebe". In contrast to GÖPPERT, SORAUER was unable to find any difference in the longevity of the intermediary tissue caused by the method of grafting. The dead tissues or cavities that are sometimes found in old grafts were due to the stock and scion having been fitted so closely together that the wound had been healed rapidly by the first wound callus alone, and without the formation of any wood parenchymatous tissues in the space between the components. HERSE (1908) stated that the callus tissues developed in splice grafts and veneer grafts enter the space between the wood surfaces from the cambium, and show a tendency to separate the components. Uniting on the external sides, the cambia then engulf the intermediary tissues, which soon die.

SORAUER stressed that his examinations of bud grafts and rind grafts, in contrast to those of his predecessors, showed that all the elements capable of growth participate in the formation of wound callus and "Kittschicht".

With regard to the establishment of union after bud grafting and rind grafting, SORAUER distinguished between wound callus and "Kittschicht". The first growth at the wound surfaces he presumed to be wound callus uniting both components. Callus meristem in combination with the cambium of the bark flap was to form the "Kittschicht" proper by extruding the wound callus. In the cases investigated by SORAUER the stock cambium and a number of incompletely differentiated wood elements had adhered to the bark flaps. The cells destined to become wood elements would contribute to the formation of lignified parenchyma ("Kittschicht") in the interior folds. This conception of the process was not shared by MENDEL (1936), who contended that the newly formed callus is converted to permanent tissue. VÖCHTING (1892) stated that wound parenchyma in a bud graft is formed from both the stock and the scion. The new cambium in the parenchyma, however, was assumed to originate solely from the scion. The union of grafts was said to occur in the same way. The sole difference being that only the tissues of the cambial zone would participate in the new growth if the graft components had a fully developed wood cylinder. KABUS (1912) arrived on the whole at the same conclusions as SORAUER and VÖCHTING. Concerning callus formation in woody species he said: "Bei der Holzpflanzen dagegen ist das Cambium wachstumsfähig, das Holz nicht." He assumed the initiative to the union of the components to originate in the scion.

VÖCHTING also introduced the matter of corresponding pits between cells of different origins in grafts. He confirmed the occurrence of such pits in the graft of a stem on root in *Beta vulgaris*. STRASBURGER (1901) had also made the same observation in several species. He also succeeded in showing plasmatic connections (plasmodesmata) between cells of rind origin when grafting *Abies nobilis* on *Abies pectinata*. The correctness of this observation was subsequently questioned by MEYER (1902), and MEYER & SCHMIDT (1910), among others. An investigation of the status in perichlinal chimaeras which confirmed the views of STRASBURGER, was carried out by HUME (1921). FUNK (1929), too,

confirmed the occurrence of plasmodesmata between cells of different origins in grafts of *Petunia* and *Datura*.

KÜSTER (1903—1925), as well as SCHMITTHENNER (1907) and STEFFEN (1908), confirmed SORAUER's observation that all living plant parts are able to contribute to the formation of callus under stimulation from a wound, provided, according to KÜSTER, their membranes are not lignified. SCHMITTHENNER found the cambium and the secondary phloem to be the chief callus-producing elements. In common with STEFFEN, he observed a rapid callus formation from the pith of *Ribes* grafts.

Referring to a similar observation made earlier by HERSE, OHMANN (1908) found that the callus formation originated primarily in cells of the cambium. In the same year, however, HERSE (1908) published a more comprehensive treatise which partly contradicted this earlier statement. HERSE also studied wound healing and the union of the rind. He described the cork cambium parallel to the wound surfaces in the rind as being formed by the participation of all the living elements present, and he concluded that, in principle, there is no difference between wound cork and callus.

Primarily OHMANN and HERSE both suggested that the penetration of the contact layers (necrotic tissue) on the surfaces of the graft components occurs by crowding and compression. HERSE, however, abstained from discussing the matter of resorption. MÄULE (1896) considered the union of two callus edges covered with a cork layer to be a process of disintegration and resorption. The occurrence of some sort of resorption is a possibility suggested by most later scientists.

OHMANN was not able to observe initiation of the cambial union. He noticed a differentiation of tracheid-like elements in the callus tissues, but a zone corresponding to that in which cambium was formed later did not participate in these differentiations. Cells that were no different to ordinary callus cells were first formed in this zone, but they gradually developed into woody elements. HERSE conceived the cambial growth to occur in a similar way—by a meristematic zone in the united callus first producing parenchymatous tissue only. HERSE also found that the cambial activity round a wound started earlier than in other places in the stem, and remained more active until the wound was healed. He stated that the cambium deflects outwards as a result of the great activity at the edge of the wound, and that callus cambium is formed in connection with this cambium. If junction with the other cambium is achieved rapidly, no further deflections will occur, but otherwise the callus cambium will turn inwards, since it tends to follow the upper side of the callus when this penetrates between the wood surfaces.

BRADFORD & SITTON (1929) suggested that the union of successful grafts may be equalled to wound healing under favourable conditions. The cambial activity is the main process, but callus formation has also been observed in the cortex, pith, and xylem rays, and from not fully differentiated xylem elements. The final healing, *i.e.* the formation of a continuous cambium, is completed through a zone of parenchymatous tissue which is sometimes a product from the morphological inner side of the cambium, and sometimes, at slow healing, from cortical parenchyma.

PROEBSTING (1926, 1928), as well as BRADFORD & SITTON, investigated grafts that for some reason were defective. PROEBSTING showed that grafts of pears

on quince often appeared to succeed, but that the cambial union gradually decomposed. In many graft combinations where stock and scion united poorly, he noticed an abnormally large portion of parenchymatous tissue in the union zone. He could often see twisted vessels in the region of junction, mostly when one of the components was more vigorous. This, he stressed, did not mean that the union was less vital. In the main BRADFORD & SITTON made similar observations. The cambial union of graft components that were known to show incompatibility mostly broke towards the end of the growing season. Next year they often reunited, but with each season increasingly seldom. Pieces of parenchyma, often suberized, were left between the expanding stock and scion. HERRERO (1951) suggested that the breaks in incompatible graft unions were initiated in adjoining cambial cells of stock and scion. MOSSE & SCARAMUZZI (1956) stated after close investigations: ". . . that necrosis begins in the phloem at some distance from the cambium, that it spreads inwards towards the cambium along rays and is able to reach the cambium and initiate new breaks in the woody tissue at times when the rate of cambial activity is slowed down as a result of seasonal or other causes".

Further investigations on incompatibility have been made by *i.a.* MCCLINTOCK (1948), SAX (1954 a), THIEL (1954), STIGTER (1956), MOSSE (1958), PITCHER (1960), and BUCHLOH (1962). MCCLINTOCK budded peaches on stocks of plum in the late summer. The scion united normally with the stock and the bud burst in the following spring, but in mid-June the leaves turned chlorotic on the newly formed shoot, which subsequently withered entirely. Simultaneously the stock, which had been cut back entirely in the spring, displayed dying root tips. A microscopical investigation showed that the union of xylem tissues was mostly complete, whereas the phloem tissues had never united. Thus the bud received sufficient water to enable it to burst in the spring, whereas the root growth could not be sustained on account of an insufficient supply of nutrient. In grafting different cucumber species onto each other STIGTER observed that certain combinations were able to unite if leaves were left on the stock. Otherwise the junction of the phloem became deficient. PITCHER has found some combinations of *Acer*-species to grow well until the stock was entirely cut back. STIGTER and PITCHER both presumed that the leaves of the stock produced some substance necessary for a proper union. Incompatibility may be overcome by using compatible interstocks (see *e.g.* KRÜSSMANN 1954, and MOSSE) but SAX has shown that this does not always prove to be true.

Around 1930 several investigations into the anatomy of the graft union, mainly in herbaceous plants, were reported. KOSTOFF (1928, 1929/30) stated that most of the callus was formed from the stock, which was thought to be due to an insufficient supply of water to the scion during the initial stage of union. After union had been completed, however, the vigour of the scion was superior to that of the stock. Cambial union first occurred in the lower part of the callus tissue.

Upon observing that intense callus development took place only when brown, dead cell remnants occurred on the wound surfaces, FUNK (1929) concluded that decomposition products activate the division of underlying cells. He thus supported HABERLANDT's (1923) theory on wound hormones. In common with FIGDOR (1891), FUNK considered the occurrence of flattened cells in the new

tissues of the contact zone to be a result of bilateral pressure, and, like OHMANN, he distinguished two stages in the development of the union, a primary and a secondary stage, the first one relating to the initial union of the wound surfaces, and the second to the union of vascular tissues.

SIMON (1930) was able to obtain union between *Solanum melongena* and *Iresine Lindeni* in spite of their distant relationship. The union was not continuous, but an insulating cellulose layer permitting a certain exchange of water was formed between the components. This layer was broken in places where increment was particularly rapid, *i.e.* in the cambium and phloem regions. No absorption of the contact layer occurred, such as is noticeable with closely related graft components. At the points of breach it was observed how the vascular connections between the components developed. SIMON said concerning this process (p. 150) that union is only established with bundles which are able to produce new vascular elements, and that vascular strands may even extend towards meristem in which new vascular elements have not yet been differentiated. The author further writes concerning the process that the establishment of vascular union may start without any preceding junction of parenchyma tissues. This statement was meant to disprove the earlier assumption that a union between living tissue is a prerequisite for the communication of stimulus from cell to cell through plasma connections. In an earlier publication (1908, p. 302) SIMON has assumed the upward conduction of water to be the factor releasing the vascular differentiation. He now concludes that the direction of differentiation is regulated by some sort of a growth hormone which is emitted from active meristems only.

The comprehensive work published by KRENKE (1933) was first presented in Russia in 1928. After a careful re-editing by the author, it was subsequently published in German. KRENKE discussed critically the work of previous researchers and presented detailed investigations of grafts in the family *Solanaceae* and in monocotyledons, especially *Tradescantia*. KRENKE rejected the term callus used in association with graft unions (*cf.* chapter V:C).

KRENKE observed an enlargement of old cells to be the first wound reaction. He assumed this to be due to an easing of the pressure from adjacent tissues. Divisions and increment are then noticeable in several layers of cells beneath the wound surface. Referring (p. 355) to similar observations made by *e.g.* JÄGER (1928), he showed that cells far advanced in differentiation into wood elements may undergo divisions. This reference, however, appears to have been erroneous. Instead, JÄGER found after certain investigations that the cells considered by many previous researchers to be "delignified" were actually cells developed from the cambium, but not yet lignified. KRENKE further stated that the callus formation is more intensive in the neighbourhood of vascular bundles than in purely parenchymatous tissue. Closeness to vascular tissue in one component may also initiate division in purely parenchymatous tissue in the other component. KRENKE was of the opinion that all living tissues are able to participate in the formation of callus, but that the tissues may react very differently, their age being of great significance. Contrary to FUNK, he did not interpret the flattening of cells in the regeneration tissue as a result of bilateral pressure. The form was instead supposed to be caused by a certain position of the cell nuclei at the time of the divisions. The breach in the contact layer has usually been initiated by tissue originating from a vascular bundle.

KRENKE was of the opinion that the breach may occur purely mechanically, or by resorption of the contact layer, these processes being parallel.

The union of xylem elements was considered by KRENKE to occur in two different ways: 1) A cambium is formed in the intermediate tissue in connection with the cambial tissues in stock and scion. This new cambium develops xylem and phloem elements in the regular way. 2) Oblique cells develop by cross-connections (anastomoses) a network between the vascular bundles in both components. Both types of unions may occur simultaneously in the same object. Also growth processes in the phloem were described in detail. The author dwelt at length on the influence of various stimuli on the cell division activity and on differentiation. He also penetrated the problem of polarity in the tissues, a subject which has also been dealt with by *i.a.* MÄULE (1896), ROTHE (1924), KAAN ALBEST (1934), JOST (1942), BLOCH (1952), JACOBS (1952), SAX (1954 b), and SAX & DICKSON (1956).

The investigations of *Nicotiana* grafts by CRAFTS (1934) indicated that callus could be formed from parenchymatous cells in all parts of the stem: pith, phloem xylem, cortex, and cambium. The regenerative stimulant appeared to originate from the ends of the young, growing vascular elements, and new tissue of a similar kind was differentiated only in contact with these elements. Both the phloem and the xylem cells were short at the beginning of the process, as were also the surrounding isodiametrical cells. No slime bodies typical of secondary phloem were noticeable in the short, newly formed sieve tubes. Simultaneously with the differentiation of uniting phloem and xylem elements, divisions of intermediary callus tissue produced a cambium, the direction of which was determined by that of the surrounding phloem and xylem. The union zone of many grafts was characterized by root initials surrounded by parenchymatous cells containing large amounts of starch.

SASS (1932) studied the process of union in "piece-root tongue grafts" in apple. Instructive photographs exemplified his observations. The grafting was carried out in winter with dormant material. Dormancy was soon broken, and after two days in a temperature of +18° C, the first signs of activity were observed in the bark tissue (the author used the term bark for all tissue outside a more or less distinct wood cylinder). SASS stated that all callus is produced by tissues external to the wood cylinder, and that the cambium plays a minor rôle in this context. All living parts of the bark, except the periderm, are able to proliferate. It is only exceptionally that the space between the scion and the stock is completely filled with parenchymatous tissue during the first year. No proliferation from xylem rays were detected, nor from any other xylem elements or from the pith. All the "filler callus" between the components originated from the bark. SASS wrote regarding the union of cambia (p. 369): "Along the cut edges of the old cambium, the adjacent callus cells undergo several divisions radially, producing several layers of narrow, tangentially elongated cambium-like cells. This activity extends tangentially to callus cells farther away from the respective cambia of the stock and scion. The callus between the members is finally bridged by a distinct, cambium-like layer of deeply staining cells with large nuclei . . . In view of the structure and subsequent activity of these cells, they constitute a true cambial region". At best the cambial union was complete after three weeks, but the time required for complete union varied widely.

SHARPLES & GUNNERY (1933) studied cleft grafts of *Hibiscus* and *Hevea* and made observations similar to those made by SASS earlier, with the difference, however, that callus was observed to develop from rays in both the phloem and the xylem. Callus also developed from the pith, but only to a minor extent. The main portion of the callus tissue originated from the phloem part of rays. The stock and the scion produced equal amounts of callus. No sign of cambial activity was observed until the callus tissue was complete.

The investigation of *Nothopanax* grafts by JULIANO (1941) largely confirmed the results obtained by SHARPLES & GUNNERY, with the single exception, however, that a considerable callus formation occurred from the very big pith of *Nothopanax*, particularly in the areas contiguous to the xylem. In old individuals, however, no proliferation occurred in the pith.

SWINGLE (1940, 1952) presented two summarizing articles on regeneration and vegetative propagation in various species, in which attention was also paid to grafting. BLOCH (1941, 1952) presented summaries of literature pertaining to wound healing which also included grafting. In his first article BLOCH stressed several times that the cell divisions are always parallel to the wound surface: "Cell division is always parallel to the surface of the wound or internal centres of necrosis in the early phase of wound tissue activity. It was shown that the polarizing influence from the wound is exerted upon the cell as a whole, and that the plane of division becomes visible by the configuration of the cytoplasm before it becomes evident in the mitotic figure." This matter is also discussed in the second article, where it is stated that other directions of division may occur, particularly in the late stages of wound tissue formation, and in special situations. The possibility of dedifferentiation of cells already differentiated, which has also been mentioned by *e.g.* KRENKE, is discussed in detail and then summarized as follows: "Contemporary research has shown that dedifferentiation may be induced in most mature, living cells by wounding. Even specialized cells, such as thick-walled lignified elements, may in this process become delignified and thin-walled." The problem has been discussed further in the second article. Referring to a comprehensive investigation by BUVAT, BLOCH stated that every cell of an angiosperm plant should, if not degenerated, possess the power of dedifferentiating more or less completely under special conditions. Investigations carried out by BLOCH have shown cells of an idioblastic character that do not dedifferentiate completely in wound tissues. Cells of this kind containing fats and tannin occur in *Ricinus communis*. When the plant is wounded, these cells may divide and transmit their contents to the daughter cells. BLOCH further referred to investigations which showed that the bridges of vascular elements that are formed in wound tissue run in a polar direction from the upper to the lower side of the wound. The tendency of parenchymatous tissues to develop a more or less tracheid-like character has frequently appeared in the material under investigation by the author.

The investigations carried out by CAMUS (1949) concerning the influence of the bud on dedifferentiation and differentiation was also mentioned by BLOCH. CAMUS grafted buds of *Cichorium intybus* on isolated pieces of roots containing only old parenchymatous tissues, which were dedifferentiated and redifferentiated to vascular elements under the influence of the bud. This stimulating effect could be obtained also in cases when the bud was separated from the old tissues by a semipermeable membrane of cellophane. A complete union con-

sequently seemed unnecessary for a transfer of stimulance between the members.

ROBERTS (1949) presented in a comprehensive report a large number of works mainly concerning physiological occurrences in conjunction with grafting. Many problems in this field still remained unexplored. ROGERS & BEAKBANE (1957) referred to a large number of studies which mainly concerned the mutual influence between stock and scion in fruit trees. An investigation by BRIX (1952) has clearly shown that hereditary qualities are never influenced by grafting. Other investigations on heteroplastic graft combinations and the influence exercised by the two graft components have been published by *i.a.* MERGEN (1954 c), HOLST & SANTON (1959), PITCHER (1960), SCHÖNBACH (1960), EVANS *et al.* (1961), and AHLGREN (1962).

The investigations by ARTSCHWAGER (1951) of unions between *Parthenium argentatum* and *Helianthus annuus* were carried out on the basis of the work by KRENKE mentioned above, and it was largely of a confirmative nature. ARTSCHWAGER first observed transfusion windows contiguous to vascular bundles, and through these initial parenchyma unions xylem elements were differentiated in the direction of the nearest vascular bundle. New phloem elements occurred close to the xylem elements, but the differentiation was slower. To begin with only narrow, elongated parenchyma cells were formed.

The healing process after bud grafting of roses was described by BUCK (1953). He found callus formation from rays on both the xylem and the phloem sides and from incompletely differentiated phloem and xylem elements. The cambium, however, did not participate in this process. The major portion of the cambial cells as well as the new elements last formed were destroyed in both the stock and the bud eye in the grafting. BUCK was unable to detect any intact cambium either on the bark flaps or on the wood surfaces immediately after the operation. The major portion of the callus tissue developed from the stock. The union of callus tissues from both sides was observed after five days and cambial union after 10—14 days. Concerning the differentiation of the cambium through the callus tissue, he refers to SASS's paper on the subject.

A study of the potentialities of various tissues to proliferate was made by BARKER (1954). It concerned basswood. He stated that parenchyma in the wood is able to develop callus only if there is a large amount of parenchymatous cells in the vicinity, *e.g.* in so called pith-flecks in the xylem caused by some previous damage to the cambium. The boundaries between the annual rings often contained more parenchymatous tissue than the rest of the wood. Consequently callus was often produced from them. Proliferation from the xylem rays occurred only if they were connected with active elements elsewhere. Normal wound healing of debarked material would take place by repeated divisions of recent cambial derivatives. The major portion of the callus tissue appeared to originate from the rays, but this was assumed to depend on their advantageous position in regard to nutrient supply and conduction. BARKER was of the opinion that wound healing, at least in basswood, is a function of the cambial zone. The statement made by several scientists that the rays should be the most active parts in wound healing he considered to be erroneous according to his own findings that they are unable to develop callus except under special conditions. LARUE (1936) investigated the capacity of proliferation from various parts of the stem in a great many species.

There were wide differences, but the cambial zone was active in all the species containing a cambium.

To my knowledge SEVEROVA (1958, 2nd edition, 1st edition in 1951) was the first to make any anatomical investigations into grafts of coniferous species. Her investigation was based on the Russian edition of KRENKE's work. SEVEROVA suggested the following active elements: cambium, ray cells, and pith parenchyma. The formation of callus from both components was rapid, and the space between the components was filled completely. Referring to KRENKE, she stated that the cell division intensity was highest where vascular tissues from both sides meet, at which points the contact layers are also first penetrated. This is shown in a rather sketchy illustration by an arrow indicating the point of contact between phloem elements of the graft components. When the grafting had been well performed, it took about three weeks for the cambia to unite.

MERGEN (1954 a) investigated unions in grafts of *Pinus elliottii*. The grafts were veneer side grafts with very young material, both the stock and the scion being about ten months old. When the first graft was investigated one week after the operation, the callus development was already pronounced, and transfusion windows had been formed between the components. "Parenchymatous cells from the medullary rays, phloem rays and the cortex were particularly active in bridging the contact layer and in forming direct connections between stock and scion tissues" (p. 240). Some activity was also observed in the cambium. The space between the components was mostly filled with callus originating from "medullary rays", and after three weeks the major part of the space had been filled. Simultaneously the cambia were also united in the lower part of the graft where the flap from the stock covered the wedge-shaped part of the scion. Callus was produced by both components, most of it by the stock. Exposed pith, too, participated vigorously in the callus formation. Five weeks later the union was almost complete. After six weeks the contact layer had been entirely eliminated, continuous cambial union was established, and phloem, cortex and periderm from both sides formed continuous layers.

Comprehensive investigations of unions in various types of grafts in poplar have been carried out by BRAUN (1958, 1959, and 1960 a). The age of the graft material varied between one and four years. The first part of the investigation concerned side slit grafts. The slit was made tangentially in the stock, and so deep that some wood adhered to the bark flap.

Only the stock participates in the first callus formation, and the early-wood, cambium, and young parts of the rind are particularly active. The parenchyma cells in the old parts of the rind start to divide somewhat later. The intermediary tissue is consistently growing faster on the wood side than on the bark flap side. After 14 days the intermediary tissue starts to divide according to a definite pattern. On account of the vigorous proliferation on the wood side, the scion is pressed outwards to the bark flap. BRAUN stressed the importance of the flap for a successful union. A locally faster growth in the flap approximately at the level of the scion cambium achieves a breakage of the contact layer. Stretching, bursting, and resorption are involved in this process. When the development has reached this stage, the first sign of activity is noticeable in the scion. The cambia are united by growth advancing from both sides towards the midsection. "Der vom Kambium ausgehende Reiz überträgt sich auf

angrenzende Parenchymzellen und veranlasst sie den Character von Kambiumzellen anzunehmen (homoiogenetische Induktion). Die vor dem Kambiumenden liegenden Parenchymzellen erfahren eine Rückdifferentierung, sie unterteilen sich zunächst ... mehrmals, die Teilungsprodukte sind wieder plasmareicher und besitzen erneut die für meristematische Zellen typischen grösseren Zellkerne." (*Cf.* SASS, the quotation on p. 11 above, not referred to by BRAUN). Phellogens on both sides united in a similar way, but usually the vascular cambia had already united. Complete unions have been formed in 45 to 65 days. The middle stage in the establishment of the union appeared to be the most critical, *i.e.* when the buds of the scion began to burst before vascular connections were established.

The second part of the BRAUN investigation concerned veneer side grafts and splice grafts. In these grafts intermediary tissue is formed solely from the inner layers of the rind, the cambium, and the early wood of the stock. The space between the stock and the scion is soon filled entirely by this tissue. As in the case of the side slit grafts, the scion in a veneer side graft is passive until the contact layer has been broken—except for some activity in the outer parts of its pith, where a meristematic zone is often formed. This zone occasionally affects the advancing cambium of the stock. Union between parenchyma tissues was observed after 25 to 50 days, whereas complete cambial union was not achieved in the veneer side grafts until after 45 to 90 days.

The last part of the investigation (1960 a) concerned four other types of grafts, but nothing essentially new was reported. BRAUN divided the process of union into three stages:

a) the establishment of primary contact

b) the increasing pressure between the graft components

c) the formation of normal tissue connections (union formation)

In one paper (1960 b) BRAUN has summarized his findings from these investigations. BRAUN has also presented papers on the water conditions in the scion and the stock (1961, 1962 a), and on the most advantageous time for grafting (1962 b).

LAUNAY (1961) presented an anatomical investigation of graft unions in *Pinus pinaster*. The tissues active in union formation were cambium, rays, pith, and resin ducts.

In a previous paper I have summarized the experiences obtained during the examination I am now about to present which are of importance in the practical work of grafting (DORMLING 1962).

Finally, a number of investigations concerning grafting methods and the practical side of grafting will be mentioned. GARNER's monograph on grafting (1959) contained descriptions of a large number of grafting methods. Grafting methods for conifers are dealt with in the works published by MIROV (1940), SYRACH LARSEN & MAGIUS (1944), KIELLANDER (1946), STEFANSSON (1952), ANDERSSON & JANSSON (1952), SCHRÖCK, KOOTZ & HOFFMANN (1954), MERGEN & ROSSOL (1954), MERGEN (1954 c, 1955), ZAK (1955), HOFFMAN (1957), RYABCHINSKAYA (1957), FOWLER (1959), ORR-EWING & PRIDEAUX (1959), LESKINEN (1960), PROKAZIN (1960), GATHY (1961), GUINAUDEAU (1961),

NIKLES (1961), and WEBB (1961). Grafting with semisucculent material in the summer has been proved successful by *i.a.* MERGEN (1954 b) and LESKINEN (1960). FISCHER & KOBERT (1960) have conducted promising investigations into a method of obtaining grafts of spruce on clonal stocks by grafting on pieces of root. The importance of stock activity for autumn grafting of spruce has been investigated by NIENSTAEDT (1959). NAESS-SCHMIDT & SØEGAARD (1960) studied the influence of the height of the grafting point on the development of the scion.

III. Material and methods

The material used in the investigations has been treated according to the methods most commonly used in the grafting of conifers in greenhouses. The grafts have also been treated uniformly. The main part of the material investigated has been grafted specially for the purpose of this investigation, but other material, particularly old pine grafts (2—3 years) and spruce grafts which have displayed certain growth deficiencies, have also been used.

The main series was grafted in 1958 and 1959 in the spring. Although Scots pine and Norway spruce were grafted both years, the spruce series of the first year failed and was therefore excluded. Only one method of grafting was used in the first year, *viz.*: Veneer side grafting with an upward cut in the stock flap, as shown in Figs. 1—2 and 6—7. In the second year the pine grafts were performed according to the same method as in the preceding year, whereas the spruce was grafted with a downward cut in the flap, as shown in Figs. 3—5. In addition to the veneer graftings carried out in the second year, a series of side slit graftings were done on pine according to the method shown in Figs. 9—11, as well as on a few specimens of spruce. In 1960 a few series of side slit graftings with a tangential incision in the stock were carried out (mainly for other purposes) on both pine and spruce (Figs. 12—14). A limited number of these grafts have been investigated as a supplement to the previous series. A further description of how the grafts were executed in the different cases is given in the text under the illustrations.

In 1958 a series of Scots pine was grafted on March 25th and consisted of 50 grafts. The stock material originated from Vimmerby (south-eastern Sweden). All the scion-wood was collected from the same tree, Röskär 2 (approximately 70 years old) at Bogesund northeast of Stockholm.

In 1959, on March 31st, 75 veneer side grafts of Scots pine were carried out. The stock material originated from northern Sweden, and the scions were collected from two 70-year-old trees at Bogesund, Röskär 3 and 4, which were grafted on 25 and 50 stocks respectively. On April 1st, 20 side slit graftings were carried out with the same kind of scions, but with thicker stocks, also from northern Sweden.

Norway spruce was grafted on two occasions in 1959. The first graftings were carried out on March 9th, and comprised 50 plants. The stocks originated from Fiskeby (south-eastern Sweden) and the scion-


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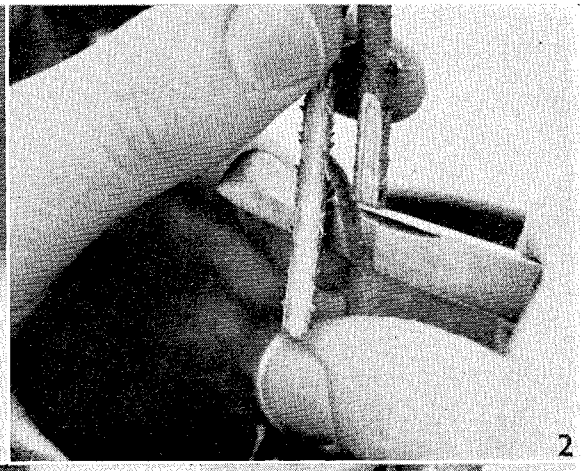
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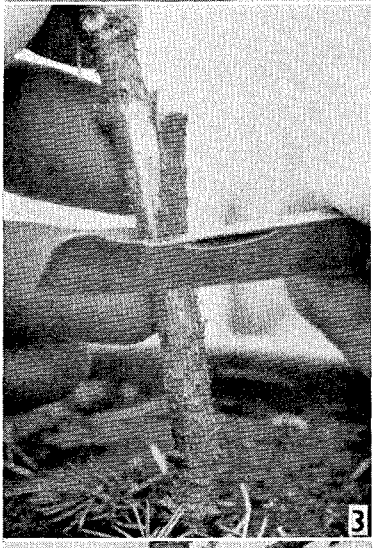
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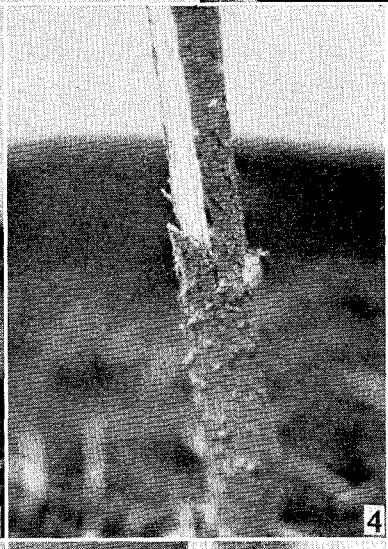
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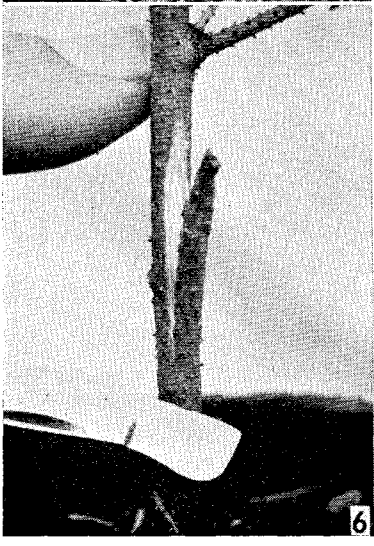
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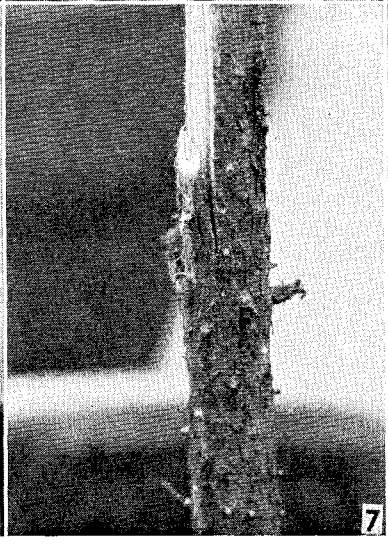
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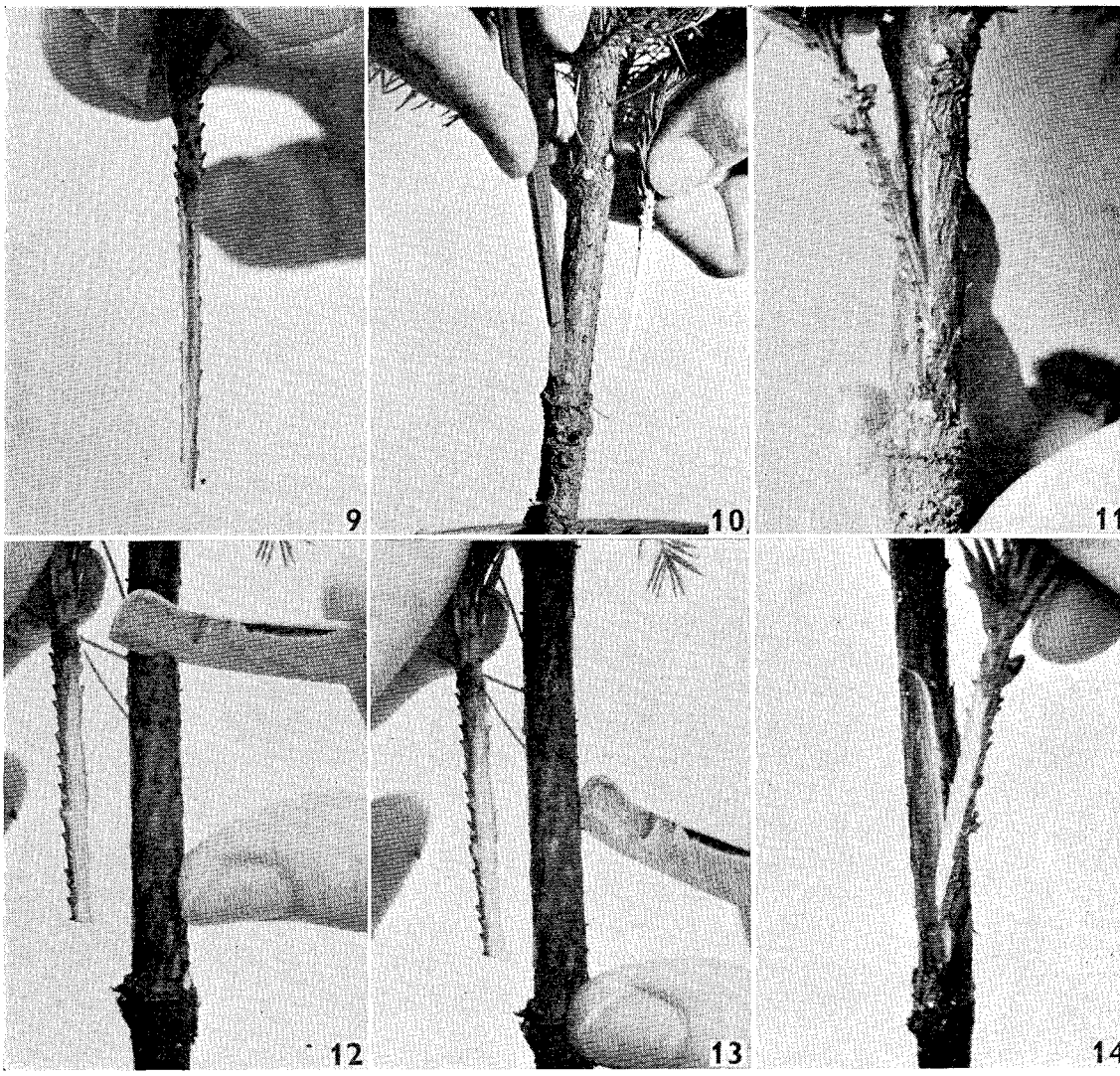


Figs. 1—8. *Veener side grafting.* 1. The cut scion. 2. The stock is cut to fit the scion. 3. Shaping the flap with a downward cut. 4. Appearance of flap after cutting according to 3. 5. Scion and stock matched. 6. Shaping the flap with an upward cut. 7. Appearance of flap after cutting according to 6. 8. Norway spruce graft, six weeks old.

Läggympning. 1. Tillskuren ympkvist. 2. Snittet i underlaget anpassas till ympkvisten. 3. Tillskärning av fliken med nedåtriktat snitt. 4. Flikens utseende efter tillskärning enl. 3. 5. Ympkvist och underlag passas samman. 6. Tillskärning av fliken med uppåtriktat snitt. 7. Flikens utseende efter tillskärning enl. 6. 8. Granymp, sex veckor gammal.

Figs. 9—14. *Side slit grafting.* 9. The cut scion. 10. Radial incision into the stock. 11. Scion being inserted under the bark flap. 12—13. Tangential incision into the stock. 14. Scion being inserted under the bark flap after a tangential incision into the stock. *Cf.* appearance of incisions in 11 and 14.

Sidsticksympning. 9. Tillskuren ympkvist. 10. Radiärt insnitt i underlaget. 11. Ympkvisten passas in under barkfliken. 12—13. Tangentiellt insnitt i underlaget. 14. Ympkvisten passas in under barkfliken efter tangentiellt insnitt i underlaget. Jfr insnittens utseende i 11 och 14!

wood was collected from a 70-year-old spruce at Bogesund. The unions being rather unsatisfactory, a new series of 25 grafts was made on April 7th. Whereas the stock material was from the same provenance, the scion-wood was collected from a fast-growing 30-year-old spruce at Bogesund.

In all cases the stocks were so advanced that the buds had begun to burst, and in many cases 1—2 cm long shoots had developed. The stocks of the veneer side grafts were designated as 2/1/1, which means that they had been growing for two years in a seed bed, one year as transplants, and one year in pots. The potting was done at the turn of the months of May and June in the year prior to grafting. In January the pots were moved into a greenhouse where the temperature was kept at approximately + 5° C to begin with, and then gradually raised so that it was approximately + 18° C in the day-time and + 10° C at night shortly before grafting. The scion-wood was collected immediately before grafting and showed no signs of bursting buds.

The grafts were tied with raffia or plastic tape, and sealed with grafting wax. They were placed in a closed case. One week after grafting air was admitted which was then gradually increased. Six to seven weeks after grafting the glass was removed. The grafts remaining in mid-June were moved to a bed out of doors, where they were planted without pots. At the same time the stocks were cut back to half, and subsequently trimmed accordingly as the individual scion developed. If the scion developed vigorous shoots during the first year, the stock above the junction was cut back entirely in the first summer. Most of the stocks, however, were not trimmed until the second summer, and this applies in particular to spruce.

To begin with samples from the 1958 grafts were taken every week, commencing one week after grafting, and continuing for a period of five weeks. After that three samples were taken at intervals of 14 days, and during the rest of the season one sample a month. Three specimens were taken each time.

The Scots pine veneer graftings of 1959 were mainly carried out for the purpose of obtaining an increased knowledge of the growth process during the first period after grafting. Two samples from this series were therefore taken every day during the first 14 days, and then two samples every other day for a further period of 14 days.

The side slit grafts were sampled by selecting one specimen every other day seven times, then one sample every third day three times, and finally one every fifth day six times.

The first spruce series of 1959 was sampled in the same way as the

pine veneer grafts of the same year. One specimen instead of two was taken from the second series, but the intervals of sampling were the same. Also old grafts were examined in all series where surviving grafts were available.

The pieces of stem affected by the graft cuts were divided into segments (ca. 5 mm long) for fixation. Being of no importance for the study of the union, parts of the stem on both sides of the junction were removed. The segments were fixed in CRAF according to the following formula.

A. chromic acid	0.8 %	B. formalin (40 %)	20 %
acetic acid	6 %	distilled water	80 %
distilled water	93.2 %		

Both the solutions A and B were prepared separately and mixed in the proportion of 1: 1 immediately before fixation. This fluid appeared to be better for tender tissues, *e.g.* cambium, than the formalin—acetic acid—alcohol solution (FAA) mostly used for examinations of this kind. The fixing fluid was renewed after 24 hours, and the material was left in the solution for at least 48 hrs.

Dehydration was carried out by the ethyl alcohol—tertiary butyl alcohol method after the fixing fluid had been carefully rinsed out with ordinary water. The segments were finally embedded in paraffin with a high melting point (70°—72° C). The material generally appeared to be too hard for immediate sectioning. The blocks were therefore submerged in water for about one month after the paraffin had been removed so as to expose the lower part of the graft segment. This treatment made the pine grafts easy to cut with an ordinary rotary microtome. The spruce stems, however, were still too hard for sectioning. Several methods were tried to make them soft. The simplest and most effective method appeared to be to treat them with a preservative composed of equal parts of glycerin, ethyl alcohol and distilled water (KISSER 1926). After the fixing fluid had been washed out, the segments were gradually brought up to 50 % alcohol before they were transferred to the preservative. They were left in the preservative for at least 14 days before dehydration was continued. After the paraffin blocks had been submerged in distilled water as described above, it was possible to section also the spruce grafts satisfactorily. The cross-sections were always cut in series, starting from below, whereas the longitudinal sections were made perpendicular to the graft cuts. Both kinds of sections were usually 15 μ thick. They were stained with safranin—fast green on slides and mounted in Canada balsam.

IV. The anatomy of young stems of Scots pine and Norway spruce

A brief description will be given here of the anatomy of young stems of Scots pine and Norway spruce. Special attention will be paid to dissimilarities between the species and to details which have proved important for the union of graft components.

Figs. 16—17 show drawings of the lower part of a veneer side graft in horizontal, semi-tangential and radial sections. Plate I: 1—2 consists of photographs of cross-sections from one-year-old branches of pine and spruce, and Plates I: 3—8 and II: 1—5 show details of special interest in the stems.

In the following description each part of the stem will be treated separately, beginning from the centre: pith, xylem, cambium, phloem, cortex, and periderm.

a) *Pith* (medulla)

The pine pith is composed of parenchyma cells of the same kind as found in the cortex, except for the resin ducts. Plate I: 3—4 shows longitudinal sections through pith and cortex from the same scion of pine. Both are visible in cross-section in Plate I: 1. Some of the pith cells contain tannin and some even chloroplasts. Virtually all pith cells have living contents and they are able to divide again if the adjacent cells become damaged. The cells filling the leaf and branch gaps are of the same character.

The first difference observed between pine and spruce with regard to the pith was that in spruce, a considerable part of the young branch volume is composed of pith. In one-year-old branches the wood merely consists of a thin cylinder around the large pith. The pith of spruce furthermore has an entirely different and more complex structure. This is shown both in the cross-section in Plate I: 2 and in the longitudinal section in Plate I: 6. Two main types of cells are distinguishable: firstly large cells, mostly extended in the direction of the stem, and with thin walls containing cellulose, and secondly short cells with more or less heavily thickened, lignified walls. The latter category of cells occurs in groups, which on one side border on the periphery of the pith. The

cells are large and numerous at the periphery, but decrease in size and number towards the centre. The walls of the innermost, smallest cells are also heavily thickened. The cell groups are arranged step-wise in the pith. Only a few of the large, thin-walled cells contain living contents. Many of the cells that are still alive contain chloroplasts and tannin; the dark cells in Plate I: 6 are of that type. It is remarkable that many of the thick-walled cells also have living contents. All around the periphery of the pith there is a perimedullary zone—a sheath of 2—4 rows of vertically elongated cells which are similar to the lignified pith cells in all respects except for the elongated shape. They have accordingly only small simple pits. At least some of them have living contents. In Plate XIV: 8 the perimedullary sheath is clearly visible in a cross-section, and Plate I: 7 shows a detail of the sheath in a longitudinal section. The same type of parenchyma cells also fills the leaf gaps.

b) *Xylem* (wood)

The woody elements of conifers are entirely composed of tracheids characterized by their bordered pit-pairs. Parenchyma tissues in the wood of pine and spruce occur only in the rays and in conjunction with the resin ducts.

The common rays are uniseriate in both genera (only one cell wide in cross-section) and they contain both parenchyma cells and ray tracheids, the latter usually occurring along the margins of the rays. Mostly, they are absent in the first annual rings. The parenchyma cells are thin-walled in *pine*. The pit-pairs formed between axial tracheids and the ray parenchyma are large, and cover the major part of the cross-field. Minor thickenings (never lignified) occasionally occur in the walls of the ray parenchyma, but they cover only a small part of the whole wall surface. Cells in contact with vertical resin ducts never have thickenings of this kind. In *spruce*, however, the parenchyma cell walls of the rays are heavily thickened and equipped with a rather large number of small pits such as seen in the cross-field. When completely differentiated, they are rather similar to the cells in the perimedullary sheath, only they are more narrow and extended radially in the stem instead of longitudinally.

Rays in radial section are shown in Plate I: 5 (pine) and Plate I: 8 (spruce), and in tangential section in Plate II: 1 (pine) and Plate II: 2 (spruce). Both the tangential sections show rays containing resin ducts in addition to the usual uniseriate ones. According to their form in tangential section, the rays containing resin ducts are often called "fusiform rays", but from their appearance in cross-section they are usually known as "multiseriate rays", *vide* Plate II: 4 (pine) and II: 5 (spruce).

The wood of pine and spruce contains both vertical and horizontal (radial) resin ducts, the latter enclosed in rays. Together they form an anastomosing system. Plate II: 3 shows a radial section of pine with a vertical duct intersected by a radial one. The cavity in the ducts is surrounded by epithelial cells, all of which are alive and thin-walled in pine, whereas in spruce the walls lignify fairly soon, except for a few solitary rows of cells. In pine the vertical ducts are associated with strands of thin-walled parenchyma cells. This is not the case in spruce. The number of the ducts may differ between various individuals of the same species, but pine wood generally contains more vertical and horizontal ducts than spruce wood. In one-year-old branches of spruce no ducts at all have been observed, whereas young branches of pine exhibit a large number, *cf.* the cross-sections in Plate I: 1—2. CHATTAWAY (1951) has previously made similar observations. More detailed descriptions of the wood anatomy in these and other conifers have been presented by GREGUSS (1955).

c) *Cambium*

The initial layer of the cambium is partly composed of vertically extended cells producing tracheids and sieve cells (the fusiform initials), and partly of short cells producing the rays (the ray initials). The cells produced on both sides of the initial layer divide a further number of times; they are spoken of as xylem and phloem mother cells respectively. In the cambium, new rays are initiated by reduction of solitary, short fusiform initials to ray initial cells (BANNAN & BAYLY 1956). The vertical resin ducts are developed from xylem mother cells which do not differentiate into tracheids in the ordinary way, but divide to shorter elements while retaining their parenchymatous character. In speaking of cambium or cambial region in the following, this means, unless otherwise defined, the entire division active layer. The organization of the cambium is similar in pine and spruce, except that the multiseriate rays are less numerous in the latter species, and entirely lacking in one-year-old branches. The cambia of the gymnosperms are described in greater detail by, among others, BANNAN & BAYLY (1956) and BAILEY (1954).

d) *Phloem*

The phloem of gymnosperms consists of sieve cells, phloem parenchyma and rays containing parenchyma cells and albuminous cells, the latter corresponding to ray tracheids in the xylem, and in structure

similar to sieve cells. Functionally, they are considered similar to the companion cells in angiosperms (*vide* ESAU 1960). Phloem parenchyma develops in vertical strands from phloem mother cells. A particularly large number of such cells are developed during a certain period of each growing-season. In cross-sections they are therefore often seen as »bands» in the phloem, *vide e.g.* the stock in Plate II: 4. Uni- and multiseriate rays occur in the phloem as well as in the xylem. The multiseriate rays contain a resin duct which ends in the phloem as a bladder-like structure, the resin cyst. This cyst is gradually enlarged by the epithelial cells and the cells in the surrounding layers dividing and extruding the external tissues. The resin cysts first established may extend far into the cortex (*cf.* THOMSON & SIFTON 1925). In somewhat older stems the horizontal resin ducts are often enlarged into series of cysts. Multiseriate rays with terminal resin cysts are shown in cross-sections in Plate II: 4 (pine) and Plate II: 5 (spruce), in radial section in Plate II: 3 (pine).

In one-year-old branches of spruce there are no multiseriate rays, nor are there any resin cysts. Multiseriate rays occur in pine, however, but the resin cysts are small and often comprise only a small number of parenchyma cells at the end of the rays that have not yet separated. The stocks of both species exhibit resin cysts, but these are more numerous in pine.

The sieve and albuminous cells are generally functional for one growing-season only. The farther out in the stem they are pushed by cambial growth, the more they are compressed and deformed. The phloem parenchyma and the ray parenchyma extend simultaneously. The phloem of gymnosperms has been studied in detail by ABBE & CRAFTS (1939). Further reference can also be made to BAGDA (1956), CHANG (1954), and HOLDHEIDE (1951).

e) *Cortex with intercepting leaf traces*

The ground tissue of the cortex is largely the same in the two species. Some cells, particularly in the scions, contain chlorophyll, others tannin.

Vertical resin ducts are evenly distributed in a ring in the cortex, *cf.* Plate I: 1—2. The ducts on both sides of the leaf and branch traces branch out and follow the traces, whereas the main duct continue further into the cortex. There are no connections between the vertical ducts of the cortex and the radial ducts of the phloem (*cf.* THOMSON & SIFTON 1925).

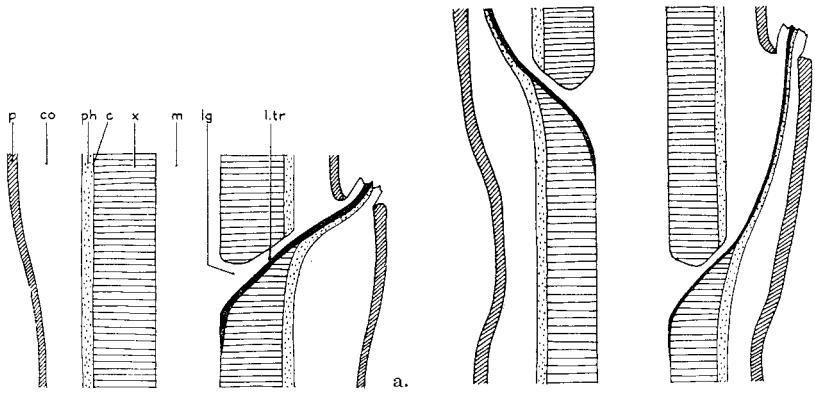


Fig. 15 a and b. Leaf traces in Scots pine and Norway spruce respectively. Radial sections from one-year-old shoots. (Outlined in principle.) Key to signs on page 135.
Bladspår hos tall resp. gran. Radiära snitt från ettårsskott. Schematiserat. Teckenförklaring på sid. 135.

