WOUND HEALING IN HIGHER PLANTS

ROBERT BLOCH
Yale University

INTRODUCTION

In higher plants, wound tissues formed over artificial or naturally developing injuries are of common occurrence, and their formation has long been described. They usually consist of comparatively simple structures which have attracted the interest of workers in both theoretical and practical botany (108, 168).

The writer feels that in a review discussing the problem of wound healing much emphasis should be laid on those processes which take place in cells and tissues in the immediate neighborhood of the wound, *i.e.*, on the physiological and structural changes which precede and follow the beginning of meristematic activity, including both the phases of degeneration and tissue reorganization. Here the first physical and chemical effects of tissue interruption may be studied, *e.g.*, the degeneration and necrosis of cells, the formative effect of these processes on adjacent healthy cells, and the influence of other external and internal factors on meristem formation and wall differentiation.

Besides superficial formation of scar tissues, more general reactions of a compensating or regenerating character occur, when deep injuries or the removal of embryonic regions interrupt or affect essential tissue and organ communications, or isolate part of the organism. These processes, though related to the problems of wound healing and of great theoretical and practical interest, cannot be discussed at length in this article, particularly as valuable information has become available in recent reviews on tissue and organ cultures, regeneration and vegetative propagation (188, 47, 104, 173).

The majority of mature, vacuolate plant cells, without being separated from the mother organism, are capable of rejuvenation, *i.e.*, they can be induced to divide and to resume growth, though to different degrees in various cell types, and also depending on the location within the plant. Information is thus obtained as regards the potential character of cells, cell layers and tissues at successive stages of development and in relation to each other. In this sense, experimentally induced wound healing may be justly called a study of cellular reactivity or competence in relation to plant organization, and it would appear that such studies should be of considerable advantage in our attempt to gain an understanding of the developmental basis of plant structure.

Under comparable conditions of growth, one and the same plant type usually exhibits some uniformity of reaction, but considerable differences occur between various plant types. Of particular interest are certain tissue changes resembling wound reactions which occur in apparently intact organs. Examples of these are the early stages of normal cork formation and certain intumescences.

Well known types of wound healing are the following examples: (1) In the terminal growing regions of shoot and root, the outermost, completely undifferentiated parts of the indeterminate meristems may reproduce parts lost by injury completely and more or less directly from cells abutting on the cut surface. (2) Further distant from the apex the responses become more complicated. Wound repair here is often effected by "secondary" meristems, *e.g.,* through a cork phellogen or through cambia and calluses from primary or secondary tissues. Original differentiation is influenced in various ways by both inner and outer conditions, and may become inhibited as well as accelerated. (3) In plants or organs of low reactivity or in maturated zones, cells of the ground tissue may not divide at all. It has been found, however, that in many cases redifferentiation, such as specialized thickening and chemical changes in the wall, may still be induced, and the tissue pattern near the injury may thus become partly restored.

The formation of the meristem is usually accompanied by some degree of differentiation, especially in the wall. More frequently specific cell and tissue types are produced. This adaptation of differentiating or mature tissues to the new conditions created by the injury in a fashion of controlled rejuvenation and redifferentiation is a characteristic feature of wound healing and cellular behavior in higher plants. This behavior would seem to explain why generally in plants cell and tissue forms of reparation tissues do not differ much from those found normally; they are as variable in degree and quality as the mother structures on which they arise, giving evidence of the developmental potencies of these at the time when the injury occurred.

Experimentally induced wound healing is a valuable tool in the analysis of the cytological, histological, and physiological sides of tissue development and the causes and mechanics of cell division and differentiation. By this method it is possible to reproduce, under controlled conditions, tissue structures within limited areas, and to investigate cell division and growth conveniently in large, more or less vacuolate cells. Though only in its beginning, this method has already yielded tangible results and thrown light on fundamental processes, such as the changes which precede the rejuvenation of cells, the mechanism and plane of nuclear and cell division, and the problem of subsequent controlled redifferentiation.

ORGAN STRUCTURE AND WOUND RESPONSE

Stems

Following Mohl's (130) early and exact description of periderm formation in natural and artificial wounds, numerous attempts have been made to describe and analyze the sequence of anatomical and physiological changes after wounding. Storage organs, such as potato tubers and kohlrabi stems, are suitable material for the study of the wide variety of phenomena connected with phellogen formation and structural regeneration. Here the processes during the formation of the temporary barrier of collapsing and suberizing cells, the metabolic changes during subsequent meristem formation, and the influence of lepto- and wound hormones have been extensively studied. External conditions (humidity, light, temperature, access of oxygen) influenced the traumatic response both qualitatively and quantitatively, as was also evident from various wound treatments which affected transpiration or facilitated or reduced the exchange of gases.

It is now generally agreed that certain metabolic changes in the cells abutting on the cut surface (enzyme activation, increase in the rate of cytoplasmic streaming, transformation of carbohydrates and nitrogenous substances, and changes in acidity) are accompanied by increased oxygen absorption and carbon dioxide production, and that access of oxygen is essential in this process.

Furthermore, changes of a necrobiotic type usually occur in a number of cells which have suffered irreversible changes in permeability, coagulation of protoplasm, and infiltration of the intercellular spaces with sap. Cells in such regions may subsequently degenerate and die, and their contents and membranes may undergo further postmortal changes which probably affect the metabolism of adjacent healthy cells.

It has been found that satisfactory suberization and wound cork formation in the potato proceed best under relatively high humidity and temperature conditions (4, 196, 187); exposure of wounded parts also would appear to facilitate the exchange of gases and respiration (87).

Heat production in wounded parts of plants has been reported; in potato such an inflammatory condition reaches its maximum soon after wounding, decreasing with the distance from the injury, and reaching the norm again after about two days (43).

Excessive humidity creates a hyperhydric condition in plant cells, promoting cell proliferation but reducing cell division and differentiation. Periderm formation in submerged dicotyledonous plants, however, is possible (151).