In spruce, sclerenchyma cells sometimes occur in the cortex, and then always in connection with leaf traces.

With regard to the occurrence and appearance of leaf traces, the dissimilarities between spruce and pine are considerable. So far as the latter is concerned, however, the term "leaf trace" is not quite correct. The trace passes to a dwarf branch (short shoot) carrying two leaves (needles). It would perhaps be more correct to call them "dwarf branch traces" in pine, but I prefer to use the less awkward term "leaf trace", which should hardly give rise to any misunderstanding. (Sometimes, however, remnants of the true leaf traces of the bracts are also visible in the sections, see the small trace outside that marked »l.tr» in Plate I:1.)

The leaf traces are more numerous in spruce than in pine, but the volume of each leaf trace is larger in the latter species. Since the leaf trace in pine forms a wide angle with the stele it will soon leave the cortex. The angle of the leaf trace in spruce, however, is very acute, and remains longer, first in the phloem of the branch, then in its cortex. *Cf.* drawings in Fig. 15. In both spruce and pine the thickness of the cortex of young and needle-covered branches is highly variable, because the leaf traces move the cortex tissues outwards. On the outside of the branches this looks to the naked eye like ridges running parallel to the axis of the stem below each needle or pair of needles. In a cross-section it has the appearance of folds. The folds directed outwards in spruce are narrower, and above all, they contain a smaller amount of living tissues than those in pine (*cf.* both cross-sections).

f) *Periderm*

Both pine and spruce already develop *phellogen* (cork cambium) in the shoots during the first summer. In pine it is produced from the subepidermal layer. The cells of the phellogen are square, slightly extended tangentially in the cross-section, and square or slightly oblong in the radial longitudinal section. They are filled with plasma, and contain a relatively large nucleus. Externally the phellogen produces three or four rows of thin-walled cells—the *phellem*. The walls of these cells soon suberize and they loose their living content. Inwardly the phellogen produces some rows of cells of essentially the same character as the cortex cells—the *phelloderm*. The *periderm* thus developed in the first year retains its protective function for six or seven years, sometimes even longer (*cf.* BAGDA 1956). Later on new phellogens are developed in the inside layers by divisions first in the cortex, and then also in the parenchyma of the non-functional phloem. They are restricted and scale-like, overlapping each other, and forming a typical scale bark. The periderm of young spruce twigs differs from that of pine, in that the part outside the phellogen is much heavier. In the ridges this layer is composed of large, thin-walled cells, whereas the crevices between the ridges contain rather small, thick-walled sclerenchyma cells. The periderms later on formed in spruce are of the same type as in pine. The first developed periderms of the two species will be seen in Plate I: 1—2.

V. Scots pine

A. General

In 1958 and 1959 the *veneer side grafts* produced very good results. In 1958 the buds burst on all the grafts, which were left undisturbed for 3 or 4 weeks so as to permit observation of this phenomenon. In 1959 the result was slightly inferior, three grafts being dead when the time came for transplanting into beds. Eight grafts, all with scions from Röskär 3, had not developed any shoots even by that time, but the needles of the preceding year were a lush green. Seven of the grafts developed shoots during the course of the summer, whereas on the eighth, although still green, the terminal bud was dead, and there were no visible newly formed buds even in the autumn.

The *side slit grafts* all healed, but they were generally weak.

Fig. 16 shows in principle how the lower part of a well-cut *veneer side graft* appears in a cross-section and a semi-tangential longitudinal section immediately after grafting. Fig. 17 shows in a radial longitudinal section the two methods of cutting the stock flap already presented in Figs. 3—4 and 6—7 respectively. The higher up on the stem, the more superficially are the components affected by the graft cuts. Both the veneer side graft series were carried out according to the method demonstrated in Figs. 6—7. Grafts, 1 and 2 years old, performed according to the other method of fashioning the bark flap (Figs. 3—4) have also been investigated, as well as 1 to 3-year-old grafts of the type used in the series.

Fig. 18 shows drawings of *side slit grafts* in cross-section, a and b corresponding to the graft methods shown in Figs. 10—11 and 12—14 respectively. The series comprising 20 grafts was carried out according to the first method.

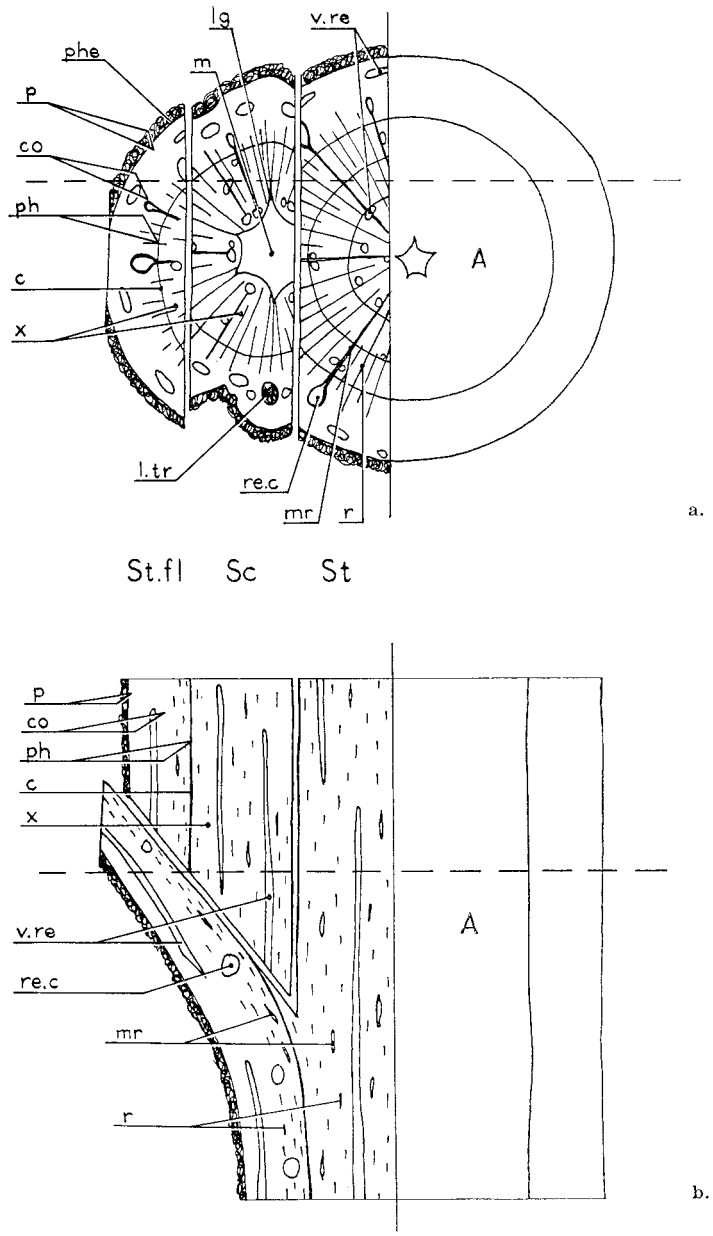


Fig. 16 a and b. Cross section and semi-tangential section respectively from the lower part of a veneer side graft (Scots pine). The dotted line marks where the two sections touch each other. Key to signs on page 135.
A = part of the stock cut away before fixing.

Tvärsnitt resp. semi-tangentiellt längdsnitt från nedre delen av läggymp (tall). Den streckade linjen markerar var de båda sektionerna berör varandra. Teckenförklaring på sid. 135.
A = vid fixeringen bortskuren del av underlaget.

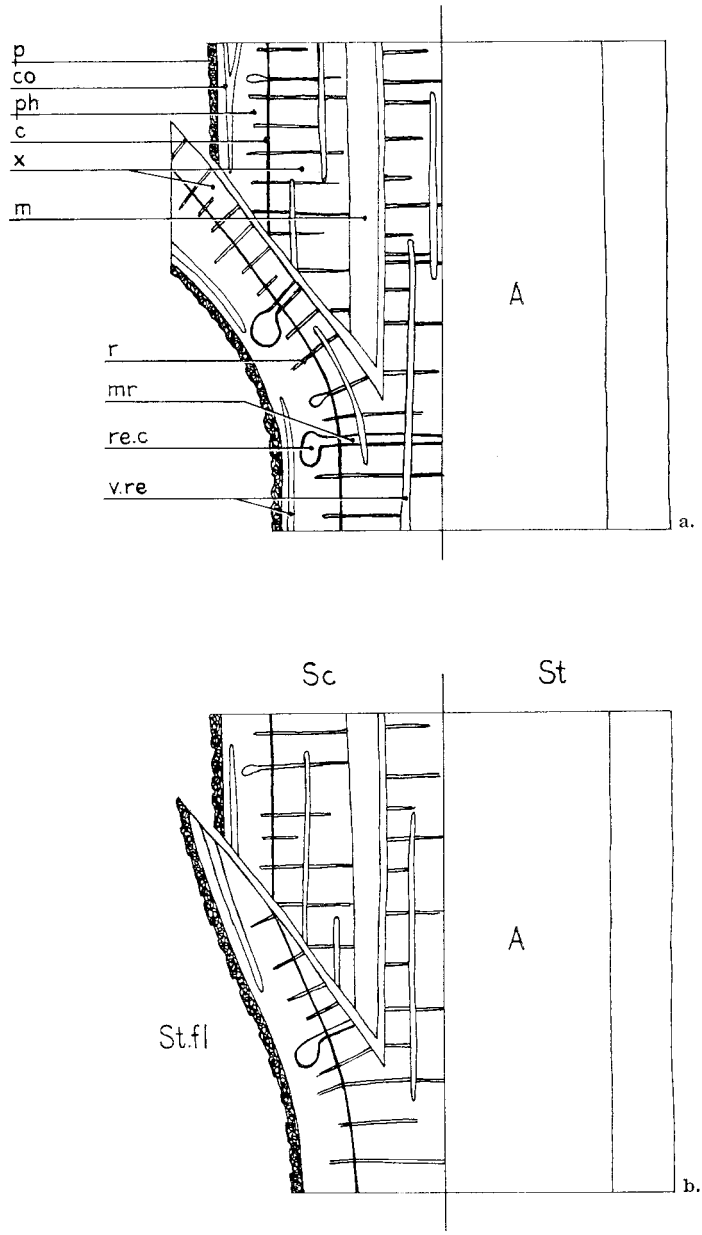


Fig. 17 a and b. Radial sections from the lower part of veneer side grafts.
a. Stock flap cut upwards.
b. Stock flap cut downwards.
Key to signs on page 135.
A = part of the stock cut away before fixing.

Radiära längdsnitt från nederdelen av läggympar.
a. Underlagsfliken tillskuren med uppåtriktat snitt.
b. Underlagsfliken tillskuren med nedåtriktat snitt.
Teckenförklaring på sid. 135.
A = vid fixeringen bortskuren del av underlaget.

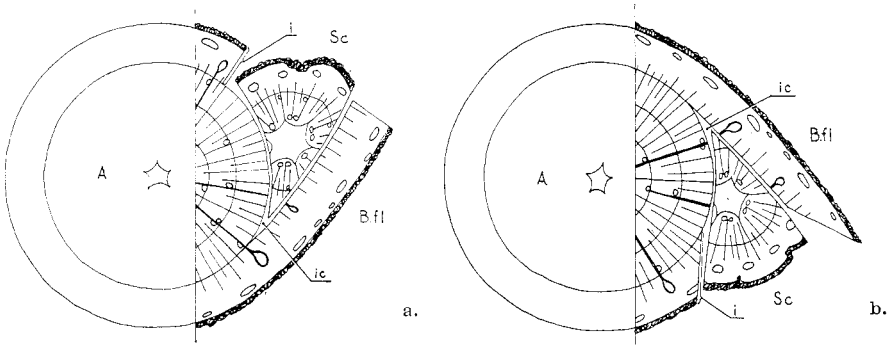


Fig. 18 a and b. Cross sections from side slit grafts.
a. Radial incision in the stock bark.
b. Tangential incision in the stock bark.
Key to signs on page 135.
A = part of the stock cut away before fixing.

Tvärsnitt av sidsticksympar.
a. Radiärt insnitt i underlagets bark.
b. Tangentiellt insnitt i underlagets bark.
Teckenförklaring på sid. 135.
A = vid fixeringen bortskuren del av underlaget.

B. The normal course of union

1. Insulating dead tissues on the cut surfaces of the scion and the stock

However well the components have been cut and tied, there is always some space between them almost everywhere, and it is only in spots that they are pressed close together. Comparatively large contact surfaces occur between the flap of the stock and the scion in veneer side grafts. The wedge-shaped lower part of the scion forces the flap outwards. The flap and the short cut surface of the scion are consequently pressed against each other. The bark flap of side slit grafts possesses great flexibility. The binding will affect it so that it attaches closely to the surface of the scion.

The first reaction immediately visible to the naked eye while the grafting is proceeding, is the extrusion of *resin* from the severed resin ducts. The resin partly fills the space between the scion and the stock. No investigations have been made in this context into the part resin plays for a successful grafting. However there is nothing to show that the resin constitutes a barrier between the graft components. On the contrary it may serve as a sealing—grafting may be carried out successfully without the sealing by grafting wax (KIELLANDER 1946, GARNER 1958, LESKINEN 1960). The fixing fluid and alcohols used in the preparation of the material have dissolved the resin almost entirely, and thus removed it from the slides. This problem will be dealt with further in the discussion.

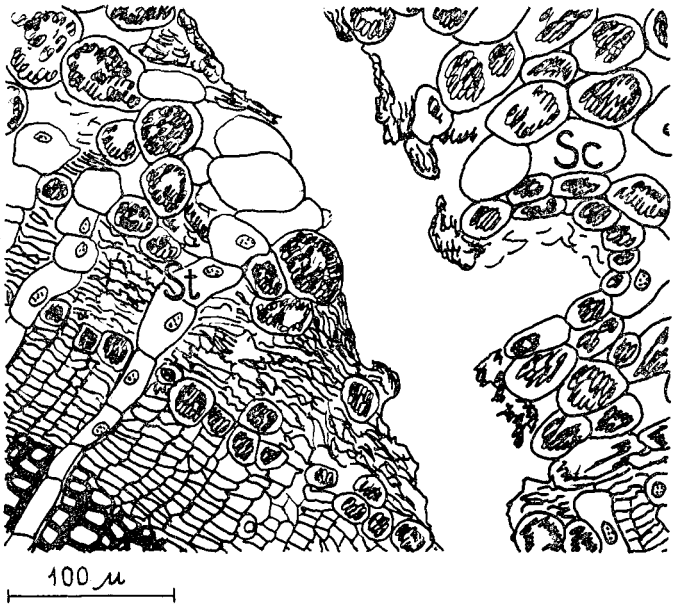


Fig. 19. 1 day. Cross section—camera lucida drawing. Enlarged ray cells outermost in phloem of stock. Contact layer over the rest of the wound surface.
1 dag. Tvärsnitt. Teckning efter preparat. Förstorade stråleceller ytterst i floemet hos underlaget. Isoleringsskikt på sårytan i övrigt.

A continuous, more or less heavy layer of wounded and dead cells soon forms on the cut surfaces of both the components. The thickness of this *contact layer* depends on several circumstances. The first day after grafting the contact layer is most noticeable in places where cells or entire cell groups have been damaged by cutting. It is most clearly distinguished in the *cortex* and *phloem* of the stock. In the phloem, all the sieve cells adjacent to the cut surface, also those in the functional phloem, will form part of the contact layer. Some of the fine-structured cells of the *cambial region* are always damaged by the graft cut. In side slit grafts some of the cambial cells in the stock become damaged when the bark flap is loosened from the wood, and some are chrushed when the scion is inserted between the wood and the flap, and when the graft is tied. If the grafting knife is sharp, and if, by fast and accurate work, the cut surfaces have not been exposed to long drying, it is often possible to find rays, the outer cells of which appear to be fairly unaffected by the cutting. Sometimes the cells are already noticeably enlarged one day after grafting. Fig. 19 shows a cross-section with a ray in the stock which was cut at the periphery of the phloem. Outside the ray (at the top in the illustration) a rather heavy

contact layer is visible in the cortex, and on the inside there is a thick layer of non-functional phloem.

In the outer parts of the cortex there is often a number of cells which gradually suberize and wither. This layer definitely reaches its greatest development in the stock, where it is also first visible. Plate V: 4 shows an example of an eight-day-old graft. Suberization of old cells (*i.e.* cells fully developed before the tissue was wounded) has been observed in the cortex only. The fully developed wound periderm in the cortex contains both old and recently formed suberized cells. This matter will be discussed further in the chapter "Phellogen formation".

Callus tissues, of whatever kind they may be, soon cover their own surface with a thick or thin (depending on the position) cork layer (periderm) if they do not reach immediate contact with other parenchyma tissues.

It is also possible to speak of *primary* and *secondary* contact layers. The first category is entirely composed of cells present in the tissues before the wounding. They include cells which have been damaged directly or indirectly by the operation, and cells (in the phloem) which are incapable of dividing. The secondary contact layer, however, is a product of recently developed tissues formed only when so located that they have no possibility of uniting immediately with other tissues.

Vertical resin ducts occur abundantly in the cortex. When the grafting cut severs such a duct, a large number of the epithelial cells are exposed without being touched by the knife, *cf.* scion in Fig. 19. There is consequently no contact layer formed by damaged cells from the outset. The same holds true for the resin cysts at the ends of the horizontal resin ducts. The vertical resin ducts are generally more abundant in the scions, whereas the resin cysts are more numerous in the stocks.

The *pith* is often exposed in the scion. Here severed cells and some less active cells will compose a contact layer.

A continuous contact layer can never be formed in the *xylem*, at least not in the sense indicated earlier. The tracheids are dead cells after full differentiation. The living part of the wood is composed of rays, resin ducts and strands of parenchyma cells around the resin ducts. When damaged, they too will naturally develop a contact layer on their surface in the same way as found in other parenchyma tissues. The occurrence of *tyloses* (parenchyma cells expanding through the pits of adjacent tracheids) in tracheids near the cut surfaces should perhaps be discussed in this context. In some cases it has been observed that old tracheids contain both cell plasma and nucleus, and at a closer study, also a thin cellulose cell wall pressed up against the wall of the

tracheid. This must be interpreted as a formation of tyloses from the rays, or from the parenchyma strands around the vertical resin ducts. This does not appear to be a common occurrence in pine grafts (*cf.* RAATZ 1892, DANIEL 1928). CHRYSLER (1908) has found tyloses in cones of Scots pine after wounding, but never in the stems of the species.

When proliferation and cell division start, the growing cells will push the dead tissues in front of them until the tissues from both the graft components meet, when their contact layers will fuse. The existence from the outset of a joint contact layer (naturally composed of parts from both sides) is found in places where unlignified parts have been placed very close together in the grafting, *e.g.* the bark flap and scion pith in Plate X: 6. To attain a complete union the contact layers must somehow be broken by pressure or by absorption. A contact layer of dead cells is often broken by underlying proliferating cells which enter the space between the graft components. There they may establish connection with cells formed in the same way from the other component. Growing cells from the one component may also affect the contact layer of the other and break it.

The remnants of the contact layer in grafts already healed are therefore mostly scattered over a rather large area of a section, and they cannot provide any exact information as to where the union first occurred, or which cells originate from the one or the other side. Fig. 20 is a drawing of a section of a 28-day-old graft, the same as shown in Plate VI: 6. The remnants of contact layers have been marked specially. In one to two weeks younger grafts in Plates V: 12 and VI: 3—4 the contact layers are easily discernible.

2. Cell enlargement

As mentioned in the preceding chapter, enlargement is the first visible reaction of living cells. This enlargement is most conspicuous in the epithelial cells of severed resin ducts, particularly in the vertical ducts in the cortex of the scions. The stimulus to enlargement of the epithelial cells extends over a sizeable part of the duct above the place of wounding. Plate III: 1 shows a wounded resin duct in the scion of a two-day-old graft, where the cells in the interior edge of the duct are enlarged. Some distance further up the duct is no longer cut, but enlarged epithelial cells are still evident. Approximately 120 μ from the section in Plate III: 1, where the duct is entirely filled with cells, a fork has developed. Both the main duct, now relatively far from the wound surface, and the small branch duct are filled with cells even at a point about 40 sections,

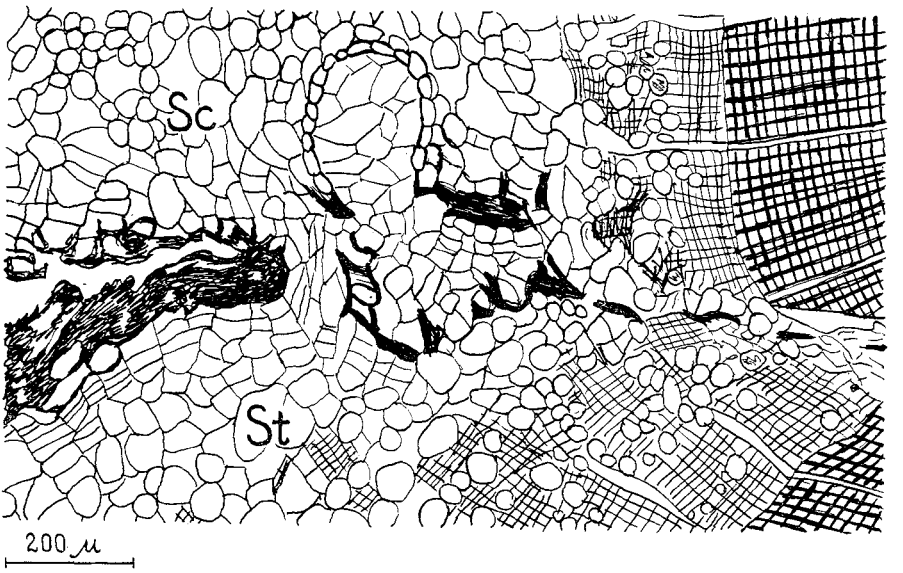


Fig. 20. 28 days. Cross section—camera lucida drawing. Good parenchyma union. Expanding tissues from stock and scion have broken the contact layer. Remnants (strongly marked in the drawing) pushed in different directions. *Cf.* Plate VI: 6, a photo from the same section.

28 dagar. Tvärsnitt. Teckning efter preparat. God parenkymatisk förening. Expanderande vävnader från båda ympkomponenterna har brutit upp isoleringsskiktet. Resterna (kraftigt markerade på teckningen) förskjutna i olika riktningar. Jfr fotot från samma snitt, pl. VI: 6.

i.e. 600 μ, above the point where the duct was wounded. Plate III: 2 shows the 50th section from the point of wounding and here the cell enlargement is most persistent on the side of the duct facing the wound surface. This has also been observed in a large number of grafts. The photograph in Plate III: 3 is taken from a longitudinal section through the lower part of a three-day-old graft. The section passes through the centre of a vertical resin duct in the scion cortex. This resin duct has been almost cross-cut in the grafting. The epithelial cells have enlarged and closed the duct entirely.

Severed rays, too, may display cell enlargement at an early stage (Fig. 19), both the uniseriate and multiseriate rays containing resin ducts as well as the cyst-like terminals of the latter (Plate III: 6). Cell enlargement may occur also in other parts of the cortex besides the resin ducts. The section shown in Plate V: 4 was obtained from an eight-day-old graft where a ridge of the type occurring below the short shoots (needle pairs) has been cut through. Throughout the entire length of the cut ridge, approximately 1 mm, the cells adjoining the wound surface have entered into the space between the components by enlargement, and

divisions, too, have occurred in these outer cells. Sometimes cells underneath the wound surface also enlarge considerably. The further course of the healing process in the cortex is discussed under the heading "Phellogen formation".

In the cambium, it is only the rays that undergo immediate, noticeable enlargement. The wound surfaces of the stock in side slit grafts consist of exposed cambium, where the first reaction of living cells is manifested as an enlargement of the ray cells. Plate XI: 2 shows a longitudinal section through the lowermost part of the graft zone. Cells enter into the empty space from a ray on the wood side. In Plate XI: 4 a cross-section shows how cells intrude from a multiseriate ray on the phloem side. In the scions the reaction of the epithelial cells of the resin ducts is the same as that described above in connection with the veneer side grafts.

The cell enlargements are less distinct in the pith.

3. The first cell divisions

The next stage in the development is that the enlarged cells adjoining the wound surface, and cells situated several layers inside begin to divide. It is quite usual to find cell divisions 3 or 4 days after grafting, particularly in the rays of phloem and cambium. In a couple of cases divisions have occurred in an equally short time in the pith of the scion. Divisions in other active parts, such as resin ducts and resin cysts in cortex and phloem respectively, as well as in ordinary cortex cells, mostly start somewhat later than the divisions of the rays in the same individual. Divisions in both the stock and the scion occur at an early stage, in many grafts even earlier in the scion than in the stock during the initial stage. This is rather remarkable, since the scion was in complete dormancy at the time of grafting, whereas the stock was so far advanced that new shoots had developed, and even some cambial activity in the form of newly differentiated tracheids was discernible in some individuals.

Plate IV: 1 shows a scion (veneer side graft) four days after grafting. A ray has been cut near the cambial zone, and two nuclei are discernible in different stages of division. Several divisions were observed in the rays of the scion of the same graft, and a couple of divisions in the same tissues of the stock. Two more veneer side grafts, four days old, were investigated, but no divisions were noticeable. Resin ducts in the cortex in the lower parts of the grafts, however, were entirely filled with cells, and division had probably occurred.

Plate II: 6 shows an entire cross-section of a five-day-old graft. In the upper side of the scion, a leaf trace is found close to the wound surface. Several rays emerging from the leaf gap have been severed in the grafting, and the cell division activity is very vigorous here as well as in the external cortex. Examples of this activity are given in the two following photographs. The cut shown in Plate II: 7 was situated 23 sections below that in Plate II: 6. One cell at the extreme end of a ray has enlarged, and the nucleus is dividing, while a nucleus in the cambial region of another ray has just divided, and a new cell wall is being established between the daughter cells. Plate II: 8 originates from a point 42 sections above that in Plate II: 6. Here the leaf trace has moved far out in the cortex. A cell containing chlorophyll and located immediately inside the trace is dividing. A total of approximately 20 cells in division has been found associated with this leaf trace. Most of the sections studied show clearly that several divisions have occurred earlier in the region of the leaf trace. During this great activity of the scion not one cell division has been observed in the opposite tissue of the stock. On the other side of the graft, towards the bottom of the full-view photograph, Plate II: 6, no divisions have been found in either component, but a cut resin duct filled with cells has been observed in the scion. Here, too, a leaf trace is discernible, although so far away from the wound surface that rays emerging from the gap have escaped being cut in the grafting.

Plate IV: 2 originates from the lower part of a six-day-old graft where the cambia of the components have not fitted together at all. In both the flap and the main part of the stock, one side of the cut cambium borders on the pith of the scion. In the flap opposite the pith, one cell in a ray is dividing, and in the same ray two daughter cells from a newly divided cell can also be seen. A dividing cell is found in the pith as well. Many divisions were observed in the following sections both in the pith and on either side of the stock opposite the pith. Higher up, where the matching of the cambia is slightly better, divisions occur in the rays of the scion. Plate III: 5 shows a resin duct from the same scion filled with cells and Plate V: 1 a dividing cortex cell. In the cortex of the stock, too, divisions occurred.

The eight-day-old graft in Plate III: 6 exhibits callus formation in a resin cyst of the stock. Plate III: 4 shows a longitudinal section from the lower part of the scion of a seven-day-old graft with a vertical resin duct in the cortex filled with cells, and with one cell rather high up in the duct in process of dividing. Originating from the same graft, the

cross-section in Plate IV: 4 shows an enlarged ray cell in the stock in process of division.

The middle cells of the rays are the most active in forming callus. Plate VI: 1 shows the appearance of proliferating rays in the phloem in a tangential section. Their middle cells have shown the most activity, and the initially uniseriate rays have expanded and become fusiform.

It happens that cells in resin ducts and rays of the xylem sometimes divide and develop callus abundantly. Plate IV: 7 gives a general view of the lower part of a graft, seven days old, with a severed vertical resin duct on the left side of the stock. Plate IV: 8 shows in higher magnification the area immediately below the scion. The cells in the resin duct have enlarged and are dividing, and a telophase can be seen in the photograph. It is not unusual to find callus developed from parenchymatous tissues in the xylem of the stock, from the rays, particularly from the multiseriate ones, and from vertical resin ducts; this is less usual in the scions. Callus is sometimes developed in the scion from severed leaf gaps in the xylem.

Side slit grafts investigated show early and vigorous division activity in both of the components. Plate X: 6 is a high magnification of a cross-section of a four-day-old graft where the bark flap touches the cut pith of the scion. Divisions are visible in a ray cell of the flap (telophase) and in a cell in the pith of the scion (metaphase). Plate XI: 2 originates from the same graft and shows proliferation from the wood side of the stock. Plate XI: 4 shows proliferation in both multiseriate and uniseriate rays on the phloem side. The stocks have consistently displayed great activity in the inner part of the corner. Mostly the cells of both the phloem side and the xylem side participate. Likewise most of the divisions in the scions occur in their inner part. Examples are shown in Plate X: 7—a division at the extreme end of a ray—and in Plate XI: 5—a division in the cortex just on the boundary of the phloem. (Divisions at the boundary between the phloem and the cortex have been a common occurrence in all the grafts investigated. It is often difficult to determine to which of the tissues a cell belongs. This matter will be dicussed in the following paragraphs.)

No divisions have been observed on the wood side of the stock where the wood of the scion has been closely pressed onto the stock. When the pith of the scion has been cut on the side facing the main part of the stock (the wood side), divisions are found in the stock opposite the cut pith, *vide* Plate XI: 3. In most cases the exposed pith, too, shows activity. On the side of the radial incision into the stock, called here the *incision face* (*cf.* Fig. 18 a), divisions also occur in rays and in

the cortex at an early stage. Plate XI: 6 shows an initial uniseriate ray at the incision face of a six-day-old graft where several divisions have occurred.

In the scions of side slit grafts, cell division activity generally starts later in the external parts of both of the cut surfaces (outside point 3 and 4, see Fig. 21) than in the other parts. Both of them have usually had poor contact with proliferating tissues in the counterpart. The resin ducts at the wound surfaces in the cortex, however, are already at an early stage clogged by expanding epithelial cells.

The cells of the *cambial region*, except for the ray cells (see above), are remarkably inactive during the inital stage of callus formation. Gradually, however, when divisions have started in the surrounding cells (rays) and the cambial activity has begun in the undamaged adjacent parts, a certain amount of division seems to begin also in the cambial region close to the wound surface. (This refers to *veneer side grafts*, but it is also applicable to *the scion of side slit grafts*. The course of development is slightly different in the stock of side slit grafts; see below.) In the immediate proximity of the wound surface, the fusiform initials and the xylem and phloem mother cells show repeated, transverse divisions (*cf.* NEEFF 1914). The divided cells then behave as other parenchyma cells near the wound and sometimes give rise to large callus masses. The cells of the cambial region are not able to participate in the callus formation until this transformation has taken place. The transformation is by no means always complete. A junction of callus cells originating from tissues external to the cambium has often occurred before the callus formation from the cambial region has become of major importance.

Plate IV: 5 shows a tangential section from the lower part of a nine-day-old graft. The scion is cut in the outermost part of the wood, and at the bottom the cut reaches the undifferentiated cells. They have divided into small irregular daughter cells, which now begin to differentiate. In the stock, the lowest part of the cut has reached outside the cambial region, the cells of which have developed into an irregular mass of callus by divisions in all directions. In the cross-section shown in Plate IV: 6 from an eight-day-old graft, irregular parenchyma cells can be seen in the cambial region of the stock. Plate IV: 3 shows a radial section from the upper part of a seven-day-old graft where the cut has touched the cambium of the stock, and where a couple of rays end in the area. Yet all the undifferentiated cells appear to be active.

Initial callus formation from the cambial region has been seen to occur only from cut rays in this area. However, when a large mass of

callus has already been formed, it is impossible to identify the cells which initiated the division. Moreover, it is not unusual to find unions between cells of cortical and phloem origin (rays) after 10—15 days, whereas hardly anything has happened in the cambial region.

Conditions are slightly different in *the stock of side slit grafts*. The bark has been loosened from the wood in the cambial region in which some cells have been destroyed. The proportion of cambial cells adhering to one or the other side varies. When the still undifferentiated xylem cells adhere to the wood, it is at least possible to study how they participate in the callus formation at the innermost part of the corner (Plate X: 8). Proliferation virtually never occurs from the areas where the cut wood of the scion is attached to the wood side of the stock, not even from the rays, *vide e.g.* Plate XII: 3, 5 and 6. If the pith of the scion has been cut on the side facing the wood of the stock, however, the callus formation from the latter often becomes vigorous, and both ray cells and other cells in the cambial region participate, *cf.* Plates XI: 3 and XII: 5. On the phloem side, too, cells other than those of the rays may divide. The photographs in Plate X: 10 and 11 are examples taken from a 12-day-old graft.

One type of parenchyma has not yet been mentioned, *viz.* the *vertical phloem parenchyma*. Almost without exception these cells contain tannin, which gives them a dark colour in a fixed material. Initially their cross-section area is not larger than that of ordinary phloem cells, but accordingly as they are pushed outward by the cambial growth, they are enlarged in the same way as the ray cells. They may react in a parallel way at an earlier stage if tissues in their immediate proximity are wounded. Plate X: 9 shows an entirely intact part from a stock. Other portions of the same stock are visible in Plate X: 10—11. The magnification is the same in all these photographs. It can be seen clearly that the last formed parenchyma cells in the phloem are considerably enlarged in both sections shown in Plate X: 10—11. ABBE & CRAFTS (1939) have found in *Pinus strobus* that by renewed meristematic activity the phloem parenchyma cells jointly with ray cells successively develop the cork cambia which form the phellem in the outer bark. The dark colour of the cell contents renders direct observation of divisions in these parenchyma cells more difficult, but it is easy to establish that these cells are able to participate in the callus formation—the cells containing tannin produce files of cells of the same kind, *cf. e.g.* Plate XIII: 3 and 9. In side slit grafts it is not unusual for the division activity in the bark flap to start a good distance inside the

wound surface. A continuous meristematic layer is formed jointly by the ray cells and the phloem parenchyma, *cf.* Plate XII: 5.

It has consequently been established that all living cells in Scots pine possessing an active cell nucleus have a possibility to divide under the influence of the stimulation initiated by wounding. (The reservation "possessing an active cell nucleus" has been added with due consideration to the functional sieve cells which have living cell plasma, whereas their nuclei degenerate at an early stage. This also applies to the albuminous cells of the rays in the functional phloem.) A compilation of the cell division intensity in various tissues in the proximity of the wound surfaces during the first period after grafting is presented as a supplementary to the corresponding chapter on spruce (Table 1, p 77).

4. Phellogen formation

Matters concerning the formation of periderm on the wound surfaces in the cortex will be treated here in close context.

The reactions to be seen in the cortex of the stock and scion after grafting are similar to those which occur when the stem has been wounded superficially. Divisions may develop in every undamaged cell close to or immediately underneath the wound surface.

Enlargement of cells close to the wound surfaces is a rather common occurrence in the scions, and divisions in the cells that enter the space between the components also occur. Plate V: 4 shows cells of this kind advancing from the scion side, while Plate V: 5 shows a division of a superficial cell in the same scion. Cells located immediately underneath the wound surface may also enlarge, and the first divisions produce cells that enlarge strongly and push the external dead tissues outwards. Plate V: 8 shows an example where 13 days after grafting proliferation has been vigorous in both components. Callus formation of this extensive kind from the cortex has been observed in connection with leaf and branch traces only. In Plate V: 8 the section through the scion passes immediately below the level where a leaf trace is leaving the stele; in the stock a branch trace has proceeded outwards and in the present section its main part is in the outermost part of the cortex. A leaf trace in the scion in Plate XII: 2 has been split. A callus mass of a similar kind has entered from the phloem-cortex boundary. It is not always, however, that the proximity to leaf and branch traces causes such callus formation in the cortex as described, although the appearance of traces near the wound surfaces mostly gives rise to increased cell division. Essential conditions for an extensive callus formation

are that the atmosphere around the wound shall be kept humid, and that the wounded surface is not exposed to drying for any length of time during the grafting.

It is much more usual for the first divisions to occur some distance inside the wound surface both in the scion and in the stock (Plate V: 2—3). However, they have no definite angle to the wound surface. This is evident from the divisions shown in these two photographs and from divisions studied in a large number of other sections (see also Plate V: 1 and 5). Nor is there any specific place in the cortex where the cells are at first to divide. The first divisions in the cortex occur within 4—7 days.

Some days later a continuous strand of actively dividing cells can be observed inside the wound surface. This strand runs fairly parallel with the wound surface, see Plate V: 6. Contrary to the very first divisions described above, most of the divisions in this meristem occur parallel to the plane of the latter. This meristem will function in the same way as an ordinary phellogen and produce a number of cell rows in either direction. Outermost in the cortex, junction is attained with the phellogen present there, which, however, plays no active part in the formation of the new phellogen on the wound surface. No divisions have been observed in the cells of the old phellogen in the early stage, and not until some time after the new phellogen has been formed does a union of the two parts occur.

Deeper in the cortex, where the actively dividing layers are more superficially located in both scion and stock, junction is soon established between the newly formed phellogens. In the 13-day-old veneer side graft, from which Plate V: 7 is taken, definite phellogen union has been established over rather long distances on one side. The union is so good that it must in fact already have taken place at least a couple of days earlier. The junction of cortical cells occurs 10—20 days after grafting in places where the fit of the graft components renders junction possible. This union does not immediately take on the character of a continuous phellogen, the first cells to attain contact with each other being more in the nature of an irregular callus. As soon as the junction has been established the cells in the region of unification participate in the organized dividing activity which characterizes the phellogens on both sides. Plate II: 4 shows a good union of phellogens.

When the first divisions are superficial and a certain number of large, irregular cells has been formed, the phellogen is established inside these cells. The first cells formed will thus constitute a part of the layer which is insulated from the inside stem by the phellogen. Plate V: 8

shows how phellogen is established at the base of the callus tissues in both components. The same process is going on in the scion shown in Plate XII: 2, where vigorous divisions occur in one plane at the base of the callus mass. An example of a slightly older graft (17 days) is shown in Plate V: 9. Large, deformed cells occur outside the phellogen of the stock, and in the scion the phellogen has been developed through a resin duct which was first filled with cells. It sometimes happens that cells in the part of the cortex which will later constitute a portion of the layer insulated by the phellogen enlarge and divide a couple of times, after which their activity ceases.

It was said in the chapter dealing with the formation of contact layer that the layer of dying cells in the cortex generally was heaviest in the stock, where it also first became clearly visible. Similarly the divisions which produce the phellogen also start deeper in the stock than in the scion. The reasons for this may be several: 1) In most cases a piece of the cortex in the stock is not covered by the scion, and is therefore subject to exposure and withering. 2) The cortical tissues of the stock are older, at the time of grafting three or four years old, whereas the scion is only one year. 3) The stocks are forced, their annual growth is in full progress, and their water consumption is therefore high in comparison with that of the unforced scions. The first reason cannot be excluded entirely, but may be regarded as only a contributory cause: divisions may start superficially also in the scion when it is displaced in relation to the stock, *cf.* Plate V: 6, whereas the phellogen is formed at some distance inside the wound surface of the entirely covered stock. Divisions in the outermost cells of the wound surface are rare in the cortex of the stock, and enlargement of old cells pushing them forward in front of the wound surface has never been observed. The second explanation may appear to be the most plausible one—the young cells of the scion have superior vitality. It should be added, however, that a distinct phellogen with clearly developed derivatives mostly occurs earlier in the stock, where the supply of water and nutrients from the roots is superior. Comparative investigations of graftings with forced and unforced stocks are needed to provide a definite answer as to the importance of whether or not the stocks are forced.

When the stock and the scion do not cover each other in the cortex so completely that a union of newly formed phellogens is possible, the phellogen proceeds by differentiation of the callus originating from cells located deeper in the stem, primarily from the phloem rays. In side slit grafts this occurs regularly in both stock and scion at the union of bark flap and scion, as well as at the incision face. In the grafts investigated,

the incision face has rarely been entirely covered by the cut surface of the scion. Here phellogen develops even in callus tissues originating from the cambium. This also happens in the part of the scion facing the wood. The tissues, which then endeavour to heal the wound on both sides, are covered with heavy layers of cork which have to be penetrated before union can be achieved (Plate XIII: 9). All exposed living tissues are covered in the same way. Plate VIII: 4 shows a two-year-old graft where union has been achieved on one side during the first year, whereas no connections have been formed on the other side, in spite of vigorous growth in both of the components. This growth has so far only had the effect of pushing the original graft components apart.

At the union of scion and stock it often happens that large, dead pieces of tissue are embedded and isolated from the living tissues by cell layers of the same appearance as that of the phellogens at the exposed wound surfaces, *cf.* Plate V: 10.

5. *Further callus formation and the union between parenchymatous tissues*

It has been stressed repeatedly in the preceding chapters that the intensity of cell division may vary widely in the different parts of an individual. Leaf and branch traces appear to be active elements which stimulate divisions in adjacent tissues when wounded. Divisions start very soon in rays emerging from leaf gaps. Activity seems to be particularly vigorous in the boundary between the phloem and the cortex outside a leaf trace, as shown in Plate V: 11. The ridge located in the cortex below an emerging leaf trace belongs to the more active parts. Active leaf traces no longer exist in the stocks, but the few branch traces that occur near the cut surfaces may also be surrounded by active tissues in the cortex. This great tendency to develop callus around branch and leaf traces also provides better possibilities for a rapid union of the graft components where such branch and leaf traces are present at the wound surfaces (Plates V: 8 and XII: 1). A vigorous development of callus from the scion at an early stage is nearly always connected with a leaf trace.

The first union (transfusion windows) in veneer grafts usually occur between cells that originate from rays outside the xylem (uniseriate as well as multiseriate rays and the resin cysts at the ends of the latter) and from the cortex and its resin ducts. The unions occurring at an early stage between cortex-derived tissues were discussed in the preceding chapter. It is quite usual for junctions of this description to be the first

to occur. Unions in the cortex may for a long time be the only ones that occur over large parts of a graft.

All the cells that are formed initially near the wound surfaces are of a parenchymatous nature, and, given the necessary conditions, they all possess the same inherent possibility of achieving union with the newly formed cells of the counterpart. It is consequently not unusual to find junction between cells that may originate from widely different parts of the stem if tissues of the same kind have not been fitted together from the outset. Concerning veneer side grafts, unions of callus tissues originating from rays in the phloem of one component and from the cortex (ordinary cortex cells or resin ducts) of the other are a common occurrence. Plate V: 12 shows a longitudinal section of a 14-day-old graft where a vertical resin duct is cut axially in the cortex of the scion. It is entirely filled with cells which have subsequently united with newly formed cells from the rays of the stock. In the section shown in Plate VI: 2, union has occurred between the cambial region of the scion and the cells of a resin cyst in the stock flap. Junction of cells originating from the pith of the scion and from the stock bark flap, especially the rays, is common in side slit grafts, *e.g.* Plate X: 11. In this type of graft, union also occurs regularly between callus tissues from the cortex of the scion and from rays of the bark flap (Plate XII: 4). In Plate IV: 2 a junction of parenchyma cells in a ray of the stock flap and the pith of the scion is just about to be established in a veneer graft.

In places where tracts of cortex and phloem are pressed against each other (cortex—cortex, cortex—phloem, phloem—phloem), union may occur by a comparatively small number of divisions, and large callus formations never occur there (Plates VI: 3, II: 4). Unions of large parts of the wound surfaces can never occur simultaneously, since the thickness of the contact layers and the ability of cells of the various tissues to divide vary a great deal. For this reason remnants of the contact layers are always found between the places where breakage has occurred a long time after the first union. Depending on which side has been proliferating most vigorously, pieces of the contact layers are pushed to one side or the other (Plate VI: 6 and Fig. 20). The three-week-old graft, from which the section in Plate VI: 3 is obtained, differed in appearance at different levels. Sometimes a more vigorous callus formation had occurred, as in Plate VI: 4, but generally union had been established at an early stage on both sides of the graft, sometimes between tissues originating from the cortex, sometimes between tissues from the phloem and the cambial regions, or with a couple of transfusion

windows simultaneously, as in the sections photographed. Plate VI: 5 shows a section through the centre of the graft at the exposed wood surface—there is no callus tissue between them. It is quite usual to find that no cells have been formed between the wood surfaces when the junction on the outsides is rapid. Plate VI: 11 shows an example from a six-month-old graft.

When the cut surfaces of the stock and the scion have not been properly fitted, the result is nearly always a callus formation which is larger on one side, the least favoured side. (Endeavours have always been made when grafting to fit the cambia to one side if the scion has been weaker than the stock.) The scion is then extruded from the stock, and a large slot is formed between the wood surfaces. The callus mass penetrates between the wood surfaces *e.g.* as on one side of Plate VI: 10. Proliferation from the pith of the scion, from cut leaf and branch traces in the wood (Plate IX: 4), from xylem resin ducts (Plate IV: 8) and from xylem rays (Plate VI: 7—8), may contribute towards filling up the space. However, it cannot always be said that it is the presence of a large space that initiates great proliferation in parenchyma cells of the wood. In the four-week-old graft shown in Plate VI: 7—8, the rays and the resin ducts of the stock have formed large masses of callus. Before fixing, the lowermost part of the graft was split into two halves, one of which was cross-sectioned, and the other longitudinally sectioned. Plate VI: 8 shows one of the cross-sections. The largest mass of callus has been formed at the boundary between the last annual rings. The longitudinal section in Plate VI: 7 passes through the other cut edge of the same annual ring. These masses of callus have no connection with the parenchyma or the cambial layers external to the wood. Plate VI: 7 shows the formation of a strand of cells of a cambial character in the middle of the callus, with subsequent divisions producing cells of a more uniform shape. The scion has been pushed outwards by the vigorous callus formation, and there are only a few weak points of union between the main part of the stock and the scion in the cortex region. Higher up, where the annual ring boundary in the stock was not cut and the callus formation remained less intensive, the junction of parenchyma in cortex and phloem was good. The union of the stock flap and the short, obliquely cut surface of the scion, however, showed the greatest advance (*cf.* the next chapter).

The ability of the stock to proliferate from parenchyma in the wood has appeared to vary considerably. To a certain degree this apparently depends on the path of the cut—whether specially active parts have been cut, as in the graft shown in Plate VI: 7—8, the boundary of

the last annual ring, or, as in Plate IV: 8, a large resin duct. A cut annual ring boundary, however, does not always produce callus, *cf.* Plate VI: 11. A comparison of the appearance of the annual ring boundaries in Plate VI: 8 and 11 reveals quite large dissimilarities. In Plate VI: 11 the transition from the wood of one annual ring to that of the following is fairly even, and it is possible to follow the rows of tracheids straight through the boundary areas. In Plate VI: 8, on the other hand, the border between the annual rings is interrupted. Broken rows of tracheids are interpolated by parenchyma cells. This behaviour is the consequence of some damage done to the cambium, probably caused by drying in connection with the potting in the previous spring. Several of the stocks potted simultaneously exhibit the same defect. There were thus more parenchyma cells than normal at the periphery of the annual ring, which might explain the great ability to produce callus.

In the scions the power of the wood and pith parenchyma to form callus varies, even among scions originating from the same tree.

When the cut on the stock of a veneer graft has been so superficial that it touches the cambium only, the space between the components is always filled, mostly by tissues emerging from the rays that have been cut (Plate VI: 9), but also by the intrusion of tissues from the outer edges. In the upper parts of the graft zones, the cuts are usually superficial.

In the side slit grafts it is less common that rays and other cambial cells located in the stock opposite the cut xylem of the scion form callus. A large portion of the parenchyma cells at the wood surface become crushed when the scion is inserted and tied. At the point where the pith of the scion has been exposed opposite the wood of the stock, however, callus formation, as mentioned earlier, occurs. This proliferation opposite the cut pith seems to indicate that the contact with living cells in the pith may initiate divisions in the rays and in incompletely differentiated xylem cells in the stock. Another possible explanation may be that several cells have been destroyed where the wood of the scion has been pressed against the stock. The space for proliferation has then been rather limited, at least immediately after grafting and until callus formation in more active areas has occurred to such an extent that the scion has been raised from the stock as shown in Plate XIII: 1. There are many instances where activity in one graft component has influenced the other component to formation of callus and differentiation of the newly formed cells. Plate VII: 5 shows an example from the lower part of a veneer graft, where parts of the scion phloem and cortex have been placed between wood elements in the stock. A branch trace has been

cut in the latter, and the effect on the callus formation in the scion is clearly visible.

We have seen earlier how the junction of parenchyma may be effected by a few cell divisions on both sides when parts capable of proliferation are closely fitted together. When very active portions are cut, however, cell division immediately becomes so vigorous that the mass of callus is able to push the graft components apart before union has been established. The firmer the binding, the earlier the union. Thus when a large space between the wood surfaces has been formed by vigorous proliferation in the outer sides, the callus tissue intrudes and fills the space, in so far as intensive divisions in the wood parenchyma and in the pith of the scion have not occurred simultaneously. When the parts of the graft components that are able to proliferate and unite (areas outside the wood cylinder) have been less satisfactorily fitted together, a large formation of callus always occurs before union has been possible. A space between the wood surfaces which is filled with intruding tissues is then a natural consequence. This is practically always the case in side slit grafts where the insicion face has never been fitted closely to the phloem and cortex of the scion (see Fig. 18 a). Callus tissue enters the space between the wood surfaces both from the outer side and from the vigorously proliferating tissues in the innermost corner. Plate XII: 6 shows a 17-day-old graft where the innermost corner is entirely filled with callus. The stock has formed phellogen at the incision face and a vigorous callus formation has been initiated in the scion, which, if continued, would have forced the scion outwards. The large space between the wood surfaces would then be filled with callus from both edges, and the whole graft would finally have about the same appearance as that of the graft shown in Plate XIII: 10.

The tissues formed in different ways between two exposed wood surfaces (alternatively the pith of the scion) and their fate when engulfed by the cambia will be discussed in chapter V: D.

6. Union between vascular tissues

a. *Veneer side grafts*

After parenchyma union has been established, the coalescence of the cambia of the graft components is the next stage in the progress towards the complete healing of the graft wound.

In places where the cambia of the graft components have been well fitted together and where the union of parenchyma has occurred at an early stage in the surrounding area, it is possible after three weeks,

sometimes earlier, to observe how short, more or less deformed tracheids have differentiated close to the contact layers between the components. There is no real junction between these newly differentiated cells. Plate VII: 1 shows a longitudinal section of such a contact area between the scion and the main part of the stock in a 17-day-old graft (the contact surfaces have become separated during preparation of the material). In sections from superficial parts of the same graft there are good parenchyma unions. Plate VII: 2 is a cross-section of the flap side of a three-week-old graft. Newly differentiated tracheids occur on both sides, and the contact layer has just been broken outside the cambial region, and a transfusion window has been formed.

In all grafts investigated where the buds of the scions have begun to burst, the union of cambia has started.

At the time of the grafting the cell divisions in the cambia of the stock had in most cases started, but only little growth had taken place, possibly one or two rows of tracheids. At approximately the end of the next three weeks, when fusion of the cambia of the two graft components was about due, several rows of tracheids had been established and the cambia thus moved outwards. The cambial activity was mostly very moderate in the scions, partly because the scions were in dormancy at the time of grafting, and partly because of the reduced supply of water. If the cambia of the components are fitted accurately at grafting, it happens that the cambium of the stock grows away from the scion cambium. This is illustrated by some drawings in chapter V: E (Fig. 32 p. 73). Plate VI: 5 shows an example of a three-week-old graft where the cambia had originally been fitted closely together on one side (on the left in the photograph), while on the other side the cambium of the scion had projected beyond that of the stock. Now, it is instead on the last-mentioned side that the cambia are accurately placed and a bridging might soon occur, whereas on the left side the increment of the stock has forced them far apart. The cambium is pulled slightly forward when a leaf trace emerges from the wood cylinder. Plate VII: 3 is obtained from a section slightly subjacent to the section in Plate VI: 5. A leaf trace in the scion has been severed with the result that the cambia have nearly united on the side where the cambium of the stock has departed from that of the scion by faster growth in other parts of the graft.

The leaf traces are able to effect union between vascular tissues on their course through the phloem and the cortex. Plate VII: 4 shows a longitudinal section which has passed peripherally through a leaf trace in the scion. Contiguous to the contact surface of the stock there are

some recently differentiated, short tracheids. (In other sections of the same series the newly formed tracheids will be seen in contact with the main tracheids of the trace.) Here the graft cut of the stock has passed through the cambial region. Straight opposite the leaf trace, tracheids have been differentiated in the stock, but this is not the case with the rest of the cut-surface. Plate VII: 6 gives another example of the power of one graft component to influence the cells of the counterpart to differentiate (the photograph is of a section just outside that shown in Plate VII: 5). Opposite the cut branch trace in the stock wood, tracheids are differentiated in the callus tissue of the scion. No connection was observed between the stele of the scion and these newly differentiated tracheids.

Plate VII: 7 is a longitudinal section of the same four-week-old graft and shows a part of the union between the scion and the stock flap. The cambial strand differentiated in the flap has united with the cambium of the scion, and tracheids from both of them lie close to one another without any contact layers in between. No union between cambia or between newly differentiated tracheids in the scion and the main part of the stock has been observed. The vigorous callus formation from wood parenchyma in the stock of this graft, discussed in the previous chapter (p. 46), has forced the scion outwards. This effect, however, was greatest in that part of the graft which was longitudinally sectioned. Here union has been established only in the cortex. In the cross-sectioned part (Plate VI: 8) a junction in the cambial region is imminent.

Cross-sectioning puts a great deal of strain on the cambia and on still weak unions in the cambial region. The heavy parenchyma junctions in the cortex and the phloem usually remain firm, whereas the first xylem unions easily rupture. Breaks often occur also in the cambium. The transition from soft to hard material (easy and hard to cut respectively) in combination with firm union in the external parenchyma causes a collapse in the cambial region when cross-sectioned, *e.g.* Plates II: 4, VIII: 1. Longitudinal sectioning does not produce a similar strain, because it follows the direction of the tracheids.

Plate VII: 8 shows a complete fusion of cambia at the flap of a five-week-old graft. Here the cambia have started to produce united vascular tissues—both xylem and phloem. Vascular unions with the main part of the stock have also occurred in this graft, but they are so weak that they have been damaged in the sectioning (Plate VIII: 1). The parenchyma unions in the same section are now so complete that the union zone is difficult to detect, but some remnants of the contact layers are discernible. (See the arrows.)

It is only in places where the cambia are well matched that the union is as easily achieved as outlined above. When the cambia are farther

apart, the picture becomes more complicated. A broken cambium induces adjacent parenchyma cells to undergo dedifferentiation and resume division. The entire process has been described by BRAUN (1958), see pp. 14—15 above. Thus the cambium extends by induction from one cell to another laterally as well as vertically (upwards and downwards) through the callus tissue. It may therefore appear in a single cross-section as if no junction had occurred between a meristematic strand and a rather closely situated cambium. Upon studying adjacent sections, however, it becomes apparent that union has been established.

This does not imply that influence from an existing cambium is a prerequisite for the formation of cambium in a mass of callus. Many scientists working with callus cultures (*e.g.* BALL 1950, GAUTHERET 1957, STEWARD *et al.* 1958) have shown that a stele may be formed gradually in a callus mass even when separated from the mother organism. Even in the absence of contact with external tissues, cambia may also occur in callus masses which have been formed between the wood surfaces of the graft components. The meristematic strand shown in Plate VI: 7 is probably a preparatory stage before the differentiation of cambial derivatives has been initiated (see also chapter D).

It is definitely clear, however, that a cambium strand originating in a callus mass in front of a broken cambium is a result of an induction from this old cambium. Plate VII: 10 shows how the cambium of the stock has turned outwards to establish contact with that of the scion. Plate VII: 11 is another section from the same graft, approximately 2 mm below the previous one. Here, too, a union is achieved between meristematic strands from both sides. In the section first mentioned, tracheids have been differentiated in connection with the cambium of the stock. In the last-mentioned section there are newly formed tracheids in tissues originating from a leaf trace in the scion. No junctions, however, have occurred in any of the adjacent sections between the new tracheids developed from both components; only various degrees of parenchyma union and part unions of cambial strands and of phellogen. Plate VI: 2 shows how callus from the cambial region of the scion has united with the callus in a resin cyst in the stock flap. A strand of elongated meristematic cells now passes through this callus tissue in the direction of the stock flap cambium, and a union of the strands from both sides is established. Originating from the scion differentiation of tracheids has started in the stock flap callus close to the junction with the scion.

The nature of the undifferentiated callus cells is the same wherever they are developed. Each broken cambium tends to expand in an

adjoining callus tissue, and when a union is established with callus of different origin, the cambia advance from both sides through the tissues, irrespective of their origin. It also seems possible that a stimulus may be transferred through parenchyma tissues from one edge of cambium to another, thus influencing the directions of the expanding cambia.

The direction of the cells in the union zone has been studied also in longitudinal sections. Even in very smooth unions the direction of the first cells to unite is oblique. Tracheids of anomalous shape may be knotted together onto cyst-like formations with a number of parenchyma cells in the centre, which often constitutes a point of origin for new rays. The direction of the tracheids is with few exceptions from the scion downwards to the stock, and to a minor extent from the stock upwards to the scion (Plate IX: 3). This point will be further discussed in chapter VII: E.

In the cases described above, the cambial union has taken place without interference, in spite of the relatively large distance between the cambia. Plate VIII: 2 shows an example where the cambial fitting between the main part of the stock and the scion was initially good. The callus formation has been vigorous in the stock, but weak in the scion. A firm binding has forced the callus mass to extrude towards the scion, some tissues of which have been compressed. It is noticeable how the heavily pressed cambium of the scion has produced compressed tracheids arranged in oblique rows. The cambium of the stock has followed the callus mass outwards, but turns in towards the advancing cambium of the scion.

A parenchyma union with the other graft component and its cambium, however, should not be regarded as a prerequisite condition for the subsequent turning inwards of a cambium that initially turns outwards. In a normal wound-healing process, too, the cambium usually turns outwards first, because of the stronger tissue formation at the edge of the wound. Very soon, however, it deflects inwards to follow and cover the wood surface. On one side of Plate VIII: 3 (at the top of the photograph) the union of the cambia of the scion and the stock, both in the main part and in the flap, has taken place in the same way as shown in Plate VIII: 2. On the opposite side junction has been established on the flap side only. There the cambium of the main part as well as in the union zones previously mentioned has first turned outwards and then inwards. A clear difference, however, can be observed: In the union zones in the upper part of Plate VIII: 3 the first cells to turn inward are laterally extended toward the scion but in the lower part the cells have their normal vertical orientation. In Plate VIII: 2 the undifferentiated cells in

the cambial union are extended towards the scion cambium. It appears as if the cell orientation in these cambial bridges is influenced by the cambial region of the counterpart. Wherever cambia become united laterally by differentiation of connecting parenchyma tissues, the cells extend in the way described above.

No real unions between vascular tissues occurred in the seven-week-old graft shown in Plate VIII: 2, but the parenchymatous unions were mostly satisfactory. The rather vigorous growth in the scion cambium (7—8 rows of tracheids in Plate VIII: 2) has been possible without any junction with the vascular tissues of the stock.

The cambial activity is always more vigorous near a wound surface than in the rest of the stem. This has been observed in many previous investigations (*e.g.* HERSE 1908) and is also confirmed here. In the scion, too, the cambial activity close to the wound starts earlier than in the other parts. The cambia of the graft components usually meet at a certain angle. Through the more vigorous cambial activity at this point, the angle is soon filled, and the united cambia form an even cylinder round the two components, *vide* Plate VII: 9.

When the cambia are located far apart and a meristematic strand is developed through a uniting callus mass, its derivatives in the zone of union usually retain their parenchymatous nature longer than the contiguous cambia. Differentiations on the xylem side are easier to study in an early stage of development than those on the phloem side. Undoubtedly the junction on the phloem side, too, is frequently maintained by parenchyma cells, even when united tracheids have developed on the xylem side. There are, however, examples indicating the reverse. Plate VII: 12 shows a detail of the zone of union eight sections above that shown in Plate VII: 10. Union of the newly differentiated tracheids on both sides has not occurred, but on the phloem side, the union is complete and sieve cells are differentiating. The nuclei of the new sieve cells have started to degenerate (at this stage they are heavily stained by safranin).

When the stock flap is cut as shown in Fig. 17 a (*cf.* also Fig. 30), union between the flap and the scion can take place in lateral direction only. Straight inward-upwards there is a piece of the stock wood which constitutes a barrier. All the newly formed cells in the stock flap will therefore be directed towards the edges where the unions occur. This also applies to the scion in places where its cambium fits up with the wood surface of the flap. Plate X: 1 shows a longitudinal section passing near the centre of such a graft. The longitudinal axis of the newly formed cells in the flap has not the same direction as that of the cells formed during the previous year. Most of the new trach-

eids are cross-sectioned or obliquely sectioned, whereas the older ones are cut longitudinally. Plate X: 2 shows the heavy growth at the outer edge of the union zone of the same graft. On the other hand when the stock flap has been cut as shown in Figs. 17 b and 31, union can occur between the whole of its cambium and the cambium along the entire short cut surface of the scion. A successful union then has the appearance as in Plate X: 5, which shows a section through the centre of the graft. Complications that may arise during union with the flap will be discussed further in chapter V: E.

To obtain a sucessful grafting result, it is not necessary that cambial unions or even parenchyma unions shall be established on both sides of the graft during the first growing season. When the scion is smaller than the stock, the cambia have always been fitted rather accurately on one side, and often at least if the cut surfaces differ greatly in size, the graft components unite on one side only. Several years may then pass until union on the other side is established. The newly formed tissues in both components cover their surfaces with heavy cork and a great deal of force is needed to break this layer (see *e.g.* at the top of the photograph in Plate VIII: 4).

In the upper parts of the graft zones, and occasionally also in some places further down, both the stock and scion may heal over their own cut wounds without uniting with their counterpart. The scion must be completely united with the stock at some point to be able to further growth. Gradually, however, the pressure becomes so great that the cork layers are broken. The living cells underneath the cork layers appear to be able to contribute to the breakage by decomposition and absorption of cork material. Plate VIII: 5 shows both sides of a two-year-old graft some distance above the middle of the graft zone. On the side turned downwards the cambia were united in the second year, whereas only parenchyma junctions occurred on the other side. Plate IX: 1 is obtained still further up. The wound surfaces of both the components have been healed over in the first year. Increasing pressure has forced the cells to turn outwards, and the cork layers have broken at the point where the pressure was heaviest. During the next growing season, the cambia would have united. The union proceeds here in the same way as the union of so called natural grafts, where two stems with closed cambial rings have been pressed against each other. The cambial ring divides, and the two edges turned outwards to unite with the cambial edges of the counterpart. A rather interesting phenomenon concerning the direction of the cells has been observed in a couple of cases, in which a cambium has divided and

united with that of the other component. Cells developing straight opposite the counterpart are parenchymatous, horizontally elongated (like the ray cells), and arranged with their long axis towards the other graft component. On the sides of this "division layer" the cambia have turned outwards (*cf.* Plate IX: 2).

Generally there are two possibilities for a union of the cambia in a veneer graft. 1) The broken cambia of both components are so close to each other that an almost direct bridging may occur. Only a few, short cells produce the first parenchyma union, and the new cells adhering to the broken cambia of the components continue to divide. The divisions in the union zone soon acquire the same character as that of the adjacent cambia in the stock and the scion. 2) Meristematic strands from the cambia of both parts develop towards each other through a conjunctive parenchyma tissue. The two growth processes described cannot be clearly distinguished.

b. *Side slit grafts*

The cambial union takes place principally in the same way as in veneer side grafts, except that the picture mostly becomes more complicated because of the differences in the mutual position of the cambia. After grafting by the method used in the series investigated (radial incision in the stock), the first cambial unions are obtained with the part of the scion cambium seated in the inner corner. Mostly it is in the lower part of the graft zone that the first cambial union is established. If, however, the scion has been shaped so that no cambium is left in the lower part of the wedge that is inserted between the bark flap and the wood, the first unions occur higher up, where cambium is present in the inner part of the scion.

The union of the cambia in the corner is seldom entirely free of complications. After the grafting, the cambium of the stock may be found more or less intact on the phloem side (flap) or the wood side. The major portion of the cambial region follows the flap when the cambium is in the active stage at grafting, which was the case in most of the grafts investigated. Some of the cambial cells may be damaged in grafting, so that no complete cambium is present in the corner of the stock immediately after the operation. The scion has two free cambial edges directed inwards to the corner, one faces the wood side of the stock, the other its flap. (To facilitate the discussion of cambial union in side slit grafts, these two cambial edges and the other two places where the cambium of the scion may be exposed have been numbered from 1 to 4

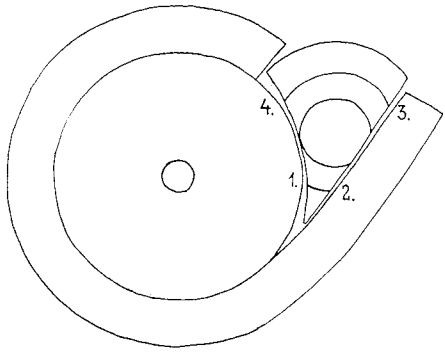


Fig. 21. Side slit graft. The four places where the scion cambium may be exposed are numbered. *Cf.* Plate XI: 1.
Sidsticksymp. Numrering av ympkvistens fyra blottade kambiekanter. Jfr pl. XI: 1.

according to the drawing in Fig. 21.) The width of the part of the scion cambium which faces the corner (distance between 1 and 2), appears to have been important for the mode of development of the connecting cambial strand in the corner.

In the 20-day-old graft shown in Plate XII: 7, the stock cambium has followed the flap and produced some tracheids and sieve cells in the inner part of the flap. A meristematic strand running in an arch towards the cambium of the bark flap, has emerged from the part of the scion cambium (1) which faces the wood side (*cf.* Fig. 22 a). No tracheids have differentiated, and divisions appear to have ceased in the part of the bark flap located between the point of union with the meristematic strand from the scion cambium 1 and the point of contact at 2. At point 2 the cambium of the flap has nearly united with that of the scion, and has developed some groups of tracheids, which have no connection, however, with the newly formed tracheids in the scion. In the flap cambial activity and differentiation is apparent also in the contact with the scion pith. Further out in the flap and external to the scion pith, there is no continuous meristem (Plate XII: 8). Solitary parenchymatous unions occur at point 3. Plate XII: 9 originates from a section approximately 2 mm above the previous ones. Here the corner is not entirely filled with cells. The stock cambium follows the flap, and (beyond the limits of the photograph) it turns inwards in the same way as in Plate XII: 7. In this and the following 200 sections (3 mm) there was no union between the stock and the scion at point 2. At a higher level, union was again established by the advancement of tissues from the scion between the flap and the scion wood, which connect a meristematic layer further out in the flap. Still higher up, Plate XII: 10,

tissues from the scion at point 2 are seen protruding underneath the flap, although meristem is lacking at its inner surface. Divisions have started farther out in the phloem of the flap in the same way as in the graft shown in Plate XII: 5.

In the 24-day-old graft shown in Plate XIII: 1, the major part of the inner corner has been filled with callus from all directions. Plate XIII: 2 is a detail of an adjacent section showing the union of cambia at point 2. United vascular tissues are also present. Meristematic strands had developed in several places in the callus masses at the corner. It was still impossible to determine which one of them would take the lead at various levels. Both sections have been obtained from the middle of the graft zone. Lower down, where the inner part of the scion was smaller, cambial strands developed from point 1 in the same way as shown in Plate XII: 7.

When there is no cambium on the inner part of the scion, the cambium in the stock mostly follows the flap, as shown in Plate XIII: 4. Deviations from the straight course of the cambium may occur if tissues in the flap have died, as in Plate XIII: 3, which was obtained from a section lower down on the same graft. (Plate XIII: 3 is located 2.5 mm from the bottom of the scion, Plate XIII: 4 approximately 11 mm above.) In the lower part of the graft zone the phloem side has contributed vigorously to the callus formation in the corner. Meristematic strands have developed in several places in the callus, particularly in the parts at the bottom of the grafting zone (Plate XIII: 3). The leading strand follows the flap. Plate XIII: 3 also shows a complete union of the scion and the stock at point 3. The cambium of the scion spreads into the flap. The cell layers situated between this and the meristematical strand in the inner part of the flap are more of a phellogen character. About 1 mm above the section just discussed there is no longer any union at point 3, and the phellogen continues unbroken inwards to the pith of the scion.

No vascular tissues have yet been developed in connection with the cambial strands in the lower part of the graft (Plate XIII: 3). The vigorous tracheid formation higher up (Plate XIII: 4) from an almost normally active cambium consequently has no connection with the tracheids in the stem underneath—except laterally.

Approximately 4 mm above the section in Plate XIII: 4, cambium is present in the inner part of the scion (Plate XIII: 5). Emerging from point 1 of this cambium, meristem extends in an arch similar to that shown in Plate XII: 7. The stock cambium, however, passes unbroken along the side of the inner corner in the flap, and the meristem

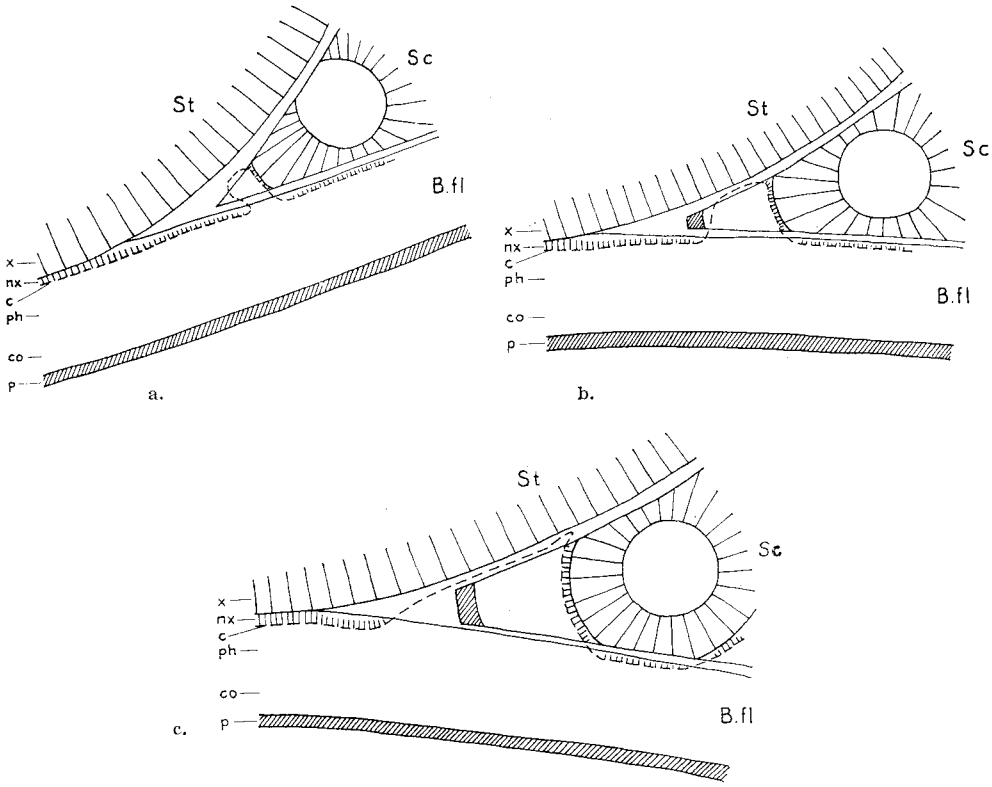


Fig. 22 a—c. Side slit grafts. The principle of the cambial union in the innermost corner. At grafting the stock cambium accompanies the bark flap. Callus tissue fills the corner (not shown in the drawings).

a. The inner part of the scion is narrow. The cambium at pt. 1 (*cf.* Fig. 21) extends semicircularly towards the cambium of the flap. Between their point of union and the less complicated union at pt. 2, the cambial activity in the flap is suppressed.

b. The scion is wider. The cambium in the corner forms a wider arch.

c. Still wider scion. Long distance for the cambia to bridge.

Key to signs on page 135.

Sidsticksympar. Principen för kambiernas förening i inre vinkeln. Vid ympningen följer underlagskambiet med barkfliken. Kallusvävnader fyller vinkeln — ej markerat i teckningarna.

a. Ympkvisten smal i sin inre del. Kambiet vid pt. 1 (se fig. 21) utbreder sig halvcirkelformigt mot kambiet i fliken. Mellan deras föreningsställe och den mer okomplicerade föreningen vid pt. 2 undertrycks kambieverksamheten i fliken.

b. Ympkvisten bredare. Kambiet i vinkeln beskriver vidare båge.

c. Ännu bredare ympkvist. Lång sträcka för kambierna att överbrygga.

Teckenförklaring på sid. 135.

from point 1 has instead joined up with the scion cambium at point 2. Immediately above, however, the cambium in the flap has been broken. The meristem strand from point 1 has reached the stock cambium in the same way as described earlier (*vide* the section shown in Plate XIII: 6 which is located 0.3 mm above the one in Plate XIII: 5). At

point 2 complete union has been established between vascular tissues. Plate XIII: 7 shows a section at a further 1 mm higher level where the meristem from point 1 has taken a shorter path toward the stock cambium. The wider the cambium of the inner part of the scion, the wider is usually the arch formed by the meristem from point 1, see Fig. 22. When the inner part of the scion cambium is wide, a large portion of the external tissues are involved as well: phloem, cortex, and portions of cork. The cambia usually unite inside a large mass of this kind. Tissues of a phellogen character are developed around the dead parts by the phellogen present in the scion and by the ray and phloem parenchyma in the flap. In most cases the phloem elements in the flap that have been in contact with the cork also become incorporated in the dead tissues, and thus become isolated from the organism.

When the stock flap is loosened from the wood at grafting, it may happen that a large portion of the cambium adheres to the wood surface, particularly at the innermost corner. This frequently occurs when the cambial activity has not yet started. In such cases the cambium follows the wood surface and turns towards the scion at point 1. Plate XIII: 8 shows an example from a six-week-old graft. The scion cambium at point 1 has first turned inwards to achieve contact; at point 2 it has turned towards the flap, which contains a complete cambium united with that of the scion at point 3. A more vigorous cambial activity in the stock occurred in this graft only in the graft zone and contiguous to it. In the rest of the stem there are at most only signs of initiated differentiation in the first tracheid row of the year. This is shown by a photograph of the region of the incision face (Plate XIII: 9).

It usually takes rather a long time before junctions are established between the incision face of the stock and the scion at point 4. The cambia are far apart, and tissues capable of division are seldom placed exactly opposite each other. The Plates XII: 3 and 6, XIII: 4 and 9 show examples of the mutual position of the cambia of scion and stock at the stock incision face and the scion at point 4 in different grafts. All the photographs originate from sections 10—16 mm above the base of the scion. When the wound tissues established on both sides have no possibility of uniting, they develop a cover of cork layer. Growth, however, continues in the cambial regions. At point 4 the scion is lifted from the wood surface of the stock by its own proliferation. Callus enters from this point between the graft components, and the same tissue from other sources may also assist. Callus from the cambial region of the incision face may also enter the space. Masses of callus tissue from both sides will eventually unite. A union has thus been

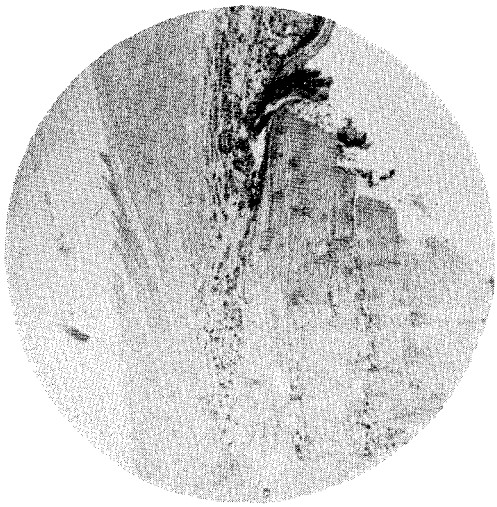
established in the eight-week-old graft shown in Plate XIII: 10, and the cambium has entirely encircled the graft zone for a short distance. In this case the scion has not been inserted to as great a depth as in several of the grafts shown previously. In many grafts union at the incision face may occur at the lower part of the graft zone where the scion has usually been placed more superficially than at the upper part, *vide* Plate XIII: 3.

The first cambial union in side slit grafts carried out according to the method shown in Fig. 18a occurs between the cambia in the flap and the inner part of the scion. If the flap is entirely loosened from the stock, which is usually the case when a stock is in growth at the time of grafting, the cambium follows the flap to begin with. It is soon broken, however, by a meristematic strand emerging from the scion cambium at point 1. The scion cambium at point 2 establishes direct union with the cambium of the flap. The latter gradually develops further, and eventually establishes connection with the cambium of the outer part of the scion at point 3. Cambial union usually occurs at the incision face only after a long time has passed, when extensive formation of tissues from both sides has taken place.

7. The healing of the cut stock

After the scion has started to manifest firm union with the stock by developing new shoots, the stock is trimmed successively. When the growth of the scion is good, the stock is already cut back entirely in the first summer; otherwise this is postponed until the next season. The last piece above the scion is removed by a slanting, upward-pointing cut. The wound surface heals in much the same way as that of the wounds left by lopped branches. Callus masses enter from all sides over the exposed wood surface. Some photographs will be shown here of grafts as they appear three growing seasons after grafting (the stocks were cut back in the second season).

Figs. 23—26 are all from the same graft. An almost radial section through the centre of the graft is shown in Fig. 23 where only a slight extrusion of the external tissues of the scion is visible. The next photograph of a section 0.4 mm outside the previous one shows, however, that these extruding tissues are not the ones that are going to produce the layers covering the wood surface (Fig. 24); instead the covering tissue originates principally from the stock itself. The next section (Figs. 25—26) has been taken a further 0.6 mm closer to the periphery from the upper and the lower side of the oblique surface respectively. The callus mass on the upper side is extensive here, and the cambium



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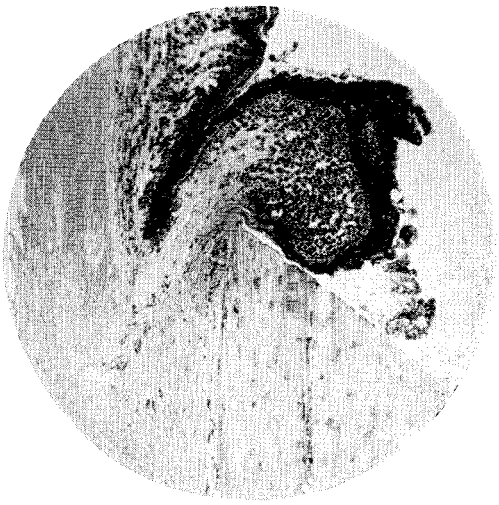

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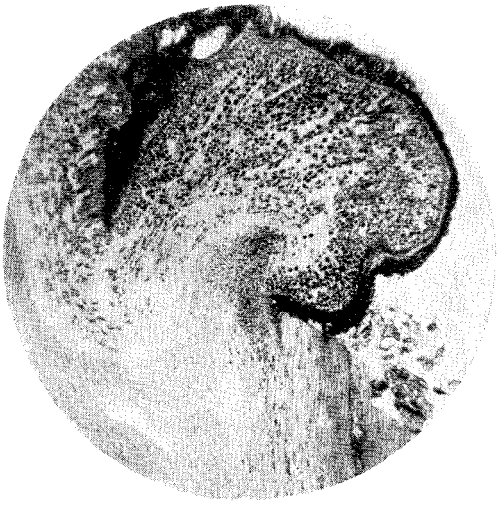

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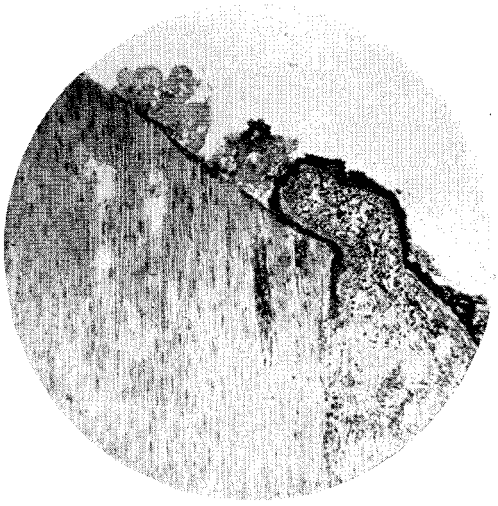

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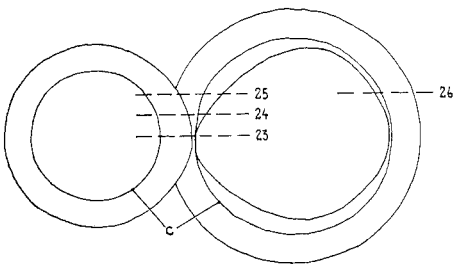
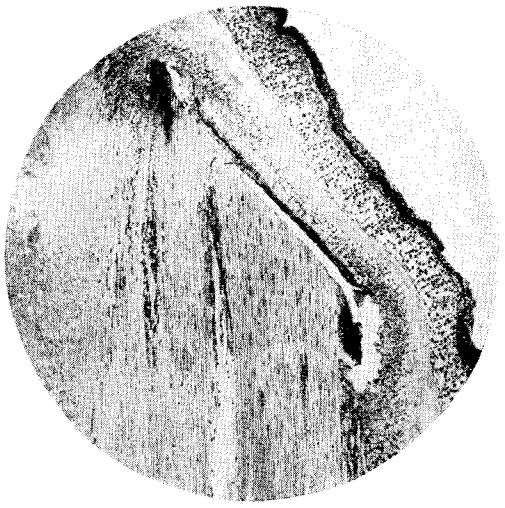


Figs. 23—26. Healing over the cut stock of a 3-year-old Scots pine graft. Longitudinal sections. × 22.5. The drawing shows position of photographs as seen in a cross-section. 23: No healing at all. 24: Healing tissue originates from the stock only. 25: Most vigorous growth from the outermost part of the stock in contact with the scion. 26: Poor healing at side turned away from scion.

Övervallning av det avskurna underlaget hos 3-årig tallymp. Längdsnitt. × 22,5. Skissen visar snittens läge i ett tvärsnitt. 23: Ingen övervallning. 24: Övervallningsvävnaderna härstammar från underlaget självt. 25: Kraftigaste tillväxten i yttre kontaktområdet med ympkvisten. 26: Svag övervallning vid den sida som är vänd från ympkvisten.

27.



28.

Figs. 27—28. Healing of the cut stock of a 3-year-old Scots pine graft, somewhat more advanced than that shown in Figs. 23—26. × 16.5. 27: Cross-section—lateral healing. 28: Tangential longitudinal section—complete healing.
Övervallning av det avskurna underlaget hos 3-årig tallymp, något längre kommen än den i fig. 23—26. × 16,5. 27: Tvärsnitt. Övervallning i sidled. 28: Tangentiellt längdsnitt. Fullständig övervallning.

in it has begun to extend. Callus tissue has started to grow over the wood surface from the lower side of the stock facing away from the scion. Straight opposite the latter, the healing is still very slight, but becomes increasingly vigorous on the sides.

The sections shown in Figs. 27—28 are obtained from another graft where the healing was slightly more advanced. Tissues from all sides will eventually cover the entire wood surface. The cambial edges unite, and a closed stem will be developed as shown in Fig. 28. Fig. 27 shows a cross-section from the lateral healing rather high up on the oblique surface.

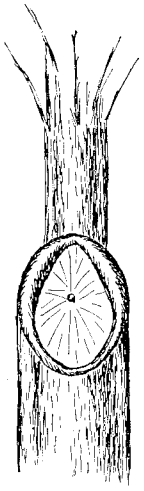


Fig. 29. Healing of the wound surface of the cut stock.
Övervallning av sårytan hos det avskurna underlaget.

The healing over has always appeared to be most vigorous from either side of the stock (right and left as seen from the scion) and slowest from the side facing away from the scion. The drawing in Fig. 29 shows the progress of the healing as seen from the outside.

Parenchyma in the wood can never participate in these growth processes, since the few living cells that occur at the cut surface will immediately wither and die. For the

same reason there are never any connections between tissues in the old wood and the healing masses, which are moreover covered by an insulating cork tissue themselves.

C. The terms intermediary tissue and callus

The term intermediary tissue (intermediäres Gewebe) used for tissues located between two graft components, was first introduced by GÖPPERT (1874). The term was accepted by OHMANN (1908) and SORAUER (1875, 1921). The latter, however, preferred the term "Kittgewebe", but the meaning of the word remained rather obscure. The original term, intermediary tissue, was again used by KRENKE (1933) and in the sense of the word applied by him, adopted by BRAUN (1958), as well as SEVEROVA (1958), and others.

Regarding union after splice grafting of two *Sorbus* species, GÖPPERT wrote on p. 2 in his treatise that union was achieved by means of a rather thick-walled parenchymatous tissue. In the second year the annual rings in the two branches had united directly and enclosed this cell tissue.

Because of its connecting properties and its position, he called the tissue "intermediäres Zellgewebe". When he subsequently showed intermediary tissue in his illustrations, they always referred to old grafts and tissue seated between the originally exposed wood surfaces of the grafts. OHMANN used the term intermediary tissue exclusively for tissues between the two wood surfaces.

SORAUER's definition of "Kittschicht" is to be found in his "Handbuch der Pflanzenkrankheiten" (in the 4th edition on p. 825): "Das neu entstehende, teils von der Unterlage, teils vom Edelreis gelieferte Gewebe, welches die Verkittung der beiden künstlich verbundenen Glieder bewirkt, wird 'Kittschicht' oder, nach GÖPPERT, 'intermediäres Gewebe' gennannt." An account of SORAUER's concept of wound callus and "Kittschicht" formation in bud grafts and rind grafts was given in the literary review (p. 7). In his account of grafting tissues located between two exposed wood surfaces were also called "Kittschicht".

KRENKE explains on pp. 356—357 in his treatise *his* concept of intermediary tissue. He definitely denounces the words "Kittschicht" and callus in this connection. He might possibly accept the term primary callus (according to his classification of callus tissues quoted below) but he was of the opinion that the regeneration tissues developed after grafting differ from those produced at the healing of an open wound.

The term intermediary tissue (or "Zwischengewebe"), however, would indicate both its place of formation and its morphological and physiological importance—it is a true intermediary stage before subsequent differentiation.

In the preceding account of the process of union I have intentionally avoided the word intermediary tissue or any other term that would distinguish the new formation at the wound surfaces of grafts from those contiguous to other wound surfaces. On the contrary, there seem to be no fundamental differences. It has appeared that all cells, irrespective of their origin, have the power to effect union of graft components, and to obtain union with cells in the other graft components whatever their origin may be. Vascular cambia as well as cork cambia may develop in tissues of any origin. It is true, certainly, that new formations between two graft components may assume different appearance to that of the callus at an open wound surface. The callus tissues in grafts have a relatively protected position against excessive drying. More tissues than those which usually profilerate in an open wound participate in the callus formation, *e.g.* the wood parenchyma and superficial cells in the cortex. The new cells are often large and have thin walls. Differentiation occurs in callus tissues independent of their position—in the junction of a graft or in an open wound.

KRENKE states (*loc. cit.*, p. 357) that union of two graft components can occur not only by means of the intermediary tissue mentioned but also by means of true callus in the periphery of the graft wounds. This statement was apparently not founded on any of his own observations. KRENKE worked only with herbaceous plants, and he was consequently only rarely confronted with phellogen formations in the cortex. It is probable, therefore, that the formation he thought to be "true callus in the periphery of the graft wounds" was actually callus produced by the cortex, which finally brings about a healing of a phellogen type.

HERSE, too, stated that no distinction could be made between callus and what he called wound cork. I myself would prefer to define a callus formation as a "wound cork" or a "wound periderm" when the divisions in it have assumed a regular pattern. A phellogen has thus developed, and suberized products have been deposited externally.

Tissues between exposed wood surfaces did not occur in KRENKE's herbaceous graft material. These tissues are originally of the same character as all other newly formed tissues at the wound surfaces. It is only the conditions for their further development that change when the cambia close up on the outside. They will then remain as real intermediary tissues such as observed by GÖPPERT.

KRENKE defined callus as follows: "Kallus ist jede durch Wundreizung hervorgerufene interorgane Bildung, die durch Wachstum und Zellteilungen enstanden ist". The same author also considered all living cells capable of participation in the formation of callus. The latter has been found true also in respect of pine. Referring to this statement and to what has been said above, it must be unrealistic to make a definite distinction between tissues formed at graft wound surfaces and those found at open wounds.

Naturally there is nothing to prevent tissues developed from the wound surfaces of both components in a graft zone from being called intermediary tissue, as long as one realizes that the formations are nothing but an ordinary wound-healing process going on from both sides under particularly favourable conditions, and that the intermediary tissue could just as well also be called callus. The concept of intermediary tissue should, however, in my opinion be limited only to such tissues as in one way or another are formed between two exposed wood surfaces (*cf.* the next chapter).

The term callus is, no doubt, somewhat diffuse, and is used to indicate wound-healing tissues of various kinds and at various stages of development. KRENKE used a classification of callus tissues (*loc. cit.*, p. 234). According to this classification a callus is called *primary* until a cambium is formed within it. When the callus cambium has developed derivatives, the callus is called *secondary*. In the primary callus an immediate cell transformation may occur, *e.g.* by suberization and lignification. It is then reasonable to call it a *transformed primary callus*. If no regular cambium is developed in the callus, and irregular meristematic elements which continue to transform are established, KRENKE calls this *differentiated primary callus*. KRENKE himself considers this classification directly applicable to "intermediary tissue".

The first formations at the wound surfaces of grafts should undoubtedly be called primary callus. When cambia start to develop within these formations, they advance towards the secondary stage. In rapidly healing grafts one finds nothing but primary callus, which first produces the parenchyma union and then the cambial union. As soon as the cambial junction has been achieved one can no longer speak of callus tissue in this context. The formations which heal the cut stock must be regarded as entirely secondary. In accordance with SORAUER, it would be better to speak of healing edges ("Überwallungsränder"). When primary callus formations at the cut surfaces of the two components do not unite with each other very rapidly, the divisions some distance inside the surface of this tissue assume a phellogen character. The

cambium from the unwounded part advances into the callus, which then passes into the secondary stage. The callus cells on the outside of the phellogen are suberized, and may be called "transformed primary callus". In the tissues enclosed between the wood surfaces of the graft components, immediate cell transformations (*transformed primary callus*) occur, as well as irregular meristematic elements (*differentiated primary callus*). Also secondary callus is sometimes present: vascular nodules may be formed and cambia which have first turned in between the wood surfaces may be cut off by the fusion of cambia outside the wood surfaces (*cf.* next chapter).

D. Tissues between the wood surfaces of the graft components

In the following all tissues which are established in one way or another between the cut or exposed wood surfaces (on the scion side also the cut pith) will be called *intermediary tissues*. The term will apply here only to the special position of the tissues.

Often there is already a minute space between the wood surfaces from the outset. It is not necessary for a successful grafting that this gap should be filled with cells, as is shown by the six-month-old graft in Plate VI: 11. Indeed, the case is often the reverse, in that a very rapid healing often results in a lack of tissues between the wood surfaces. Nor is it necessary that there should be an initially large space for the development of tissues, since very strong proliferation may force them apart. If the surfaces are pressed firmly against each other, however, the development of cells will be inhibited.

It has appeared in an earlier connection that the intermediary tissue can develop from parenchyma in the wood of both components, from exposed pith in the scion, from cut leaf and branch traces, and from tissues seated outside the wood cylinder. The cells which intrude from various directions into the space between the wood surfaces seldom achieve complete union with each other. Remnants of the contact layers mostly appear here and there (*cf.* Plate IX: 4 and 7). The callus masses developing from various points cover their surfaces with thin cork layers, as will be seen in Plate VI: 10. The intermediary tissues naturally cannot establish any true junctions with the exposed wood surfaces, but their cells sometimes adhere closely to the wood and fill in the cut tracheids. Generally, however, the intermediary tissues develop thin cork layers on the surfaces adjacent to the wood. These layers are only broken in places where the wood parenchyma has participated in the formation of callus. After the cambia have closed

on both sides, the intermediary tissue may retain parenchymatous connections with the tissues on the outside through rays in the newly formed wood.

Most of the cells in the intermediary tissue do not retain their strictly undifferentiated form for any appreciable length of time. The surface cells are suberized, as mentioned above; many others soon lose their living contents, and their walls lignify, but do not assume a tracheid character. Others which remain alive are incrusted with tannin, but a few in common with the ray cells, may long retain an unchanged character. It also happens that callus cells assume a more or less tracheidal appearance although they have no contact with any meristematic zone. The cells which are seated far out in contact with the rays of the new wood, stay alive longest. Plate IX: 7 shows intermediary tissue from a three-year-old graft. Most of the cells are dead, but a few, mainly at the outer margins, are still alive.

Not infrequently cambial strands occur in the intermediary tissues without having any connection with the cambium on the outside. Regions in which the meristematic activity continues may in cross-sections assume the appearance of islets surrounded by dying and tannin containing tissues. A region of this kind may be seen in the middle of the intermediary tissue in Plate IX: 4. Sections immediately above and below that in Plate IX: 4 show several cell divisions in the region. Plate IX: 5 and 6 are obtained from the same graft. The section in Plate IX: 6 is approximately 13 mm above that shown in Plate IX: 4, and the section in Plate IX: 5 is situated between the two. In the intermediary tissue in Plate IX: 5 only a few cells with living contents are left, mainly at the edges, and in contact with some rays at the wood surfaces. The section in Plate IX: 6 is passing through another meristematic centre in the intermediary tissue, which centre is not connected with that shown in Plate IX: 4. A number of tracheids have been differentiated.

Several meristematic centres may occur close to each other in the intermediary tissue (*cf.* Plate IX: 8). The cells in the nodule-like formations are extended and bent, but entirely closed circles are rarely seen. A remarkable fact about these structures is that the xylem is always seated on the outside of the cambium, and the phloem inside. Differentiation of xylem elements continues as long as space is available, but the formation of new tissues on the phloem side gradually decreases, and the existing sieve cells are compressed.

These formations in the intermediary tissues cannot be regarded as synonymous with the nodules ("sfäroblasts" according to LAGERBERG

1943) that occasionally appear in the outer parts of the stem. In this case the meristem is established as a ring, but an entirely closed ring with phloem on its outside. More accurately it is a sphere, since the formation is round like a ball (*cf.* LAGERBERG). A broken leaf or branch trace may constitute the centre around which the formation starts. The nodule may continue its growth for a long time—as long as the surrounding cells are able to supply water and nourishment. Plate IX: 10 shows a section through the centre of a nodule obtained from a one-year-old veneer graft. The nodule occurred in the uppermost part of the stock flap, which was shaped as in Fig. 17b, and was completely united with the scion. Measurements have shown it to be nearly spherical. This structure, as well as the formations in the intermediary tissues mentioned earlier, all lack connection with the cambium of the stem or its vascular elements. They are consequently entirely dependent on the surrounding parenchyma for their supply of water and nutrients.

Cambia between the wood surfaces of the graft components may become isolated by the cambium of one component turning into the space between the wood surfaces and subsequently establishing junction with the cambium of the counterpart—not with its end, however, which lies between the wood surfaces, but at a place further outwards. The cambium part thus cut off from outward connection continues to grow as far as space permits, and it may also spread downwards and upwards in the intermediary tissue. Plate IX: 11 shows how a cambium emerging from the stock has been intercepted by the union of an outer part of this cambium with that of the scion. How large a part of the xylem in the intermediary tissue has developed after the union on the outside can be clearly distinguished. The position of the stock cambium at the time of union with the cambium of the scion is marked with arrows. The pith of the scion has been compressed to make room for the expanding tissues. Approximately one mm further down, the stele in the intermediary tissue is entirely isolated from the vascular tissues on the outside (Plate IX: 12). The cambium has developed an arch, with the small phloem part turned inwards.

No cambial strands have yet been developed in the intermediary tissues of the 15-week-old graft shown in Plate VI: 10, but the division activity is vigorous in the three clearly separated callus formations. The cambium from the scion on the left side in the photograph has first started to expand inwards and then bends outwards in order to meet the advancing stock cambium. There has been no union at all higher up on this side, and the entire cambium developing from the scion enters between the wood surfaces. When cambia of both the graft

components have finally united, some cambial tissue will definitely remain inside and become isolated in the same way as described above. In the two other parts of the intermediary tissue, cambia would probably have developed spontaneously.

Needless to say, one has also to consider the possibility that some of the spontaneously developed cambia in the intermediary tissue may establish union with the cambium of either component, even though no direct evidence to this effect has been found in this material. After such a junction has been established, it would not differ in appearance from a cambium turning inwards from the outside. There is certainly no fundamental difference between the cambia developed spontaneously in the intermediary tissue and those from the exposed cambial edges. Thus the union between the cambia of two graft components through a callus mass need not necessarily be achieved solely by the advancement of the cambial edges; it can also be established by the participation of cambia developed in the callus.

In side slit grafts the intermediary tissues often reach a great volume. The callus originates mainly from the innermost corner and the outer part of the scion (point 4 according to Fig. 21), but parenchyma and less differentiated cambial derivatives on the wood surface of the stock, as well as wood parenchyma in the scion, may participate. The tissues continue to expand, thus forcing the scion away from the stock until a union between cambia from point 4 and the incision face is achieved (Plate XIII: 10). When the pith of the scion has been cut through in the part turned towards the wood side, its callus formation is often considerable, as is also that from the rays in the stock situated straight opposite.