Haberlandt used the technique of washing the injured surfaces which results in reduced cell division and metabolic activity in cells adjacent to the layer of crushed and degenerative cells. The interpretation of this effect, however, is contradictory. Lutman (122) emphasized that washing may remove the wound substances from the surface as well as other essential substances contained within the cells; but one important result was greatly reduced wound respiration. Steward, Wright and Berry (170) studied this effect in potato discs placed in air or water, or placed in air after preliminary washing; they found the amount of respiration related to the number of air spaces infiltrated with water. If all air spaces are filled, only little oxygen has access to the tissue. It appears that the result of an infiltration with tissue sap instead of water is rather different, for we know that in this case numerous cell divisions occur. This is in agreement with Ruhland and Ramshorn's findings (153), who reported that the application of tissue sap increased respiration greatly; they attributed this phenomenon to the presence in the juice of wound hormones or growth factors which regulate respiration.

It is natural that during progressive suberization and periderm formation the entry of oxygen should become considerably impeded. Thornton (175) found that oxygen regulates the dormancy of the potato in such a manner that during the progress of suberization the entry of oxygen into the tuber is actually retarded, while the sprouting of the buds is promoted.

Much early work was done on wound repair and regeneration in terminal growing points, but some more recent reports on wound healing of apices have been somewhat contradictory. Mirskaja (129) described a case of regeneration of the terminal stem meristem of *Tradescantia guianensis* which was comparable to the well known method of direct regeneration in wounded root tips. Linsbauer (119) and also Pilkington (143) reinvestigated these processes in herbaceous monocotyledons and dicotyledons, and confirmed the former author's earlier findings, that only a limited portion of the apex above and between the youngest leaf primordia is capable of reproducing the terminal meristem; generally new growing points are formed from parts of the original meristem which have remained intact.

Bloch (17) investigated cell reactivity in the primary stem tissues of a monocotyledon, *Tradescantia fluminensis*. All living vacuolate cells, including epidermis, collenchyma and sclerenchyma, were capable of returning to a meristematic condition and of forming storied cork, though to a lesser degree in the older internodes. Formation of calcium oxalate crystals, not in the form of normal monoclinic raphides, but as tetragonal trihydrate, was combined with the resumption of meristematic activity. Cells surrounding the internal vascular bundles, normally richer in cytoplasm than the adjacent parenchyma, differentiated into thick-walled lignified elements.

The wound tissues of woody stems are known for their extensive dimensions, the high degree of differentiation, and the frequent irregularity of elements produced. Both cambium and primary and secondary tissues take part in their formation. Methods of callus formation in grafts were reported by Sass (155) and Sharples and Gunnery (163); the former author found that in apple grafts the callus was derived from all the living tissues located outside the xylem, the cambium itself contributing very little; the latter authors described the method of callus formation in cleft grafts and stripped surfaces of *Hibiscus* and *Hevea;* here callus was formed mainly from the medullary rays. Mendel (126) studied callus and wound gum formation in *Citrus* grafts.

In practical tree surgery best results were obtained with vigorous specimens and when operations were carried out during spring or early summer (171, 124, 36). Wray (195) and also Paterson (141) investigated the structural changes which occur after pruning. The latter author, discussing the advantages of live-pruning in *Picea excelsa,* reported that live-pruned branches occluded more rapidly causing less distortion of the grain than dead-pruned ones.

A. B. Brown (28) studied cambial activity in relation to wounding in *Populus balsamifera;* the presence of living bark, developing buds and leaves distal to the wound had a promoting influence on local wound cambial activity. This responds to the stimulus of gravity in the same way as normal cambial activity, and the author infers that hormone action is here involved. Besides this, another local stimulating effect on cambial activity was exerted by dying cells of the cortex, where wound substances might be active.

Willison (191) reported fall spray injuries in peach trees that were due to treatment with 1:7 lime sulphur mixture, which prevented the periderm from developing over the leaf scars.

Poulter (144) investigated wound healing in alfalfa, white clover and red clover stems in relation to cutting and pasturing. In red clover the amount of dying pith cells is large and wound cork formation very slow, so that late autumn injuries do not properly heal.

Roots

Roots, both normal and air roots, particularly of monocotyledons, furnish excellent examples of different types of wound responses (14, 15, 16, 19). Generally there seems to exist a correlation between normal phellogen formation and the capacity to form wound cork. In extreme cases, however, neither is formed. In such a case the response to wounding may be simple suberization or metacuticularization of the ground parenchyma cells abutting on the wound (*Allium cepa*), or cell expansion and considerable structural redifferentiation may occur (air roots of orchids). In the cortex and axial strand even heavily impregnated cells may dedifferentiate (air roots of *Araceae* and orchids). A well developed endodermis, however, usually acts as a barrier preventing the wound stimulus from passing over to the axial strand. Deep cortex wounds accelerate the differentiation of endodermal cells and may promote activity in the pericycle, even when the cortex cells themselves are incapable of dividing (air roots of orchids).

Wounding of root tips of *Faba vulgaris, Lupinus* sp. and other plants has, according to Fourcroy (55, 56), an inhibiting effect on the differentiation of the elements determined to be the future first vessels, but it accelerates the development of the ontogenetically later elements which are not directly affected by the injury.

Taubenhaus and Ezekiel (174) described pathological enlargement and wounds in tap roots of cotton caused by acid soil (pH 2–4). Gore and Taubenhaus (65) studied the proliferation thus induced in cambium, phellogen and ray cells.