The longevity of the intermediary tissues is highly variable, and depends on the completeness of the connections with the tissues on the outside. The cells seated at the extreme edges of the intermediary tissue and connected with rays in the wood in the union zone, should have the same possibility of continuing living as the cells of the pith, which are fairly long-lived in pine. The isolated cambia remain active as long as the space and the supply of water and nutrients permit. For how long a time after grafting living cells may be found has not been established, since the oldest grafts examined were only three years old.

E. Some observations on the shaping and fitting of the graft components

Two methods of cutting the stock flap of veneer side grafts are shown in Figs. 3—7 and 17. In the case where the flap is shaped with an upward cut, the resultant wound surface will not be covered by the scion,

and wood will adhere to the entire flap. When the flap is cut according to the other method, the wound surface will be turned inwards and placed against that of the scion. There will be no wood to prevent a good union between the flap and the scion. The drawings shown in Figs. 30—31 present the original status as appearing in cross-sections at various levels.

When the flap is cut as in Fig. 30, union between it and the scion can only occur on the sides (Fig. 30d), since the wood in the flap forms an obstruction elsewhere (*cf.* Plate X: 1 and 2, which are obtained from the centre and the edge respectively of such a graft). The cambial edge of the scion will not remain passive, however, if it fails to achieve contact with the cambium of the stock, neither will the cambium of the stock flap. On the contrary, the cells of these cambia seem to be stimulated by such failure. Plate X: 3 shows a longitudinal section through the centre of a three-year-old graft where the original situation was as illustrated in Fig. 30. The tissues of the scion have grown enormously, and the tracheids are extended laterally towards the junctions on the sides—in the present section they have been cross-cut. The flap has been forced into an increasingly horizontal position, and its cambium has been very active. After one or more years of growth the cambial edges may possibly have united outside the wood that now separates them. An already large knot on the stem would have reached considerable dimensions by that time. Plate X: 4 shows a cross-section from graft contemporary in age with a flap cut in the same way. The section passes straight through the horizontally extruded wood in the flap. Tissues from the side penetrate where the wood of the scion has been cut, while higher up, the intact scion cambium is advancing outwards. The old wood in the flap may be either forced out by the growth, or more likely embedded. When the wood part of the flap is so large as to make even lateral junctions difficult, the picture may become more complicated. The cambium of the scion may bend outward-upwards along the flap (*cf.* Plate IX: 14 showing a section through

Figs. 30—31. Sections of lower part of veneer grafts showing relations between cambia of scion and stock flap when the latter is shaped with an upward cut and a downward cut respectively (just grafted, simplified). a: Radial section, *cf.* Fig. 17. b—d: Cross sections at the levels marked in a. 30: Wood adheres to flap at all points only lateral unions possible (d). 31: Parenchyma union may be established along the whole flap. Cambia may unite completely.
Snitt genom nederdelen av läggympar visande relationerna mellan kambierna i ympkvisten och underlagsfliken, då den senare tillskurits med uppåtriktat resp. nedåtriktat snitt (utgångsläget, schematiserat). a: Radiära snitt, jfr fig. 17. b—d: Tvärsnitt på olika nivåer markerade i a. 30: Ved ut igenom hela fliken. Sammanväxning möjlig endast i sidled (d). 31: Parenkymförening kan ske utefter hela fliken och kambieförening kan ske utan komplikationer.

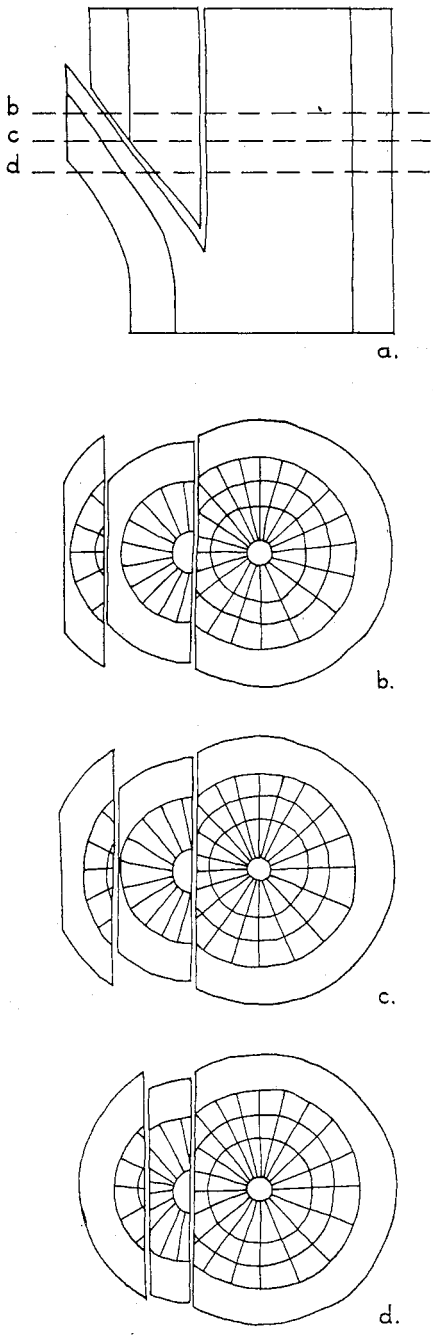


Fig. 30

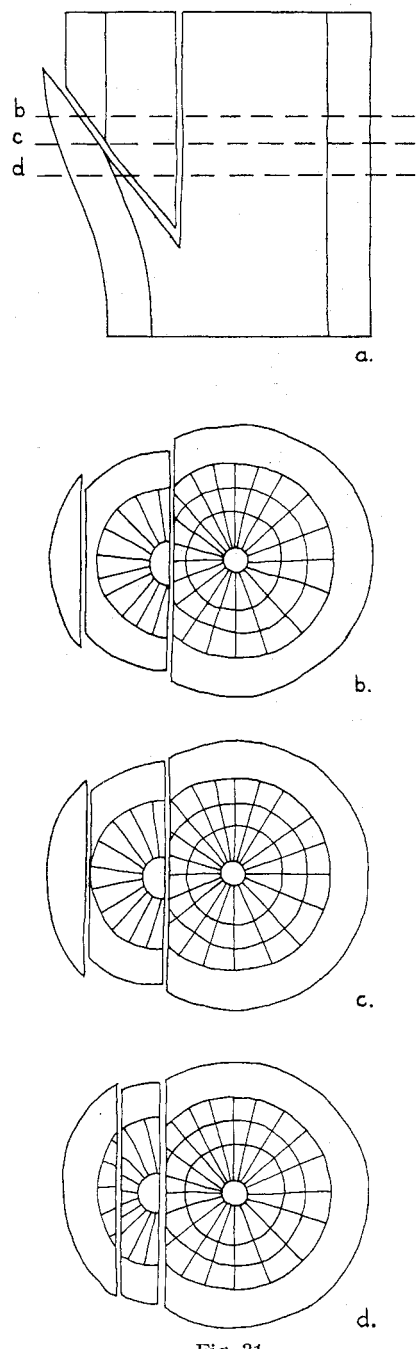


Fig. 31

the centre of a $4^1/_2$-months-old graft). Union can be achieved at the edges in two ways, and the same graft can be used to exemplify both. On one side the cambium both of the stock flap and the scion have grown laterally (that of the scion has first curved upwards and then united outside the old wood, Plate IX: 13). On the other side the cambia have united above the wood of the flap (Plate IX: 15). The general direction of the cells has become extremely complex here, and it would have taken a long time before the cambial activity assumed a normal course of growth.

Complications of this kind are seldom found in grafts where the flap is cut according to the second method. As the drawings in Fig. 31 show, tissues capable of proliferation are meeting at each level, and cambial unions are usually established as easily as in the graft shown in Plate X: 5. It may happen, however, that the union does not immediately become complete on both sides as in the graft in Plate VIII: 3. This may also be the case when the stock flap is cut with an upward stroke, but it is somewhat more common when the flap is cut as in Fig. 31, the reason being that it is not so firmly pressed against the scion as in the first case. If the flap is made with an upward cut, it has a certain flexibility due to the wood sliver, which acts like a spring in pressing together the scion and the stock. If the flap has been made with a downward cut, however, the surfaces of the scion and the stock fit together better; the flexibility given by the wood sliver can be compensated for by a firm and steady binding.

The heavier growth of the stock cambium in relation to the weaker growth in the scion during the period shortly after grafting has been discussed on p. 49. The cambium of the stock frequently outgrows that of the scion if the cambia are fitted accurately from the outset. The position of the cambia of veneer grafts immediately after grafting, and their mutual position after 3 or 4 weeks, are shown in the drawings in Fig. 32. One might therefore conclude that it would be better to have a scion that is bigger than the stock, or at least to make the cut in the scion wider than the cut in the stock. With the material usually available this is impossible if the grafting is to be done at the lower part of the stock.

In side slit grafts, the most complex step in the healing process has proved to be the union between the scion at point 4 and the incision face of the stock. The surfaces are seldom placed so that they cover each other completely or even partly. When the incision into the stock is nearly radial, as was the case in the grafts investigated, the exposed wood surface and the incision face are nearly perpendicular to each

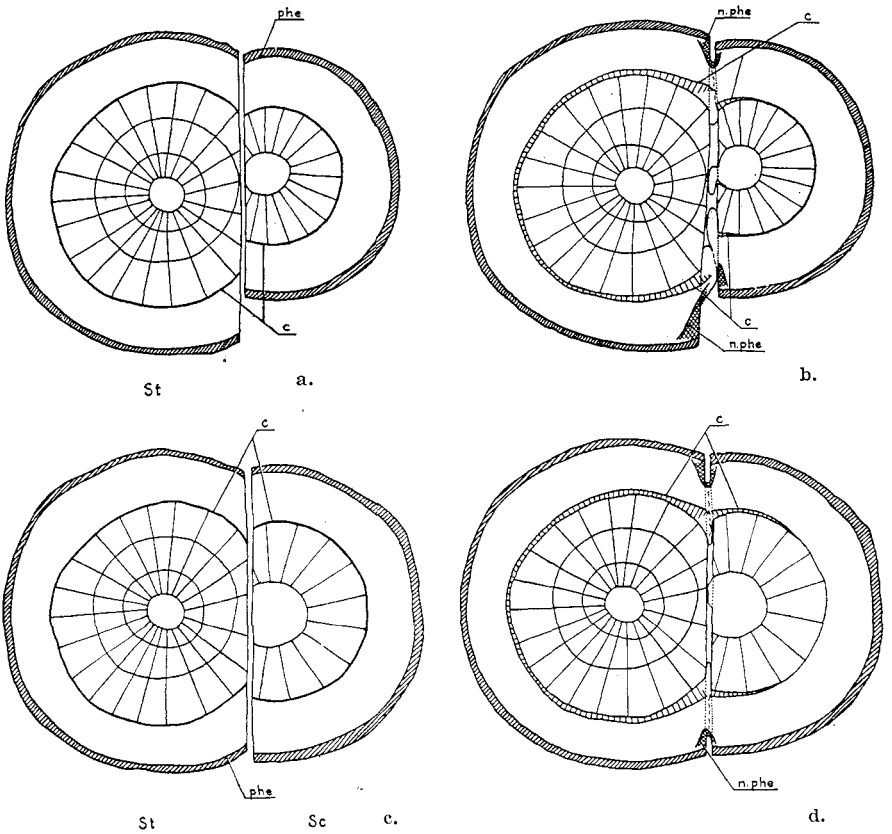


Fig. 32. Simplified illustrations of the cambial growth in veneer side grafts. Cross sections.

a—b. Large stock, small scion.

a. A common situation when just grafted, the cambia matched on one side, the cambium of the scion inside that of the stock on the other side.

b. After about three weeks. The cambium of the stock, growing faster, has left that of the scion behind on the upper side. On the lower side vigorous development of callus—the graft components have been pushed apart. Cork cambia united on the upper side.

c—d. Stock and scion rather equal in size.

c. Ideal situation. The cambium of the scion outside that of the stock on both sides.

d. After about three weeks. Opposing cambia ready to unite. Cork cambia united.

Key to signs on page 135.

Schematiska illustrationer av kambietillväxten hos läggympar. Tvärsnitt.

a—b. Grovt underlag, klen ympkvist.

a. Vanligt utgångsläge hos nyympad planta — kambierna sammanpassade i en sida, ympkvistens kambium innanför underlagets i den andra.

b. Efter ca tre veckor. Kambiet hos underlaget växer starkare, har vuxit ifrån ympkvistens i den övre sidan. I den undre kraftig kallusutveckling — ympkomponenterna skjuts från varandra. Korkkambier förenade i övre sidan.

c—d. Underlag och ympkvist av ungefär samma grovlek.

c. Idealiskt utgångsläge. Ympkvistens kambium utanför underlagets i båda sidorna.

d. Efter ca tre veckor. Kambierna mitt för varandra redo att förenas. Korkkambier förenade.

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other. The scion is mostly inserted in its entirety inside the incision face. There are only the dead tissues of the outer bark facing the latter, and the cambia to be united will be kept far apart (*cf.* Fig. 18a). In order to obtain improved cambial agreement, it would be better to make a tangential incision in the stock, as shown in Fig. 18b. (The reason for the scion in Fig. 18b being inserted from the opposite side in relation to Fig. 18a is that the grafting in the two cases has been performed from different working positions, compare Figs. 10—11 with Figs. 12—14. The mode of operation is, of course, in principle of no importance for the shaping of the cut.) The contact surfaces fitted at the incision face after a tangential incision would correspond to those of a veneer side graft. Plate XIII: 11 and 12 show examples of union under such circumstances. In both cases the junction at the incision face (the lower part of the section) is very good.

VI. Norway spruce

A. General

As already mentioned in the chapter on "Material and methods", the results of union in spruce grafts performed for the present investigation were not so good as those obtained with pine. In the first series of 1959, six out of ten remaining grafts were dead at the time of transferring out of doors. Only one of the four surviving grafts had developed a shoot, and the other three had only the green needles from the year before. The other series was more successful. The four grafts that had not been fixed were all alive, three of them, however, carrying only last year's green needles. Both series were comprised of veneer side grafts, the flaps of which were cut as shown in Figs. 3—5 and Fig. 31.

In addition to the series mentioned above a few side slit grafts from the spring of 1960 have been investigated. They had been executed according to the method demonstrated in Figs. 12—14 and Fig. 18b. Parallel with the series of 1959, some side slit grafts were also performed according to the method in Figs. 10—11 and Fig. 18a, although with negative results.

B. The normal course of union

1. Insulating dead tissues on the cut surfaces of the scion and the stock

As in pine grafts, contact layers develop over all the cut surfaces of spruce grafts containing living tissues. However, they can never be distinguished in the parenchymatous tissues in the wood of spruce (the ray cells, the epithelial cells of the resin ducts, and the cells of the leaf gaps), since they have a more firm, lignified wall structure. The pith, too, remains entirely passive. Some of the large, thin-walled cells subsequently collapse, but the pith cells do not participate at all in the callus formation, and for that reason the dead tissues cannot be regarded as an insulation layer. In the cortex, phloem and cambium, the picture is largely the same in both the species. Plate XIV: 5 shows an example of the formation of a contact layer.

2. Cell enlargement and the first cell divisions

The most active cells adjacent to the wound surfaces soon begin to enlarge. Plate XIV: 1 from a two-day-old graft shows expanded ray cells in the stock flap and enlarged epithelial cells in a severed resin duct in the cortex of the scion.

The first cell divisions follow immediately. They occur at about the same time in the rays outside the xylem, the resin ducts in the cortex, and in the ordinary cortex cells (*cf.* Plate XIV: 2—4, which shows examples of cell divisions in the scion of a four-day-old graft). Quite considerable callus masses may have developed after a further couple of days, as in the six-day-old graft shown in Plate XIV: 5. There the stock has been most active, particularly the rays that have been severed in the phloem. Some phloem parenchyma cells have also participated. A resin duct immediately inside the wound surface in the scion has been entirely filled up with cells, and some divisions have occurred in the external cortex. Higher up, the cell division activity was considerable also in the scion.

The epithelial cells of the resin ducts in the cortex of the scion react intensively. Some days later the ducts opened by the graft cut have been closed again by cells that have enlarged and divided. The stimulus is transmitted upwards in the ducts. A resin duct of a scion which was studied four days after grafting, had been severed in the extreme lower end of the scion. The duct was entirely filled up to 1 cm above the cut, and at this point cells were dividing. A few centimetres higher up, effects of the graft cut in the form of enlarged epithelial cells could be observed.

The examples shown indicate that the scions react at least as quickly as the stocks, often even more rapidly. In the four-day-old graft from which some of the photographs discussed above have been obtained, dividing cells were observed in the scion only. Enlarged cells and cell groups were found here and there in the stock.

No divisions in cells of the rays or resin ducts of completely differentiated wood have been observed in spruce. There is thus an essential difference here between spruce and pine. In the latter species vigorous callus formation frequently occurs from wood and pith parenchyma. The fact that no proliferation can occur in spruce depends in all probability on the structure of the tissues concerned, which has been described in chapter IV: a and b. The parenchymatous ray cells cannot contribute to callus formation in spite of their living contents. The heavily thickened cell walls constitute a directly visible obstacle. When

the graft cut has been shallow, so that the wood is exposed at the cambial region, no callus will be formed even from this exposed wood surface (see Plate XIV: 9).

However, the thickening of the walls in the ray parenchyma does not proceed as rapidly as in the surrounding tracheids. If the stocks have been so far advanced before grafting that their cambia have been active for some time, it may happen that solitary ray cells in newly formed xylem enlarge and start dividing (*cf.* Plate XIV: 6). Taken as a whole, however, this is of minor importance.

The pith of the scion does not either show any sign of cell division when it is severed. The number of thin-walled living cells in it is low. These cells do not become activated for division even when proliferating tissues in the stock have been seated close to the pith; the callus masses from the counterpart intrude and compress the pith cells (*cf.* Plate XIV: 8). In old grafts it is quite usual to find the pith shrivelled and mutilated (if it has been cut in the grafting), particularly when the union fails to become complete fairly soon after grafting (*cf.* Plate XV: 7).

As in pine, all the cells of the cambial region may participate in the formation of callus. However, the change in the mode of cell division

Table 1. Intensity of cell division in different tissues of grafts of Scots pine and Norway spruce.

Tissue	Pine	Spruce
Periderm	—	—
Cortex, ground tissue	+++*	+++*
Cortex, resin ducts	++++*	++++*
Phloem, rays	++++*	++++*
Phloem, vertical parenchyma	++*	++*
Phloem, completely differentiated sieve cells	—	—
Cambial region, rays	+++	+++
Cambial region, other undifferentiated or incompletely differentiated cells	++	++
Xylem, rays	+	—(+)
Xylem, resin ducts	+	—
Xylem, completely differentiated tracheids	—	—
Pith, leaf and branch gaps	++	—

*Tissues influenced by leaf and branch traces show greater activity than others.

++++ very high intensity of cell division
+++ high intensity of cell division
++ intensity of cell division varies, in pith, leaf and branch gaps of pine divisions occur at an early stage, otherwise not until neighbouring tissues have started to divide.
\+ divisions in variable amount can occur but often fail to appear.
(+) when late grafted, ray cells in the newly formed xylem may divide
— no divisions

described on p. 39 has to take place first. The most extensive proliferation takes place, at least in the beginning, from rays and other parenchymatous tissues outside the cambium.

Table 1 shows a comparison of the cell division intensity in various tissues of Scots pine and Norway spruce.

The youngest *side slit graft* investigated was 17 days old. The photograph in Plate XVI: 9 of this graft shows a remarkably weak activity in both the stock and the scion (*cf.* the equally old pine graft in Plate XII: 6). In all investigated samples of spruce the space in the innermost corner was considerable. This is a consequence of the low tissue flexibility both of the stock bark and of the scion. No divisions have occurred in the bark flap of the graft shown in Plate XVI: 9. The tendency to form callus from the bark flap varied widely in the grafts studied. It appears as if thick bark has greater power to proliferate—the small number of specimens investigated, however, does not allow of any definite conclusions on this point. The air-filled space in the corner undoubtedly causes some drying of the flap tissue, which is perhaps of minor importance when the bark is thick. When cell divisions occur in the flap, all the living cells participate in the manner described above for pine. No callus formation has been observed from the wood side of the grafts. The incision face, and the part of the scion that covers it, are entirely on a par with the wound surfaces of a veneer side graft.

3. Phellogen formation

The development of periderm over the wound surfaces in the cortex proceeds largely in the same manner in spruce as it does in pine. In spruce, however, the first divisions, with only a few exceptions, occur some distance inside the wound surfaces. The greatly enlarged cells that are common in pine when a leaf trace is present contiguous to, or immediately inside the wound surface (p. 41), are never found in spruce.

Complete union of cortex-derived cells has been established on the left side of the 16-day-old graft shown in Plate XIV: 8. New phellogen is developing (at present most visibly in the stock). Well developed phellogen occurs in the 18-day-old graft in Plate XIV: 9 over the wound surfaces of both stock and scion, and the union between them is complete. The divisions creating the phellogen start far inside the edge of the wound surfaces when these are exposed and do not cover each other. The left part of Plate XIV: 9 shows how phellogen in the stock has been formed by callus originating from rays in the phloem. Large parts of old phloem are now located outside the phellogen.

4. Further callus formation and the union between parenchymatous tissues

The importance of leaf and branch traces for the formation of callus as discussed in the corresponding chapter on pine, applies equally to spruce. The leaf traces in the scion are numerous. Several of them will in each graft be so placed in relation to the cut surfaces that they will exert influence on the formation of callus and the union. Some of the first parenchyma unions observed have apparently occurred through the influence of a leaf trace (*cf.* Plate XVI: 7 from a ten-day-old graft). The callus formation initiated by the leaf and branch traces of spruce never assumes any complicated forms; there are never any large "inflated" cells as in pine (*cf.* Plate V: 8). The role played by the leaf and branch traces in the final union of grafts is possibly even greater in spruce than in pine. This will be discussed more comprehensively in a later chapter.

As in the case of veneer grafts on pine, the first parenchyma unions mostly occur outside the cambial region between tissues originating from phloem rays and the cortex; 10—15 days after grafting the first junctions have been established.

Union soon occurs between the scion and the stock flap where tissues capable of proliferation meet. In the contact zone between the scion and the stock flap, the callus development was in most grafts more vigorous in the scion than in the stock. Plate XIV: 7 shows a tangential section through the phloem of the scion of an eleven-day-old graft where the phloem is in contact with the stock flap. Vigorous new formation from the rays in the scion can be observed, whereas the stock is almost passive. The graft in Plate XV: 1 is twice as old. It shows a complete union between callus tissues over the entire line, from which it is clear that the scion has produced the major portion of the callus, particularly in the outer parts.

It appears that it is more difficult to obtain a good fit between scion and stock with spruce than it is with pine. The spruce scions are mostly much thinner than the stocks. It is especially the parts between the wood and the periderm which are capable of proliferation and they are essentially smaller in the scions than in the stocks (*cf.* the width of the bark of the scions and stocks in Plates XIV: 8, 9, and XV: 9). In grafting one always endeavours to fit together the *cambia* at least on one side. In the grafts studied, however, it is mostly the *outer edges* that have been fitted together, with the result that the cambium of the scion projects outside that of the stock on one side, and is far inside on the other, frequently so far inside that tissues capable of prolifera-

tion do not meet (*cf.* Plate XV: 9). Parenchyma union has occurred rapidly on the left side of this graft, and vascular coalescence has also been established without any great difficulty. On the right side, however, large masses of callus have developed from both parts, and it is clear that union would hardly have taken place during the first growing season.

As already mentioned, the callus development in *side slit grafts* is poor. In many of the specimens investigated, the proliferation is most extensive along the incision face and the adjoining part of the scion. Good union is soon established there, as shown in Plate XVI: 9—11. Some of the circumstances influencing the callus formation from the flap are discussed on p. 78. In several side slit grafts the bark flap dies fairly rapidly after grafting. Occasionally some cell divisions have occurred before then, but sometimes it withers without previous activity. Plate XVI: 9 shows a small part of the flap in which most of the cells have lost their living contents. The scion persists by means of the union with the stock established at the incision face. In the graft in Plate XVI: 11 the scion has achieved junction with both the incision face and the flap. The innermost corner, however, has still, after four weeks, not been filled with callus. An example where proliferation has been vigorous from the flap, however, is shown in Plate XVI: 12.

5. Union between vascular tissues

Union between vascular tissues occurs in the same way in spruce as in pine, at least as far as the immediate junction of the cambia in the stems of the graft components is concerned. Only a few examples, therefore, will be given here. Plate XV: 3 shows laterally extended tracheids in the stock directed towards the newly differentiated xylem cells of the scion. The cambial union is not yet complete. A longitudinal section from the lower part of the same 22-day-old graft illustrates the uniting trends occurring between the cambium of the stock flap and the cambium in the lower, obliquely cut part of the scion (Plate XV: 2). It will be seen how tissues from the cambial region of the latter enter between exposed wood in the scion and some less active parts in the stock flap (mainly non-functional phloem). Further down in the flap, the formation of new tissues is vigorous, and some short tracheids have been differentiated in the callus of the flap. Four weeks after grafting the junctions may in parts have the apparance as in Plate XV: 4. A prerequisite condition is that the cambia are well matched. The radial section in Plate XV: 5 shows a good junction of the latter at the flap. Such a union is possible only when the flap has been made with a downward cut as in Fig. 31.

The first cambial unions in *side slit grafts* made with a tangential incision in the stocks occur at the incision face, where the tissues are closely fitted and proliferation is vigorous.

The part played by *leaf* and *branch traces* in the achievement of vascular unions in pine grafts was mentioned on p. 49. Their importance appears to be still greater in the grafts of spruce. In this species the leaf traces are more numerous, and they furthermore leave the stele of the scion at a more acute angle than in pine (*cf.* p. 26 and Fig. 15). This means that the possibility of a leaf trace ocurring close to the wound surface is considerably greater in spruce than in pine. Unions achieved through leaf and branch traces are most usual in cases where the cut in the scion is relatively superficial. Plate XVI: 8 shows a union produced by a leaf trace in the scion. Junctions of this kind generally extend some millimeters above and below the leaf trace during the first growing season, whereafter they continue to extend more and more.

The picture becomes more complicated when leaf traces situated far out in the cortex of the scion produce vascular unions with the stock (after having previously contributed to the parenchyma union). Plate XVI: 1—6 shows a series of sections from a graft at the beginning of its second growing season. The first photograph shows a leaf trace in the cortex of the scion. Heavy cork formation occurs on both sides between the graft components. The second photograph was taken 18 sections further up (section thickness 15 μ), and shows a parenchyma junction between the components. Yet another 18 sections higher up, the leaf trace is seated half-way between the cambia of the graft components (Plate XVI: 3). Fifteen sections higher (Plate XVI: 4), it is seen moving towards the cambium of the stock subsequently to be incorporated with the vascular tissues of the latter (Plate XVI: 5 and 6, the sixth and 13th sections respectively above the one shown in Plate XVI: 4). This has happened within a distance in height of approximately 1.5 mm. The distance between the cambia of the graft components at the time of investigation varied between about 1.6 mm at the level where the leaf trace is leaving the stele of the scion, and about 1.0 mm where the leaf trace is incorporated with that of the stock. The more vigorous dividing activity of the parenchyma cells around a leaf trace near a wound surface has produced a union between the graft components at a relatively early stage at the higher level. Failing this early connection, the tissues farther down have developed periderm on their surfaces, and the continued growth has moved the cambia apart. The meristematic activity around the leaf trace has obviously induced the potential

cambium in the leaf trace to start producing new vascular elements, and this stimulus has been communicated to the uniting callus mass. For a union to take place such as shown in the photographs, impulses also from the stock must be presumed. In Plate XVI: 2, the direction of the leaf trace already appears to be affected by the stock. The mutual arrangement of elements in the vascular bundle of the leaf trace has also been influenced, the trace having twisted half a turn before its incorporation with the stele of the stock. Fig. 33 shows in principle such a "moving leaf trace" as seen longitudinally. In another series of cross-sections studied, a leaf trace has emerged straight opposite the stock (the cut in the scion has consequently been so superficial that the cambium remains unaffected). One can see how the phloem, mainly seated on the exterior of the trace, and facing the stock, divided gradually, and moved over to the sides of the trace, until finally, at the entrance into the stock, it becomes entirely reversed in relation to its original direction.

The moving leaf traces are of a common occurrence in spruce grafts and they have been observed even in places where a regular union of the cambia has taken place.

C. Tissues between the wood surfaces of the graft components

When tissues occur between the wood surfaces of spruce grafts, it is always a case of their having entered from regions outside the wood cylinder. Thus there are never any unions between these tissues and rays or leaf gaps at the wood surfaces (*e.g.* Plate XV: 8). Differentiation of xylem and phloem from cambia in arches also takes place here, but these cambia always appear to have, or have had, connection with the cambium on the exterior. Two formations of this kind are found in the intermediary tissues in Plate XV: 11. The uppermost formation is that which is best developed at the level at which the photograph was taken. It is obvious that a part of the scion cambium has been isolated inside the union produced by a leaf trace and has bent inwards. About one mm higher up it has connected with the outside cambium, which then developed a narrow arch between the wood surfaces. When the union occurs rapidly on both sides, no tissues are formed between the wood surfaces. However, since the fitting together of graft components, frequently differing in size, has been difficult, the union in many grafts has not been completed on more than one side during the first year. Tissues from both of the graft components may enter the space from the other side and become cut off from their mother cambia when the final union occurs (*cf.* the corresponding chapter on pine).

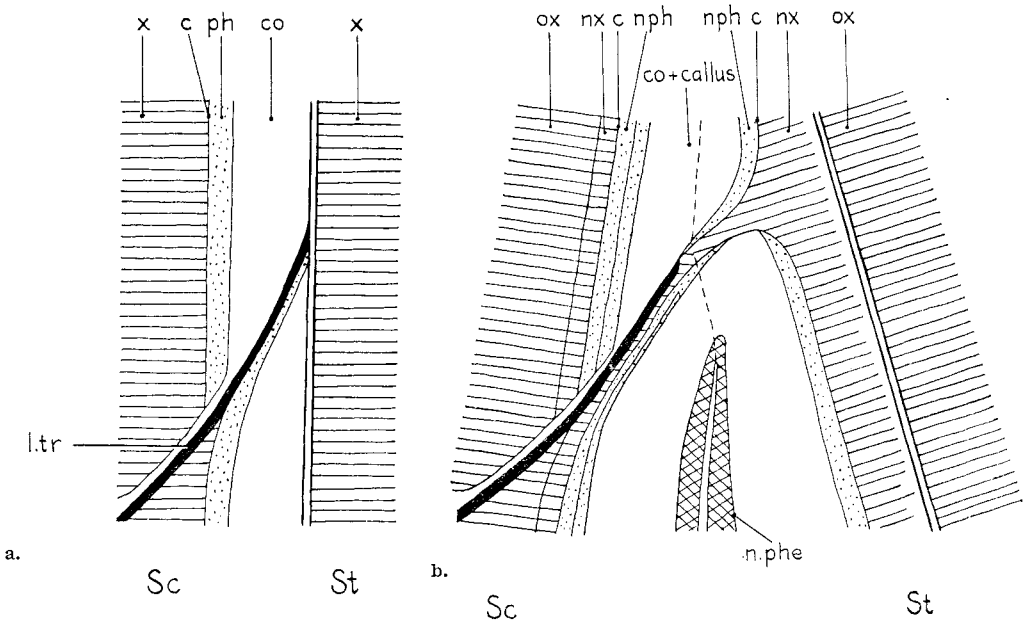

Fig. 33 a and b

Fig. 33 a and b. "Moving leaf trace" in spruce graft. Longitudinal sections (outlined in principle). a: situation just at grafting, b: drawn from the series of cross sections of a 14 months old graft presented in Plate XVI: 1—6. The trace describes a bow laterally (not shown in this drawing).

a. A leaf trace of the scion cut in cortex. The cut into the stock deep, in the present section wood borders upon the scion cortex.

b. Stock wood surface healed over. Callus formation around leaf trace of scion has been vigorous which stimulated the adjoining tissues of the stock to increased activity. Parenchyma union was established. The potential cambium in the leaf trace has started to produce vascular tissues and influencing the callus tissues outside to regular divisions and differentiation. Some kind of stimulus has been communicated between both cambia through connecting parenchyma. Vascular tissues have been differentiated in fixed directions from both sides. The dotted line marks the approximate border between scion and stock.

Key to signs on page 135.

»Vandrande bladspår» hos granymp. Längdsnitt, schematiserat. a: utgångsläget, b: konstruerat efter den serie tvärsnitt från en 14 månader gammal ymp, som presenteras i pl. XVI: 1—6. Spåret beskriver en båge i sidled, tas ej hänsyn till i denna principskiss.

a. Bladspår hos ympkvisten avskuret i kortex. Snittet i underlaget djupt. Ved gränsar här till ympkvisten.

b. Underlagets vedyta övervallad. Kring ympkvistens bladspår har kallusbildningen varit livlig, vilket stimulerat intilliggande underlagsvävnader till ökad aktivitet — parenkymförening har etablerats. Det potentiella kambiet i bladspåret har trätt i funktion och även influerat kallusvävnader utanför till ordnad delning och differentiering. Genom det sammanbindande parenkymskiktet har någon form av stimulans förmedlats mellan de båda kambierna. Ledande vävnader har differentierats i bestämd riktning från båda håll. Streckade linjen markerar ungefärliga gränsen mellan ympkvist och underlag.

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D. Some observations on the shaping and fitting of the graft components

The discussion concerning the shape of the flap of veneer side grafts in pine (pp. 69—70) is also applicable to spruce. The existence of a large wood sliver in the stock flap may give rise to many strange formations. The advantage of cutting the flap downwards is clearly shown in Plate XV: 5.

Usually it is more difficult to get a good fit between the cambia of the stock and scion in spruce than it is in pine. Last year's shoots are often very slender in spruce, and are moreover enclosed in a relatively deep layer of dead tissue which cannot contribute to callus formation. Another difficulty which has been discussed earlier is that the bark layer of the scion is generally thinner than that of the stock, and their cambia will not match if the outer edges are fitted together. The cut in a stock that is thicker in relation to the scion is moreover rather shallow, and as the bark is cut almost tangentially, its width at the surface of the cut is increased still further. The graft in Plate XIV: 8 shows an example where a good fit could have been arranged by placing the scion straight opposite the wood surface of the stock instead of seating it on one side. If, on the other hand, the cut in the stock had penetrated deeper into the wood, it would have been necessary to place the scion at the side (not so far, however, that its outer edge would run parallel to that ot the stock) in order to get a fair fit at least between the cambia on one side. This way of cutting must be avoided, however.

The consequences of too deep an incision into the stock are shown in Plate XV: 10, which is obtained from the lower part of a one-year-old graft. The flap and the main part of the stock have united outside the scion on one side, but still the cambium of the scion has not been placed sufficiently far out on the other side to render an immediate union possible. The xylem in the scion has had two growth periods, the second one after union with the stock had been obtained. It can be observed as a false annual ring in the scion. Grafts as poorly fitted as this one usually fail to develop.

A relatively superficial incision into the stock has consequently appeared to be advantageous in the grafts investigated. (All stocks in these grafts have been thicker than the scions.) An incision in the stock which barely exposes the wood, or removes only a thin sliver of wood provides a contact surface better suited to that of the scion. The spruce stocks have not shown any tendency to proliferate from exposed wood surfaces, not even from surfaces where the grafting knife has only peeled off the bark close to the cambium, see Plates XIV: 9 and XV: 6. Nat-

urally, the scion must be placed right opposite the stock as in Plate XV: 6. There is no risk that the scion will be forced away from the stock by abundant callus formation from an exposed cambium or from rays in the wood. Firm binding, however, is necessary in order to prevent lateral tissues from entering between the components and thus forcing the scion away from the stock. Superficial cuts of this kind cannot be recommended for pine grafts because of the vigorous proliferation from the entire wound surface that would ensue.

A question that is often discussed is whether it is advisable to cut so deep into the scion that the pith is exposed. This investigation does not show any evidence that cutting through the pith would involve great risk, particularly if a better fit between the cambia can be obtained. In some cases where the buds of the scion have failed to develop, the pith was found to have been cut through and to have shrunk. At the same time, however, the fit of the cambia had been poor, and this was probably the primary cause of the failure of the graft.

It is a common occurrence in spruce grafts that the scion persists without developing any shoots during the first summer. The apical bud of such a scion is normally dead and so too are mostly the larger lateral buds. Scions which survive the first summer and winter in this state occasionally develop shoots next spring from buds established during the previous summer immediately below the dead buds, or weak lateral buds that have grown stronger. Alternatively, and what seems more likely, is that these small buds had not been able to produce any shoots last year, only new buds. In most grafts of this kind the vascular connections have appeared to be established at a rather late stage, and they have often been very weak. At the time of investigation in the spring following on the grafting, some grafts contained only a few solitary junctions produced by leaf traces. Parenchyma unions naturally occurred over rather long distances in all the surviving grafts. Poor fitting of the cambia mostly seems to cause the cambia to require a longer time to effect junction, and this means in turn that the buds receive too little water to be able to develop shoots. In the graft shown in Plate XV: 11, the fit between the cut surfaces of the scion and the stock is very poor. On short distances there are cambial unions, all of which are produced by leaf traces as in Plate XV: 11. The scion has now (the second spring) developed a shoot from a lateral bud.

The ability to develop adventitious buds is poor in spruce. It happens quite frequently, therefore, that grafts which survive the first summer without developing shoots have no possibility of continuing to grow

after the first buds have died. They may persist for a few seasons by means of the green assimilating needles they bore at the grafting. Plate XV: 13 is obtained from a similar graft after its second summer. A superficial cut in the stock has been matched with an all too superficial cut in the scion. Only weak vascular union was established in the first year. During the second year the union was strengthened.

Poor fitting of graft components, however, could not have been the cause of all the cases in which the scions persisted without developing shoots. It appears that some trees are more difficult to propagate by grafting than others, and their proportion of grafts on which the buds do not burst in the first year is also larger. This may be due to the fact that the cells in the scions from these trees have lower ability than normal to start a division, that the buds of the scions are poorly developed, or that the scion-material has been damaged in some way before or after collection from the mother trees. Incompatibility between certain mother trees and the stock, *i.e.* too great physiological differences, may also be a possible cause, although it is very rarely, if ever, observed in grafts between components of the same species (*cf.* BRADFORD & SITTON 1929).

Experience has shown that scion-wood of spruce from northern Sweden is more difficult to graft successfully. The annual shoots are usually so short that the graft cuts must be made in the two-three-year-old parts of the twigs. Grafts of this kind are not included in the ordinary series, but they are included in the group of grafts investigated with regard to union difficulties. In the latter group there were cases in which the cambial fit of the components appeared to be good, but the union was still slow and incomplete, and no shoots developed in the first summer. Plate XV: 12 is obtained from the lower part of one of these grafts. The scion contained two annual rings at grafting. The incomplete union can be explained as due to the fact that the parenchyma cells of the two-year-old scions possess considerably lower vigour and therefore have a lesser capacity for renewed division activity than scions of ordinary one-year-old shoots. The factor of light may perhaps also play a rôle in this context—the trees in the north develop their shoots during 24 hours of light. The transfer to the region of Stockholm implies great differences in respect of the light conditions.

In the introductory chapter it was mentioned that the *side slit grafts* of spruce performed according to the same method as used for the series of pine side slit grafts, did not heal. The incisions made in the stocks were radial, and the entire scions were placed inside the cut surface as in Fig. 18 a. The investigations of grafts with tangential

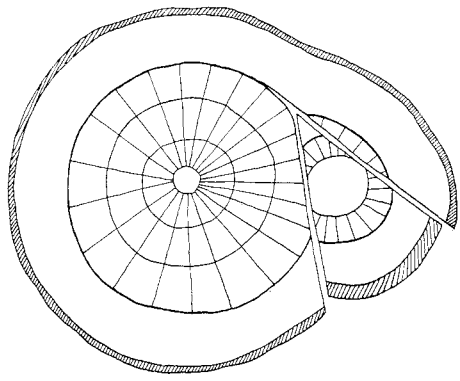

Fig. 34. Side slit graft. Tangential incision effecting part of the wood of the stock.
Sidsticksymp. Tangentiellt insnitt som tar med del av veden i underlaget.

incision in the stock (Fig. 18 b) have shown that the main union occurred at the incision face and that proliferation has been poor elsewhere. The method first used did not allow of any junctions at the incision face in the early stage, which caused the failure of the graft. For grafting spruce, it would certainly be useful to make a tangential incision which included also a part of the wood (*cf.* Fig. 34). This would provide a better contact surface for the scion, and the empty space in the inner corner would be reduced.

VII. Discussion

A. Conditions initiating cell division. Callus formation

1. Growth substances

The basic mechanism initiating cell division when a plant individual has been wounded appears to be of a very complicated nature. HABERLANDT (1923) suggested the presence of special *wound hormones* developed from the decomposition products of damaged cells. BONNER & ENGLISH (1938) and ENGLISH, BONNER & HAAGEN SMIT (1939) proceeded on the basis of this hypothesis, and finally succeeded in isolating from wounded tissues an active substance, a dicarbonic acid, which they called *traumatic acid.* ENGLISH (cited by BLOCH 1952) has later isolated an additional number of dicarbonic acids which appeared to be variably active as wound hormones. However, it has lately been questioned strongly whether any special hormone or *auxin* is active in wound healing, *cf. e.g.* AUDUS (1959). Instead, growth substances of the kind (*indoleacetic acid* and the like), which are active in all cell reproductions, appear to possess a stimulative effect also on the callus formation at wound surfaces. Although many attempts to facilitate the union of grafts by treatment with auxin have failed, AUDUS mentioned some successful experiments with apple and plum, experiments with *Juniperus* and *Rhododendron* conducted by KRUYT, and experiments with grapes carried out by MÜLLER-STOLL. In both of the last-mentioned cases root initiation was reported to have occurred in the region of junction as a result of the auxin treatment. *Kinetin,* isolated in 1955 by MILLER and his co-workers, is a substance which has attracted great interest in recent years. It has a strong influence on the cell division activity, but only in the presence of indoleacetic acid. SKOOG & MILLER (1957) compared the effects of kinetin and indoleacetic acid in tissue cultures inoculated with these substances. Indoleacetic acid produced increased callus and root formation, but inhibited the shoot development, whereas kinetin stimulated the shoot development, but produced fewer roots. Experiments with auxin on spruce grafts have been initiated at this Institute, but no positive results have yet been obtained. The rôle of auxin in xylem differentiation will be discussed under the heading "Union of vascular tissues and cambia".

It has long been known that the cambial growth in a stem is always stronger close to a wound than elsewhere, *cf. e.g.* HERSE (1908). The same author also stated that the divisions in the cambium in spring started earlier in the proximity of wounds than in other parts of the stem. The investigations reported here have shown that divisions in the cambia of scions which were dormant at the time of grafting, always started first close to the wound surfaces. The entire cambial growth was strongest near the wound surfaces in both scion and stock. Apparently the conduction of growth substances and, of course, nutrients to the wound area is increased. The factors releasing the cell division at wound surfaces are still far from fully explored.

2. Regions at the wound surfaces with superior callus formation

The present investigation has shown the initial cell division to be most vigorous in regions which are known as storage places for nutrients and best suited for conduction. Parenchyma cells in rays, and in leaf and branch traces, constitute storage places for plant nutrients. The rays that connect with leaf traces (rays emerging from leaf gaps) must be held to be the most suitable ones for conduction, and the quantities of nutrients stored in their cells are large. In the boundary between cortex and phloem, where the oldest rays end, vigorous callus formation is frequently observed, especially in rays emerging from leaf gaps. KRENKE (1933) found that in the herbaceous plants with scattered vascular bundles which constituted his experimental material, the most vigorous formation of new tissue emerged from parenchyma adjacent to vascular bundles. KABUS (1912) had already made the same observation, but did not wish to ascribe this to the nutrient conditions. HABERLANDT (1923) also stressed the importance of the vascular bundles for the cell division activity, and considered that the phloem was of the greatest importance in this context, because of its production of what he called lepto-hormone. KRENKE showed that the entire vascular bundle, phloem as well as xylem, has the power of inducing divisions in the surrounding parenchymatous tissues.

The leaf and branch traces in conifers may be compared to the scattered vascular bundles in certain herbs when passing through the phloem and the cortex. The parenchyma cells surrounding them also divide vigorously when the tissues have been wounded.

The rays maintain the lateral connections between the various parts in the stele of the stem. From the point of view of conduction, their cells are consequently better situated than *e.g.* the vertical parenchyma cells

in the phloem. The vertical parenchyma certainly plays a part in the production of callus, but I have never observed divisions in the vertical parenchyma that had not been preceded by a division of the ray cells. It would thus seem probable that the vertical parenchyma is activated by induction from cells under division.

In most cases it is not the ray cells exposed in the functional part of the phloem which are most apt to divide but sooner the cells of rays that have been cut further out in the stem. The stock of the spruce graft in Plate XIV: 5 and 6 shows an example of the ray activity in various positions. Possibly an explanation is to be found in the extension of cells associated with the normal development of the stem. The further out in the stem a ray cell is moved by the cambial growth, the larger is its volume and the nearer the time when it will be ready to take part in the formation of a new scale of periderm. The outer cells in the rays would thus appear to possess a greater potential power of division through wounding than is the case with the inner cells. Great activity from the outermost parts of the rays is frequently seen in the boundary zone between phloem and cortex. Some additional viewpoints on the part played by the rays in the formation of callus and phellogen will be discussed in the following.

The epithelial cells of the vertical resin ducts in the cortex and of the horizontal canals in the phloem have appeared to react very rapidly, and they often develop large amounts of callus. GAUTHERET (1957) suggested that parenchyma cells in connection with secretory canals were less differentiated (*e.g.* they contained no starch) than other parenchyma cells, which may explain their great power of dividing. The importance of the epithelial cells of the formation of callus is discussed in a special chapter (p. 103).

3. The mutual influence of the graft components before union

The intensity of the cell division is to some extent dependent on what kind of cells in the counterpart adjoin a certain part of the wound surface. The graft components seem to be able in one way or another to exercise some influence on each other long before any unions occur. CAMUS (1949) showed that such an induction is possible, and that active tissues in *e.g.* a bud (= one graft component) could induce tissues in a counterpart to dedifferentiate and start dividing. Without this contact, the counterpart (old parenchymatous tissues without connection with vascular elements) would certainly have remained entirely passive. SIMON (1930) followed the same line of reasoning (*cf.* p. 10

above) when he suggested the possibility of an induction transfer between the graft components without previous union. The formations at the wound surfaces of the stock and the scion are consequently not wholly influenced by the qualities and changes in their own part only, but are highly dependent on the activity in their counterpart as well. This is the essential difference between the healing of an open wound and the formation of a graft union.

In normal cases divisions in the external regions of the stock cortex start some distance inside the wound surface, *cf.* p. 41. Under the influence of a very active region in the scion, however, also superficial cells may be induced to divide, *cf. e.g.* the spruce graft in Plate XVI: 10, where the cortex of the stock is influenced by the activity around a leaf trace in the scion.

The stocks of side slit grafts in pine do not proliferate uniformly over the whole of their exposed wood surface, *cf.* p. 47. No callus at all is formed where cut wood in the scion is in contact with the exposed wood surface, whereas both ray cells and incompletely differentiated xylem cells form callus when placed in contact with cut pith in the scion. The pith cells of pine are active in callus formation and may influence the opposite stock tissues. In places where scion wood has been placed against the stock, most of the tender tissue on the surface of the latter must have been destroyed. This has not been the case opposite the pith, where the newly formed cells also have more space to expand since the pith cells may be compressed (Plate XIII: 1). The conditions in side slit grafts are discussed further on p. 93.

The experiments carried out by KRENKE showed that the entire vascular bundles can affect the surrounding parenchyma. If the vascular bundles were severed by the graft cut, however, only the parenchyma of the phloem, but not of the xylem, would participate in forming callus. Yet the xylem as well as the phloem are able to induce cell division in the counterpart. No such influence from the xylem has been observed in pine and spruce—plants with a closed wood cylinder. In pine, however, it happens that branch traces that have been severed in the wood of the stock, where the traces are composed of tracheids and parenchyma only, proliferate vigorously, and are able to affect the parenchyma in the counterpart (*cf.* p. 50 and Plate VII: 5—6).

4. Callus formation from wood and pith parenchyma

Callus formation in pine also occurs from parenchymatous cells in in the wood. Such proliferation is not found in all grafts, however, and where it does occur, it is only rarely that all of the parenchyma tissue

touched by the graft cut participates. It is mostly found in the stocks, and particularly in those with vigorous growth. Multiseriate rays, vertical resin ducts, and regions where more parenchymatous cells than normal have developed because of some damage in the cambium, together with branch and leaf gaps are the most common points of origin for callus formations from the wood surfaces. This largely agrees with the observations made by BARKER (1954) concerning proliferations from parenchyma in basswood, *cf.* p. 13 above. MERGEN (1954 a) found that the space between the wood surfaces of grafts of young material of *Pinus elliotti* was filled with callus mainly originating from "medullary rays", apparently identical with leaf gaps. The pith of the scion is often severed, when it nearly always exhibits cell divisions.

In spruce, however, I have never observed any callus formation from parenchyma in the wood. The major portion of the parenchyma cells of the spruce wood exhibits heavily lignified walls. BLOCH (1952), however, stated after studies of a large number of works on the subject that most of the living cells can be dedifferentiated even if the walls are heavily lignified (p. 12 above). The lignified parenchyma cells in the spruce grafts investigated have never undergone any dedifferentiation leading to resumed division. No callus formation from the pith of spruce has ever occurred in the material studied.

According to the findings in many previous investigations of grafts, the woody plants differ considerably with respect to proliferation from wood and pith parenchyma. Differences between individuals may occur within one particular species. Thus, for instance, SASS (1932) found no callus formation from parenchyma in the wood or the pith in grafts of apple, but he mentioned that another research worker (FISK, unpubl.) had described proliferation from parenchyma in the wood of that species.

5. Callus formation from the cambial region in veneer grafts

BARKER (1954) suggested on the basis of his investigations that the cells of the cambial region, and not the ray cells, are the most active in the healing of wounds (*cf.* p. 13 above). His investigations, however, covered the regions of xylem and cambium only. The investigation reported here, as well as earlier investigations by *e.g.* SHARPLES & GUNNERY (1933), JULIANO (1941), and MERGEN (1954a), have shown that rays in the phloem play a decisive rôle in the healing of grafts in several species. The callus formations which effect the first unions between parenchyma tissues in veneer side grafts of pine and spruce, originate with few exceptions from rays in the phloem and/or from the

cortex. Thus the first parenchyma unions generally take place outside the cambial region.

The contribution by the cambial region to the formation of callus is very slight in well-matched veneer grafts. The conditions in the formation of callus from the cells of the cambial region have been discussed on p. 39. All cells in the cambial region may contribute to the callus formation, but the fusiform initials, and the xylem and phloem mother cells, have to pass repeated transverse divisions before they are ready to divide in the irregular way characteristic of primary callus. In well-matched grafts, callus tissues originating from tissues external to the cambium of the two components had united before this process was completed. The new formations at the wound surfaces in the cambial regions will therefore effect an almost immediate fusion of the vascular tissues provided the cambia are seated so that they face each other reasonably well. The first cells to unite in the cambial regions are always short and isodiametric, and they consequently differ from the normal, fusiform cambial cells.

Considerable callus formation originating from the cambial region occurs in veneer grafts of pine and spruce only when the cambial regions of the graft components have not been able to reach union relatively soon in the manner described above. Several scientists (MERGEN 1954a, SASS 1932, SHARPLES & GUNNERY 1933, JULIANO 1941), who worked with veneer grafts or other kinds of grafts with similar wound surfaces (tongue grafts, cleft grafts), found in several different woody species that the cambium is less active as a callus producer than the tissues on its exterior. BRAUN (1959), however, found in *Populus* that the major portion of the callus mass originated from the cambium and the youngest parts of the phloem and the xylem.

6. Callus formation in side slit grafts

The tissues in the stocks of the side slit grafts have been exposed in a different way. An incision is made in the bark, which is then loosened from the wood. If the cambium is in full activity when the operation is performed, the bark loosens in the youngest parts of the xylem. If the cambium is dormant or less active, it may attach to the wood, either completely or partly, which is less favorable in grafting.

SAX & DICKSON (1956) produced an excellent illustration showing how the cambium follows the bark when loosened from the wood. A bark ring was removed from an apple tree with white wood, and replaced with an equally large ring from a tree with red wood. All the

new wood formed inside the grafted bark ring was red. White wood, however, was developed in the vertical seam, which shows that a new cambium can be formed in a callus, mainly developed, according to SHARPLES & GUNNERY, from the rays in the exposed wood surface.

In side slit grafts of *pine*, ray cells and xylem mother cells, as well as incompletely differentiated, not yet lignified tracheids can participate in callus formation on the wood side of the stocks. Activity first becomes visible in the rays. In most cases it is only in the innermost corner and straight opposite the severed pith of the scion that the tissues mentioned above proliferate, see p. 91. On the bark flap side, too, proliferation may occur from all living elements. On this side it is not so important which parts of the scion are situated straight opposite the bark flap as it is on the wood side, but an obvious stimulation to increased division in the flap may be observed in places where it is in contact with living elements in the scion.

In side slit grafts of *spruce* I have not found any proliferation at all from the wood side of the stock. As in pine, the cambial region mostly followed the flap, but its cells appeared to have been extensively damaged in the grafting operation. Later on the cambial region also began to wither, probably due to the large, empty space left in the corner. As the scion is hard, it does not conform to the wood surface of the stock. This may be the explanation of the remarkable passivity of the flap. A minor change in the method of grafting, which would reduce the empty space in the corner, has been described on p. 87.

In principle I agree with the earlier research workers who contended that all living parts of plants can start division and formation of callus under suitable conditions. Neither in pine nor in spruce, however, have I observed any divisions of living cells with lignified walls, or any definite proof that tracheids that are already visibly lignified, would be able to dedifferentiate. It is clear, however, that tracheids that have not yet reached such an advanced stage in their differentiation as to become lignified, are able to dedifferentiate and develop callus. These observations agree entirely with those made by JÄGER (1928). I do not wish, however, to reject entirely the contention that dedifferentiation of lignified cells might also be found in pine and spruce, as well as in many other species (*cf.* BLOCH 1941, 1952). Sieve cells lose their power of dividing when differentiation has proceeded so far that their nuclei have started to degenerate, although the cells remain alive (ESAU 1953, 1960).

BRAUN's investigations (1958) of side slit grafts in *Populus* species showed callus formation from all exposed living cells in the stock, and

most vigorously from the wood side, where the early wood has usually been cut through. When the cut had instead passed through last year's wood, however, proliferation occurred from the sides only, and union was delayed. A method of incising the stock as used by BRAUN is recommended on p. 00 for side slit grafts in spruce. Proliferation from the wood surface never occurs in spruce stocks whether the cut in the wood is deep or superficial. The main concern here is to arrange the best possible contact surface for the scion, and the smallest possible empty space in the corner. At the same time the cambia of the scion and the stock should be fitted together fairly well at the incision face, *cf.* Fig. 34. This lastmentioned point was not observed by BRAUN, but it is probably not so important in *Populus*, where unions are always preceded by vigorous callus development and growth in the stock, while the scion remains almost passive. This leads to a change in the mutual position of the graft components. In spruce, where the callus formation is rather moderate in both the components, is it necessary to fit the cambia together fairly well. The cambium of the scion may be placed slightly outside that of the stock so as to compensate for the more vigorous growth of the stock, but never as far outside as shown in BRAUN'S drawings of *Populus* grafts.

The description given by BUCK (1953) of the callus formation in rose bud grafts is no different to the conditions I have found in side slit grafts of pine, except for the fact that the cambium of pine mostly follows the flap without suffering much damage. This, however, does not imply that the cambium will continue its division activity unchanged. According to the conditions present some parts of the cambium may be suppressed, while other parts continue their cambial growth pattern. Cambial unions with the scion can be achieved by differentiation of new cambial strands through the callus tissues in the corner. An excellent illustration of this development will be found in a series of sections (Plate XIII: 3—7) from a graft describedon pp. 57—59. See also Fig. 22.

It was mentioned on p. 40 that it is fairly common for divisions to occur in side slit grafts of pine some distance inside the wound surface in the flap. This means that the cells from the cambial region that adhered to the flap when this was severed from the wood, have died as a result of damage received in the grafting operation or from shrivelling on account of an insufficient supply of water. Ray cells and vertical parenchyma cells in the nonfunctional phloem may give rise to considerable amounts of callus in the flap (*cf.* Plate XII: 5). When phellogen is formed in the phloem of old stems, it proceeds in the same way. The remarkable thing about these divisions in the flap is that the rays,

he cells of which undergo divisions, lack any connections inwardly with the functional phloem, cambium, and xylem. If the flap attains junction with the outer part of the scion (point 3 according to Fig. 21), cambium from the scion may spread through the newly formed tissues. The section in Plate XIII: 3 shows an example of this. There was no junction some millimeter higher up in the same graft (above the branch trace in the scion) and the phellogen was intact right through to the pith of the scion, where callus masses from both components were united.

This course of events in the flap may provide some further elucidation of the part played by the rays in the formation of callus in the phloem. Here the rays lack any connections whatsoever with the cambium and vascular tissues, but they are still able to proliferate. The vertical parenchyma also participates, but the rays apparently react first (p. 90). These cells can hardly be said to be well placed from a point of view of conduction. Some water and nutrient must be assumed to be conducted through the parenchyma cells. This is, *inter alia*, a pre-condition for the life and growth of the nodules that occasionally occur in the outer parts of the stems (p. 68). In bark flaps, the outer parts of which have no junctions with the scion over long distances, lateral conduction through the parenchyma must be assumed a prerequisite, to prevent the flap from shrivelling. This often occurs in pine whereas in spruce the flap dies if no union has been established at an early stage. Tissues which continue to live, are always bordered on the exterior by periderm developed from phellogen originating in the cortex and phloem parenchyma.

7. *The intensity of callus formation in the two graft components. Parenchyma unions*

Previous investigations of graft unions have shown differences in the species in respect not only of the tissues in the graft components that may contribute to the callus formation, but also in the extent of the cell divisions in both the graft components, and in the mode of union induction (*cf.* literature review). In pine and spruce, divisions at the wound surfaces start almost simultaneously in both scion and stock after 3 or 4 days, sometimes even earlier in the scion than in the stock, eventhough the latter component had been growing at the time of grafting, whereas the scion was still dormant. Generally, however, it is the stock that produces the largest quantities of callus, but the scions may be very active within limited areas (when leaf traces adjoin the wound surfaces). It also happens that the scions produce very large

amounts of callus, after the first parenchyma junctions with the stock have been established.

It has repeatedly been stressed by BRAUN (1958, 1959, 1961, 1962 a) that the first parenchyma unions are effected by activity in the stock only. In grafts of pine and spruce, however, the unions are obviously established by reciprocal activity, but in occasional cuts a superior activity in one graft component may give the impression of its being the sole source of union in the area. It must also be regarded as having been proved that active tissues on one of the graft components may stir the other component to an activity that would not occur otherwise. The influence on the stock of the activity around the leaf traces in the scions is most clearly noticeable. The generally rather great activity in the stocks may influence the scions, provided the contact layers on the surfaces of the graft components are not too heavy.

BRAUN (1958, 1959) stressed the great importance of the pressure for the union of two graft components. In the *Populus* grafts he investigated, increased pressure between the components was developed by a vigorous formation of callus almost exclusively from the stock. The union developed only when the pressure grew sufficiently strong. In grafts of Scots pine and Norway spruce, however, union is usually established after only a few cell divisions on both sides. There is no great increase in the pressure in such cases, but a pre-condition is that tissues capable of proliferation have been closely fitted together and that the graft has been tied firmly. The relatively early unions between the stock flap and the scion often found in grafts of pine and spruce are certainly a result of the flap being forced outwards by the scion, which has caused them to become pressed closely together.

Where tissues capable of proliferation have not been fitted together at grafting, or where the binding of the graft has been unsatisfactory, large masses of tissue are gradually formed from both the stock and the scion (from the latter, however, only provided junction with the stock has taken place in other places in the graft zone). A pressure greater than that obtaining at the early unions is required for these tissues to unite, since their surfaces are coated with heavy cork layers. Independent of pressure and position in relation to the counterpart, vigorous formation of callus at an early stage may occur in specially active areas in both the graft components, *cf.* above. This callus effects a rapid union, if the graft components are well matched and securely tied.

Eight to ten days after grafting the first parenchymatous unions may be expected to have been established in well matched and firmly tied grafts of Scots pine. The healing in Norway spruce is usually

somewhat slower. Fifteen days after grafting there are parenchymatous unions in all the greenhouse grafts that have any prospects of developing further.

B. Phellogen formation

The formation of phellogen at a wound surface may be preceded by a vigorous development of callus composed of large, irregular cells, a layer of which some distance inside the surface starts to divide regularly, producing tissues characteristic of a periderm. The cell divisions may also proceed from the beginning according to a regular pattern (often, however, with the exception of the very first division, regarding which see below). This is usually the case when divisions start some distance inside the wound. The new formations then assume entirely the same character as that of the phellogens which would have been established in these tissues a few years later. (The normal development of new phellogens is described on p. 27.)

It has often been stressed that the first divisions in a wound meristem always occur parallel to the wound surface (*cf. e.g.* BLOCH 1941, 1952). The very first divisions in the cortex, especially in pine (*cf.* p. 42), however, have appeared to occur without any such predetermined direction. When divisions start superficially, an irregular cell mass is often formed in which divisions may occur in all directions. The first divisions in rays often proceed with the new cell walls perpendicular to the direction of the ray; in the cambial regions the fusiform cells first divide transversally, the new cell walls running fairly perpendicular to the wound surface. In those regions, however, where the first divisions have not been able to achieve union between the graft components, the divisions soon assume a regular character, and the newly formed cells will be arranged in rows. Divisions take place according to the same pattern as in a phellogen, but mostly more rows of cells are produced than in an ordinary phellogen. BLOCH (1952) also pointed out the similarities between the cell arrangement in periderm and wound tissues, and that the cell walls in both cases were often positioned straight opposite each other, so that four cell walls met at one point.

The similarities that have been observed between normal phellogens and periderms on the one hand, and wound phellogens and periderms on the other, lead to the assumption that there is no fundamental difference between these formations. Further, when new phellogens are formed in unwounded stems, the dedifferentiation, the cell enlargement, and the first divisions of cells in the cortex and phloem may be regarded as callus formation. According to KRENKE (*cf.* p. 65) callus formation

is a result of stimulation from a wound. The nature of the stimulus is not fully known (see pp. 88—89). It is probable that a stimulation of the same kind is present in normal phellogen formation, possibly arising from breaks in the tissues as a consequence of cambial expansion.

After the first callus fusion has occurred in the outer parts of the graft zone, the cells in the united tissues soon start to divide regularly more or less parallel to the wound surface. Already before the union of the callus has been established, there are mostly fairly distinct deposits of phellogens along the wound surfaces in the cortex of the graft components, and they now achieve union. In most cases the cork cambia unite earlier than the vascular cambia, which SOE (1959) has found true also in some species of deciduous trees after scoring in the stem. The cork cambia of pine and spruce grafts are often well united after 15 to 20 days, while the first signs of unions of well matched vascular cambia appear after 20 days, and often a week or so later. BRAUN (1958) stated regarding side slit grafts of *Populus* that the wound periderms mostly united only after the vascular cambia had achieved union, while in veneer side grafts (BRAUN 1959) the union of cambia and phellogens occurred about simultaneously. In *Populus*, as well as in pine and spruce, the old periderm in the periphery of the stems did not participate in the formation of the wound periderm, and union of old and new phellogens was not established until the wound periderm was almost complete. Also in grafts of apple, the old periderm has appeared to be inactive (SASS 1932).

C. Dedifferentiation and differentiation

As it is possible in principle for most living cells to lose their specificness (to dedifferentiate), to divide and form callus, all newly formed callus cells are initially entirely unspecified. They may differentiate in various directions under different influences. Callus tissues may unite irrespective of the type of the original tissues, and cambia and phellogens may differentiate through callus tissues of any origin. When entirely dissimilar tissue parts adjoin each other, *e.g.* the cambial region of the one component and the cortex of the other, parenchyma union may occur quite soon and the cambia from both sides spread through the uniting tissue. Newly formed cells, that have reached a certain degree of specialization, can again dedifferentiate under the influence of an advancing cambium. This is a common occurrence when union in some part of a graft has proceeded slowly—Plate XIII: 3 shows an example.

Before the union between the outer part of the scion and the park flap was established, the formations in the flap had developed a periderm character. Now, when the scion and the flap have united, the flap cells in contact with the scion cambium are dedifferentiated successively, and the cambium extends through the flap tissues. The vascular differentiation will be further discussed in the following.

D. The formation of vascular nodules in the intermediary tissue

Differentiation in the intermediary tissue of pine was shown in chapter V: D. In his studies on tissue cultures of Jerusalem artichoke GAUTHERET (1957, 1959) found nodules with the same cell arrangement when the original explant was a fragment of xylem. The nodules occurred in secretory canals, the centre of which differentiated into phloem, while the peripherical cells became tracheids. The latter consequently are formed in contact with the old tissue, *i.e.* xylem. Finally, a cambium is formed between the phloem and the xylem. GAUTHERET (1959) observed that new cambia in tissue cultures are generally formed in connection with newly differentiated phloem strands and then turned towards the original explant if this is of a xylem character but turned away from the explant if this consists of phloem.

In pine, the intermediary tissue is developed mostly from parenchyma in the wood. Plate IX: 9 shows in a higher magnification one of the nodules in Plate IX: 8 where some phloem cells have been differentiated and a cambial strand has developed in an arch with the phloem on the inner side of the arch. In the other two nodules shown in Plate IX: 8, several tracheid layers have been deposited but most of the phloem cells appear to have been crushed.

As mentioned in chapter V: D, it is not only spontaneously developing cambia that extend in such inverted arches, but also cambia, which have been enclosed between the wood surfaces (Plate IX: 12). Arches with the same tissue arrangement are found also in the innermost corner of side slit grafts (Plate XIII: 5).

E. Union of vascular tissues and cambia

A broken cambium always tends to spread and form a closed unit. It was mentioned on p. 93 that divisions at the cambial regions are almost immediately able to effect a union of the vascular tissues when the cambia of the graft components are placed close to each other. The short cells on the xylem side are often differentiated immediately to tracheidal elements, and newly formed tracheids of this kind from

both the graft components may adjoin each other without to unite. A real union of tracheids (= tracheids with mutual pits) is formed by the fusion of young, undifferentiated cells which then differentiate simultaneously. An initial xylem union of this kind often occurs between cells which have not been deposited from any distinct cambial zone. This is in agreement with the findings by SIMON (1908), KAAN ALBEST (1934), SINNOTT & BLOCH (1945), and JACOBS (1952). The first cells connecting the two cambial edges are parenchymatous. The complete vascular union is a result of influence on these cells emitted from the nearby unwounded tissues. The fact that auxin is the factor stimulating xylem differentiation has been made definitely clear by JACOBS (1952, 1961). When the cambia have been well fitted together, the uniting tissue may be composed of a very small number of cells.

SASS (1932) and BRAUN (1958, 1959) have observed cambial bridging achieved by a meristematical activity that extends tangentially from the cambial edges of both the stock and the scion (see "Literature review", pp. 11 and 14—15 respectively). The two investigators have stated that a connecting strand of meristematical cells is present before union between vascular tissues has been established. In the present investigation a "homoeogenetic induction" like that described by BRAUN and SASS has been found in cases where the cambial edges of the components were separated by a larger mass of parenchyma. Even before parenchyma union a stimulus may be transferred between the vascular tissues of the graft components, and thus determine the direction of cambial extension (SIMON 1930, HAYWARD & WENT 1939). The cells of the advancing cambial zones, which are influenced by another cambium, are in cross-sections observed as laterally extended towards the source of induction (Plate VI: 2, VIII: 3).

When longitudinal sections are studied it is obvious that the direction of the first uniting tracheids is mainly oblique from the scion downwards to the stock, and to a minor extent from the stock upwards to the scion (Plate IX: 3). JACOBS (1952, 1961) has shown the close relationship between xylem differentiation and auxin movement. The auxin moves mainly basipetally in the stems, but there is also a small acropetal movement, the relation between downward and upward transport being about 3: 1. Several scientists have found the xylem regeneration around a wound to be strictly basipetal (SIMON 1908, KAAN ALBEST 1934, JOST 1942, SINNOTT & BLOCK 1945). JACOBS, however, have found that the acropetal auxin movement is paralleled by a slight acropetal xylem differentiation. The cell arrangement in the studied graft junctions in pine and spruce confirms this statement.

Differentiation on the phloem side is mostly slower than on the xylem side, which has been stated earlier also by SIMON (1908), KAAN ALBEST (1934), and ARTSCHWAGER (1951). The first sieve cells do not appear in the region of union until the divisions have assumed a cambial character. The union in the phloem is therefore maintained for some time by parenchyma cells. ARTSCHWAGER (1951) found this phenomenon in grafts in the *Compositae* family, where these parenchyma cells, however, are narrow and elongated. In pine and spruce grafts the cells were of a callus character, often slightly elongated, but shorter than normal sieve cells. The first sieve cells mostly had approximately the same outer dimensions as the callus cells.

So far we have only discussed the union of cambia in which the continuity has been broken. Also a completely intact cambium, however, can be broken up under the influence of another intact or broken cambium. In so called natural grafting, intermediary parenchyma tissues will be extruded. The cambia of the components divide and bend outwards to the sides where they unite. It was described on pp. 81—82 how leaf traces exposed in the bark parts of spruce scions activate parenchyma tissues in the stock to differentiate into vascular tissues, finally to become incorporated with its stele. The cambium of the stock divides to receive the leaf trace. Often the cambial edges of the graft components do not achieve union with each other in certain parts of a graft zone, especially in the upper parts of the zone, and in one side of grafts consisting of components of widely differing thicknesses. In such cases one or both of the cambia enter between the wood surfaces. Upon continued growth the cambia will unite in the same way as in natural grafting.

Even without influence from another cambium, a broken cambium always spreads through contiguous parenchyma tissues, but these new cambial cells do not extend laterally. As a result of the great activity at the wound surfaces, broken cambia mostly turn outwards to begin with (*cf.* HERSE 1908). This may be seen most clearly in the stock, which is the component with the faster growth. At the wound edge the cambium grows faster than in the rest of the stem. If union with the counterpart fails to materialize, or is too weak, the parenchyma tissues extend over the exposed wood surface of each part, and the cambium follows. The healing over of the cut stocks proceeds according to the same pattern.

The importance of various methods of cutting and fitting together the scions and the stocks for the result of the union has been discussed in chapter V: E (pine) and chapter VI: D (spruce). Although more difficult

to apply in practice, a good cambial fit is much more important in grafts of spruce than in pine, the reason being that the callus development in spruce grafts is usually weaker. The greater the ability of the graft components to produce callus, the better are the conditions for cambial unions over long distances. *Populus* is an example of a species possessing great power of proliferation. In the side slit grafts studied by BRAUN (1958), cambial union could be achieved thanks to the vigorous callus formation from the stocks. Extremely vigorous callus formation from the stocks sometimes occurs in pine grafts, but has mostly proved less desirable, in that the scion may simply be extruded. This can be prevented to some extent by binding the graft firmly, particularly if the grafting has been done carefully by fitting the cambia well together. It was also mentioned on p. 85 that too superficial cuts in the stock should not be made when applying veneer side grafts in pine, since they easily produce heavy callus formation over the entire wound surface, which may lead to the extrusion of the scion.

F. The epithelial cells of the resin ducts

The epithelial cells of the resin ducts in the cortex and the phloem often play a great part in the production of callus in grafts of pine and spruce. The distribution and direction of the resin ducts in various tissues of both species has been described in chapter IV. According to this description vertical ducts occur in xylem and cortex only. The statement made by ESAU (1953, 1960), among others, that vertical ducts may be present in the phloem of conifers, is wrong, at least in respect of Scots pine and Norway spruce. Horizontal resin ducts enclosed in rays occur in both xylem and phloem, and are directly connected via the cambium. The resin cysts, developed when the horizontal ducts expand in the phloem, may possibly be conceived as vertical ducts in single cross-sections. In three *Pinus* species investigated, incl. *Pinus silvestris*, BAGDA (1956) found neither vertical nor horizontal ducts in the phloem. However, he observed "dilatation" of many rays in the phloem after the second year, and stated that most rays are uniseriate during the first year. Upon investigating tangential sections through the youngest phloem and the cambium, one will find that some rays are fusiform, *i.e.* they are two (or more) cells wide in the middle, but one cell wide in the upper and lower edges. These rays constitute connections between the horizontal resin ducts on both sides of the cambium. THOMSON & SIFTON (1925) interpreted this to mean that no anastomoses occur between the horizontal resin ducts of the xylem and the phloem, and that there is continuity in the tissues only. The dilata-

tion of rays observed by BAGDA is probably the same phenomenon as that described above (p. 25), *i.e.* an expansion of the resin ducts in multiseriate rays into resin cysts. One of the illustrations in the paper written by BAGDA, called "Mik. 4", would also seem to justify this assumption (the ray is marked "Mstr").

The epithelial cells around the resin ducts in the phloem are consequently ready to divide without any wounding of the stem. THOMSON & SIFTON (1925) also discussed the occurrence of "cambial" activity around the resin cysts in the phloem, and around the vertical ducts in the cortex. When the ducts are wounded, resin is first excreted, whereupon the epithelial cells almost immediately start to expand, and very soon divide. Primarily, it appears to be a function intended to close the ducts from the environment, but these new formations seem to be of identically the same character as the callus formations from other tissues, and they nearly always contribute to unions when suitably positioned in relation to the counterpart.

G. How and when should grafting be carried out?

In the chapters dealing with "observations on the shaping and fitting of the graft components" (p. 69 and p. 84 respectively) some recommendations have been given concerning the method of grafting with a view to obtaining the conditions most conducive to a good union from an anatomical-histological point of view. A repetition of these recommendations is therefore unnecessary, but some supplementary viewpoints may be added.

The water conditions in stems and scions have been closely investigated by BRAUN (1961, 1962 a). Until parenchyma unions are established with the stocks, the scions are restricted to their own water reserves. The water in the scions moves from the inner to the outer tissues, and from the basal parts towards the top. Accordingly, the lowest parts of the scions, that are in contact with the stocks, are most exposed to drying. It is consequently of great importance that the union occurs rapidly, and that the atmosphere around the grafts is kept humid until the junction is complete, in order to prevent the scions from drying out.

Of the two graft components, it is actually only the stocks that can be chosen and treated before grafting. The scion-wood usually has to be accepted as it is, the matter simply being to propagate certain trees. It goes without saying that the scion-wood should be as fresh as possible when grafted, or, when this is not possible, stored in the best way. It is

also clear that the scions should have no growing annual shoots at the grafting, since this would mean too great a loss of water.

The stocks, however, may be treated in various ways. The stocks mostly used when grafting in the greenhouse are four years old, in the field they are often somewhat older. The stocks are consequently generally much thicker than the scions. The difference in the size of the components of *spruce* grafts is often very great, which renders it difficult to obtain a good fit (*cf.* chapter VI: D). Young, smaller stocks are therefore to be preferred. It has also appeared that young cells have a greater power of dividing, which is an additional reason for using young stocks. The treatment of the material during its growth is certainly of the greatest importance, since stocks in good condition produce callus more vigorously than poor stocks.

The scions of the grafts investigated here have been placed as far down on the stocks as possible. This is the usual practice when grafting in the greenhouse, and also the most common procedure when grafting in the field, at least in Sweden. The interesting investigation carried out by NÆSS-SCHMIDT & SØEGAARD (1960) on Douglas fir (*Pseudotsuga taxifolia*) showed that the result of union in "high grafting", 91 per cent survival, was considerably superior to that of "low grafting", 46 per cent survival. On the basis of information obtained from the anatomical investigations of grafts, it may be assumed that the young tissues in the upper parts of the stocks have had greater power of proliferation. It is also probable that the size of the graft components was more equal in these positions.

Methods for grafting succulent or semi-succulent material (young twigs with incompletely lignified woody cylinders) have been described by MERGEN (1954 b), ZAK (1955), FOWLER (1959), and LESKINEN (1960). From an anatomical point of view such a technique is advantageous—only young cells capable of proliferation are present in the healing zone. Good results have been reported, but obstacles to a wider use are *e.g.* the time of grafting, and difficulty in collecting the scion material. Sometimes, however, this possibility could be of great value.

The time of grafting and the treatment of stocks prior to grafting are other interesting points. The stocks of the grafts investigated here had been forced so far that they had all developed 1—2 cm long, new shoots. It appeared, however, that the cell division activity at the wound surfaces started at least equally as early in the unforced scions, which probably shows that it is unnecessary to force the stocks before grafting in order to obtain successful results. A small, comparative experi-

ment comprising 48 pine grafts and conducted in the spring of 1960 also provided similar indications, and an even slightly superior increment of the scions grafted on the unforced stocks. The NIENSTAEDT (1959) investigation on spruce (*Picea abies* and P. *glauca*) grafted in the autumn, also showed that activity in the stocks at grafting is of minor importance. The stocks were given various treatments during the months prior to grafting: long day (*i.e.* in growth at the time of grafting), short day (*i.e.* in rest, although soon interrupted after the transfer of the plants into the green house). The number of successful unions obtained from the differently treated stocks wase about equal. The continued development of the scions, however, may be affected by variations in day length and temperature after grafting.

BRAUN (1962 a) has made thorough investigations into the most advantageous time for grafting poplar in the field. Two periods of excessive cambial growth is observed during the growing season, and grafting is best carried out just at the beginning of these periods (in the mentioned case from the end of April to mid-May and from the end of June to early July). This agrees with the practice in greenhouse grafting of conifers. The grafts are made when the buds of the stocks have just begun to burst, and the cambial activity has been found to start simultaneously.

VIII. Summary*

The majority of the grafts investigated were made in a greenhouse in the spring of 1958 and 1959, with a minor supplementation in 1960. Being forced, the stocks, mostly four years old, had new annual shoots measuring 1—2 cm at the time of grafting. The scions consisted of one-year-old shoots in complete dormancy.

Two different methods of grafting were applied: veneer grafts and side slit grafts. Each type of graft was done in two ways and investigated, *cf.* Figs. 1—14 and 16—18. After having been fixed in CRAF (for recipe see p. 21) for the purpose of anatomical studies, the graft zones were embedded in paraffin and cut in 15 μ thick cross-sections and longitudinal sections, which were stained in safranin and fast green, and mounted in Canada balsam.

From the grafts of 1958 three specimens were taken for examination every week during 5 weeks, and then at intervals of 14 days to one month for the rest of the summer. In order to follow the course of growth accurately during the first stage, specimens for examination were taken daily from the grafts of 1959 for the first 14 days, and then every other day for a further period of 14 days. The process of union growth has been followed completely during the first season after grafting. A number of 1—3-year-old grafts were also investigated.

The main features of the anatomy of young stems of Scots pine and Norway spruce have been reviewed in chapter IV, with particular attention paid to the ability of the various tissues to contribute to the union of graft components and to differences between the species in this respect. The various anatomical details such as observed in cross-sections as well as in tangential and radial longitudinal sections are presented in the drawings in Figs. 16—17. Plates I and II: 1—5 show full pictures and details of both the species.

Resin excretion from severed resin ducts is the immediate reaction at the wound surfaces. There is nothing to show that the resin constitutes a barrier between the graft components; on the contrary, it serves as a sealing. As it has mostly been dissolved and removed from the material by fixing solvents and alcohols, no resin was found in the microscope slides.

Contact layers consisting of directly or indirectly damaged cells are developed on the cut surfaces in the cortex, phloem, and cambium of

* A short summary concerning experiences of importance for practical grafting was given in the author's publication "Grafting Methods for Scots Pine and Norway Spruce" (1962)

both the graft components. In the phloem, both the functional and the non-functional, a large number of sieve cells will constitute a part of the layer, on account of their inability to participate in callus formation. In Scots pine, contact layers also occur over severed parenchyma tissues inside the cambium, *viz.* rays, resin ducts, and pith.

Enlargements of cells adjacent to the wound surfaces is the first noticeable reaction from the living cells. The epithelial cells of cut vertical resin ducts in the cortex react specially quickly (Plate III: 1—3). As early as one day after grafting they are clearly enlarged, and they soon clog the duct entirely, often at a long distance from the place where the duct has been wounded. Cell enlargements at an early stage are also common in practically all thin-walled, parenchymatous cells situated adjacent to the wound surfaces.

Cell divisions appear close to the wound surfaces in both stock and scion 3—4 days after grafting. The scion often shows the first divisions and most activity during the first days after grafting. In Scots pine, it is quite clear that the first cell divisions occur in rays of the phloem, sometimes also in cambial parts of the rays, but some later epithelial cells of resin ducts in the cortex and ordinary cortex cells divide as well. In Norway spruce, divisions occur simultaneously in all the tissues mentioned above.

The initial cell division is most vigorous in regions known as storage places for nutrients and best suited for conduction. The cells surrounding leaf and branch traces, and the cells of rays that emerge from leaf gaps are particularly active in the formation of callus (Plate II: 6—8). On the whole, the stocks produce a larger volume of callus before union than the scions, but leaf traces adjacent to the cut surfaces of the latter component induce a locally larger formation of callus.

Rays that have been cut far out in the phloem mostly form more callus than those which have been cut closer to the cambium, or in the cambial zone (Plate XIV: 5—6). The boundary between phloem and cortex is a very active zone (Plate V: 11).

The very first cell divisions do not occur at any special angle in relation to the wound surface; especially in Scots pine (Plate V: 1—3 and 5), where the initial callus formation is often very extensive. Soon, however, divisions proceed according to a definite pattern, in which the new cells are established with their walls almost parallel to the wound surface (Plate V: 6—8). This is the first stage in the development of cork cambium (phellogen).

The cambial region plays a subordinate rôle as a callus producer in veneer grafts. Generally callus tissues from both the graft components

outside the cambium unite before the necessary change in the mode of cambial cell division (p. 39) has occurred. In the stocks of side slit grafts, however, the bark has been loosened from the wood in the cambial region, the cells of which can give rise to vigorous callus formation in Scots pine. This process is initiated by ray cells, but soon the major portion of the cambial cells participate to such extent as they have not been damaged in the grafting. The Scots pine stocks produce callus from both the wood surface and the bark flap (Plate XII: 1), whereas callus production in Norway spruce stocks has been reported to occur from the flap only, and even there it is mostly sparse (Plate XVI: 11). If the incision in the stock is made tangential to the cambium, the conditions at the incision face are equal to those in veneer grafts (Plate XVI: 10). Radial incision gives usually rise to essential formation of callus from the cambia of both the components in consequence of the poor cambial fitting.

Callus formation from parenchyma of the wood or pith occurs only in Scots pine, where it can sometimes be quite extensive. The scion pith is particularly active when severed. In the stocks, vigorous callus formation has been observed in some cases when more parenchymatous tissues than normal were present in the wood as a result of some damage suffered by the cambium during growth. In some of the cases investigated, this occurs in annual ring boundaries (Plate VI: 8).

A comparison of the tendency of various tissues to produce callus in both the species is presented in Table 1 (p. 77). Great activity in one graft component has appeared to induce contiguous tissues in the counterpart to increased activity already before direct union is achieved between the tissues concerned. It is consequently a matter of influence communicated through a not too heavy contact layer, and without plasmatic connections between the cells.

Unions between parenchymatous tissues have been reported 8—10 days after grafting. Fifteen days after grafting there are parenchyma unions in all the greenhouse grafts that have any prospect of developing further. Only cells newly formed after grafting are able to unite. In veneer grafts, the first unions occur between cells originating from tissues outside the cambial region. They are mainly developed from the cortex and the phloem part of the rays. In side slit grafts with a radial incision in the stock bark (Fig. 18 a), the first unions develop between the callus from the stock cambial region in the bark flap, and between callus from the cortex, the phloem rays, and the pith of the scion (Plates XII: 1, X: 11), In side slit grafts with tangential incision in the stock (Fig. 18 b). unions also occur at the incision face in a way similar to that in veneer

grafts. Newly formed cells may unite irrespective of the nature of the tissues from which they originate.

Union of phellogen. Through the parenchyma unions in the outermost parts of the graft wounds, phellogen is differentiated which connects the cork cambia that have developed, or are in process of development on the wound surfaces of the graft components. Complete unions of phellogen occur 15—20 days after grafting. The phellogens at the periphery of the stems do not participate in the formation of the new ones, and a union of new and old phellogens occurs only gradually.

Unions of vascular tissues have been reported after approximatively three weeks in well-matched grafts. When the fit has been less satisfactory, union may take 5—6 weeks. In well-matched grafts it is common that divisions in the cambial region are able to promote the union of vascular tissues almost at once. Only a small number of short, irregular cells are then formed. It is often noticeable that newly formed tracheids have united before any true cambial union has been established. When the cambia are situated farther apart, they spread through intermediate parenchyma tissues towards each other by induction from one cell to another. This causes the cells to dedifferentiate and start dividing again. Differentiation of tracheids on the wood side often follows the cambial strands, while connection on the phloem side is maintained for some time by parenchyma cells which only gradually differentiate into sieve cells.

Since the stock cambium had already entered the active stage at grafting, and since the stock furthermore has a greater supply of water and nutrients than the scion, its cambium will be able to deposit several new rows of tracheids until such time as union is possible. This means that the cambium of the stock outgrows that of the scion when the two cambia are placed right opposite each other at grafting. If the scion cambium is placed outside that of the stock, the cambium of the latter will soon catch up with it (Fig. 32, Plate VI: 5).

The first unions of vascular tissues in veneer grafts are often found between the stock flap and tissues situated at the short, cut surface of the scion (Plate VII: 2, 7).

Neither parenchyma unions nor cambial unions occur simultaneously over the entire cut surfaces of the grafts; the first unions occur where the tissues have been placed closely together, and where the most active tissues adjoin the cut surfaces.

Leaf traces appear to play an important part in the establishment of vascular connections, especially in Norway spruce, where they occur in large numbers and remain long in the cortex tissues before departing from the stem (Plate XVI: 1—6, 8, Fig. 33).

The cambial unions in the innermost corner of side slit grafts become more or less complicated depending on the mutual position of the tissues in the graft components. When the flap is loosened from the wood, the cambium usually sticks to the flap. In its upper part, at least, the scion has two free cambial edges directed inwards to the corner, one towards the flap and one towards the wood side. Fig. 22 shows how cambial unions are achieved, *cf.* Plate XIII: 5—7.

Intermediary tissues. It is not necessary that the space between the wood surfaces of the graft components should be filled with callus tissues (Plate VI: 11). On the contrary the space usually remains empty when the tissues heal rapidly. The intermediary tissues which nevertheless occur, originate in Norway spruce exclusively from tissues on the exterior of the wood cylinder which have expanded in between the wood surfaces. In Scots pine, parenchyma cells in xylem resin ducts, xylem rays, leaf and branch gaps, and pith, as well as tissues external to the wood cylinder, participate in the formation of intermediary tissues (Plate VI: 7—10). Vascular nodules are often formed in the intermediary tissue, particularly in pine. On these nodules, xylem is situated on the exterior and phloem on the interior of the cambial sheath (Plate IX: 8—9). The tissues that intrude between the wood surfaces are often followed by cambium which becomes separated from its original cambium when this unites with the cambium of the other graft component. These isolated cambia form arches with the same cell arrangement as that of the spontaneously developed nodules (Plate IX: 11—12).

Healing of the cut stocks. In the summer of the year after grafting, the stocks are cut back with an oblique cut immediately above the uppermost point of contact with the scion. The wound thus caused is healed over from all sides in the same way as the wound of a cut branch (Figs. 23—28). In the cases investigated, only tissues originating from the stock have participated in the process. The edge of callus is most heavily developed on the two sides adjoining the scion; it is weaker in front of the scion and weakest on the side facing away from the scion, *cf.* Fig. 29.

Shaping the stock flap of veneer grafts. The flap may be shaped in two ways, as demonstrated in Figs. 3—4 and 6—7, respectively. Of these two, the downward cut in Figs. 3—4 is definitely to be preferred. In the second case, a sliver of wood will adhere to the entire flap and will obstruct a smooth union between the flap and the short cut surface of the scion, *cf.* Figs. 30—31. Plates IX: 13—15, and X: 1—4 show examples of disturbances that occur when the flap is made with an

upward cut. The wood sliver must either be walled in or expelled by the expanding tissues. Plates X: 5 and XV: 5 show examples of a smooth union obtained from a downward cut in the flap.

Fitting the cambia of veneer grafts. Good fitting of the cambia is in veneer grafts a prerequisite for a rapid union of the graft components. This does not imply, however, that the cambia of the scion and the stock should be placed exactly straight opposite each other from the outset, as mentioned above. It is better that the cambium of the scion is placed so that it extends a short distance outside that of the stock, so as to compensate for the more vigorous growth of the latter component (Fig. 32 c—d).

It has proved to be considerably more difficult to arrange a good fit between the graft components of Norway spruce than between those of Scots pine. Difficulties arising in the grafting of Norway spruce are primarily due to the fact that the stocks have been considerably bigger than the scions. It has been possible to obtain a good fit, however, by making a very superficial incision in the stock—an incision which merely touches the wood—and then placing the cut surface of the scion straight opposite that of the stock. In Scots pine, however, such superficial incision in the stock is not advisable, since it promotes a vigorous callus formation over the entire cut surface, which impedes the union of cambia, or may even cause an expulsion of the scion. This, however, has not been experienced with Norway spruce. It goes without saying that the graft components must always be tied firmly, so as to prevent the callus from the stock from healing over the wood surface from the sides before connection with the scion has been established.

Common faults made in the grafting of Norway spruce include too deep an incision in the stock, and fitting together the outer edges of the graft components on one side in order to match the cambia. Because of the thicker bark of the stock as well as the more tangential cut made in the latter, the cambia of the stock and the scion do not fit together on either of the sides (Plate XIV: 8 and XV: 9).

A comparison between the one-year-old shoots of Scots pine and Norway spruce has shown that the bark of the latter species contains a considerably smaller portion of living tissues (see pp. 26—27 and Plate I: 1 and 2). The Norway spruce shoots are surrounded by a heavy layer of dead cells and the cortex between the ridges formed by the leaf traces is very thin. Since the extent of tissue capable of proliferation is comparatively limited in the scions of Norway spruce, a good cambial fit is more important in Norway spruce than in Scots pine. The in-

vestigation has clearly shown that young and small stocks are to be preferred in the case of veneer grafts.

The incision in the stock of side slit grafts has been made in two ways: radially and tangentially (Figs. 10—11 and 12—14, respectively). When the incision has been made radially, the entire scion will be seated inside the incision face (Fig. 18 a), and the cambial edges at this point will be placed far apart (Plates XII: 3, 6, and XIII: 4, 9). With a tangential incision (Fig. 18 b) there are possibilities of fitting the cambia so as to obtain unions corresponding to those of veneer grafts (Plates XIII: 11, 12 and XVI: 10, 11). Of the side slit grafts of Norway spruce used in this investigation, only those with a tangential incision in the stock have succeeded. The major part of the unions then occurred at the incision face, whereas the bark flap often failed. By cutting the stock so that it also includes part of the wood (Fig. 34), a better contact surface for the scion would be obtained, and less empty space in the corner.

Veneer side grafting is clearly the superior of the two methods tested and the only one to be recommended for Norway spruce. The flap should be done with a downward cut. *Side slit grafting* may be recommended for Scots pine when large stocks are to be grafted with small scions. Tangential incisions in the stocks then improve the prospects of a successful grafting.

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Sammanfattning*

Anatomisk och histologisk undersökning av sammanväxningen mellan ympkvist och underlag hos ympar av tall (*Pinus silvestris* L.) och gran (*Picea abies* (L.) Karst.)

Huvudparten av de ympar, som varit föremål för undersökning, ympades i växthus vårarna 1958 och 1959. En mindre komplettering gjordes 1960. Underlagen var mestadels fyra år gamla och hade drivits före ympningen så långt, att de nya årsskotten utvecklats 1—2 cm. Ympkvistarna var ettårsskott i fullständig vila.

Två olika ympmetoder har tillämpats: läggympning och sidsticksympning. Ympar enligt båda dessa metoder har utförts och undersökts i två varianter, se fig. 1—14 och 16—18. För de anatomiska studierna fixerades ympzonerna i CRAF (recept se sid. 21), bäddades i paraffin och snittades i 15 µ tjocka tvär- och längdsnitt. Snitten färgades i safranin och »fast green» och monterades i kanadabalsam.

Från 1958 års ympar togs tre exemplar ut till undersökning varje vecka under 5 veckors tid, sedan med 14 dagars—en månads mellanrum under resten av sommaren. För att noggrant kunna följa händelseförloppet den första tiden togs från 1959 års ympar ut två exemplar till undersökning varje dag under de första 14 dagarna, därefter varannan dag under ytterligare 14 dagar. Sammanväxnings- och tillväxtförloppet under första säsongen efter ympningen har följts i sin helhet. Dessutom har ett antal 1—3-åriga ympar undersökts.

Den anatomiska strukturen hos unga tall- och granstammar så som den ter sig i tvärsnitt och tangentiellt resp. radiärt längdsnitt återfinns i teckningarna i fig. 16—17. I sina huvuddrag är stammarna uppbyggda på likartat sätt men det finns några anmärkningsvärda olikheter som är av betydelse för kallusbildning och ympsammanväxning. Parenkymet innanför kambiet (märg, blad- och grenluckor, strålar[1], hartskanalernas epitel) består hos tall av tunnväggiga celler medan de flesta av dessa celler hos gran har förvedade väggar. Antalet hartsförande strålar är större hos tall än hos gran och saknas helt i ettårsskotten hos gran. Den förkorkade delen av peridermet hos unga skott är tjockare hos gran än hos tall. Det finns fler bladspår i grankvistar än i tallkvistar. Pl. I och II: 1—5 visar helhetsbilder och detaljer från båda trädslagen.

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* I uppsatsen »Ympningsmetoder för tall och gran» (1962) har erfarenheter av betydelse för praktiskt ympningsarbete sammanfattats.

[1] I överensstämmelse med bruket i engelskan används här ordet »stråle» i stället för det oegentliga »märgstråle». Prefixen »xylem-» och »floem-» används för att ange läget i stammen.

Hartsavsöndring från genomskurna hartskanaler är den första redan för blotta ögat synliga reaktionen vid sårytorna. Det finns ingenting som tyder på att hartset utgör något hinder för sammanväxningen, tvärtom tycks det tjänstgöra som ett skydd. Huvudparten av detta harts har lösts från materialet av fixeringsvätskor och alkoholer och har ej funnits med i de mikroskopiska preparaten.

Isoleringsskikt bestående av direkt och indirekt skadade celler utbildas över snittytorna i kortex, floem och kambium hos båda ympkomponenterna. I floemdelen, i såväl den aktiva som inaktiva, kommer dessutom en stor del silceller att ingå i skiktet beroende på deras oförmåga att delta i kallusbildning. Hos tall förekommer isoleringsskikt även över skadade parenkymvävnader innanför kambiet: strålar, hartskanaler och märg.

Förstoring av celler intill sårytorna är den första märkbara reaktionen från de levande cellerna. Epitelcellerna hos genomskurna vertikala hartskanaler i kortex reagerar särskilt snabbt (pl. III: 1—3). Redan dagen efter ympningen är de tydligt förstorade och sluter snart till kanalen helt, oftast långt ovanför det ställe, där kanalen sårats. Cellförstoringar på tidigt stadium är dessutom vanliga i praktiskt taget alla intill sårytorna belägna tunnväggiga parenkymceller.

Celldelningar börjar uppträda intill sårytorna hos både underlag och ympkvist 3—4 dagar efter ympningen. Ofta är det ympkvisten som visar de första delningarna och den större aktiviteten under de första dagarna efter ympningen. Hos tall har det varit fullt tydligt att de tidigaste celldelningarna uppträtt i strålarnas floem- och kambiedelar, men bara någon dag senare har delningar förekommit även i kortex — såväl i hartskanalernas epitelceller som i vanliga kortexceller. Hos gran har delningar konstaterats i alla de ovannämnda vävnaderna samtidigt.

Celldelningsaktiviteten är störst i områden, som ligger väl till ur närings- och transportsynpunkt. Celler kring blad- och grenspår, liksom celler i strålar, som utgår från bladluckor, är speciellt aktiva kallusbildare (pl. II: 6—8). Som helhet bildar underlagen större kallusmängder före sammanväxningen än ympkvistarna, men bladspår intill snittytorna hos de senare kan orsaka lokalt stor kallusbildning.

Strålar, som blivit avskurna längst ut i floemet, bildar oftast mer kallus än sådana som avskurits närmare eller i själva kambiezonen (pl. XIV: 5—6). Gränsen mellan floem och kortex utgör en mycket aktiv zon (pl. V: 11).

De allra första celldelningarna sker inte i någon bestämd vinkel i förhållande till sårytan, i synnerhet inte hos tall (pl. V: 1—3 och 5), där den första kallusbildningen ofta är av ett mycket extensivt slag. Snart inordnas dock delningarna i ett bestämt mönster där de nya cellerna anläggs med de nya cellväggarna mer eller mindre parallellt med sårytan (pl. V: 6—8). Detta regelbundna meristem utvecklas i kortex till ett korkkambium (fellogen).