Cotyledons

Distribution and plane of cell division in cotyledons in relation to a wound surface and to the presence of vascular elements have been studied by various workers. Nakano (134), using cotyledons of *Vicia, Phaseolus, Pisum, Lupinus* and *Cucurbita,* assumed the combined action of an irritant diffusing from the wound surface (wound hormone) and a factor from the vascular bundle, probably the leptom (leptohormone). In this case the assumption was based particularly on the observation (also often reported in the older literature) that parenchyma cells situated between a vascular bundle and the wound face divide more vigorously. Badian (7), in a study of cotyledons of *Lupinus* and *Cucurbita,* confirmed these results; he also paid special attention to later phases of divisions at the cut ends of vascular bundles, whose plane is probably no longer determined by the traumatic stimulus.

In this connection it is of interest that cases have been reported in which an influence of the leptom on cell division appears unlikely, for instance, in the endosperm of *Ricinus* (134) and *Crinum asiaticum* (127).

Leaves

Woit (193) studied wound healing, cell reactivity and intumescence formation in tunnels of leaf miners in relation to leaf age; thin leaves of annuals tended to form callus, fleshy leaves and leaves of evergreens periderm. Most cell types were capable of renewed growth and division; the former was promoted when transpiration was reduced.

Wylie (197, 198) reported that the formation of a protective barrier consisting of collapsing dead cells generally preceded the formation of the meristem. In leaves of evergreens callus and wound cork formation proceeded much more slowly than in mesophytic leaves, but larger amounts were formed. In leaves of *Syringa vulgaris* (199), wounds were made which interrupted the major conductive channels; these injuries healed, but there was no formation of new vascular bridges as reported in other instances. Here the sap supply to the partly isolated portions of the blade was apparently transported through the few remaining small veins.

Jump (92) studied wound healing in leaves of *Ficus australis* and found that besides the formation of periderm, the mesophyll often proliferated into the gap, finally effecting a union of the wound surfaces.

Bloch (18, 19) investigated the histological and microchemical changes in the natural wounds of the stem-borne leaves of *Araucaria imbricata.* Longitudinal fissures appear in the 5–40-year-old leaves owing to radial expansion of the axis. A many-layered periderm, tyloses and wound gum are formed, and the membranes of lignified fibres adjacent to the wounds undergo postmortally a very gradual enzymatic breakdown.

Fritz (58) wounded the outer wall of epidermal cells of *Gasteria,* and observed that the outer layer rich in cutin became readily regenerated.

LaRue (111, 112, 113, 114) examined the structure and physiology of intumescences in leaves of poplar, *Eucalyptus, etc.* Most favorable for their development was a stagnant atmosphere with high humidity and somewhat lowered oxygen content; only occasionally was cell enlargement combined with cell division. Injection of extracts from intumescence-forming tissue, of indoleacetic acid, *etc.,* also induced intumescence formation. A comparison with cell proliferation from wounded surfaces in various stem and leaf types led to the conclusion that in various types of hypertrophic growth (galls, intumescences, tyloses, lenticel proliferation, "Perldrüsen," *etc.*) auxin besides other factors may be the immediate cause of cell enlargement.

Cunningham (40), studying histological changes in wounded or infected leaves, found that in cases of fungus necrosis in leaf spot diseases a cicatrice was not always formed, even if the plant responded with periderm formation to mechanical injury of the leaves.

Saran (154) investigated the increase in respiration which occurs in leaves of *Anacardium occidentale* soon after wounding. Young leaves (*e.g.*, 3, 8, 14 and 20 days old) respired normally at a higher rate than adult ones, but when wounded did not show an after effect. Older leaves (30, 40 and 100 days), on the other hand, showed a considerable increase in the respiratory rate after wounding, which passed off in about 2–4 hours. No histological details were given.

Audus (5) and Godwin (62) had previously shown that mechanical manipulation considerably increased the rate of respiration in cherry laurel leaves. A similar effect of mechanical stimulation was reported by Barker (9); slight mechanical pressure caused immediate increase in respiration of about 30% in shrivelled, soft-fleshed potatoes, and the rate did not return to normal for 10 days.

Hagemann (71) reviewed and investigated regeneration processes and location of root and shoot initials in a great number of leaf cuttings. The cause of the regenerative activities, according to the author, is to be sought rather in altered correlations due to isolation than in the wound stimulus or accumulation of food.

Schwarz (161) studied the structural changes in leaf cuttings, paying some attention to the problem of "directed" divisions. In petioles of *Coleus*, the plane of the wound surface or a center of necrosis does not determine the plane of divisions of cells situated between two vascular bundles, which is a continuation of the division plane of the fascicular cambium.

Fruits

Comparatively few reports on histological changes in wounded fruits are found in the older literature, although these fast and vigorously developing organs promise to be favorable material for such studies. A good deal of differentiation takes place during a relatively brief period, and great diversity of structures occurs. Of interest is the comparison of wound responses in the ovary, after fertilization, and in nearly mature fruits.

Küster (107) found long ago that the cells of the inner surface of the immature pericarp of Leguminosae (*e.g.*, *Pisum, Vicia, Lupinus, Lathyrus, Cytisus*) are very reactive. If the pods are opened and the inner parenchyma is exposed under moist conditions, the cells proliferate abundantly. In young pods masses of tissue develop and numerous cell divisions occur when a connection is made with the outside air by pricking.

Garms (61) investigated a great variety of fruit types (dry and fleshy, dehiscent and non-dehiscent, types with stony or parenchymatous endocarp), studying mainly the healing processes in the fruit wall. Wound cork or callus were readily formed in both ovules and fruits. The most vigorous response generally took place when injury occurred after fertilization, that is, after the beginning of vigorous growth. Dicotyledons formed typical phellogen, while monocotyledonous fruits showed the modified type of storied cork. Meristematic activity was most vigorous near the moist interior of the fruits; the tissue formed here was in the form of callus, while periderm was formed in the more exposed outer regions. Some time before maturity was reached the cells lost the capability to divide, though a certain variability existed, depending on the fruit type. The elements of the epidermis were usually the first to lose the ability to divide.