Kambiezonen spelar en underordnad roll som kallusbildare hos läggympar (pl. V: 7). I allmänhet hinner kallusvävnader från båda ympkomopnenterna utanför kambiezonen förena sig, innan den nödvändiga omställningen i kambiecellernas sätt att dela sig ägt rum. Hos sidsticksymparnas underlag utgörs större delen av kontaktytan med ympkvisten av blottat kambium, och därifrån förekommer hos tallsidsticksympar mycket livlig kallusbildning. Initiativet tas av stråleceller, men mycket snart kan man se större delen av kambie-

zonens celler delta, i den mån de inte skadats vid ympningen. Tallunderlagen bildar kallus både från den blottade vedytan och från barkfliken (pl. XII: 1), medan hos granunderlagen kallusbildning endast konstaterats från fliken och även där mestadels sparsamt (pl. XVI: 11). Om insnittet i underlaget gjorts tangentiellt mot kambiet så blir förhållandena vid inskärningsytan desamma som hos läggympar (pl. XVI: 10). Radiärt insnitt medför vanligtvis livlig kallusbildning från båda komponenternas kambiezoner till följd av den dåliga sammanpassningen mellan kambierna.

Kallusbildning från parenkym innanför kambiezonen förekommer endast hos tall och kan där ibland bli rätt omfattande, särskilt från märgen och från områden i veden, där det funnits mer parenkymvävnader än normalt beroende på någon skada som tillfogats kambiet under tillväxten — i vissa undersökta fall vid årsringsgränser hos underlagen (pl. VI: 8).

En sammanställning av olika vävnaders benägenhet att bilda kallus hos de båda trädslagen återfinns i tabell 1. Stor aktivitet hos den ena ympkomponenten har visat sig kunna påverka intilliggande vävnader hos motparten till ökad aktivitet redan innan direkt förbindelse föreligger mellan vävnaderna ifråga. Det är alltså fråga om en påverkan som överförs genom ett naturligtvis inte alltför kraftigt isoleringsskikt och utan plasmatiska förbindelser mellan cellerna.

Tabell 1. Celldelningsintensitet i olika vävnader hos ympar av tall och gran.

Vävnad	Tall	Gran
Periderm	—	—
Kortex, grundvävnaden	+++*	+++*
Kortex, hartskanaler	++++	++++
Floem, strålar	++++*	++++*
Floem, vertikalt parenkym	++*	++*
Floem, fullt differentierade silceller	—	—
Kambiezonen, strålar	+++*	+++*
Kambiezonen, övriga odifferentierade eller ofullständigt differentierade celler	++	++
Xylem, strålar	+	—(+)
Xylem, hartskanaler	+	—
Xylem, fullt differentierade trakeider	—	—
Märg, blad- och grenluckor	++	—

* Vävnader under inflytande från blad- och grenspår visar större aktivitet än motsvarande andra.

+++ mycket stor celldelningsintensitet
+++ stor celldelningsintensitet
++ celldelningsintensiteten varierar, men kan beträffande tallens märg och bladluckor börja på tidigt stadium, eljest först sedan intilliggande vävnader börjat dela sig
+ delningar av varierande omfattning kan förekomma men uteblir ofta
(+) när ympningen skett sent kan xylemstrålar i *årets* ved bilda kallus
— inga celldelningar.

Sammanväxningar mellan parenkymatiska vävnader har konstaterats 8—10 dagar efter ympningen. 15 dagar efter ympningen finns parenkymföreningar hos alla växthusympar, som har förutsättningar att utvecklas vidare. Endast celler som nybildats efter ympningen har möjlighet att förenas. Hos läggympar sker de första föreningarna mellan nya celler som härstammar från vävnader

utanför kambiezonen, huvudsakligen från kortex och floemstrålar (pl. V: 7, 8 och 12). Hos sidsticksympar, som utförts med radiärt insnitt i underlaget så att inga direkta kontaktytor finns mellan inskärningsytan och ympkvisten (se fig. 18 a), sker de första föreningarna mellan kallus från underlagets kambiezon i barkfliken, främst strålar och kallus från kortex, floemstrålar och märg hos ympkvisten (pl. XII: 1 och X: 11). Hos sidsticksympar med tangentiellt insnitt i underlaget (fig. 18 b) sker föreningar dessutom vid inskärningsytan på samma sätt som hos läggympar. Föreningar mellan nybildade celler kan ske oberoende av från vilka vävnader de har sitt ursprung.

Fellogenbildning. Genom det förenade parenkymet ytterst i stammen differentieras mycket snart fellogen som förenar de korkkambier som redan har bildats eller är under utbildning utefter sårytorna hos ympkomponenterna. Fullt utbildade föreningar mellan fellogen uppträder 15—20 dagar efter ympningen. De gamla fellogen, som ytterst omgärdar stammarna, deltar inte i bildandet av de nya. En förening dem emellan sker först så småningom.

Förening mellan ledande vävnader har konstaterats efter c:a tre veckor hos väl sammanpassade ympar. Då sammanpassningen varit mindre god, kan 5—6 veckor erfordras för denna slutliga förening. Hos väl sammanpassade ympar är det vanligt att delningarna i kambiezonen nästan omedelbart bidrar till föreningen mellan ledande vävnader (pl. VII: 2—3 och XV: 4). Endast ett litet antal korta mer eller mindre oregelbundna celler bildas därvid. Man ser ofta, att nybildade trakeider förenats innan egentlig kambieförening förekommer. När kambierna ligger längre isär, sprider de sig genom mellanliggande parenkymvävnader i riktning mot varandra genom en induktion från cell till cell, som medför att cellerna dedifferentieras och åter börjar dela sig. Differentiering av trakeider på vedsidan följer oftast kambiestråken åt, medan förbindelsen på floemsidan till en tid uppehålls av parenkymceller, som först så småningom differentieras till silceller.

Eftersom underlagets kambium redan vid ympningen befinner sig i verksamt stadium och dessutom har god tillgång på vatten och näring hinner det fram till den tidpunkt (3—4 veckor), då kambieförening kan ske, att avsätta flera nya trakeidrader. Vid samma tidpunkt har kambieverksamheten hos ympkvisten just kommit i gång. Om ympkomponenternas kambier sammanpassas exakt vid ympningen kommer därför underlagets kambium att »växa förbi» ympkvistens,vilket försvårar deras förening. Ännu sämre blir utgångsläget om ympkvistens kambium läggs innanför underlagets. En sammanpassning med ympkvistens kambium något utanför underlagets är den allra bästa ur kambieföreningssynpunkt. Se fig. 32 och pl. VI: 5.

De första föreningarna mellan ledande vävnader hos läggympar återfinns mycket ofta mellan underlagsfliken och vävnader vid den korta snittytan i ympkvisten (pl. VII: 2 och 7).

Varken parenkymföreningar eller kambieföreningar sker samtidigt utefter hela snittytorna hos ymparna — först sker dylika föreningar, där vävnaderna legat väl samman och speciellt aktiva vävnader funnits invid snittytorna.

Bladspår har visat sig spela stor roll som förmedlare av ledande förbindelser, speciellt hos gran, där de förekommer i stort antal och länge ligger kvar i kortexvävnaderna, innan de lämnar stammen (pl. XVI: 1—6 och 8; fig. 33).

Kambieföreningen i den inre vinkeln hos sidsticksympar är komplicerad beroende på vävnadernas inbördes lägen hos ympkomponenterna. När fliken

i underlaget; det medför nämligen hos detta trädslag livlig kallusbildning över hela snittytan — även den blottade veden — vilket försvårar sammanväxning mellan kambierna eller t. o. m. orsakar att ympkvisten stöts bort. Något liknande behöver inte befaras, när det gäller gran. Man måste naturlöses från veden, följer kambiet som regel fliken. Ympkvisten har åtminstone i sin övre del två fria kambiekanter riktade inåt vinkeln — en mot fliken och en mot vedsidan. Fig. 22 illustrerar hur kambieföreningen går till vid olika bredd på ympkvistens kambium, jfr. pl. XIII: 5—7.

Mellanvävnader. Det är inte nödvändigt, att springan mellan ympkomponenternas vedytor utfylls av kallusvävnader. Det är tvärtom vanligt, att den förblir tom, när vävnaderna utanför läks ihop snabbt utan större kallusbildning. De mellanvävnader, som dock förekommer, härstammar hos gran uteslutande från vävnader utanför vedcylindern, vilka expanderat in mellan vedytorna. Hos tall deltar i mellanvävnadsbildningen såväl parenkym innanför kambiet (celler i hartskanalernas epitel, xylemstrålar, bladluckor och märg) som vävnader utanför vedcylindern (pl. VI: 7—10). Mellanvävnaderna kan undergå differentiering. Meristemstråk av kambiekaraktär uppstår ofta spontant, i synnerhet hos tall, och avsätter en tid — så länge utrymmet medger — ledande element. Kambierna ligger i bågar och avsätter xylem utåt, floem inåt (pl. IX: 8—9). De vävnader, som utifrån tränger in mellan vedytorna, åtföljs oftast av kambium, som rätt snart avstängs från sitt ursprungskambium, då detta förenar sig med kambiet hos den andra ympkomponenten. Dessa »avsnörda» kambier bildar bågar på samma sätt som de spontant uppkomna (pl. IX: 11—12).

Övervallning av det nedskurna underlaget. Under sommaren året efter ympningen skärs underlagen ner med ett snett snitt strax ovanför den översta kontakten med ympkvisten. Det uppkomna såret vallas över från alla sidor på samma sätt som en avskuren kvist (fig. 23—28). I de undersökta fallen har enbart vävnader härstammande från underlaget självt deltagit i processen. Övervallningskanten utbildas kraftigast i de båda sidor som gränsar till ympkvisten, är svagare mitt för densamma och allra svagast i den sida som är vänd från ympkvisten, se fig. 29.

Tillskärning av underlagsfliken hos läggympar kan ske på två sätt som framgått av fig. 3—4 resp. 6—7. Av dessa båda är det nedåtriktade snittet i fig. 3—4 tydligt att föredraga. När snittet görs uppåtriktat kommer en flisa av ved att ligga med ända ut i spetsen av fliken och utgöra ett hinder för en jämn sammanväxning mellan den och den korta snittytan i ympkvisten (jfr även fig. 30 och 31). Pl. IX: 13—15 och X: 1—4 visar exempel på de störningar som uppstår, då fliken tillskurits med uppåtriktat snitt. Vedflisan måste antingen vallas in eller stötas bort av de expanderande vävnaderna. Pl. X: 5 och XV: 5 visar exempel på jämn sammanväxning efter nedåtriktat snitt i fliken.

Sammanpassning av kambierna hos läggympar. God sammanpassning mellan kambierna är hos läggympar en förutsättning för en snabb läkning mellan ympkomponenterna. Därvid bör ympkvistens kambium placeras en bit utanför underlagets; se ovan under »Förening mellan ledande vävnader».

Det har visat sig betydligt svårare att åstadkomma god sammanpassning mellan ympkomponenter av gran än av tall. Svårigheterna vid granympningen har främst berott på att underlagen varit betydligt grövre än ympkvistarna.

En god sammanpassning har dock visat sig möjlig att åstadkomma genom att göra ett mycket ytligt insnitt i underlaget — ett snitt som endast tangerar veden — och att lägga ympkvisten med sin snittyta mitt framför snittytan i underlaget. Hos tall är det däremot inte lämpligt att göra så ytliga insnitt ligtvis alltid tänka på att binda samman ympkomponenterna väl, så att underlaget inte får tillfälle att valla över vedytan från sidorna, innan förbindelse etablerats med ympkvisten. Vanliga fel, som begåtts vid granympningen, har varit att snittet i underlaget lagts allt för djupt, och att ympkvistens och underlagets ytterkanter sammanpassats i ena sidan, varvid ympkvistens kambium kommit att ligga långt utanför underlagets i denna sida och långt innanför i den andra (pl. XIV: 8 och XV: 9). Snittet genom underlagets barkdel är nämligen större än motsvarande snitt hos ympkvisten.

En jämförelse mellan ettårsskotten hos tall och gran har visat, att barken hos den senare innehåller betydligt mindre del levande vävnader (jfr pl. I: 1 och 2). Granskotten omges av ett brett skikt döda celler. Dessutom är kortexvävnaderna starkt »veckade». I dalarna mellan de åsar, som bildas av bladspåren och dem omgivande kortexvävnader, är kortex mycket tunn. På grund av att de prolifieringsdugliga vävnaderna har jämförelsevis liten omfattning hos granympkvistarna, är det av större vikt att åstadkomma god kambiesammanpassning hos granympar än hos tallympar.

Undersökningen har klart utvisat, att yngre och klenare underlag borde vara att föredraga för läggympning.

Insnittet i underlaget hos sidsticksympar har utförts på två sätt: dels radiärt, dels tangentiellt (fig. 10—11 resp. 12—14). När insnittet gjorts radiärt kommer ympkvisten i sin helhet att ligga innanför inskärningsytan (fig. 18 a) och de kambiekanter, som så småningom skall förenas, att ligga långt isär (pl. XII: 3 och 6; XIII: 4 och 9). Vid tangentiellt insnitt (fig. 18 b) har man större möjligheter att sammanpassa kambierna och får sammanväxningsytor motsvarande dem hos läggympar (pl. XIII: 11 och 12, XVI: 10 och 11). Av de sidsticksympar av gran, som ympats för den här undersökningen, har endast sådana med tangentiellt insnitt i underlaget lyckats. De huvudsakliga sammanväxningarna har skett vid inskärningsytan medan barkfliken ofta dött. En snittföring i underlaget, som tar med en del av veden (fig. 34), skulle ge en plan yta som bättre passar till ympkvisten och även medföra mindre tomrum i vinkeln.

Läggympning är den klart överlägsna av de båda ympmetoderna och den enda som kan rekommenderas för gran. Fliken bör skäras till med ett nedåtriktat snitt. *Sidsticksympning* kan rekommenderas för tall då grova underlag måste ympas med klena ympkvistar. Insnittet i underlagets bark bör göras tangentiellt.

Резюме

Анатомическое и гистологическое исследование по срастанию между привоем и подвоем у прививок сосны (*Pinus silvestris* L.) и ели (*Picea abies* (L.) Karst.)

Преобладающая часть из прививок, которые были объектом исследований, были привиты в теплице весною 1958 и 1959 гг. Небольшое комплектирование было сделано в 1960 г. Подвой в своем подавляющем большинстве был четырех летнего возраста и был доведен до начала прививки до такого состояния, что его новые годичные побеги достигли длины 1—2 см. А привой представлял собой одногодичные побеги в абсолютном покое.

Были применены два различных метода прививки: *прививка вприклад* и *прививка под кору*. Прививка по способу этих двух методов была произведена и исследована в двух вариантах, см. рис. 1—14 и 16—18. Для анатомических исследований зоны прививки фиксировались в растворе хромовой и уксусной кислоты и формалина (рецепт см. стр. 21), затем укладывались в парафин и разрезались на образцы поперечного и продольного сечения толщиной в 15 μ. Образцы окрашивали в сафранине и т. н. жестком грине (fast green), а потом монтировали их в канадском бальзаме.

Из прививок 1958 г. было взято 3 экземпляра для исследований каждую неделю в течении 5 недель, а потом все остальное время до конца летнего периода интервал исследований был двухнедельный — одномесячный. Для того чтобы точно проследить как у прививок в первое время протекает процесс событий было взято из прививок 1959 г. 2 экземпляра, которые подвергались исследованию каждый день в течении первых 14 дней, а потом каждый второй день в последующие 14 дней. Кроме этого было исследовано некоторое количество 1—3-годичных прививок.

Анатомические детали у молодых стволиков сосны и ели, таковые какими человек видит их на поперечном и тангенциальном, а также и на радиальном (лучевом) продольном разрезе, имеются на рис. 16—17. В своих общих чертах стволики обеих пород построены по однообразному способу, но одновременно с этим имеется несколько различий, достойных особого внимания, т. к. они имеют значение в образовании каллюса и при процессе срастания у прививок. Паренхим, лежащий внутрь от камбия (сердцевина, сердцевинные лучи, смоляные ходы), состоит у сосны из тонкостенных клеток, в то время как большая часть этих клеток у ели имеют одеревяневшие стенки. Количество сердцевинных лучей, ведущих смоляные ходы, у сосны больше нежели у ели, причем последняя совсем не имеет их в одногодичных побегах. Опробковевшая (суберинизованная) часть перидермиума у молодых побегов ели толще нежели у сосны.

Сучья-ветки ели имеют больше листовых следов нежели сосны. Иллюстр. I и II: 1—5 показывают полные картины и детали касающиеся обоих этих древесных пород.

Выделение смолы из разрезанных смоляных ходов есть первая, уже даже невооруженному глазу, видимая реакция раневых поверхностей. Ничего не имеется, что могло бы намекать на то, что смола представляет собой какую то преграду для срастания у прививок, кажется наоборот, что она в данном случае служит как бы защитой. Большая часть смолы у исследуемого материала была растворена фиксирующими жидкостями и спиртами, а следовательно и не имелась в микроскопических препаратах.

Изоляционный слой, состоящий из непосредственно и косвенно поврежденных клеток, образуется на поверхности разреза в кортексе, флоэме и камбиуме у обоих компонентов прививки. В флоэмной части, как в ее активной так и неактивной части, имеется кроме этого большая часть проводящих клеток, которые будут также входить в изоляционный слой, потому что эти клетки не обладают способностью участвовать в образовании каллюса. У сосны изоляционный слой встречается так же и на перерезанных паренхимных тканях, с внутренней стороны камбия: сердцевинные лучи, смоляные ходы и сердцевина.

Увеличение клеток, прилежащих к раневой поверхности, является первой заметной реакцией живых клеток. Особенно быстро реагируют эпителиальные клетки, у перерезанных вертикальных смоляных ходов, в кортексе (иллюстр. III: 1—3). Уже на второй день после прививки они отчетливо увеличены и примыкают вскоре вплотную к смоляному каналу, часто далеко над тем местом где этот канал был ранен. Увеличение клеток на ранней стадии является при этом обычным явлением, практически говоря, для всех тонкостенных паренхимных клеток, прилежащих к раневым поверхностям.

Деление клеток у подвоя и привоя начинает появляться на 3—4-й день после прививки и происходит вблизи прилегания их к раневым поверхностям. Первое деление клеток наступает часто у привоя, он же имеет и большую активность в первые дни после прививки. У сосны было вполне отчетливо видно, что самое раннее деление клеток появлялось в флоэмной и камбиальной части сердцевинных лучей, а потом только несколько дней позже появилось деление клеток так же и в кортексе — как в смоляных ходах так и в обычных клетках кортекса. У ели деление клеток было констатировано во всех выше названных тканях одновременно.

Наибольшая активность деления клеток происходит в области находящейся в благоприятном положении с точки зрения питательного и транспортного состояния. Клетки вокруг листовых и веточных следов, а так же и клетки в сердцевинных лучах, которые выходят из т. н. листовых люков, являются особенно активными как образователи каллюса (иллюстр. II: 6—8). В общем и целом подвой до срастания прививки образует большее количество каллюса нежели привой, но листовой след, прилежащий к поверхности среза, может причинить локально большее образование каллюса последним.

Сердцевинные лучи, отрезанные на самой периферии флоэмы, образуют чаще всего больше каллюса нежели таковые, которые были отрезаны вблизи или в смой камбиальной зоне (иллюстр. XIV: 5—6). Граница

между флоэмом и кортексом является очень активной зоной (иллюстр. V: 11).

Самое наипервейшее деление клеток не появляется под каким либора определенным углом по отношению раневой поверхности, это относится особенно к сосне (иллюстр. V: 1—3 и 5), где первоео бразование каллюса часто имеет очень экстенсивный характер. Но вскоре все-таки деление клеток принимает определенный узор и отложение новых клеток происходит уже так, что их новые стенки принимают более или менее параллельное положение по отношению к раневой поверхности (иллюстр. V: 6—8). Эта закономерная меристема развивается в кортексе в пробковый камбий (феллогений).

Камбиальная зона у прививок вприклад играет подчиненную роль в деле образования каллюса (иллюстр. V: 7). Каллюсные ткани от обоих компонентов прививки, находящиеся вне камбиальной зоне, обычно успевают соединиться друг с другом прежде чем в камбиальных клетках произойдет необходимая перестройка их способа деления. У прививок под кору контактная поверхность подвоя с привоем состоит в своей большей части из обнаженного камбия, откуда у сосновых прививок под кору и происходит очень сильное образование каллюса. Инициативу берут клетки сердцевинных лучей, но очень скоро можно видеть, что большая часть клеток камбиальной зоны тоже принимает участие в какой то степени, зависящее от характера повреждений данных клеток при производстве прививки. Подвой сосны образует каллюс как от обнаженной поверхности древесины так и от дольки, т. е. полоски коры (иллюстр. XII: 1), в то время как у елового подвоя образование каллюса было констатировано лишь от дольки, но даже и там это было большей частью скупо (иллюстр. XVI: 11). Если срез (надрез) на подвое сделан по отношению камбия тангенциально то тогда поверхность среза (надреза) будет

Таблица 1. Интенсивность деления клеток в различных тканях у прививок сосны и ели.

Ткань	сосна	ель
Перидерма	—	—
Кортекс, основные ткани	+ + +*	+ + +*
Кортекс, эпителий смоляных ходов	+ + + +	+ + + +
Флоэм, сердцевинные лучи	+ + + +*	+ + + +*
Флоэм, вертикальный паренхим	+ +*	+ +*
Флоэм, полностью дифференцированные ситовидные клетки	—	—
Зона камбия, сердцевинные лучи	+ + +*	+ + +*
Зона камбия, прочие недифференцированные или неполностью дифференцированные клетки	+ +	+ +
Ксилем, сердцевинные лучи	+	—(+)
Ксилем, эпителий смоляных ходов	+	—
Ксилем, полностью дифференцированные трахеиды	—	—
Сердцевина, листовой и веточный люки	+ +	—

* Ткани под влиянием действия от листовых и веточных следов проявляют большую активность нежели другие соответствующие ткани.

+ + + + очень большая интенсивность деления клеток.

+ + + большая интенсивность деления клеток.

+ + интенсивность деления клеток варьирует, но что же касается сердцевины и листовых люков у сосны то начало этого действия проявляется уже на ранней стадии, а иначе таковая наступает лишь после того как уже началось деление у прилегающих тканей.

+ деление варьирующего характера может происходить, но все же таковое часто совсем отсутствует.

(+) когда прививка произведена поздно то тогда ксилемные сердцевинные лучи в древесине последнего года могут образовывать каллюс.

— деление клеток отсутствует.

такой же самой как и у т. н. прививок вприклад (иллюстр. XVI : 10). Радиальный срез (надрез) обычно приводит, в следствии плохой подгонки между камбиями привоя и подвоя, к оживленному образованию каллюса у обоих компонентов прививки в их камбиальной зоне.

Образование каллюса от паренхима с внутренней стороны камбиальной зоны встречается только у сосны и это может иногда быть довольно обширного характера, в особенности от сердцевины и от зоны древесины, в том месте где было найдено больше паренхимных тканей нежели нормально, по причине какого то повреждения, которое было нанесено камбию во время прироста — в некоторых случаях при исследовании границ между годичными кольцами у подвоя сосны (иллюстр. VI: 8).

Склонность отдельных тканей к образованию каллюса у обоих выше названных пород показана в таблице 1. Большая активность одного из компонентов прививки может, как это показало, повлиять на соприкасающиеся ткани партнера так, что активность их повышается уже прежде чем непосредственное соединение совершилось между тканями обоих компонентов прививки. Здесь речь идет о том воздействии, которое передается через, разумеется конечно, не так уж сильный изоляционный слой и при этом без участия плазматических соединений между клетками.

Срастание между паренхиматическими клетками было констатировано через 8—10 дней после прививки. У всех прививок произведенных в вегетационном домике, которые имеют предпосылки для дальнейшего развития, имеются паренхимные соединения уже через 15 дней после прививки. Возможность соединения имеют только новообразованные клетки после прививки. У т. н. прививок вприклад первые соединения между новыми клетками, образование которых происходит от тканей находящихся за камбиальной зоной, происходит главным образом от кортексовой и флоэмной части сердцевинных лучей (иллюстр. V: 7, 8, 12). У т. н. прививок под кору (вертикального надреза стволика-подвоя), которые были произведены по способу радиального вреза в подвой так, что не имеется ни какого непосредственного контакта между поверхностью надреза в подвое, с одной стороны, и привоем, с другой стороны (рис. 18a), первые соединения между каллюсом от камбиальной зоны подвоя совершаются в полоске, т. е. дольке коры, в то время как активными тканями у привоя являются прежде всего сердцевинные лучи и каллюс от кортекса, флоэмных сердцевинных лучей и сердцевины (иллюстр. XII: 1, X: 11). У прививок под кору, произведенных по способу продольного (тангенциального) вреза в подвой (рис. 18b), выше названные соединения совершаются также и при поверхности вреза, способ этих соединений такой же как и у прививок вприклад. Соединение между новообразованными клетками может происходить независимо от того от каких тканей эти клетки ведут свое происхождение.

Феллогенное соединение. Через посредство соединяющего самого крайнего паренхима в стволике начинает очень скоро дифференцироваться феллоген (пробковый камбиум), каковой соединяет таковые, которые уже имеются или находятся в процессе образования вдоль раневых поверхностей компонентов прививки (т. е. ее привоя и подвоя). Полностью образованные соединения между феллогеном появляются через 15—20 дней после прививки. Старые феллогены (пробковые камбиумы), которые

на самой крайней периферии огараживают стволики, не принимают участия в образовании новых, а соединение между ними начинает совершаться в свое время мало по-малу и протекает своим чередом.

Соединение между проводящими тканями было констатировано примерно через 3 недели у хорошо подготовленных прививок. В то время как у прививок с менее хорошей подгонкой это соединение может затягиваться до 5—6 недель. У прививок с хорошей подгонкой привоя с подвоем деление в камбиальной зоне обычно ведет почти сразу к соединению между проводящими тканями (иллюстр. VII: 2—3, XV: 4). При этом образуется лишь небольшое количество коротких, более или менее нерегулярных (неправильных, беспорядочных), клеток. Часто можно видеть, что соединение новообразованных трахеид совершается прежде чем происходит собственно само камбиальное соединение. Когда камбиумы лежать долгое время разделены между собой то тогда распространяют они себя через посредство междулежащих парехимных тканей, это распространение идет в направлении их друг к другу и ведет к тому, что клетки дедифференцируются и опять начинают делиться. Дифференциация трахеид на древесной стороне часто идет в направлении камбиального пояса, в то время как связь на флоэмной стороне задерживается некоторое время паренхимными клетками, которые только со временем мало по-малу начинают дифференцироваться в проводящие клетки.

Поскольку камбиум подвоя уже при производстве прививки находится в деятельном состоянии и кроме того имеет лучший доступ воды и питательных веществ успевает он, уже к тому времени когда соединение камбия может совершиться, отложить несколько новых трахеидных рядов. Это ведет к тому, что камбиум сдвигается наружу и удаляется от камбия привоя, с которым он был точно подогнан, но «растет вперегонку» оный, который поместился снаружи (рис. 32, иллюстр. VI: 5).

Первые соединения между проводящими тканями у т. н. прививок вприклад очень часто вновь находятся между «долькой» подвоя и тканями при короткой поверхности среза в подвое (иллюстр. VII: 2, 7).

Ни соединения паренхима, ни соединения камбия происходит одновременно вдоль всей поверхности срезов прививки — такие соединения совершаются сначала там, т. е. в тех местах, где ткани хорошо прилегали друг к другу и специально там где активные ткани находились рядом возле поверхности срезов прививки.

Листовые следы показали, что они играют большую роль как посредники проводящих связей, это наблюдается специально у ели, у которой они встречаются в большом количестве и долго остаются лежать в тканях кортекса, прежде чем они покидают ее стволик (иллюстр. XVI: 1—6, 8, рис. 33).

Камбиальное соединение во внутреннем углу у т. н. прививок под кору сложное и зависит от взаимного положения тканей между собой у компонентов прививки. Когда «долька» отделяется от древесины то и сам камбиум как правило сопровождает ее. Привой имеет, во всяком случае в своей верхней части, два свободных края камбия, направленных внутрь угла — один из них обращен в сторону «дольки», а другой направлен в сторону древесины. Рис. 22 иллюстрирует как происходит соединение камбия при различной широте его на привое (см. иллюстр. XIII: 5—7).

Средние ткани. Это совсем не обязательно, чтобы щель между поверхностями древесины компонентов прививки заполнилась тканями каллюса. Когда ткани снаружи быстро залечиваются без значительного образования каллюса то обычно бывает наоборот, что эта щель остается пустой. Те средние ткани, которые все-таки встречаются, происходят у ели исключительно от тканей, лежащих снаружи древесного цилиндра, которые экспандировали себя внутрь между соответствующими поверхностями древесины. У сосны в образовании средних тканей принимают участие как паренхим, лежащий с внутренней стороны камбия (клетки в смоляных ходах, сердцевинных лучах, листовых люках и сердцевине) так и ткани, лежащие снаружи древесного цилиндра (иллюстр. VI: 7—10). Средние ткани могут претерпевать дифференциацию. Меристемный пояс камбиального характера часто образуется спонтанно, что наблюдается особенно у сосны, и откладывает некоторое время — до тех пор пока имеется место — проводящие элементы. Камбиумы расположены в виде дуг и откладывают ксилем наружу, а флоэм внутрь (иллюстр. IX: 8, 9). Те ткани, которые снаружи входят внутрь между древесными поверхностями часто сопровождаются камбием, который довольно скоро отделяется от своего первоначального камбия, тогда как этот, позже названный, соединяется с камбием другого компонента прививки. Эти «отделенные» камбиумы образуют дуги по такому же самому способу как это наблюдается у таковых, которые образовались спонтанно (иллюстр. IX: 11—12).

Заплывание срезанного подвоя. Летом, год спустя после прививки, срезается подвой косым срезом непосредственно выше верхнего контакта с привоем. Образовавшаяся рана заплывает со всех сторон и протекает точно таким же способом как это происходит после обычной обрезки сучьев (рис. 23—28). При исследовании во всех случаях было констатировано, что в данном процессе принимают участие лишь только ткани происходящие от подвоя. Край заплыва образуется наисильнейший в тех обоих сторонах, которые граничать с привоем, слабее оный в месте находящегося прямо напротив привоя и наиболее слабый край заплыва образуется в той стороне, которая обращена от привоя (см. рис. 29).

Закройка, т. е. зарезка или надрезка, дольки на подвое у т. н. прививок вприклад может производиться двумя способами, именно так как это показано на рис. 3—4 и соответственно рис. 6—7. Из этих двух способов ясно видно, что вниз обращенный срез на рис. 3—4 имеет предпочтение. Когда же зарез делается обращенным вверх то тогда древесная пластинка будет лежать совсем в вершине-носке дольки и этим самым будет являться препятствием для равномерного срастания между долькой и короткой поверхностью среза на привое (сравни также рис. 30 и 31). Иллюстрации IX: 13—15 и X: 1—4 показывают пример тех нарушений, которые появляются при тех случаях когда долька была закроена, т. е. зарезана вверх обращенным срезом. Древесная пластинка должна или заплывать внутрь или отталкиваться (выталкиваться в сторону) экспандирующими тканями. Иллюстрации X: 5 и XV: 5 показывают пример равномерного срастания в тех случаях когда долька на подвое была закроена, т. е. надрезана вниз обращенным срезом.

Подгонка камбиев у т. н. прививок вприклад. Хорошая подгонка между камбиями подвоя и привоя у этих прививок является предпосылкой для

быстрого залечивания места раневого соединения между компонентами прививки. Но это всетаки не означает, что камбии привоя и подвоя должны точно лежать друг против друга с самого начала прививки, см. выше, наоборот лучше было бы если бы камбий привоя расположился бы немножко снаружи за приделами границы камбия подвоя, для того чтобы компенсировать прирост, т. е. рост у камбия привоя (рис. 32 с—д).

Исследования показали, что сделать хорошую подгонку между компонентами прививки у ели представляется гораздо труднее нежели это самое у прививки сосны. Трудности при прививки ели в первую очередь зависели от того, что подвой был значительно крупнее по сравнению с материалом привоя. Но опыт показал, что и в данном случае имеется всетаки возможность добиться хорошей подгонки между компонентами у прививки ели, а именно посредством очень поверхностного среза — такого среза, который только что лишь тангирует, т. е. касается древесины подвоя —, а одновременно с этим и прикладывать привой своей поверхностью надреза (среза) прямо напротив поверхности надреза (среза) на подвое. У сосны же наоборот делать такие очень поверхностные срезы у подвоя является делом не удачным, потому что именно это приводит у этой древесной породе к оживленному образованию каллюса по всей поверхности надреза (среза) — при этом также и на обнаженной древесине —, который затрудняет срастание между камбиями компонентов прививки или является даже причиной тому, что привой отталкивается от подвоя. Нечто такое подобное не является опасением в отношении ели. Само по себе разумеется, нужно всегда помнить, что компоненты прививки должны связываться хорошо и надежно, так чтобы подвой не получил возможности сделать заплыв со сторон обнаженной поверхности древесины, прежде чем связь его будет этаблирована, т. е. установлена с привоем. Обычные ошибки, которые были сделаны при прививки ели заключались в том, что надрез в подвое делался слишком глубоким, а также и потому, что внешние края привоя и подвоя подгонялись в одной стороне, в результате чего камбий привоя должен был лежать в этой стороне далеко наружу от камбия подвоя и одновременно тоже далеко внутрь от последнего по отношению другой стороны подвоя (подвой крупнее нежели черенки привоя), см. иллюстр. XIV: 8 и XV: 9. Надрез через корковую часть подвоя именно больше нежели соответствующий у черенка привоя.

Сравнение между годичными побегами сосны и ели показало, что кора у последней содержить значительно меньшую часть живых тканей (сравни иллюстр. I: 1—2). Годичные побеги ели окружаются широким слоем мертвых клеток. Причем ткани кортекса сильно «морщинистые». В «долинах» между «хребтами», которые образуются из листовых следов и ими окружающих тканей кортекса сам кортекс очень тонкий. На основании того, что пролифиэрные ткани (т. е. ткани способные образовывать каллюс) у прививочных черенков ели имеют по величине сравнительно маленький объем то в следствии этого требование делать хорошую подгонку камбия у прививок ели имеет большее значение нежели у прививок сосны.

Исследования ясно показали, что при производстве прививок по т. н. *способу вприклад* нужно бы предпочитать более молодой и тонкий подвой.

Надрез в подвое у т. н. прививок под кору был сделан двумя способами, а именно радиальным и тангенциальным способом (рис. 10—11 и соот-

ветственно рис. 12—14). Когда надрез делается в лучевом, т. е. радиальном направлении то черенок привоя будет тогда целиком лежать, сравнительно далеко, внутрь от поверхности надреза (т. е. без надлежащего соприкосновения с этой поверхностью (рис. 18 a), а те края камбия, которые в свое время должны соединиться будут лежать при этом раздельно на довольно длинном расстоянии друг от друга (иллюстр. XII: 3, 6 и XIII: 4, 9). Когда же надрез делается в тангенциальном направлении (рис. 18 b) то тогда имеются большие возможности чтобы лучше подогнать камбии компонентов прививки и таким образом получить при этом такие поверхности срастания, которые по своему характеру соответствуют (т. е. похожи или подобают) таковым у т. н. прививок вприклад (иллюстр. XIII: 11—12 и XVI: 10—11). Из тех опытных прививок ели, которые были произведены по способу т. н. прививки под кору оказались удачными только те прививки, у которых надрез у подвоя был сделан в тангенциальном направлении. Срастания произошли главным образом у поверхности надреза, в то время как долька, т. е. полоска коры часто была отмершей. При таком срезе надреза в подвое когда срез берет, т. е. прихватывает с собой и частицу древесины (рис. 34) получается плоская поверхность надреза, которая лучше прилегает при соединении ее с черенком привоя, а это одновременно приводит также к тому, что размер пустого пространства в образуемом угле тоже будет меньше.

Из этих двух методов, которые были применены при проведении опытов выявилось, что *т. н. прививка вприклад* имеет ясное преимущество по сравнению с *т. н. прививкой под кору* — при чем для прививок ели можно рекомендовать лишь только способ прививки вприклад. Корковую дольку, т. е. полоску коры нужно при этом срезать таким образом чтобы получался надрез обращенный вниз. Что же касается *т. н. прививки под кору* то этот способ можно рекомендовать для прививок сосны в тех случаях когда прививка должна производиться материалом мелкого, т. е. тонкого привоя на крупный или другими словами толстый подвой. Надрез на подвое нужно делать тангенциальный.

Объяснение касающееся значения знаков и сокращений, употребленных на иллюстрациях и рисунках см. стр. 135.

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Резюме перевел на русский язык инж.-лесовод И. Руссанов.

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APPENDIX

Key to the signs in plates and figures and other abbreviations.
Teckenförklaring till planscher och figurer jämte andra förkortningar.
Объяснение значений знаков и сокращений, употребленных на иллюстрациях и рисунках.

Sc = scion
ympkvist
черенок привоя

St = stock
underlag
подвой

St.fl = stock flap (in veneer side grafts)
underlagsflik (hos läggympar)
долька, т. е. полоска коры подвоя (у прививок вприклад)

B.fl = bark flap (in side slit grafts)
barkflik (hos sidsticksympar)
полоска, т. е. долька коры (у прививок под кору)

C = cross section
tvärsnitt
поперечный разрез

L = longitudinal section
längdsnitt
продольный разрез

RL = radial longitudinal section
radiärt längdsnitt
радиально-продольный разрез

TL = tangential longitudinal section
tangentiellt längdsnitt
тангенциально-продольный разрез

i = incision face (in side slit grafts)
inskärningsyta (hos sidsticksympar)
поверхность надреза (у прививок под кору)

ic = innermost corner (in side slit grafts)
inre vinkel (hos sidsticksympar)
внутренний угол (у прививок под кору)

cl = contact layer
isoleringsskikt
изоляционный слой

m = pith (medulla)
märg
сердцевина

x = xylem (wood)
xylem (ved)
ксилем (древесина)

ox = old xylem
gammalt xylem
старый ксилем

nx = new xylem
nytt xylem
новый ксилем

c = cambium
kambium
камбий

nc = new cambium
nytt kambium
новый камбий

ph = phloem
floem
флоэм

n.ph = new phloem
nytt floem
новый флоэм

co = cortex
kortex
кортекс

p = periderm
periderm
перидерма

phe = phellogen (cork cambium)
fellogen (korkkambium)
феллогений (пробковый камбий)

n.phe = new phellogen
nytt fellogen
новый феллогений (новый пробковый камбий)

r = ray
stråle
сердцевинный луч

mr = multiseriate ray (ray containing a resin duct)
hartsförande stråle
смолопроводящий сердцевинный луч

re.c = resin cyst
hartsbehållare
смолорезервуар

v.re	= vertical resin duct vertikal hartskanal вертикальный смоляной ход	d.	= days dagar дни
br.tr	= branch trace grenspår веточный след	w.	= weeks veckor недели
l.tr	= leaf trace bladspår листовой след	m.	= months månader месяцы
lg	= leaf gap bladlucka листовой люк	pt.	= point punkt пошт

When not otherwise stated the length of the dimension line is 500 μ.

Där inget annat angivits är måttlinjens längd 500 μ.

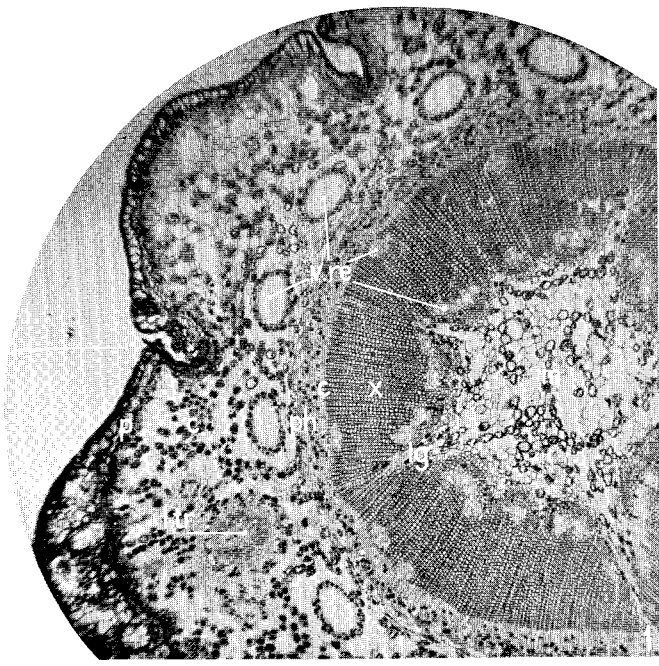
Там где ничего другого не указано то тогда нужно считать, что длина измерительной линии равна 500 μ.

Plate I. General anatomy.

1—2. Scots pine and Norway spruce respectively. C. One-year-old twigs.
3. Scots pine. RL. Pith.
4. Scots pine. RL. Cortex.
5. Scots pine. RL. Xylem with ray and vertical resin duct.
6. Norway spruce. RL. Pith.
7. Norway spruce. RL. Medullary sheath.
8. Norway spruce. RL. Xylem with ray.

Plansch I. Allmän anatomi.

1—2. Tall resp. gran. C av 1-åriga kvistar.
3. Tall. RL. Märg.
4. Tall. RL. Kortex.
5. Tall. RL. Ved med xylemstråle och vertikal hartskanal.
6. Gran. RL. Märg.
7. Gran. RL. Yttre delen av märg.
8. Gran. RL. Ved med xylemstråle.



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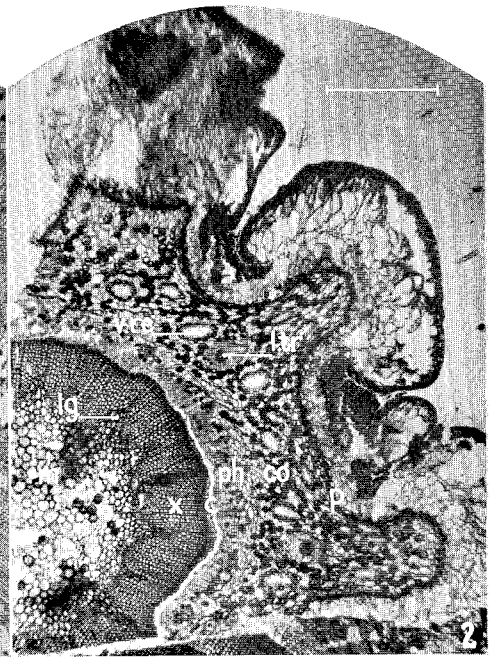

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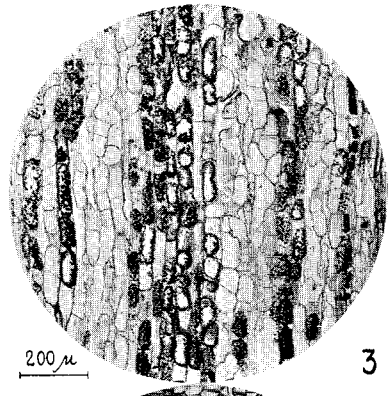

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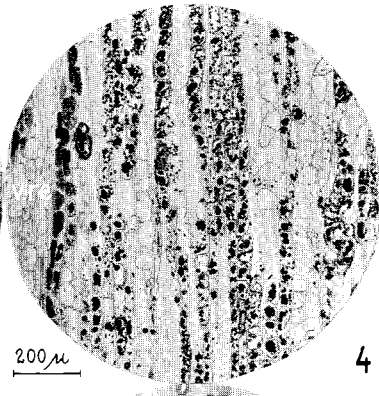

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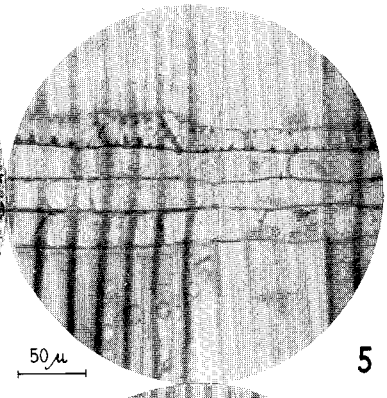

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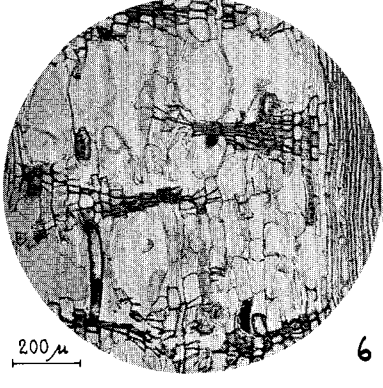

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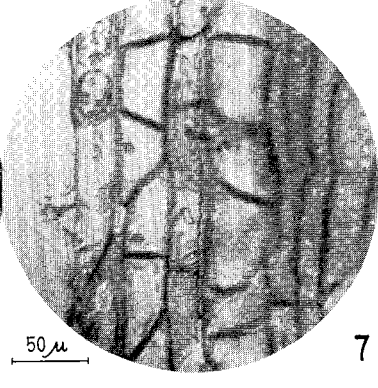

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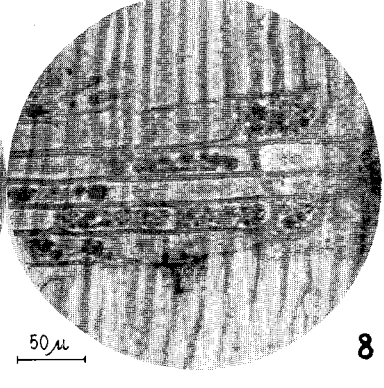

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Plate II.

1—5. General anatomy.

1. Scots pine. TL of xylem. Ray cells thin-walled.
2. Norway spruce. TL of xylem. Ray cells with lignified walls. Two thin-walled epithelial cells in resin duct of multiseriate ray.
3. Scots pine. RL. Horizontal resin duct, the outer part expanded and forming a resin cyst.
4. Scots pine. 35 d. C. In St three multiseriate rays with resin cysts.
5. Norway spruce. 46 d. C. In St multiseriate ray with resin cyst.

6—8. Scots pine, veneer graft, 5 d. C.

6. Full view of graft zone. Rays emerging from leaf gap in upper part of scion severed by graft cut.
7. 23rd section down from 6. Detail from Sc. Cell divisions in rays emerging from leaf gap, see arrows.
8. 42nd section above 6. Detail from Sc cortex with leaf trace. Telophase inside the trace, see arrow.

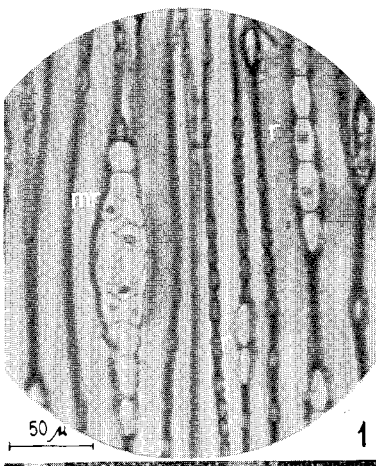
Plansch II.

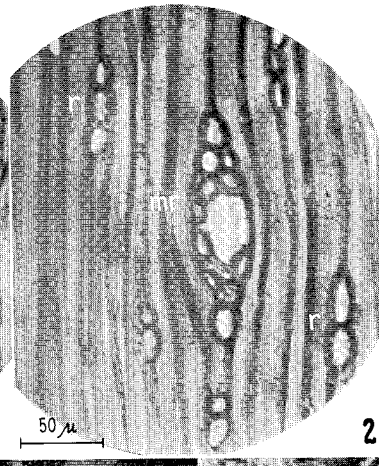
1—5. Allmän anatomi.

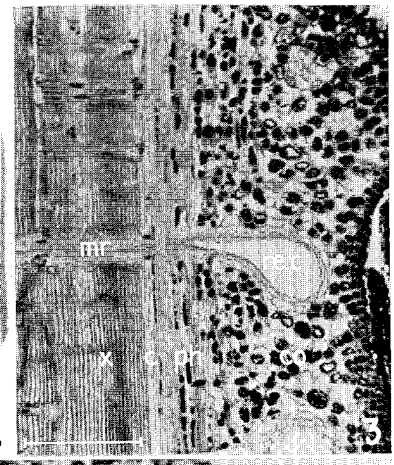
1. Tall. TL av ved. Xylemstrålarnas celler tunnväggiga.
2. Gran. TL av ved. Xylemstråleceller med förvedade väggar. Två tunnväggiga epitelceller i horisontell hartskanal.
3. Tall. RL. Horisontell hartskanal i sin yttre del utvidgad till hartsbehållare.
4. Tall. 35 d. C. Tre hartsförande strålar med hartsbehållare i St.
5. Gran. 46 d. C. Hartsförande stråle med hartsbehållare i St.

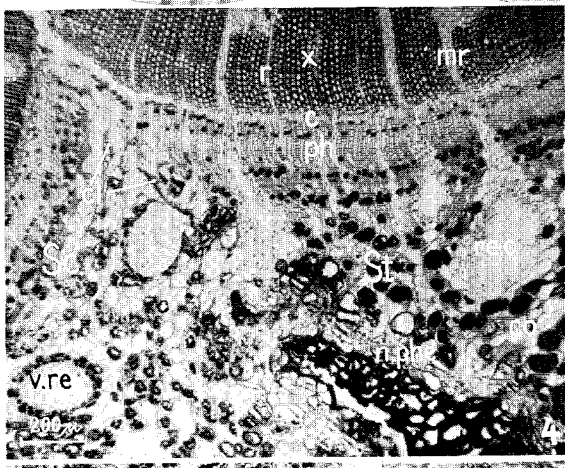
6—8. Tall, läggymp. 5 d. C.