Ulrich (178), in an extensive and valuable paper, reported similar results. Callus was formed best in fruits during rapid growth; too young fruits dropped after injury, too old ones decayed. In fruits of *Hedera helix* (179), confinement at high temperature, stagnant atmosphere, or the presence of certain gases in the air had a similar effect. Generally, presence of water vapor reduced cell division, suberization and lignification. The reactions were analogous to those known in leaves, stems, roots, *etc.*, in both physiological and histological respects. Abundant phelloderm was formed.

Spitzer (169) reported that the browning of the cut surface in apple and other fruits was due to the reaction of a chromogen and a specific enzyme.

Beth (12) investigated the effect of wounding on formation of adventitious embryos in ovaries and could not confirm Haberlandt's results in *Oenothera* where such embryos were formed after injury.

Nutman (137), however, studying changes in the developing embryo of rye, reported that the growth of the embryo sac is associated with a series of degenerative changes, and assumed that hormonal substances are liberated from the degenerative tissues. He suggested that lack of such substances may explain the arrested development of excised embryos of *Zizania aquatica* (115).

THE INDUCTION OF MERISTEMATIC ACTIVITY

Dedifferentiation

The following sections review briefly results of recent experimental work concerning the various phases and phenomena of wound tissue formation as affected by different factors.

The return of mature cells to a more or less undifferentiated, meristematic condition occurs not infrequently during normal development. The process is usually accompanied by cell division and growth, and plays an important rôle in secondary meristematic activities, as in phellogen formation, anomalous thickening growth of stems, and in regeneration. Dissolution of endosperm membranes, of inner layers of gelatinous wood fibers, and of stone cells during the ripening of certain fruits (3) are other instances.

Dedifferentiation in these cases appears of a more or less normal and spontaneous nature, and in some of the instances mentioned the cells remain alive. The term, however, has also been applied to a different category of processes, also frequently met with in wound healing, when membranes and other remainders of dead cells become dissolved by the surrounding tissue. This occurs, for example, in calluses and grafts (105, 176, 59, 104), or when during vascular development in shoots and roots the first formed vessels become resorbed (35, 41). The breakdown of cell membranes may also be caused by typical necrobiotic processes (gummosis); sometimes this process is very slow (19).

That dedifferentiation may be readily induced in most mature plant cells by wounding is not only in itself a remarkable feature, but has stimulated a considerable amount of research in the hope that under such conditions the phenomena of cell rejuvenation, cell division and growth, may be analyzed and explained.

Striking examples of induced dedifferentiation in wound tissues are the cases in which specialized cells, often thick-walled or lignified, lose their impregnation and become thin-walled and embryonic, giving rise to daughter cells which often undergo a development distinctly different from their own.

Early statements that lignified cells can neither divide again (182) nor grow (156) can therefore hardly be maintained. Numerour reports by Trécul (177), Crüger (39), Schenk (157), Schilling (159) and others indicated that the contrary could often be observed in wound healing and related activities. In lignified vessels, sclerenchyma, and endodermal cells of various monocotyledons, wounding seems rather frequently to induce dedifferentiation (14, 16). It would thus appear that in higher plants somatic cells preserve to a considerable degree developmental potencies which become realized when the cells are freed of their original correlations. The extent and the limitations of such dedifferentiation in plant cells are of great theoretical interest, although hardly systematically investigated.

Necrotic Changes and Wound Hormones

The traumatic stimulus produces, either directly or indirectly, a chain of rather heterogenous phenomena, at the beginning of which stand a number of conspicuous tissue changes near the wound surface, indicating the resumption or the stimulation of metabolic activity, but also some processes of a definite necrobiotic character. Cell expansion and cell division follow, though not necessarily together, and finally the complex of embryonic tissue once again differentiates in various ways, undergoing a process of physiological readaptation and chemical changes, of which structural redifferentiation is one visible expression. It appears obvious that interruption of tissue continuity by mechanical injury must set into motion numerous abnormal physical and chemical processes in the cells. As long as these are not sufficiently known any speculation regarding the true nature of the traumatic stimulus seems premature.

The various phases of necrotic and necrobiotic changes in the cells abutting on the wound surface are, however, of particular interest, for these processes play probably an important, though perhaps indirect, rôle in the induction of dedifferentiation and meristematic activity in the adjacent tissue. A variety of physical and physicochemical changes have been described here as early effects of injury, for example, changes in electrical potentials (106), vacuole contraction, increase in permeability and viscosity, and mechanical coagulation of the protoplasm (33, 109, 94, 104, 116, 162).

The outermost cells of the exposed tissue often atrophy and dry up quickly, but the cells and intercellular spaces beneath become infiltrated with necrobiotic products from the degenerating protoplasts, with tannin, suberin, enzymes and other substances; these products may become transported by means of vascular ducts to considerable distance into the healthy tissue, where secondary centers of meristematic activity are formed. The infiltration of air spaces is common, though Woodhead (194) takes exception to this observation. Decomposition products, wound gum and phlobaphenes, also alter permeability and the chemical character of the membranes; oxygen and water have an effect on these necrobiotic changes (19).

Externally the necrotic zone shows a brownish or brownish-red discoloration; microchemically often a positive reaction is given with phloroglucin and hydrochloric acid, owing to the presence of varying amounts of certain aldehydes, whose relationship to lignin, however, is not definite. On the other hand, tannin and phlobaphenes often mask an original lignin reaction, and such cases have been erroneously described as delignification. These processes were investigated, for instance, in air roots of *Phoenix*, leaves of *Araucaria imbricata* (19), and in *Cereus* (160). Molisch described the formation of a red pigment from a chromogen in wound surfaces of Cactaceae (132).

Similar condensation and oxidation processes probably take place in the heartwood of trees; here Goodwin and Goddard (64) reported a low basal rate of oxygen consumption.

Dufrénoy (42) studied the relation of cellular immunity to the presence of phenolic compounds formed in wound tissues; he found that in highly resistant varieties, especially of potato, fungus penetration was checked, owing to the rapid death of cells and accumulation of phenolic compounds in adjacent ones which proved highly toxic to the parasite (compare also 32).