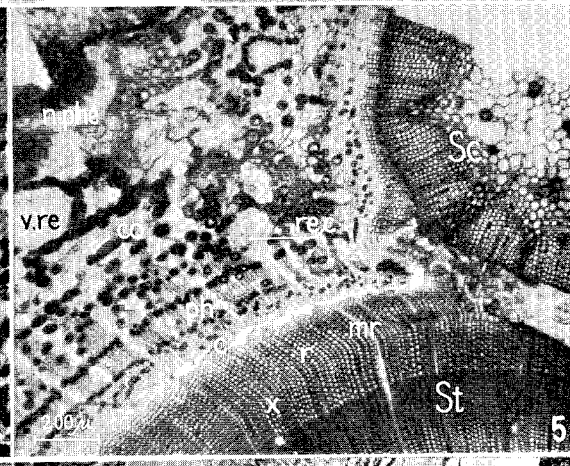
6. Översiktsbild. Ympsnittet har träffat strålar utgående från bladlucka i övre sidan av ympkvisten.
7. 23:e snittet under föregående. Detalj från Sc. Celldelningar (se pilarna) i strålar utgående från bladluckan.
8. 42:a snittet ovan 6. Detalj från Sc, kortex med bladspår. Telofas strax innanför bladspåret (se pilen).

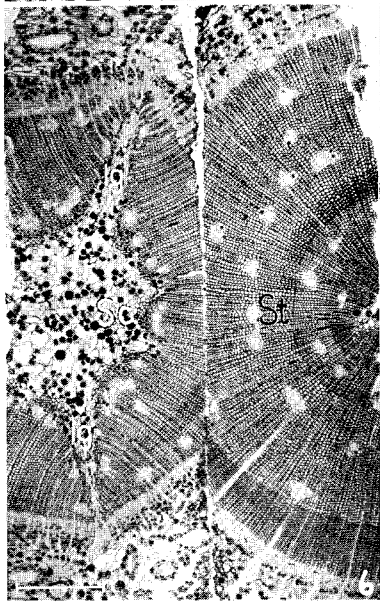

mr
50 μ
1

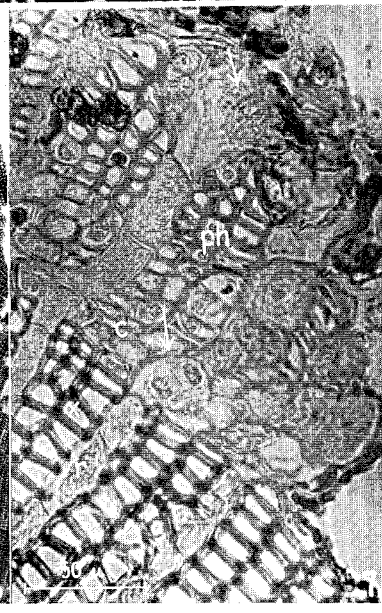

mr
r
50 μ
2


mr
x
ph
5


r
x
mr
ph
St
v.re
4


Sc
v.re
mr
r
x
St
5


St
6


ph
7

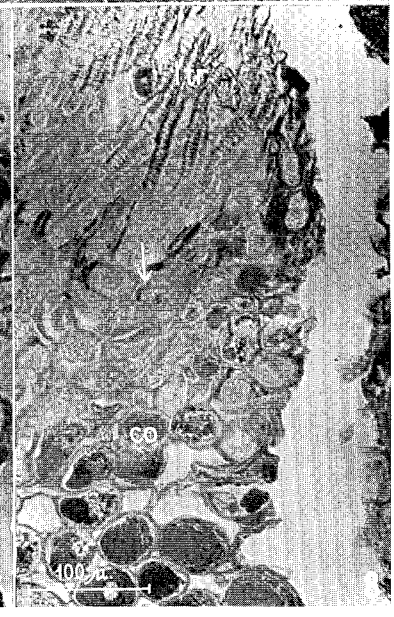

co
8

Plate III. Scots pine, veneer graft. Reactions from epithelial cells of resin ducts.

1—2. 2 d. C. 2 is the 52nd section above 1. Enlarged epithelial cells in resin duct in Sc cortex.
3. 3 d. L. Resin duct in Sc cortex cut at grafting; clogged by expanding epithelial cells.
4. 7 d. L. Callus formation from resin duct in Sc cortex. Arrow marks telophase.
5. 6 d. C. Resin duct in Sc cortex filled with cells. Anaphase at arrow.
6. 8 d. C. Enlarged cells and callus formation in cut resin cyst of St.

Plansch III. Tall, läggymp. Reaktioner hos hartskanalernas epitelceller.

1—2. 2 d. C. 2 är 52:dra snittet ovanför 1. Epitelceller i hartskanal i kortex hos Sc förstorade.
3. 3 d. L. Hartskanal i Sc kortex avskuren vid ympningen, tillsluten av expanderande epitelceller.
4. 7 d. L. Kallusbildning från hartskanal i Sc kortex. Vid pilen telofas.
5. 6 d. C. Cellfylld hartskanal i Sc kortex. Vid pilen anafas.
6. 8 d. C. Förstorade celler och kallusbildning i hartsbehållare hos St.

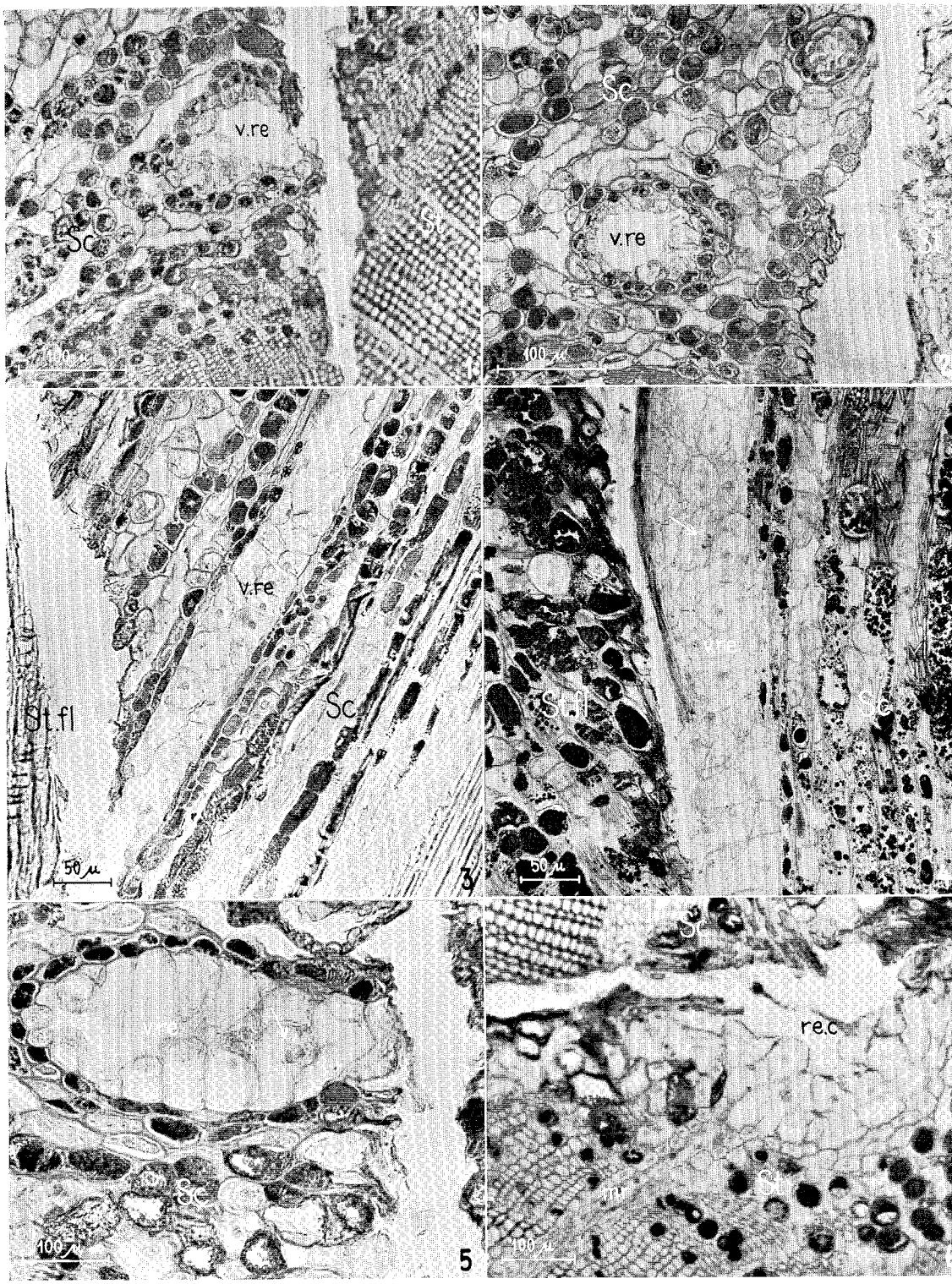

v.re
Sc
100 μ
v.re
Sc
100 μ
St.fl
v.re
Sc
50 μ
3
v.re
Sc
50 μ
100 μ
5
re.c
100 μ

Plate IV. Scots pine, veneer graft. Cell division and callus formation.

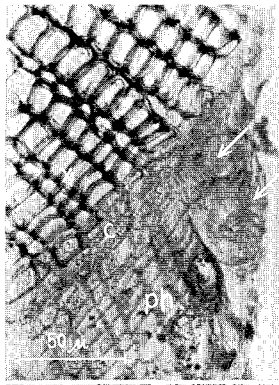
1. 4 d. C. Two divisions (metaphase and telophase) in Sc ray, see arrows.
2. 6 d. C. Two newly formed cells and telophase in St flap. Divisions in Sc pith. See arrows.
3. 7 d. RL. Callus formation in cambial region of St. Arrow indicates telophase.
4. 7 d. C. Metaphase in ray of St cambium.
5. 9 d. TL. Callus formation in cambial region of both Sc and St; irregular cells, some of which in Sc differentiating into tracheids.
6. 8 d. C. Callus formation in phloem and cambial region of St.

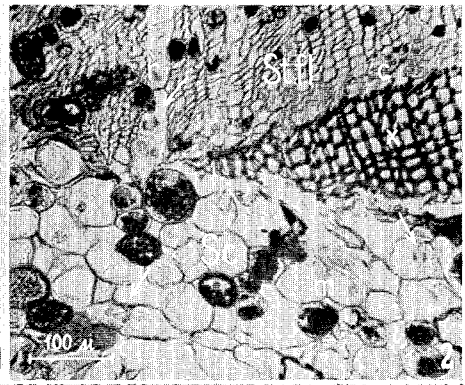
7—8. 7 d. L. Callus formation in resin duct of St xylem. 8 is a magnified photograph of the region inside the square of 7. Arrow marks telophase.

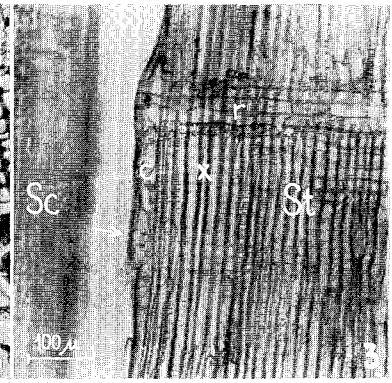
Plansch IV. Tall, läggymp. Celldelning och kallusbildning.

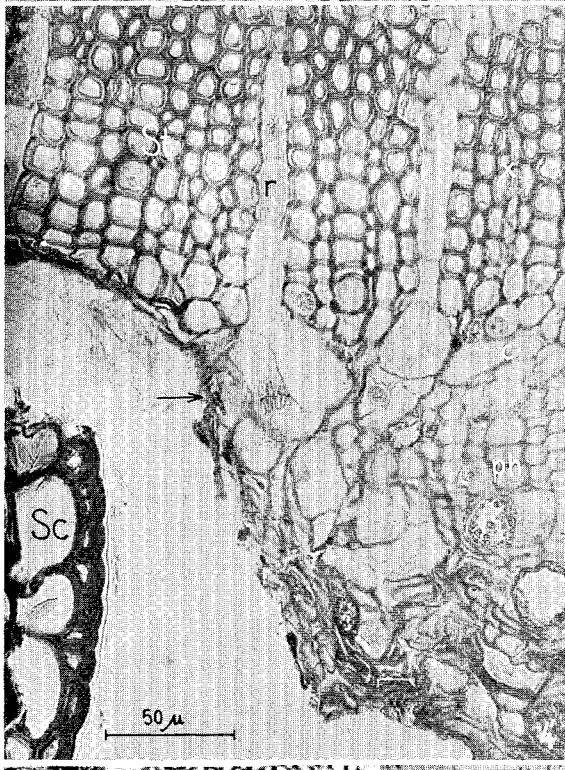
1. 4 d. C. Två celldelningar (metafas och telofas) i stråle hos Sc, se pilar.
2. 6 d. C. Två nybildade celler och telofas i stråle i St-fliken; delningar i Sc märg, se pilar.
3. 7 d. RL. Kallusbildning från kambiezonen hos St. Vid pilen telofas.
4. 7 d. C. Metafas i strålecell hos St.
5. 9 d. TL. Kallusbildning i kambiezonen hos både Sc och St; oregelbundna celler varav några hos Sc börjat differentieras till tracheider.
6. 8 d. C. Kallusbildning i floem- och kambiezonerna hos St.

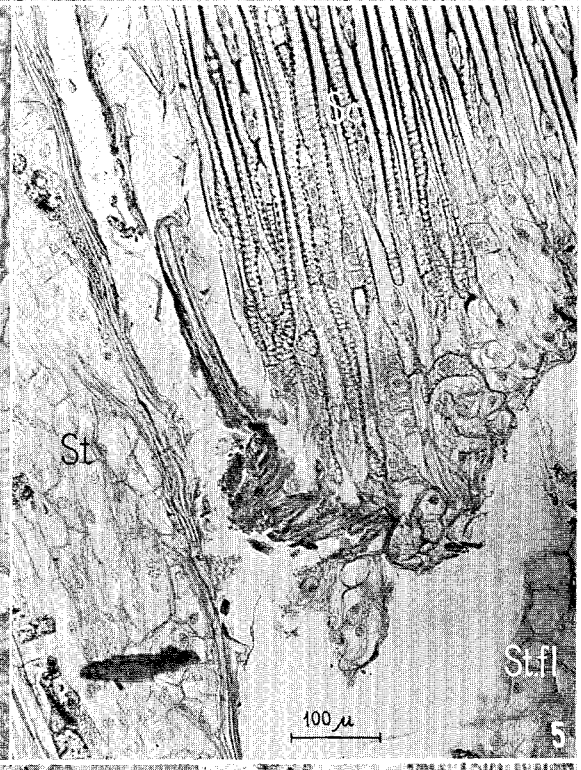
7—8. 7 d. L. Kallusbildning från hartskanal i St-veden. 8 visar förstoring av inrutade området i 7. Telofas vid pilen.

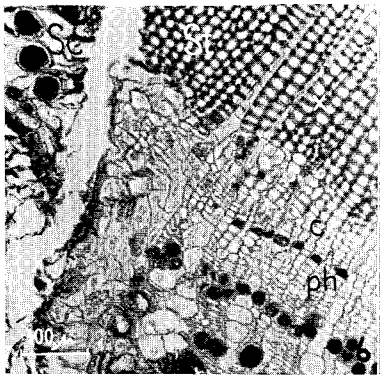

c
ph
50 µ
1

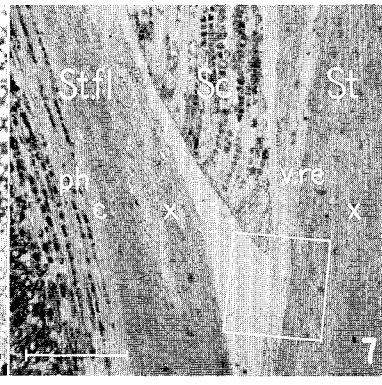

Stfl
100 µ
2


Sc
St
c
x
r
100 µ
3


St
r
Sc
ph
50 µ
4


St
Sc
Stfl
100 µ
5


Sc
St
c
ph
6


Stfl
Sc
St
ph
c
x
vrte
x
7

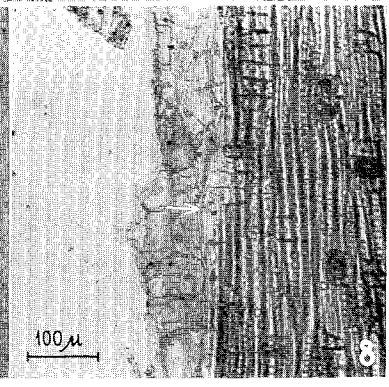

100 µ
8

Plate V. Scots pine, veneer graft. Cell divisions in cortex. Phellogen formation. Parenchyma unions.

1. 6 d. 2—3. 7 d. C. Cell divisions in cortex. Note the direction of the spindles.
4. 8 d. C. Superficial callus formation of Sc. Superficial cells of St suberized. Phellogen is forming between these cells and the undamaged cortex.
5. 8 d. C. Superficial cell in Sc in division. Note direction of spindle.
6. 10 d. C. Phellogen in St developing, see arrows. Callus formation in phloem-cortex boundary and in cortex of Sc. Enlarged superficial cells in outermost cortex.
7. 13 d. C. Union of cortex-derived callus tissues. Well developed phellogen in St.
8. 13 d. C. Extensive callus formation under influence of leaf trace in Sc, branch trace in St. Phellogen between extended cells and undamaged cortex.
9. 17 d. C. Union of phellogens.
10. 9 w. C. Phellogen surrounding dead tissues. Arrows mark the approximative border between St and Sc.
11. 10 d. C. Callus formation in phloem-cortex boundary in Sc.
12. 14 d. L. Transfusion windows between callus in resin duct of Sc cortex and in St phloem rays, see arrows.

Plansch V. Tall, läggymp. Celldelningar i kortex. Fellogenbildning. Parenkymförening.

1. 6 d. 2—3. 7 d. C. Celldelningar i Sc kortex. Obs. kärnspolarnas orientering!
4. 8 d. C. Ytlig kallusbildning hos Sc. Ytliga celler hos St suberiniseras, fellogenbildning påbörjad innanför dessa.
5. 8 d. C. Ytligt belägen cell hos Sc under delning. Obs. kärnspolens orientering!
6. 10 d. C. Hos St början till fellogen, se pilarna. Hos Sc kallusbildning i floem-kortexgränsen och i kortex. Förstorade, ytligt belägna celler ytterst i kortex.
7. 13 d. C. Sammanväxning mellan kallus av kortexursprung. Väl utbildat fellogen i St.
8. 13 d. C. Extensiv kallusbildning till följd av bladspår hos Sc, grenspår hos St. Fellogen innanför de starkt utvidgade cellerna.
9. 17 d. C. Förening mellan fellogen.
10. 9 w. C. Inkapsling av döda vävnader medelst fellogen. Pilar visar ungefärliga gränsen mellan St och Sc.
11. 10 d. C. Kallusbildning i floem-kortex gränsen hos Sc.
12. 14 d. L. Transfusionsfönster mellan kallus i hartskanal i Sc kortex och i floemstrålar hos St, se pilarna.

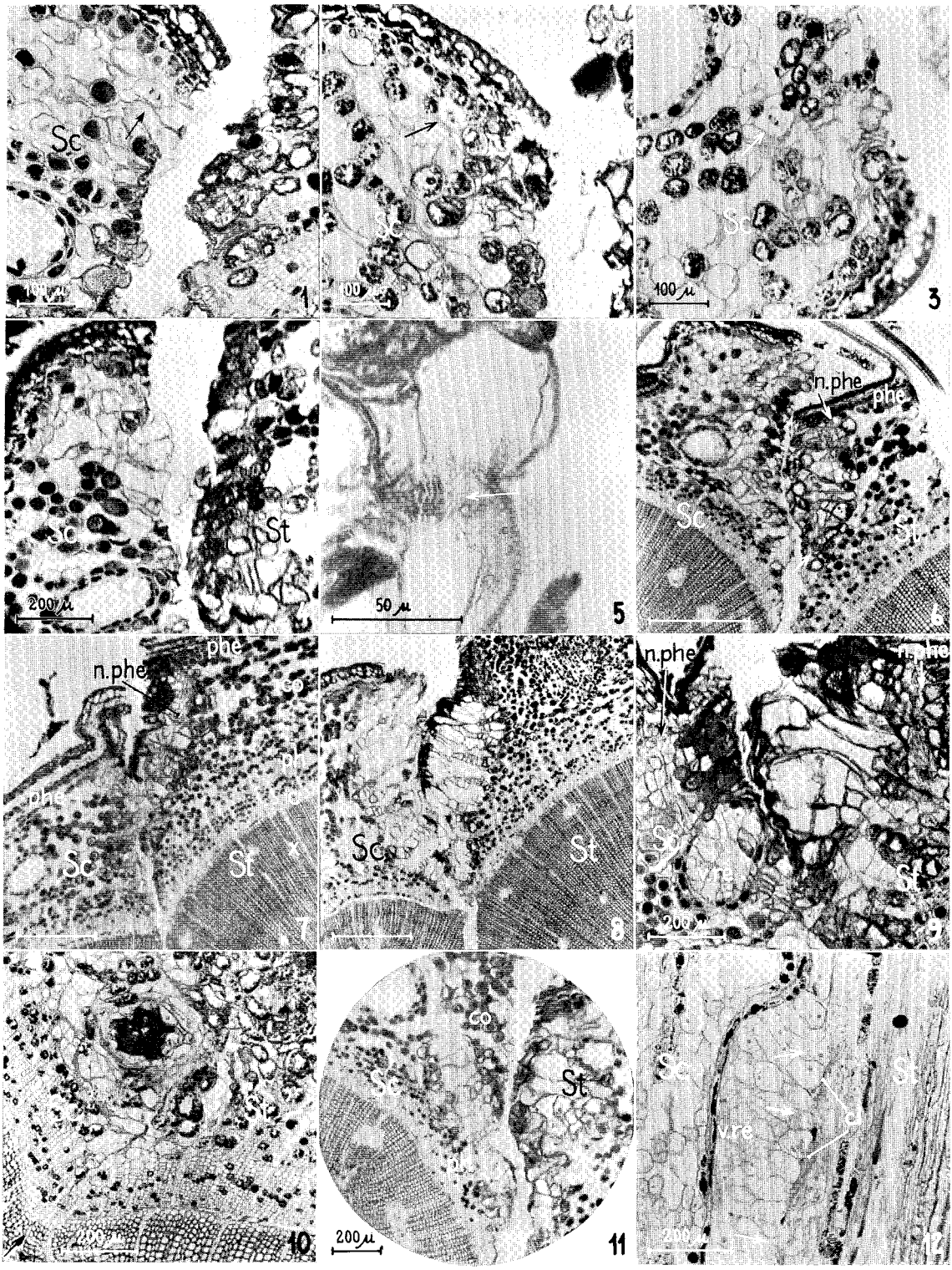

Sc
1
100 μ
3
St
200 μ
50 μ
5
n.phe
phe
6
n.phe
phe
Sc
St
7
Sc
St
8
n.phe
9
10
co
St
200 μ
11
vre
12

Plate VI. Scots pine, veneer graft.

1. 9 d. TL. Callus formation in phloem rays.
2. 35 d. C. In St flap resin cyst filled with callus and united with tissues at cambial region of Sc. Meristematical strand connecting the broken cambia, see arrows.
3. 21 d. C. United phellogens in cortex. Parenchyma union at phloem-cortex boundary of Sc and cambial region of St.
4. 21 d. C. Contact layers broken in two places (see arrows), *cf.* previous photograph.
5. 21 d. C. Cambium of St grows faster than that of Sc in the first weeks. Growth of St cambium subsequent to grafting marked with arrows. *Cf.* Fig. 32.
6. 28 d. C. Firm parenchyma unions in phloem and cortex regions. St and Sc tissues mixed. Remnants of contact layer displaced in different directions. *Cf.* Fig. 20.
7. 28 d. L. Callus formation of St wood parenchyma. Meristematical strand developed. Telophase at arrow.
8. 28 d. C. Callus formation of parenchyma at annual ring boundary and wood rays of St.
9. 9 w. C. Superficial cut in St. Intermediary tissues originating from parenchyma in wood of St and Sc. Cambial union on both sides.
10. 15 w. C. Intermediary tissues originating from pith of Sc and from tissues outside the wood.
11. 6 m. C. Complete union on both sides, no intermediary tissues.

Plansch VI. Tall, läggymp.

1. 9 d. TL. Kallusbildning i floemstrålar.
2. 35 d. C. I fliken kallusfylld hartsbehållare förenad med vävnader vid kambiezonen hos Sc. Meristemstråk bildas i vävnaderna mellan de båda avbrutna kambierna, se pilar.
3. 21 d. C. Fellogenförening i kortex. Parenkymatisk förening vid floemkortexgränsen hos Sc och kambiezonen hos St.
4. 21 d. C. Isoleringsskikt genombrutet på två ställen, jfr föregående bild.
5. 21 d. C. Kambiet hos St växer kraftigare än hos Sc första tiden. Kambietillväxten hos St sedan ympningsdagen markerad med pilar. Jfr fig. 32.
6. 28 d. C. God parenkymförening i floem och kortex. St- och Scvävnader blandade. Delar av isoleringsskikt förskjutna i olika riktningar. Jfr fig. 20.
7. 28 d. L. Kallusbildning från parenkym i veden hos St. Meristematiskt skikt bildat. Telofas vid pilen.
8. 28 d. C. Kallusbildning från parenkym i årsringsgräns och xylemstrålar hos St.
9. 9 w. C. Ytligt snitt i St. Vävnader mellan vedytorna från parenkym i veden hos St och Sc. Kambier förenade i båda sidor.
10. 15 w. C. Mellanvävnader från märg i Sc och från vävnader utanför veden.
11. 6 m. C. God sammanväxning, inga mellanvävnader.

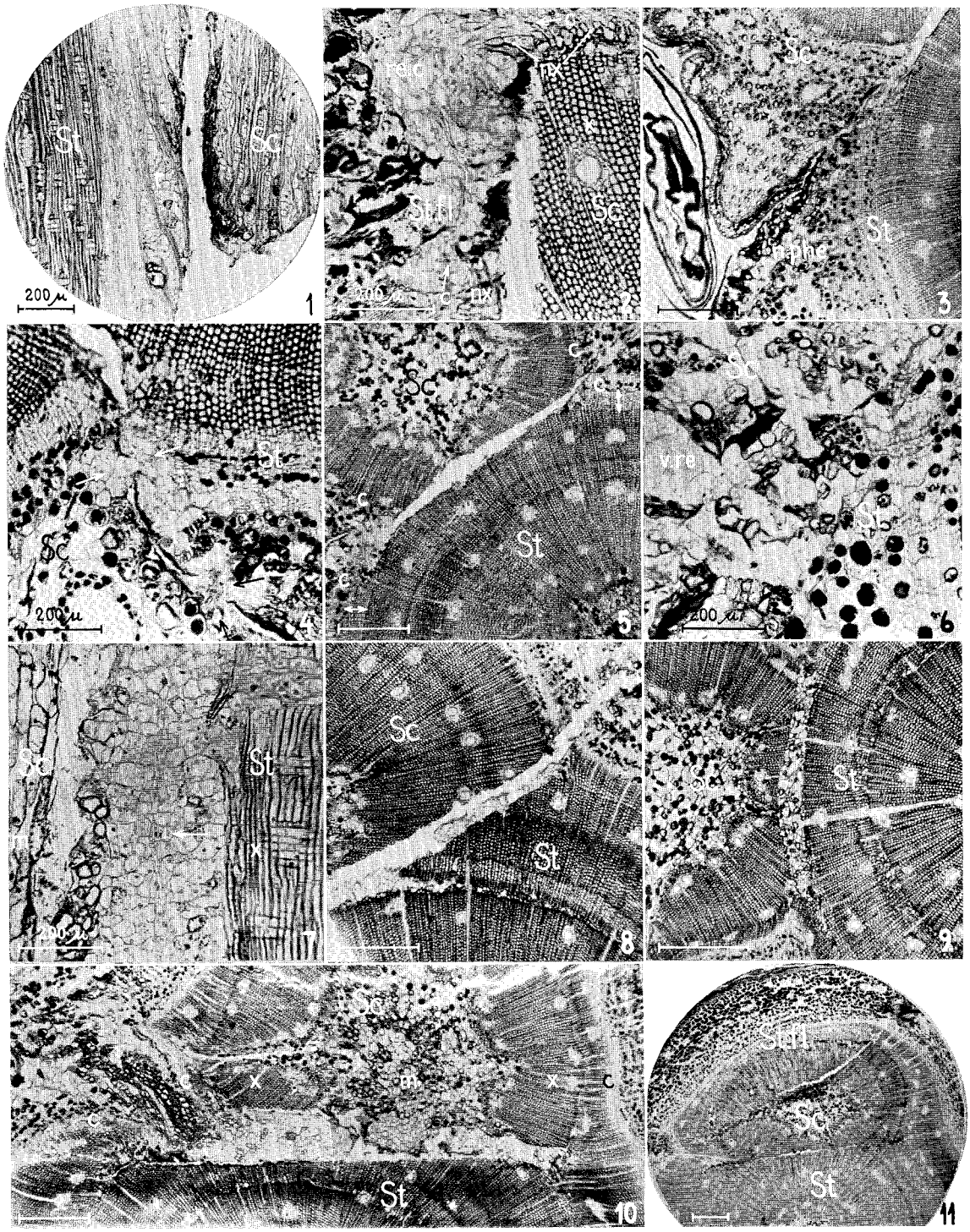

1
2
3
4
5
6
7
8
9
10
11
St
Sc
200 μ

Plate VII. Scots pine, veneer graft. Differentiation and union of vascular tissues.

1. 17 d. L. Both St and Sc exhibit their cambial regions. Irregular cells differentiate into tracheids.
2. 21 d. C. Transfusion window at cambial region between St flap and Sc. Newly differentiated tracheids in both components.
3. 21 d. C. The same graft as VI:5. Leaf trace has brought Sc cambium outwards, here nearly united with St cambium. Union of irregular tracheids is complete, see arrow.
4. 21 d. L. Tracheids differentiating in St callus in contact with leaf trace of Sc. No old xylem of the trace visible in this section.
5. 9 w. L. Branch trace in St wood cut through in grafting. Influence on callus formation in Sc.
6. 9 w. L. The formation in contact with flap in greater magnification. Section near the previous one. Influenced by branch trace tracheids differentiating in Sc callus.
7. 28 d. L. Union of St flap and Sc. Irregular cells; differentiation of tracheids. Approximate border between St and Sc marked with arrows.
8. 35 d. L. More advanced junction of the same kind as in 7. Cambia completely united.
9. 14 m. C. Good graft union.
10. 35 d. C. New cambium in St callus turning outwards to reach connection with Sc cambium. New tracheids not united. Complete union of phellogens.
11. 35 d. C. Section two mm below the previous one. Leaf trace in Sc. Cambial strands united. Tracheids differentiating in continuation with the trace.
12. 35 d. C. Eighth section above 10. Detail of the region of junction. Complete union of phloem cells (note degenerating nuclei in new sieve cells), and also of cambial strands. Xylem not united.

Plansch VII. Tall, läggymp. Differentiering och sammanväxning av ledande vävnader.

1. 17 d. L. Både St och Sc exponerade vid kambiezonen. Oregelbundna celler differentieras till trakeider.
2. 21 d. C. Transfusionsfönster vid kambiezonen mellan St-flik och Sc. På ömse sidor nydifferentierade trakeider.
3. 21 d. C. Från samma ymp som VI: 5. Bladspår har dragit kambiet i Sc utåt, nästan förenat med St-kambiet. Nya, oregelbundna trakeider förenade, se pilen.
4. 21 d. L. Bladspår i Sc. Trakeiddifferentiering hos St invid kontaktytan. Intet av bladspårets ursprungliga xylem synligt i detta snitt.
5. 9 w. L. Kluvet grenspår i St ved påverkar kallusbildningen hos Sc.
6. 9 w. L. Detalj vid fliken av snitt nära det föregående. Trakeiddifferentiering hos Sc under inflytande från grenspåret.
7. 28 d. L. Sammanväxning mellan St-flik och Sc. Oregelbundna celler, trakeiddifferentiering. Pilar visar ungefärliga gränsen mellan St och Sc.
8. 35 d. L. Längre avancerad sammanväxning av samma slag som föregående. Kambier helt förenade.
9. 14 m. C. God sammanväxning.
10. 35 d. C. Nytt kambium i St kallus böjt utåt för att nå förbindelse med Sc-kambiet. Nydifferentierade trakeider ej förenade. Fellogen fullständigt.
11. 35 d. C. Två mm under föregående. Bladspår i Sc. Kambiestråk förenade. Trakeiddifferentiering med utgång från bladspåret.
12. 35 d. C. Åttonde snittet ovan 10. Detalj från sammanväxningsområdet. Fullständig förening på floemsidan (obs! de nya silcellernas skrumpnande cellkärnor) och i kambiet. Xylemet ej förenat.

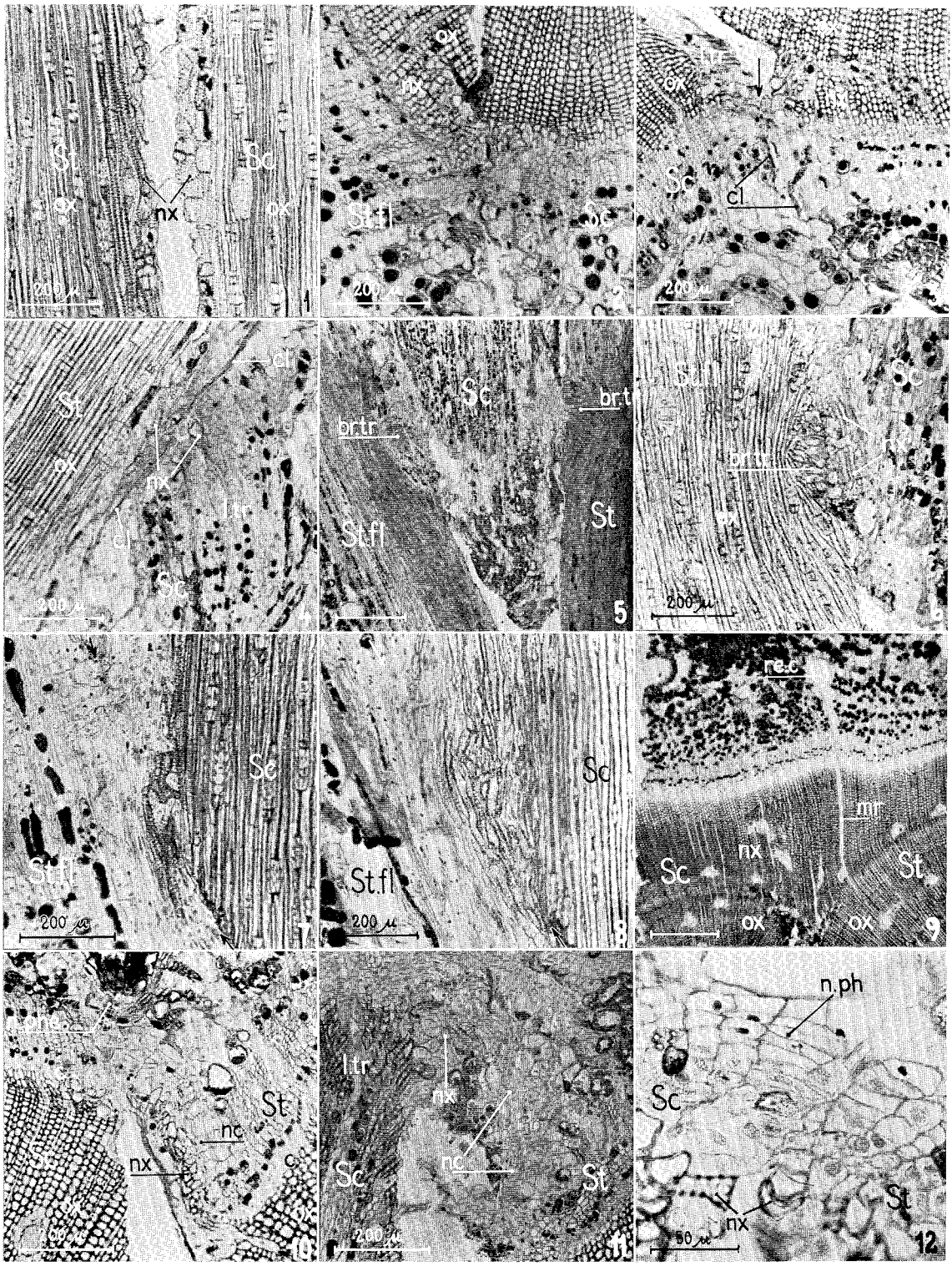
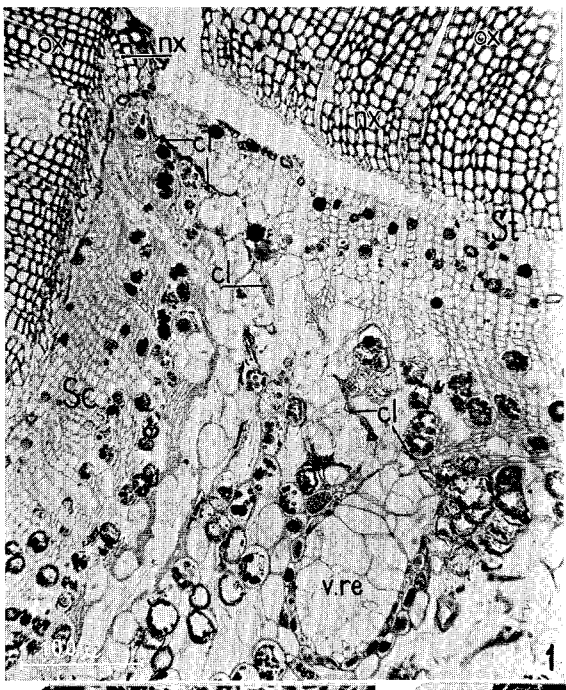

St
Sc
ox
nx
200 μ
1
ox
nx
St.fl
Sc
40 μ
2
ox
Sc
cl
40 μ
3
St
Sc
ox
nx
cl
ltr
Sc
200 μ
4
Sc
br.tr
br.tr
St.fl
St
5
Sc
br.tr
nx
200 μ
6
Sc
St.fl
200 μ
7
Sc
St.fl
200 μ
8
n.c.
mr
nx
Sc
St
ox
ox
9
nc
St
nx
Sc
200 μ
10
ltr
nx
nc
Sc
St
200 μ
11
n.ph
Sc
St
nx
50 μ
12

Plate VIII. Scots pine, veneer graft.

1. 35 d. C. Cambial union. (Break of cambial region—see p. 46.) Parenchyma well united. Note remnants of contact layer.
2. 7 w. C. Callus formation from St considerable. St cambium first pressed outwards, after union of St and Sc parenchyma turned inwards. Note horizontal elongated cells (between arrows) which unite the cambial strands.
3. 2 years. C. On one side (turned upwards) cambial union between Sc and head part of St established in the first year, on the other side (turned downwards) parenchyma union took place in the second year, but still no cambial union. St cambium turned inwards in both cases. Note direction of first formed tracheids (circles), *cf.* previous photograph.
4. 2 years. C. On one side (turned downwards) cambial union established first year, on the other side (turned upwards) still no union, heavy cork layers in contact region.
5. 2 years. C. Both sides of same graft, just above middle of graft zone. On side turned downwards cambial union second year, on side turned upwards parenchyma union only. *Cf.* next photograph, Plate IX: 1.

Plansch VIII. Tall, läggymp.

1. 35 d. C. Kambieförening (brott i kambiezonen vid snittningen). God parenkymatisk sammanväxning. Märk resterna av isoleringsskikt!
2. 7 w. C. Stor kallusutveckling från St. Kambiet först tryckt utåt, efter parenkymförening mellan St och Sc böjt inåt. Märk de horisontellt sträckta cellerna (mellan pilarna) som förenar kambierna!
3. 2 år. C. I uppåtvända sidan kambieförening mellan Sc och huvuddel av St första året, i nedåtvända parenkymförening andra året men ännu ingen kambieförening. St-kambiet har svängt inåt i båda fallen. Märk orienteringen hos först bildade trakeiderna (cirklarna), jfr föregående bild!
4. 2 år. C. I nedåtvända sidan kambieförening första året, i uppåtvända sidan ännu ingen förening, korkskikt isolerar.
5. 2 år. C. Båda sidor av samma ymp, strax ovan mitten av ympzonen. I nedåtvända sidan kambieförening andra året, i övre endast parenkymförening. Jfr nästa bild, pl. IX:1!


ox
nx
cl
St
Sc
v.re
1


St.fl
Sc
ox
nx
St
2

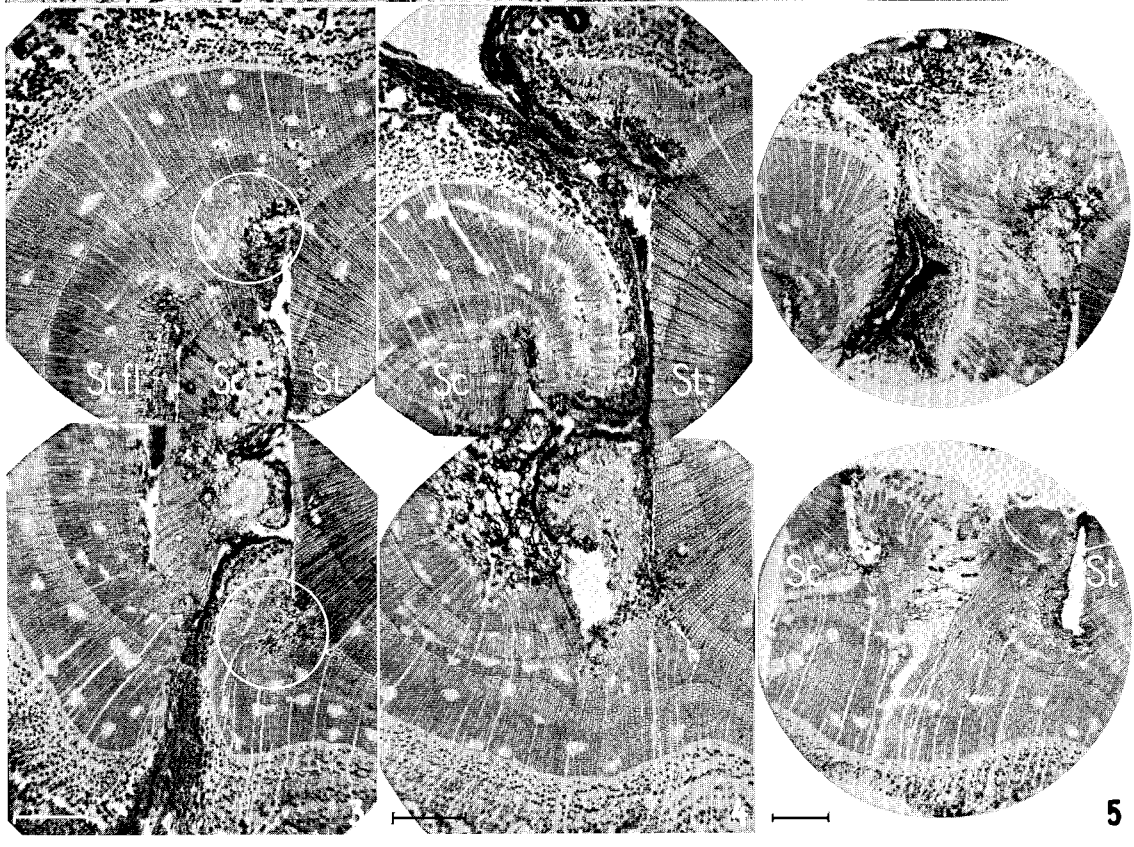

St.fl
Sc
St
Sc
St
Sc
St
5

Plate IX. Scots pine, veneer graft.

1. 2 years. C. Section 6 mm above that of Plate VIII: 5. St and Sc at first healed separately. Cambial growth pressed them together, union as in "natural" grafting.
2. 6 m. C. St cambium divided to reach connection with Sc cambia on the sides. Note elongation of parenchyma cells.
3. 11 w. TL. Direction of tracheids in union zone—from Sc downwards to St, from St upwards to Sc.

4—6. 19 w. C. Tissues between wood surfaces mostly developed from wood parenchyma. 4: 10 mm above Sc base. Region with dividing cells in centre; 5: 10 mm higher up. Narrow space between wood surfaces, no divisions; 6: 3 mm above 5. Tracheids differentiating, meristematical activity.

7. 3 years. C. Living cells in intermediary tissues only at the outer margins (downwards and upwards in the photograph).

8—9. 14 m. C. 3 vascular nodules in intermediary tissue. Xylem outwards, phloem inwards in the archs. Square in 8 marks area magnified in 9 — only phloem is differentiated. In the other two mainly xylem.

10. 11 m. C. Vascular nodule in St flap. Xylem inwards, phloem outwards.

11—12. 3 years. C. Part of St cambium isolated after cambial union on the outside. Arrows in 11 mark location of cambium at the time of junction on the outside. 12 comes from section 3 mm below 11. No vascular connection at all. Cambium bent, xylem outside, phloem inside.

13—15. 19 w. L. Basal part of graft zone. St flap cut as in Fig. 30. 14: Section through the middle, 13 and 15 through peripherical parts. Sc cambium turned up along old wood in flap. In 13 lateral union with cambium of flap, in 15 union above the wood sliver.

Plansch IX. Tall, läggymp.

1. 2 år. C. Snitt beläget 6 mm ovanför pl. VIII:5. St och Sc läkta var för sig. Kambietillväxten åstadkommer tryck, sammanväxning som vid »naturlig» ympning.
2. 6 m. C. St-kambiet delat för att växa samman med Sc-kambierna på sidan. Obs. parenkymcellernas sträckning!
3. 11 w. TL. Trakeidernas orientering i sammanväxningszonen — från Sc nedåt mot St resp. från St uppåt mot Sc.

4—6. 19 w. C. Vävnader mellan vedytorna huvudsakligen från parenkym i veden. 4: 10 mm ovanför basen på Sc. Område med delningsaktiva celler i centrum; 5: ytterligare 10 mm högre. Avståndet mellan vedytorna smalt, inga delningar; 6: 3 mm ovan 5. Trakeider differentierade, fortsatta delningar.

7. 3 år. C. Alltjämt levande celler i mellanvävnaderna, huvudsakligen i ytterkanterna nere och uppe på bilden.

8—9. 14 m. C. 3 sfäroblast-liknande bildningar i mellanvävnad. Xylem utåt, floem inåt i bågarna. 9 är förstoring av inrutade området i 8 — endast floem utdifferentierat. I de två andra huvudsakligen xylem.

10. 11 m. C. Sfäroblast i St-fliken. Xylem inåt, floem utåt.

11—12. 3 år. C. Del av St-kambium som isolerats efter kambieförening utanför. Pilar i 11 visar kambiets placering, då förbindelsen utåt avbröts. 12 kommer från snitt ca 3 mm under 11. Ingen förbindelse med xylemet utanför. Kambiet böjt — xylem utåt, floem inåt.

13—15. 19 w. L. Nederdelen av ymp, flik skuren enligt fig. 30. 14 snitt genom centrum, 13 och 15 från vardera ytterkanten. Sc-kambiet böjt upp efter vedflisan i fliken, i 13 förenat med flikens kambium i sidled, i 15 ovanför vedflisan.