Watkins and Watkins (183) described lesions in cotton roots produced with unheated or heated extracts from *Phymatotrichum omnivorum*. In the case of unheated tissue extract an enzyme seems to be responsible for the breakdown of the walls. The effect was somewhat checked by the endodermis, but meristematic activity was induced in the pericycle.

These pathological changes seem to have important bearing on the problem of wound hormones. Research in this field has been very active, particularly experimental work based on the presence, or on the results of extraction and introduction of more or less specific, degenerative or natural substances from tissues. For testing the effectiveness of plant extracts and other chemical compounds promoting cell division various tissue and organ types have been used. A considerable number of organic and inorganic compounds promoting meristematic activity were reported, and our knowledge of natural growth substances has been greatly enriched by the results of extensive research on tissue and organ cultures (188, 47).

Early observations on cell divisions in the neighborhood of dying or necrotic cells indicated a causal connection, probably a chemical influence (189, 125). Haberlandt and his students demonstrated such effects in a series of well known experiments with isolated cells and tissue pieces, in which the presence of nutrients alone was not sufficient to induce cell division. Haberlandt termed these unknown substances wound hormones, although he was careful to emphasize the complexity of the traumatic stimulus at various occasions (68). He also suggested that wound substances were active in normal periderm formation (70) and related processes. A similar influence on cell division seemed to be exerted by the leptom (leptohormones). Fitting also has repeatedly emphasized the probability of a "hormonal" effect on protoplasmic streaming and respiration in wounded cells (*e.g.*, 50, 51, 52, 53).

Injection methods were successfully employed by Reiche (145) and have been perfected since (compare 150). Reiche injected tissue sap and cell debris into plants, which induced cell division and growth wherever necrotic deposits were formed within the healthy tissue. Numerous attempts have since been made to determine the nature of the effective agents. Wehnelt (184) used the parenchymatous (unwounded) layer of cells which line the seed chamber of the immature *Phaseolus* pericarp, to test the effectiveness of various substances in inducing cell division and proliferation. A variety of organic and inorganic compounds, including filtered or heated tissue sap from *Phaseolus* leaves, chicken albumen, horse serum, haemoglobin, insulin, agar, neutral salts, *etc.*, gave positive results.

Petri (142) repeated Haberlandt's experiments with *Echeveria* and potato and concluded that the wound hormones might be oxidation products of substances normally present in the cells.

Wilhelm (190) injected various substances into the parenchymatous pith cavity of *Vicia faba*, studying the formation of chromogen in the callus tissue thus induced. Besides tissue sap, various substances of heterogeneous chemical nature, such as sugar solution or horse serum, were found to be effective; the author concluded that the cells were unspecifically irritated, and a division hormone was secondarily produced within the plant.

Mrkos (133) studied the effect of agar containing a filtrate of *Rhizopus* cultures on bud regeneration in *Taraxacum* roots and on the depth at which periderm was formed under wound surfaces of *Bryophyllum* leaves.

Orth (140) confirmed Wilhelm's results; effective were tissue sap of *Vicia faba* and *Begonia,* also technical progynon and auxin.

Jost (90), mainly using *Phaseolus* material and the method of Wehnelt, showed that several organic acids, salts and indoleacetic acid also promote cell division and proliferation.

Weissenböck and Stern (185) studied the effect of indoleacetic acid injections on cell enlargement in pith and cortical cells of the *Phaseolus* epicotyl.

Orsós (139) found that higher breakdown products of proteins, such as heat-coagulated Kohlrabi protein, Witte pepton, fibrin, and also tyrosin induced cell divisions in sterile cultures of kohlrabi tissue; this result seemed to indicate that similar compounds, probably tyrosin, may be the active component in the wound hormone and leptohormone.

Several attempts were made to extract, concentrate and purify active substances which were assumed to be the more or less specific activators of cell division. Umrath and Soltys (180) isolated a substance from Papilionaceae which induced cell division in the bean pericarp, probably in low concentration (1: 50,000). This substance was described as an oxyacid with high oxygen content; it clearly differs from the active substances prepared from fresh beans by Bonner, English and Haagen-Smit (22, 44, 23, 45, 46). The first of these substances, termed traumatin, was extracted and purified, and had the chemical composition $C_{11}H_{17}O_4N$; it was heat-stable, and induced cell proliferation in the bean pod in as low a concentration as 1: 100,000. In a later paper (45) the isolation of an active dibasic acid of the composition $C_{12}H_{20}O_4$, a crystalline substance, was reported. Synthetic "traumatic acid" was identical in physiological activity with the natural product (46). The authors indicated that this substance also induced periderm formation in washed discs of the potato tuber. In their test, which was quantitative, the authors used the height of the intumescence, and thus cell growth, rather than the number of cell divisions as a measure of the activity of the substances. The positive reactions obtained with other substances, such as those used by Jost, Wehnelt and others were explained as due to non-specific injurious effects on the cells, which liberated wound hormones in them; in such cases, however, the callus was less high than after treatment with traumatin.

Hammett and Chapman (72) emphasized that the true characteristics of a wound hormone are the ability to stimulate cell division and the fact of liberation by the trauma itself rather than by disintegration. The fact that a compound promotes only tissue growth is not considered to be sufficient proof that it is a wound hormone. The sulfhydryl group fulfills the requirements of a wound hormone best. The authors found that in root tips of beans there was a correlation between increase in cell number (here termed proliferation) and SH concentration, while there was a negative correlation between SH concentration and root growth by cell elongation. The SH reaction was intensified by wounding.

Various workers expressed the opinion that the growth substances of the bios-complex are the ones most likely to fall into the category of wound hormones affecting cell division (*e.g.,* 186). Perhaps these were the substances missing in Haberlandt's early experiments in which cells only grew but did not divide. Rippel (147, 148, 149) studied the occurrence of bios in various seeds and seedlings, and suggested that they were probably of importance in callus formation, though he made tests only with yeast cells. Laird and West (110) found that a drop of bios 2(*b*) placed on the parenchymatous lining of the bean pod induced vigorous cell divisions.

Loofbourow and collaborators (121) reported the production of "proliferation-promoting factors" ("intercellular wound hormones") which were released by yeast cells after mechanical injury. As in their former studies, when yeast cells were subjected to lethal ultraviolet or X-rays, to heteroauxin or CO_2, the substances stimulated growth, fermentation and respiration of yeast; they were probably not disintegration products of dead cells, since they were produced while most of the cells were still living.

Ruhland and Ramshorn (153) studied the stimulating effect of expressed tissue juice on wound respiration. Application of juice to wound surfaces (leaves of *Begonia,* hypocotyls of *Helianthus*) increased the CO_2 production 5–10 times and the O_2 consumption 2–5 times. Some bios fractions from yeast had similar effects. The authors suggest that such substances might become postmortally active in wounded cells, and that wound hormones might thus be instrumental in regulating wound respiration.

To summarize, it would appear that the results reported in the foregoing section are still contradictory and that the intracellular changes under the influence of the various substances, some of which might be wound hormones, are far from understood. Not only was the evidence obtained with very diverse plant material, but also often under unusual and unequal conditions. The immature bean pod tissue, which was used in the majority of cases, is a highly sensitive tissue of almost meristematic character; normally it is not exposed as in the experiments reported; if so, however, the cells, as in other Papilionaceae (107), readily proliferate and also multiply under changed relations of oxygen, water and probably temperature. It appears that some of the substances used in these tests have toxic effects, and easily destroy the cells; consequently little necrobiotic or meristematic activity follows. With substances assumed to be wound hormones the reaction was vigorous, but how these processes compare with those in tissue material in which after wounding extensive necrobiotic changes precede the occurrence of numerous cell divisions is open to question. Our knowledge of the physical and physico-chemical transmutations in injured and degenerating cells is still quite inadequate, and little is known about the character of natural substances and break-down products released into the adjoining healthy cells and how these may affect the complex mechanism of their metabolism and growth.

Cell Division

Cytokinesis. Some of the earliest visible effects of wounding are "traumatotactic" movements of nuclei and plastids toward the side of the cells facing the wound; furthermore, a considerable increase in the rate of cytoplasmic streaming. These processes are most conspicuous near the wound; after some time, though not always, redistribution of cytoplasm and nuclei may be noted (compare 57).

Nuclear changes which indicate the beginning of meristematic activity were studied by Birkholz (13), and especially by Heitz (76). This author expressed the opinion that the increase in nuclear growth is due to accumulation of sugar, and probably not to the action of wound substances.

Probably the increase in nuclear material goes hand in hand with that of the cytoplasm.

Fischer (48) reported that in leaves of *Peperomia* and *Bryophyllum* nuclear growth near the wound edge was due to swelling of the nucleus and increase in chromatic material. By supplying sugar the enlargement of the nucleus and the beginning of mitotic division could be promoted.

The mechanism of cell wall formation and nuclear division in the early stages of wound tissue activity corresponds with that often described for large, vacuolate cells by Treub, Strasburger, Bailey and others (compare 165, 37). In such cells in which the nucleus is small compared with the cell volume, the phragmoplast and the cell plate are extended across the lumen of the mother cell by means of kinoplasmic fibrils at the periphery of the phragmoplast, until contact is made with the lateral wall. In polar view the system appears as a "halo," and the fact that at telophase the daughter nuclei appear in one plane has often caused erroneous reports on multinucleate condition in wound tissues.

Less has been known about the behavior of the cytoplasm and its inclusions during division. Sinnott and Bloch (166) studied the polarization of the cell and cytoplasm by the wound in large, vacuolate, dividing cells in traumatic tissues of *Tradescantia, Kalanchoë, Bryophyllum, Coleus, Phaseolus, Petunia,* and *Cucurbita,* in both living and fixed material. They found that the plane and position in which the cells are to divide is determined and visible in the cytoplasm from early prophase. Very soon after the migration of the rounded and enlarged nucleus into the center of the cell, plasma strands may be seen which aggregate and radiate from the nucleus outward toward the walls of the mother cell in the plane of the future division. Such a cytoplasmic diaphragm, the phragmosome, was found to persist during the successive stages of mitosis. Later the developing kinoplasmic fibrils and the cell plate follow exactly the course of the phragmosome until the lateral wall is reached. It was shown by the authors that this method of division is not limited to wound tissues, but occurs in meristems of many plant types, where comparatively large and vacuolate cells divide, *i.e.,* where the amount of cytoplasm is small in relation to the size of the cell (as in pith cells in growing stem tips).

Heitz (76) reported that in dividing and regenerating cells of bryophytes, nucleus and plastids are mechanically drawn to the center of the cells as a result of the redistribution of the cytoplasm. Before the nucleus entered prophase the chloroplasts assumed positions at the two nuclear poles and multiplied. He made similar observations in traumatic tissues of *Peperomia* and *Bryophyllum.*

Plane of Cell Division. The early divisions of wound meristems are generally parallel to the surface of the wound, *i.e.*, they occur at an angle of approximately 90 degrees to the direction of possible diffusion or other gradients from the wound surface. It may be assumed, therefore, that in this phase of cell divisions the plane is determined by the shape and influence of the wound itself, in both the ordinary wound phellogen and the wound cork of the storied type. Another interesting phenomenon in this early phase is the fact that the new walls are very often laid down almost exactly opposite each other in adjacent cells. In this manner the new division walls form concentric sheaths through all the living cells which are capable of rejuvenation, thus separating the necrotic part of the tissue from the healthy portion; this arrangement is found not only beneath external surface wounds, but also around inner centers of necrosis, *e.g.*, around infiltrated air spaces, vascular ducts, bast fibers and other elements.