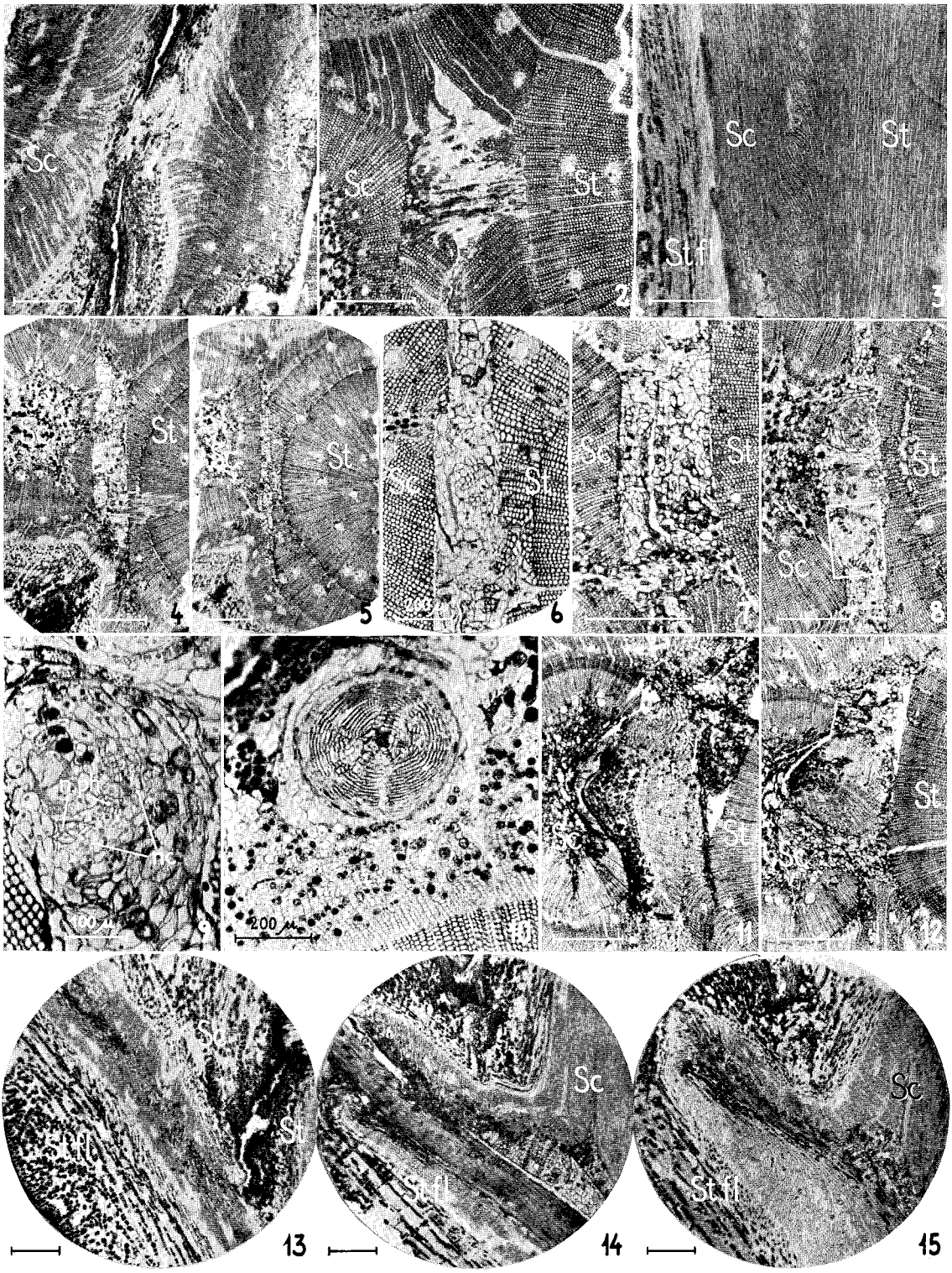

Sc
St
2
St fl
3
4
5
6
7
8
200 μ
11
12
13
14
15

Plate X. Scots pine.

1—5. From basal parts of veneer grafts.

1. 23 w. RL. Flap as in Fig. 30. Wood sliver in flap prevents union. Note orientation of new tracheids, *cf.* 3.
2. 23 w. TL from outer part of same graft as 1. Flap and Sc united, heavy growth.
3. 3 years. RL. Flap as in Fig. 30. pressed downwards by heavy growth of Sc. Horizontal elongation of tissues in Sc. Big knot formed.
4. 3 years. C. Flap as in Fig. 30. Wood sliver prevents union. Knot formation.
5. 2 years. RL. Flap as in Fig. 31. Smooth union.

6—11. Early reactions in side slit grafts.

6. 4 d. C. Division of ray cell in bark flap (telophase) and in Sc pith (metaphase), see arrows. Contact layer between graft components.
7. 4 d. C. Cell division in outermost part of ray in wedge-shaped part of Sc.
8. 8 d. C. Callus formation from wood side of St.

9—11. 12 d. C. 9: Unwounded part of St, arrows indicate last differentiated zone with vertical phloem parenchyma. 10: Callus formation in innermost corner, all cells of cambial region participate; between arrows enlarged phloem parenchyma cells, *cf.* previous photograph. 11: Callus formation from bark flap in front of Sc pith, union established.

Plansch X. Tall.

1—5. Från nederdelen av läggympar.

1. 23 w. RL. Flik enligt fig. 30. Vedflisan i fliken hindrar sammanväxning. Märk de nya trakeidernas orientering, jfr 3!
2. 23 w. TL från yttre del av samma ymp som föregående. Flik och Sc förenade, kraftig tillväxt.
3. 3 år. RL. Flik enligt fig. 30. Fliken pressad nedåt av starka tillväxten hos Sc. Horisontellt orienterade vävnader i Sc. Stor knölbildning.
4. 3 år. C. Flik enligt fig. 30. Vedflisan hindrar sammanväxning. Knölbildning.
5. 2 år. RL. Flik enligt fig. 31. Jämn sammanväxning.

6—11. Tidiga reaktioner hos sidsticksympar.

6. 4 d. C. Celldelningar i stråle i barkfliken (telofas) och i märg i Sc (metafas), se pilarna. Isoleringsskikt mellan ympkomponenterna.
7. 4 d. C. Celldelning ytterst i stråle i tillspetsade delen av Sc.
8. 8 d. C. Kallusbildning från vedsidan hos St.

9—11. 12 d. C. 9: Osårad del av St, pilar markerar senast bildade zonen med floemparenkym. 10: Kallusbildning i inre vinkeln, alla celler i kambiezonen deltar, mellan pilarna förstorade floemparenkymceller, jfr föregående bild. 11: Kallusbildning från fliken mitt för Sc märg, sammanväxning.

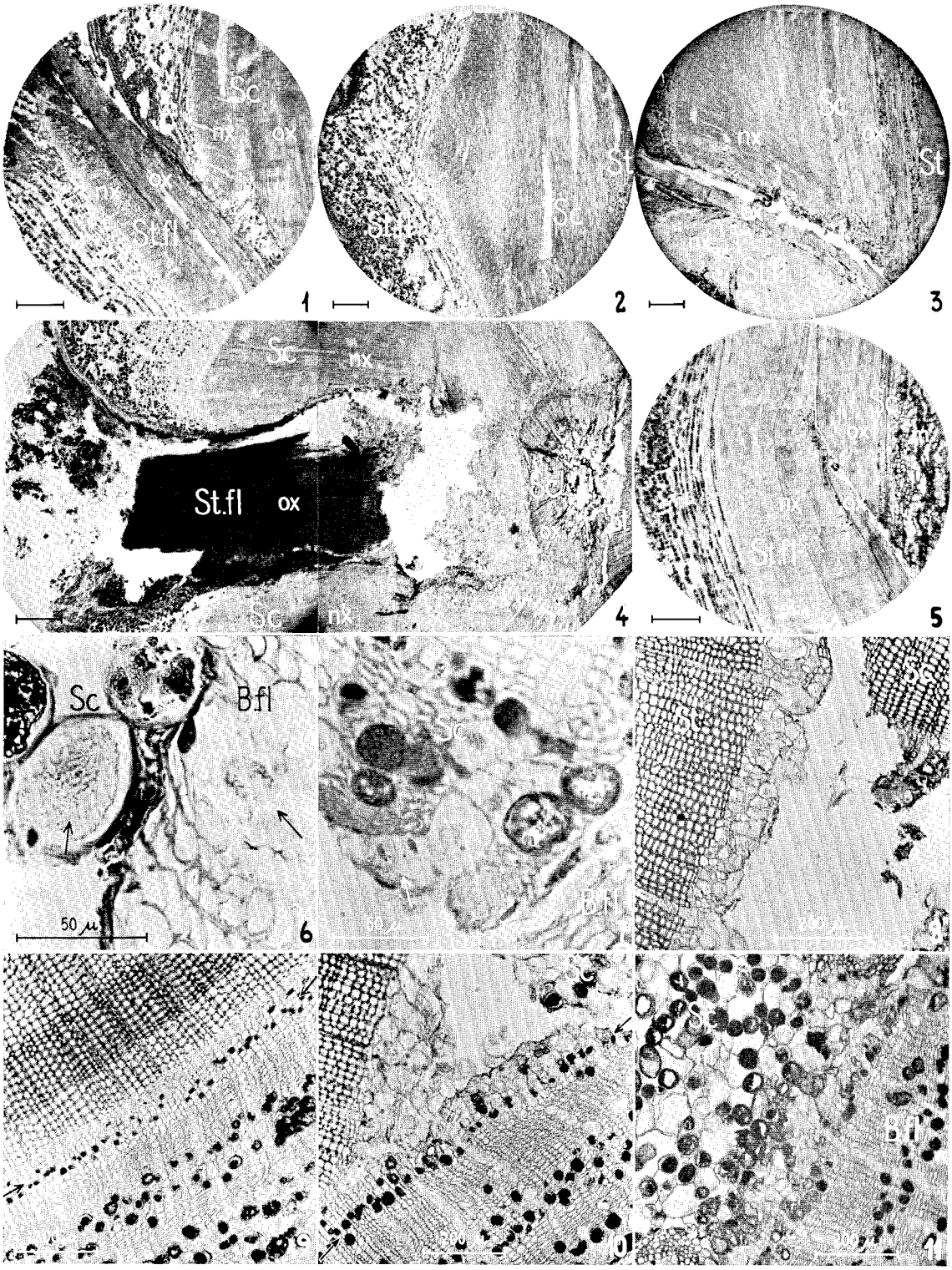
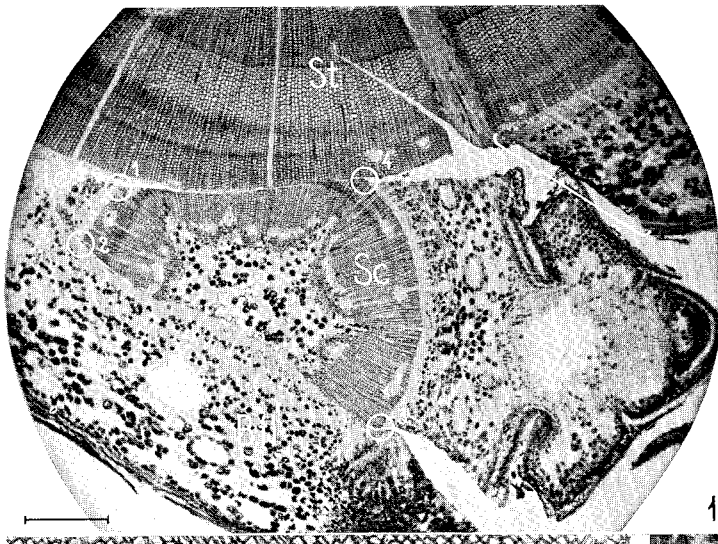

Sc
nx
ox
St.fl
1
2
3
4
5
Bfl
50 μ
6

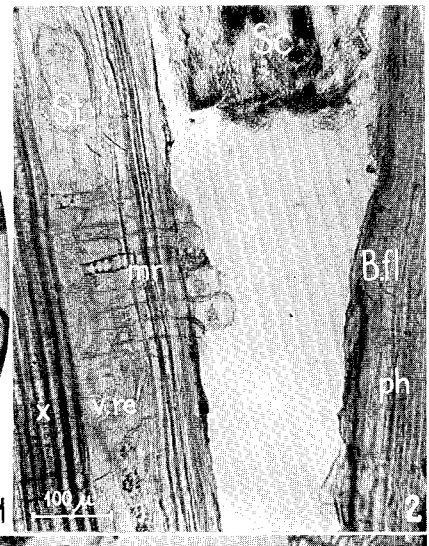
Plate XI. Scots pine, early reactions in side slit grafts.

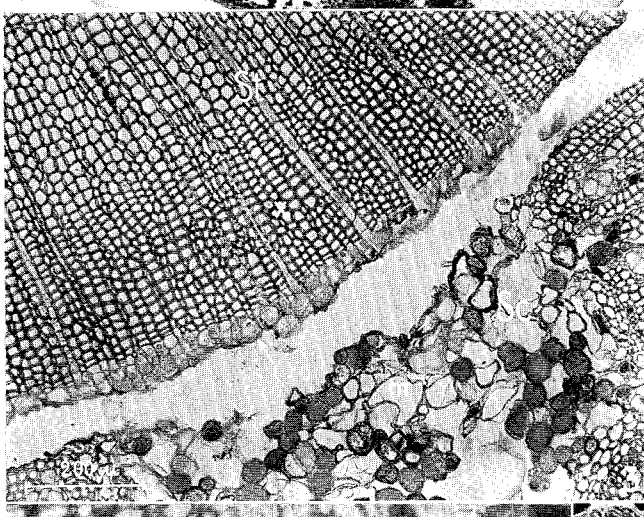
1. 4 d. C. Full view of graft, *cf.* Fig. 18 a. Exposed places of Sc cambium numbered according to Fig. 21. Note long distance between pt. 4 and cambium at incision face (i).
2. 4 d. RL. Proliferation from multiseriate ray on St wood side.
3. 8 d. C. Callus formation on wood side facing Sc pith. Telophase at arrow.
4. 4 d. C. Proliferation of cells in rays of bark flap.
5. 6 d. C. Division of cell in phloem-cortex boundary of Sc.
6. 6 d. C. Proliferation of ray at incision face of St.

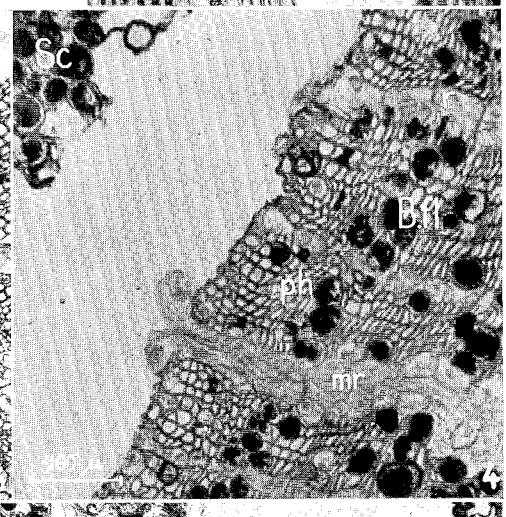
Plansch XI. Tall, tidiga reaktioner hos sidsticksympar.

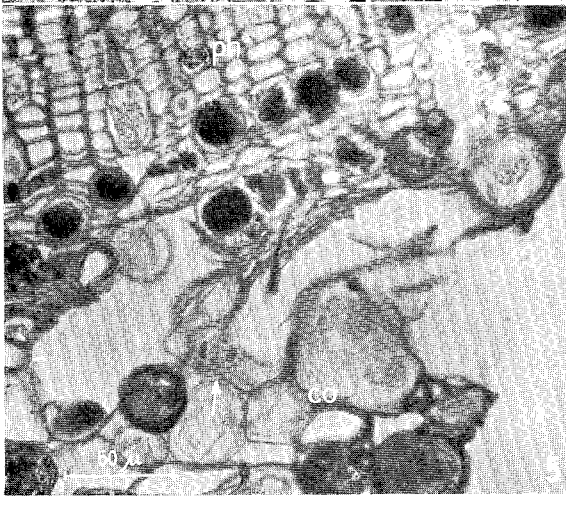
1. 4 d. C. Helhetsbild av ymp, jfr fig. 18 a. De fyra ställen där Sc-kambiet genomskurits numrerade enligt fig. 21. Obs. avståndet mellan pt. 4 och kambiet vid inskärningsytan (i)!
2. 4 d. RL. Proliferation från hartsförande stråle vid vedsidan hos St.
3. 8 d. C. Kallusbildning vid vedsidan mitt för Sc märg. Telofas vid pilen.
4. 4 d. C. Proliferation från strålеceller i i barkfliken.
5. 6 d. C. Celldelning i gränsen mellan floem och kortex hos Sc.
6. 6 d. C. Proliferation i stråle vid inskärningsytan hos St.


St
Sc
1


Sc
St
mr
B.f
ph
X
vas
100 µ
2


St


Sc
B.f
ph
mr
4


ph
co
50 µ

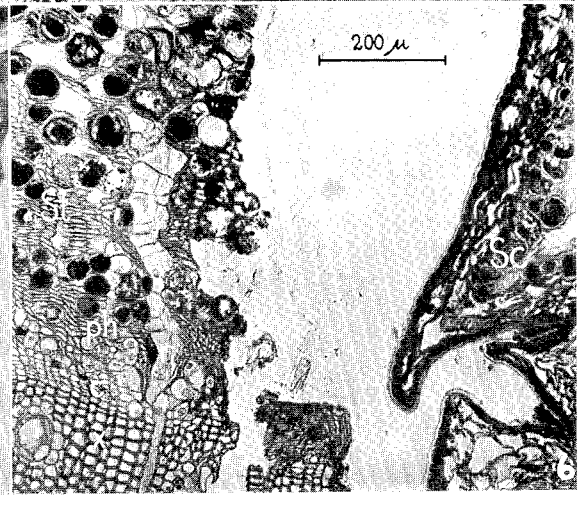

200 µ
St
ph
X
Sc
6

Plate XII. Scots pine, side slit graft.

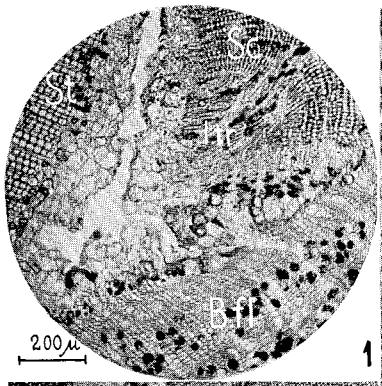
1. 12 d. C. Vigorous callus formation from both St and Sc in innermost corner, in Sc influenced by leaf trace. Parenchyma union at flap.
2. 12 d. C. Leaf trace in Sc cross-cut at grafting, large callus formation from phloem-cortex boundary.
3. 14 d. C. No callus formation from St wood side facing wood in Sc. Parenchyma union at flap.
4. 14 d. C. Parenchyma union between tissues from Sc cortex and St flap rays.
5. 14 d. C. In flap dead tissues facing Sc. Inside this region callus formed from rays and phloem parenchyma in non-functional phloem. Callus at wood side facing Sc pith.
6. 17 d. C. Innermost corner filled with callus, parenchyma union. Phellogen at incision face. Heavy callus formation from Sc at pt. 4.

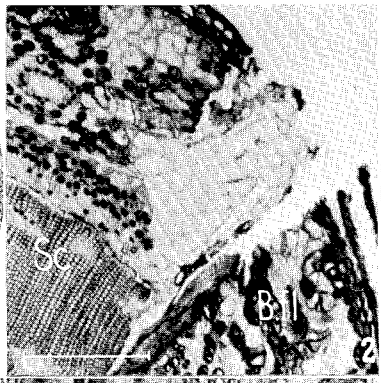
7—10. 20 d. C. 7: St cambium follows flap (between arrows marked with c). Innermost corner filled with callus. Sc cambium from pt. 1 forms an arch in direction towards St cambium in flap (arrows inside the arch). Tracheids differentiated in flap in contact with pt. 2 and in front of Sc pith. Cambia nearly united at pt. 2. 8: From the same section as 7. Pt. 3 with yet no connection and slow division activity 9:2 mm above 7. Empty space in innermost corner. Cambium follows flap. 10: 10 mm above 7. Callus from pt. 2 between Sc wood and flap. No union. Callus formation in flap as in 5.

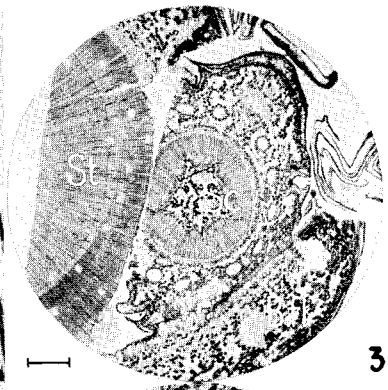
Plansch XII. Tall, sidsticksymp.

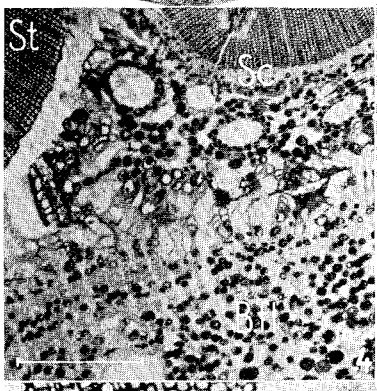
1. 12 d. C. Livlig kallusbildning hos både St och Sc i inre vinkeln, hos Sc influerat av bladspår. Parenkymförening vid fliken.
2. 12 d. C. Bladspår i Sc kluvet vid ympningen, stor kallusbildning från floem-kortexgränsen.
3. 14 d. C. Ingen kallusbildning från vedsidan hos St mitt för ved i Sc. Parenkymförening vid fliken.
4. 14 d. C. Parenkymförening mellan vävnader från Sc kortex och strålar i barkfliken.
5. 14 d. C. Kallus bildad inuti fliken från strålar och floemparenkym i inaktivt floem. Vävnader närmast Sc döda. Kallusbildning från vedsidan mitt för Sc märg.
6. 17 d. C. Inre vinkeln helt kallusfylld, parenkymförening. Fellogen vid inskärningsytan. Kraftig kallusutveckling från Sc vid pt. 4.

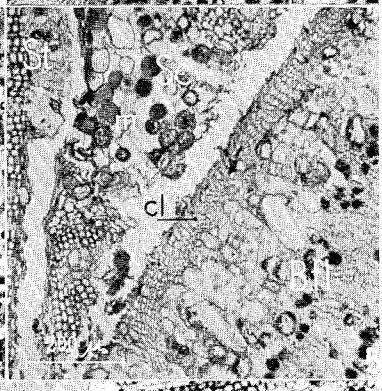
7—10. 20 d. C. 7: St-kambiet följer fliken (c med pil). Inre vinkeln kallusfylld. Sc-kambiet från pt. 1 breder ut sig bågformigt mot kambiet i fliken. Pilar på bågens insida. Trakeider differentierade i fliken invid pt. 2 och mitt för Sc märg. Nästan kambieförening vid pt. 2. 8: Från samma snitt som föregående. Vid pt. 3 ingen sammanväxning, liten delningsaktivitet. 9: 2 mm ovanför 7. Tomrum i inre vinkeln. Kambiet följer fliken. 10: 10 mm ovan för 7. Kallus från pt. 2 mellan Sc ved och barkfliken. Ingen förening. Kallusbildning i fliken liksom i 5.

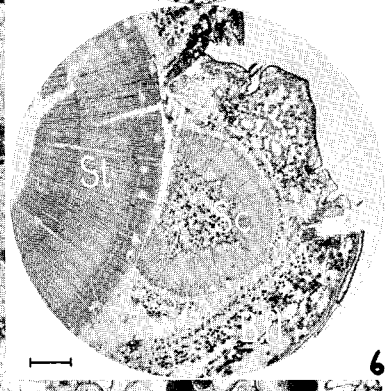

St
Sc
ht
B.fl
200 μ
1

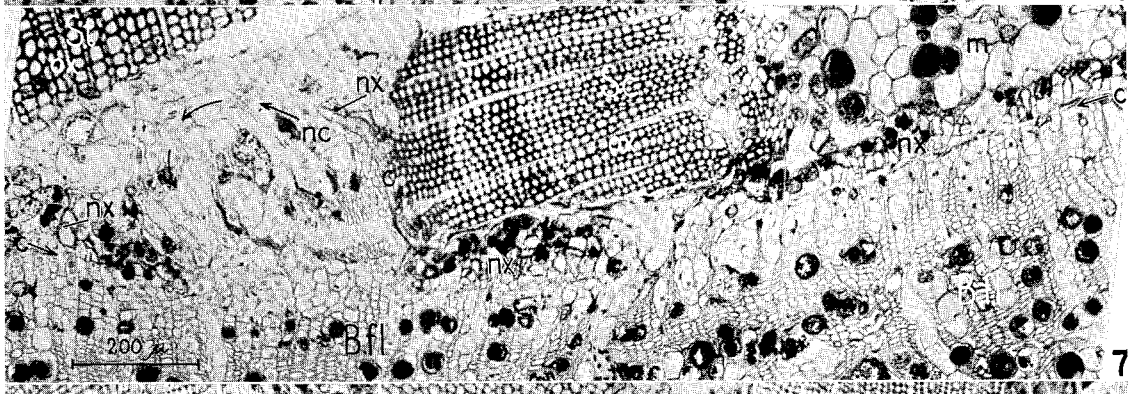

Sc
B.fl
2

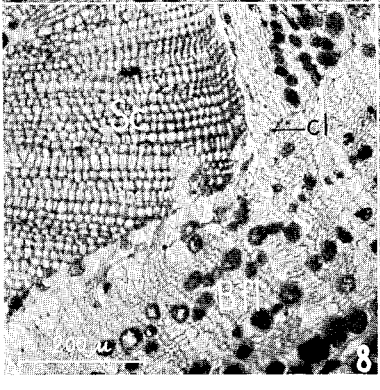

St
3

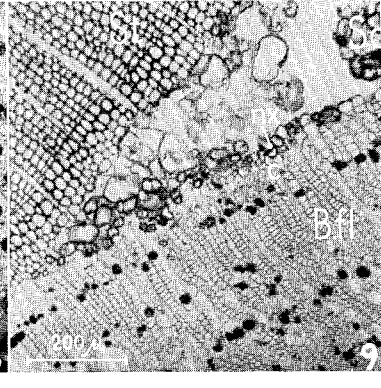

St
Sc
B.fl


St
cl
B.fl


St
6


nx
nc
m
nx
nx
200 μ
B.fl
7


Sc
cl
B.fl
8


B.fl
9

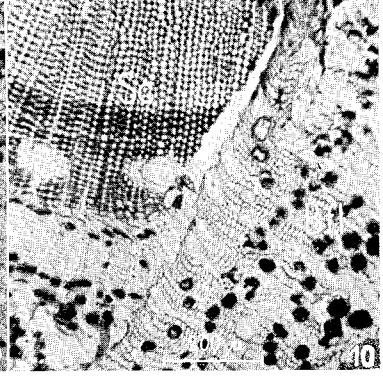

10

Plate XIII. Scots pine, side slit graft.

1. 24 d. C. Parenchyma union in innermost corner, cambial union at pt. 2. Heavy callus formation from St wood side in front of Sc pith. Pith compressed. Callus from pt. 4 penetrates into the space between the wood surfaces.
2. 24 d. C. Union of vascular tissues and cambia at pt. 2.

3—7. 34 d. C. Sections from different levels of the same graft. Approximate distance from base of Sc: 3 = 2.5 mm, 4 = 13.5 mm, 5 = 17.5 mm, 6 = 17.8 mm, 7 = 19 mm. 3: Cambial union at pt. 4; cambium in flap destroyed, phellogen grown inwards up to union between flap and Sc pith; parenchyma union at pt. 3, Sc cambium spreads into flap. 4: No union at pt. 4 or pt. 3; no cambium present in wedge shaped part of Sc; St cambium in flap unbroken. 5: small piece of cambium in wedge-shaped part of Sc — cambium from pt. 1 in an arch, united with cambium from pt. 2. 6: Broader cambial piece in Sc — wider cambial arch; broken cambium in flap united with that from pt. 1 (*cf.* Plate XII: 7). 7: Sc cambium still broader — cambial strand in a straighter course. *Cf.* 5—7 with Fig. 22.

8—9. 6 w. C. Innermost corner and incision face of the same graft. No cambial activity in St before grafting. 8: Cambium left at wood surface at grafting, cambial union at pt. 1; cambial strand formed in flap between pt. 2 and pt. 3. 9: New xylem in St only in proximity of the graft wound; phellogen in both St and Sc.

10. 8 w. C. Complete union.
11. 30 d. C. Tangential cut in St (Fig. 18 b), complete union at incision face (in circle).
12. 45 d. C. Complete union following tangential cut in St.

Plansch XIII. Tall, sidsticksymp.

1. 24 d. C. Parenkymföreningar i inre vinkeln, kambieförening vid pt. 2. Stor kallusbildning från vedsidan av St mitt för Sc märg. Märgen hoptryckt. Kallus från pt. 4 tränger in mellan vedytorna.
2. 24 d. C. Förening av ledande vävnader och kambier vid pt. 2.

3—7. 34 d. C. Snitt från olika nivåer av samma ymp. Ungefärliga avstånd från basen av Sc: 3 = 2,5 mm, 4 = 13,5 mm, 5 = 17,5 mm, 6 = 17,8 mm, 7 = 19 mm. 3: Kambieförening vid pt. 4; kambiet i fliken förstört, fellogen intill sammanväxningen mellan flik och Sc märg; parenkymförening vid pt. 3, kambium från Sc tränger in i fliken. 4: Ingen förening vid pt. 4 och pt. 3; inget kambium i inåtvända delen av Sc; St-kambiet följer obrutet fliken. 5: Litet kambiestycke i Sc; kambiet från pt. 1 beskriver båge, sammanvuxet med kambiet vid pt. 2; kambiet i fliken obrutet. 6: Bredare kambium i Sc, vidare båge; kambiet i fliken brutet, sammanvuxet med kambiet från pt. 1 (jfr pl. XII: 7). 7: Sc-kambiet ännu bredare; kambiet från pt. 1 söker sig genare väg. Jfr 5—7 med fig. 22!

8—9. 6 w. C. Inre vinkeln respektive inskärningsytan hos samma ymp. Ingen kambieverksamhet hos St före ympningen. 8: Kambiet kvar på vedytan efter ympningen, kambieförening vid pt. 1; kambiestråk bildat i fliken mellan pt. 2 och pt. 3. 9: Nytt xylem i St endast invid sårytor; fellogen hos både St och Sc.

10. 8 w. C. Väl sammanvuxen ymp.
11. 30 d. C. Inskärning i St med tangentiellt snitt (fig. 18 b), god sammanväxning vid inskärningsytan (i cirkeln).
12. 45 d. C. God sammanväxning efter tangentiellt insnitt i St.

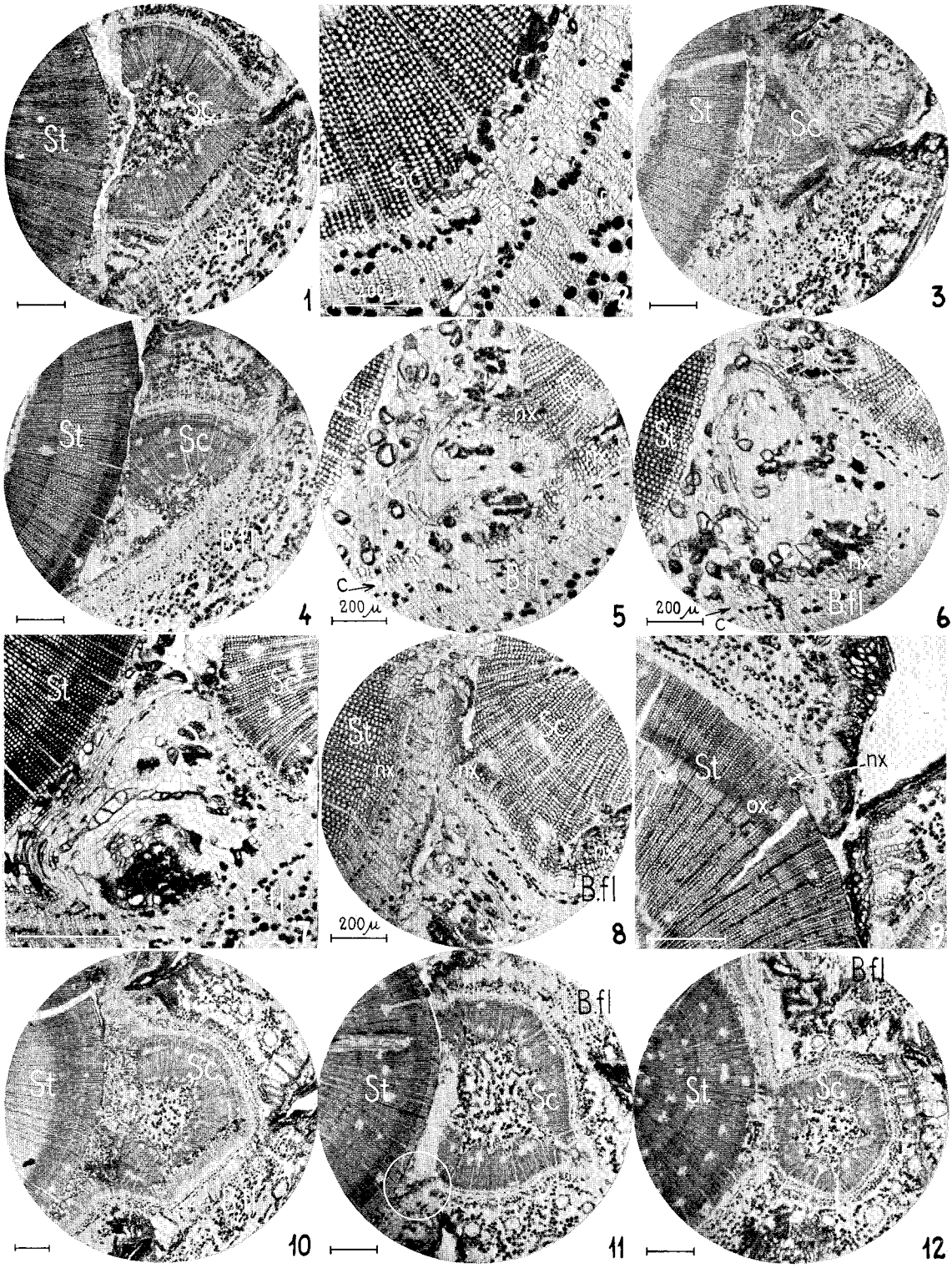

St
Sc
1
Sc
Bfl
2
St
Sc
3
St
Sc
4
nx
Bfl
C
200 μ
5
St
nx
Bfl
200 μ
C
6
St
St
nx
ox
Bfl
200 μ
8
St
nx
ox
St
Sc
10
Bfl
St
Sc
11
Bfl
St
Sc
12

Plate XIV. Norway spruce, veneer graft.

1—7. Early reactions.

1. 2 d. C. Enlarged cells in resin duct of Sc cortex and in rays of St flap.
2. 4 d. C. Cell divisions in Sc cortex, see arrows.
3. 4 d. C. Cell divisions in ray of Sc.
4. 4 d. C. Cell division in Sc cortex. Resin duct filled with cells.
5. 6 d. C. Callus formation from phloem rays in St. In Sc resin duct filled with cells. Contact layers.
6. 6 d. C. Proliferation from ray in newly formed wood and in phloem rays of St.
7. 11 d. TL. Callus formation from phloem rays at short wound surface of Sc.

8—9. Fitting of graft components.

8. 16 d. C. Outer edges of St and Sc matched on left side, cambia far apart. Callus from St intrudes into Sc pith and compresses pith cells.

9. 18 d. C. Outer edges matched on right side; cambia far apart on this side but matching on the other. Graft cut in St superficial— no callus formation from wood exposed at cambial region.

Plansch XIV. Gran, läggymp.

1—7. Tidiga reaktioner.

1. 2 d. C. Förstorade celler i hartskanal i Sc kortex och i strålar i fliken.
2. 4 d. C. Celldelningar i Sc kortex, se pilarna.
3. 4 d. C. Celldelningar i stråle i Sc.
4. 4 d. C. Celldelning i Sc kortex. Cellfylld hartskanal.
5. 6 d. C. Kallusbildning från floemstrålar hos St. Cellfylld hartskanal i Sc. Isoleringsskikt.
6. 6 d. C. Proliferation från stråle i årsveden och strålar i floemet hos St.
7. 11 d. TL. Kallusbildning från floemstrålar vid lilla snittytan nederst i Sc.

8—9. Sammanpassning av ympkomponenterna.

8. 16 d. C. Ytterkanterna hos St och Sc sammanpassade i vänster sida, kambierna långt isär. Kallus från St tränger in i och trycker samman Sc märg.
9. 18 d. C. Sc och St sammanpassade i höger ytterkant; kambier långt isär i denna sida, passar samman i den andra! Ympsnittet i St ytligt; ingen kallusbildning från vedyta blottad vid kambiezonen.

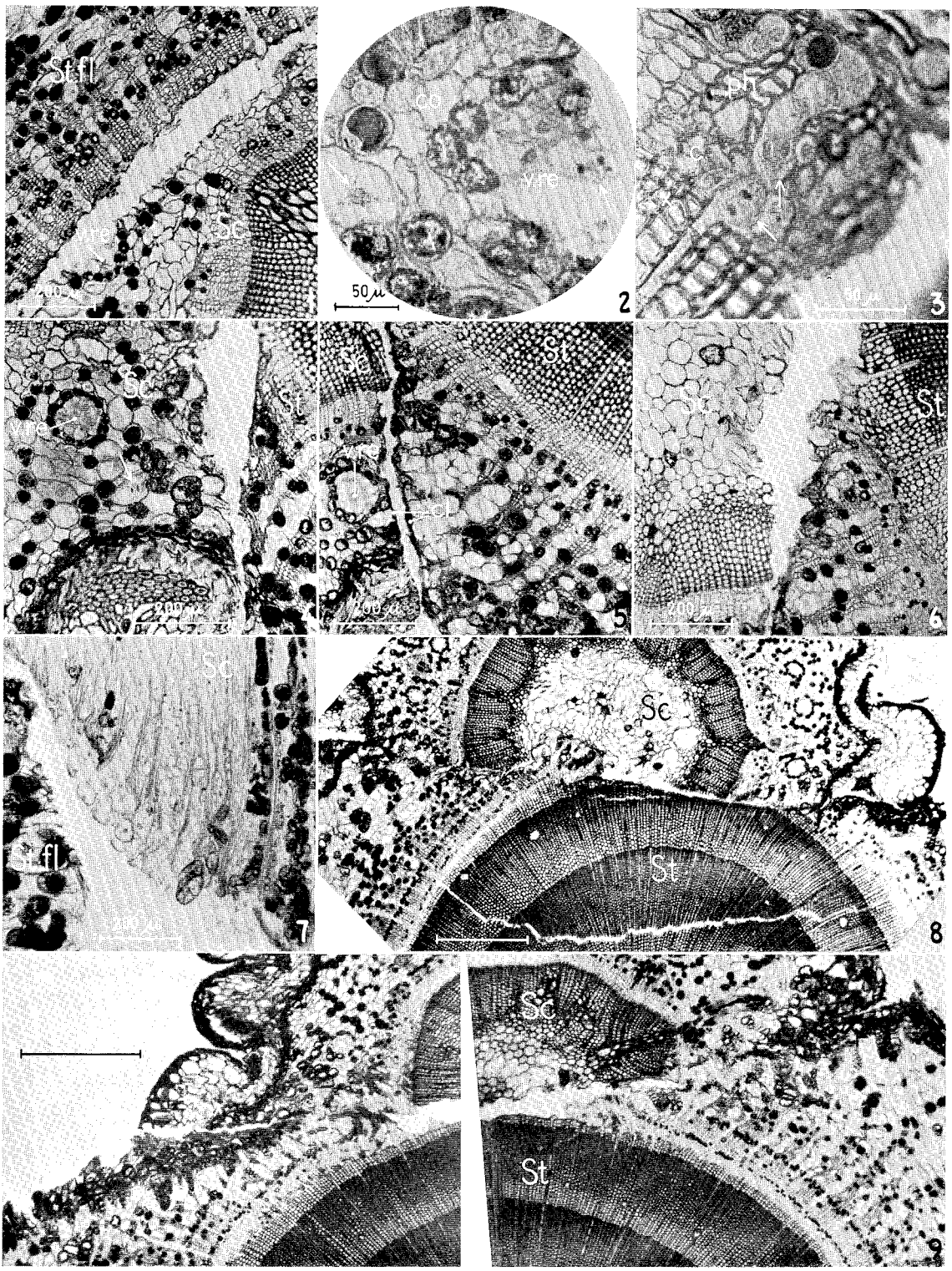

St.fl
50 μ
2
Ph
3
St
5
6
Sc
St.fl
7
8
9

Plate XV. Norway spruce, veneer graft.

1. 22 d. TL. Parenchyma union of flap and Sc. Most of the callus from Sc.
2. 22 d. L. Parenchyma union between flap-cortex and Sc-phloem, contact layer at flap originally touching Sc wood. Callus from Sc cambium intrudes between contact layer and wood.
3. 22 d. C. St cambium turning outwards, union immediate.
4. 28 d. C. Complete union of vascular tissues and of cambia.
5. 36 d. RL. Flap cut according to Fig. 31. Uncomplicated union.
6. 28 d. C. Shallow graft cut in St. No callus formed from wood exposed at cambial region. Good union.
7. 6 m. C. Parenchyma union on one side only. Sc pith shrivelled.
8. 1 year. C. Complete union. Intermediary tissues originate from both sides, each unit coated with periderm.
9. 36 d. C. Graft cut in stock too deep. Outer edges of St and Sc matched on left side but poor fit of cambia. Complete union on left side, no union at all on right side.
10. 1 year. C. Cut in St too deep. St flap and St united on side turned upwards. On side turned downwards vascular union late in the season. Note false annual ring in Sc.
11. 14 m. C. Isolated cambia in intermediary tissue. Cambial union produced by leaf trace on side turned upwards.
12. 14 m. C. Sc two years old at grafting. No new shoots developed in the year of grafting, one bud bursting at the time of fixation. Weak union in spite of relatively good cambial fitting.
13. 18 m. C. Graft without new shoots. First year weak vascular connection, strengthened in the second year.

Plansch XV. Gran, läggymp.

1. 22 d. TL. Parenkymförening mellan flik och Sc. Största kallusmängden från Sc.
2. 22 d. L. Parenkymförening mellan kortex i fliken och floem i Sc. Isoleringsskikt i fliken bildat i anslutning till ved i Sc. Kallus från Sc-kambiet tränger sig mellan isoleringsskikt och ved.
3. 22 d. C. St-kambiet böjer av utåt, nära förening.
4. 28 d. C. God förening mellan ledande vävnader och mellan kambier.
5. 36 d. RL. Flik enligt fig. 31. Okomplicerad sammanväxning.
6. 28 d. C. Ympsnitt just vid kambiet i St. Ingen kallusbildning från blottade vedytan. God sammanväxning.
7. 6 m. C. Parenkymförening endast i ena sidan. Märg hos Sc skrumpnad.
8. 1 år. C. God sammanväxning. Vävnaderna mellan vedytorna härstammar från båda kanterna, varje enhet omsluten av sitt periderm.
9. 36 d. C. För djupt ympsnitt i St. Ytterkanterna hos St och Sc sammanpassade i vänster sida, dålig överensstämmelse mellan kambier. Fullständig förening i vänster sida, ingen alls i den högra.
10. 1 år. C. För djupt snitt i St. Flik och St förenade utanför Sc i övre sidan. I nedre sidan förening mellan St och Sc på sent stadium. Märk falska årsringen i Sc!
11. 14 m. C. Isolerade kambier i mellanvävnad. Kambieförening i övre sidan förmedlad av bladspår i Sc.
12. 14 m. C. Sc med två-årsved. Inga nya skott första året, vid fixeringstillfället en brytande knopp. Trots tämligen god kambiesammanpassning klen sammanväxning.
13. 18 m. C. Ymp utan nya skott. Första året mycket liten, andra året god förening mellan ledande vävnader.

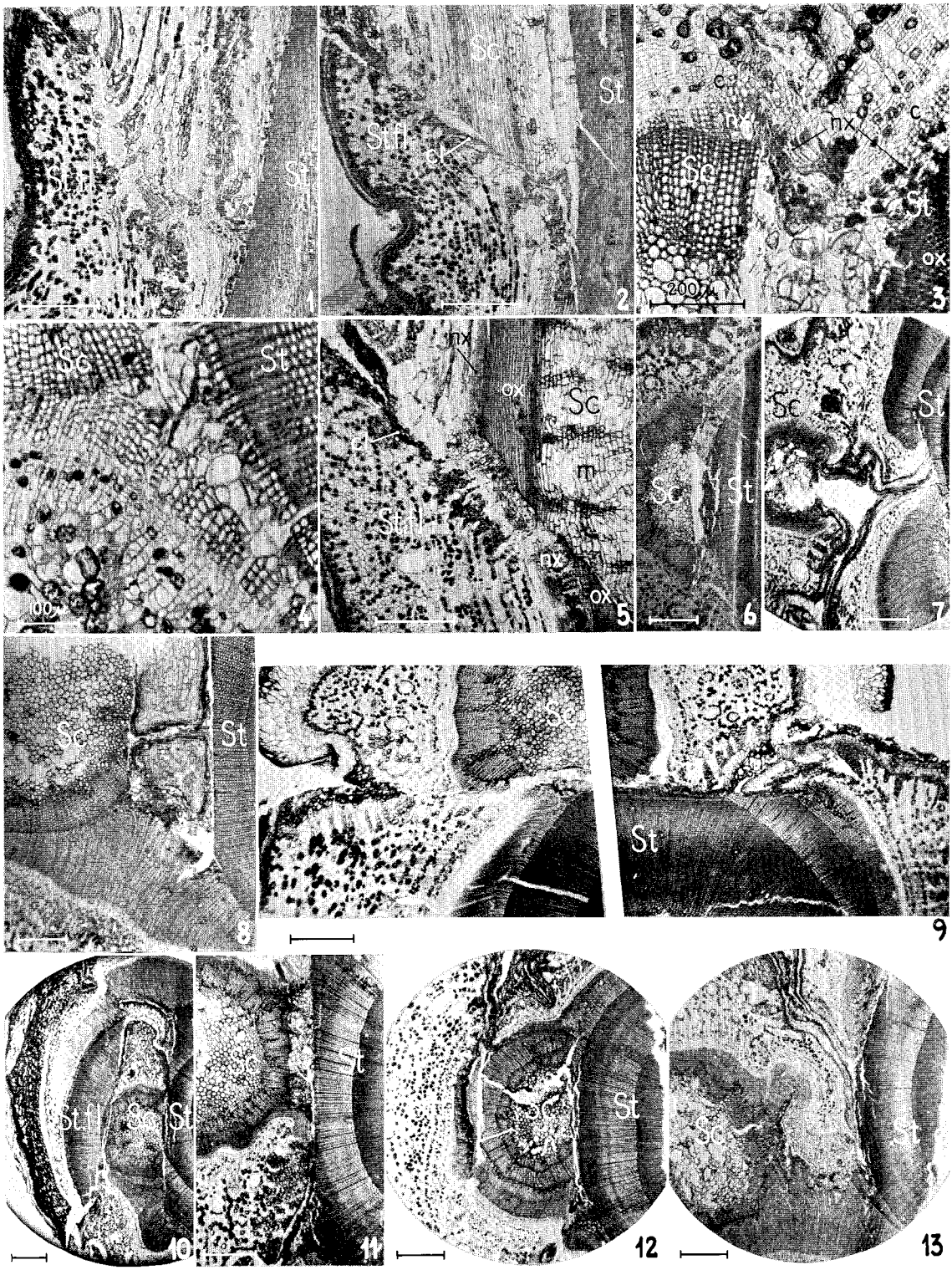

St
Sc
nx
ox
c
200μ
100μ
1
2
3
4
5
6
7
8
9
10
11
12
13

Plate XVI. Norway spruce.

1—8. Veneer graft. Unions produced by leaf traces.

1—6. 14 m. C. Series of sections with a "moving leaf trace". Growth of second year just started. Distance between 1 and 6 about 1.5 mm. 1: Leaf trace in Sc cortex; no union. 2: 18 sections above 1; parenchyma union. 3: 18 sections still higher up; leaf trace situated halfway between cambia of Sc and St. 4: 15 sections above 3. Leaf trace moved towards St cambium. 5 and 6: 6 and 13 sections above 4 respectively: leaf trace being incorporated with stele of St. *Cf.* Fig. 33.

7. 10 d. C. Early parenchyma union influenced by leaf trace in Sc. Arrows mark boundary between St and Sc.

8. 14 m. Vascular union established from leaf trace in Sc.

9—12. Side slit graft.

9. 17 d. C. Parenchyma union at incision face, bark flap inactive.

10. 17 d. C. Good parenchyma union at incision face. Callus formation influenced by leaf trace in Sc.

11. 28 d. C. Parenchyma union at incision face and at flap.

12. 35 d. C. Sometimes large callus masses are formed from the bark flap.

Plansch XVI. Gran.

1—8. Läggymp. Sammanväxningar förmedlade av bladspår.

1—6. 14 m. C. Snittserie med »vandrande bladspår». Andra årets tillväxt just påbörjad. Avstånd mellan 1 och 6 c a 1.5 mm. 1: Bladspår i Sc kortex. Ingen sammanväxning. 2: 18 snitt över föregående. Parenkymförening. 3: Ytterligare 18 snitt högre. Bladspåret mitt emellan Sc- och St-kambierna. 4: 15 snitt över föregående. Bladspåret dras mot St-kambiet. 5 och 6: 6 respektive 13 snitt ovanför 4. Bladspåret införlivas med stelen hos St. Jfr fig. 33!

7. 10 d. C. Tidig parenkymförening under inflytande från bladspår i Sc. Pilar markerar gränsen mellan St och Sc.

8. 14 m. C. Ledande förbindelse förmedlad av bladspår i Sc.

9—12. Sidsticksymp.

9. 17 d. C. Parenkymförening vid inskärningsytan. Barkfliken helt passiv.

10. 17 d. C. God parenkymförening vid inskärningsytan. Kallusbildningen influerad av bladspår i Sc.

11. 28 d. C. Parenkymförening vid både inskärningsyta och flik.

12. 35 d. C. Riklig kallusbildning från fliken kan förekomma.