Besides the wound stimulus there are other factors which influence plane and location of cell division. (I) In the neighborhood of vascular bundles which have been cut, or which run parallel and near to the wound surface, as well as in other more or less meristematic cell layers, such as pericycle and cambium, the cells divide more actively and nearer to the wound face than in other parts (*e.g.*, 138, 69, 7): This led to the assumption of active substances, *e.g.*, leptohormones diffusing from the bundles, but other factors, such as water and food relations, have here also been suggested. (II) In later phases of wound tissue activity the rules of parallelity and opposite position are often definitely abandoned, and cell division may occur in various planes, often coinciding with formation of root and shoot primordia. Here the plane of division is often related to the shape and direction of growth of the new cells. Cells released from pressure beneath the surface of a wound expand only in a radial and vertical direction and divisions occur only at an angle of 90 degrees to the longitudinal axis of the cell (96). Badian (7) emphasized that considerably later, when the original effect of the found stimulus is no longer exerted, divisions also occur in other directions, in cells whose long axis is not necessarily vertical to the wound surface.

Still another type of directed divisions during the later phases of wound tissue development coincides with the formation of tracheid and phloem bridges. In wounded roots of *Taraxacum* (176), tracheids are thus formed from entire cortex cells or their segments. According to Simon (164), not only tracheids already present, but also meristems later to form tracheids have a directing and apparently stimulating influence on the formation of such tracheid connections. Kaan Albest (93) studied the direction of connecting strands of phloem and xylem in wounded stems of *Coleus, Impatiens, etc.* She concluded that the stimulation is probably exerted by sieve tubes and xylem vessels, respectively.

Cell Growth

The basic interrelationship between cell multiplication and cell growth typical for normal meristematic activity in plants may be considerably modified by external conditions during the various phases of wound tissue formation. Wound cork which shows comparatively little cell expansion may be considered to be in many surface tissues the usual form of activity after injury. Wound callus, on the other hand, is characterized by abundant growth and proliferation and comparatively little wall differentiation. It is often temporarily formed when under excessively humid conditions transpiration becomes reduced to a minimum, but temperature seems also to play a part. This type also occurs in deeply enclosed portions of the wound, or where the cut surfaces of an injury have remained in close contact.

The outer layers of the cork meristem often expand radially toward the surface, while the innermost cells may only divide. It does not appear impossible that the infiltration of intercellular spaces with sap somehow influences the growth activities of the cells in this area, in a manner perhaps analogous to the well known effect in growing tips of seedling roots where after irritation the intercellular spaces become infiltrated with liquid, and a marked inhibition of longitudinal growth follows and cell expansion takes place in the radial direction.

Between the various forms of cell proliferation, *e.g.*, callus, natural or induced tyloses, intumescences and other hyperhydric tissues, there is no sharp anatomical distinction. In their formation various factors have been found to be important, including availability of space, high water content of the air, temperature, variations in the oxygen and water relations (172), and chemical stimulation (107, 158, 167).

LaRue (111, 112, 113) investigated the conditions under which intumescences form, particularly the moisture relations, the influence of metabolic factors and the rôle of auxin. He gives a list of plants whose stems or leaves form intumescences (114) and found that the proliferating cell walls do not become thinned out and therefore actively grow.

A simple form of "inner intumescences" often discussed in the older literature are tyloses (compare 120). They are very common, and Meyen (128) included under this term not only the natural tyloses, which, for example, occlude the vessels in ageing organs, but all other cells which proliferate into any cavity. These are usually formed after experimental wounding, where they may be seen growing into vessels, obliterating air passages, necrotic parenchyma cells, *etc.* (39, 21, 67, 81, 26). They are often combined with cell divisions and show a close relationship to the formation of necrotic and decomposition products and "wound gum" (131, 14, 17, 19, 20, 27, 1, 2). Sometimes the anatomical evidence suggests that the growth of tyloses is proceeding under some chemotropical stimulus, for instance, in material figured by Reiche (145), where tylosis-shaped cells grow along and toward surfaces covered with cell debris and decomposition products. The manner of wall growth in tyloses is somewhat comparable to the type of "intrusive growth" of cells often observed in normal tissue readjustments (*e.g.*, 135, 165).

Cell and Tissue Differentiation

The effects of wounding on differentiation are many-fold and vary considerably with the age of the organ and the distance from the injury. In young organs differentiation taking place near the injury at the time of wounding may become arrested or diverted (*e.g.*, 55, 56, 193), while an accelerating effect of the wound on metabolic activity and on structural differentiation is almost invariably seen in layers further distant from the wound beyond the zone of cells made to divide more or less actively. In older organs the effects of wounding are naturally somewhat modified and, as mentioned before, increased differentiation may be the only wound response.

The differentiation processes in the wound meristem proper take many forms. If wound periderm is formed, differences specific for the plant type occur with regard to the sequence and manner of cell division (*e.g.,* unequal divisions; storied cork; phellogen). Cell division is followed by various types of wall differentiation, especially in plants whose normal cork has these qualities.

In extensive tissue regeneration redifferentiation may be very complex. Thus Vöchting (181) has shown that the pith of the kohlrabi tuber is capable of regenerating completely the primary tissue arrangement of the tuber with all its specific elements; even a new epidermis with stomata becomes differentiated beneath the first formed phellogen.

Finally a considerable number of cases have become known in which structural redifferentiation and restoration of anatomical features is less complicated. These cases have in common the fact that in the neighborhood of the wound the cells resume development under the accelerating influence of the wound stimulus, and they later age like normal surface tissues by thickening of the membranes and by impregnation with suberin and lignin, usually in a manner characteristic for the particular plant. This has the striking result that to a greater or lesser extent the primary tissue pattern becomes restored. In some plant types all layers of the tissue do not react in the same manner; certain layers of the meristem or of the ground tissue actually exhibit a specific reactivity in this process.

Noteworthy examples of such behavior are: petioles and stems of ferns (80, 82, 83); leaves of orchids (25, 193); air roots and stems of monocotyledons (14, 16, 17, 19); fruits (61, 178); cork of Cactaceae (130, 136, 38, 77); roots of *Chelone* (123); stem of *Kleinia* (194); submerged monocotyledons (151). In wound callus and phelloderm of fruits the differentiation processes are still quite varied (61): wall thickening and impregnation, formation of specific forms of sclereids, crystal cells, tracheids, secretory ducts. With increasing age here the wound periderm becomes histologically and microchemically more and more similar to normal surface tissue; its contents, such as chlorophyll, starch, tannin, crystals, anthocyanin and fat, undergo changes similar to those in unwounded parts.

In air roots of *Philodendron Glaziovii* (14) the wound meristem derives from older cortical cells, and in their division products the redifferentiation of pitted, thick-walled, subepidermal sclereids occurs, which link up with the original sclerenchyma sheath present at the wound edge. These cells may make their appearance in the wound meristem of young roots at a time at which the original sheath at the other sides of the root has not yet appeared. Similarly in wounded air roots of *Phoenix reclinata* (19) cells within the wound tissue develop U-shaped thickenings, and these cells link up with the original superficial sclerenchyma. In the wound surfaces microchemical changes also are similar to those normally taking place. Similar behavior has been observed in roots of *Iris,* and stems and roots of *Tradescantia fluminensis.* Air roots of orchids do not form wound cork at all, but if the wounds penetrate through the exodermis as far as the living cortex, the already mature cortex cells thicken and lignify in the same manner as normal exodermis cells (16). In the instances just described cells originally destined for a different function seem to have undergone a true process of redifferentiation. There seems little doubt that the factors which bring about such structural redifferentiation must be related to those which are instrumental in normal development. The exact nature and control of this complicated mechanism are not known. In wound tissues the restoration of anatomical features near the surface appears to be linked up with oxygen and water relations which determine the fate of the dedifferentiated meristematic cells. Under favorable conditions there seems to exist some similarity with normally developing organs, and condensation and oxidation processes within the cells result in microchemical changes making them very similar to normal structures.

In layers such as bundle sheaths, pericycle, endodermis, *etc.,* differentiation is particularly likely to become accelerated by wounding. Thus in *Tradescantia fluminensis* the internal bundle sheaths which are normally thin-walled sclerify after wounding (17); this character is normally present in other members of the Commelinaceae. Other examples of characters not normally apparent but induced by wounding are the traumatic resin ducts of certain Abietineae (*Tsuga, Sequoia*). These are regarded by Jeffrey (86) and his school (see also 8) as reversions to an ancestral condition normally present in other members of the family.

GROWTH SUBSTANCES AND WOUNDING

Recent reports on work with natural and synthetic growth substances have often referred to histological changes comparable to wound structures. Some results obtained with growth substances (*e.g.,* auxin and indoleacetic acid) in inducing cell division and growth in parenchymatous tissue of *Phaseolus* and *Vicia* have been considered under the heading of wound hormones. But high concentrations of growth substances or growth substance mixtures (79) have been very generally applied in lanolin to decapitated and other wound surfaces, in which case vigorous reactions resulted due to the combined action of tissue interruption and chemical irritation. In a number of cases the effects of the growth substances were noticed at a considerable distance from the point of application, but the formation of the wound meristem did not seem to be influenced. In other instances natural meristematic activities, such as the formation of abscission layers, became even inhibited (60). In the majority of cases, however, the changes which were due to the treatment by the chemicals overshadowed the original wound reactions in the region of the injury, inducing especially vigorous cell division and growth in those cells which were normally very active in processes of wound healing and regeneration. It appears, therefore, that the stimulus provided by the growth substances may be substituted for other stimuli which exert comparable effects. The qualitative character of the histological changes is thus determined by the inherent formative organization of the plant rather than by specific properties of the chemical agents. Several workers have emphasized, from similar considerations, the non-specificity and the irritant character of many growth substances (90, 54, 6, 20, 78, 173).

Studies of histological changes similar to wound responses following growth substance treatment of wounds are contained in the following papers. Monocotyledons: *Lilium* (10, 11), *Tradescantia fluminensis* (20); Dicotyledons: *Iresine* (75), *Phaseolus* and tomato (118), tomato (24), *Phaseolus* (103), *Brassica* (84, 63).

The formation of vigorous callus growth of crown gall-like character was induced by high concentrations of growth substances in *Phaseolus* (102, 30, 31, 74) and in *Mirabilis* (73).

According to Jakeš and Hexnerová (85), callusing of ringing wounds in fruit trees can be improved by applying 1% indoleacetic acid or "Belvitan" paste to the surface of the exposed wood.

The rôle of polarity in wound callus, root and shoot formation of woody cuttings treated with growth substances was investigated by Rogenhofer (152), Fischnich (49) and Zimmerman and Hitchcock (200).

Brown and Carmack (29) also studied cambial activity in relation to a wound and to indoleacetic acid treatment.

Jost (91) reported on vessel development in decapitated epicotyls of *Phaseolus* treated with indoleacetic acid, and found that growth substances stimulated cambial activity only in general, the differentiation into vessels depending on other factors.

PLANT NEOPLASMS

The "tumorous" overgrowths obtained by prolonged or repeated treatment with growth substances often form a histological transition to related types of anomalous neoplastic growths induced by various chemical irritants or organisms, such as *Bacterium tumefaciens* (*e.g.*, 117). Besides certain systemic responses, this organism causes the formation of an unorganized type of gall; such pathological forms have often been compared with malignant neoplastic growths in animals. In the etiology of plant neoplasms, however, the significant factor is the continued presence of the irritant, the growth coming to an end when the causing agent ceases to be active; the analogy with an inflammatory tissue condition in animals is obvious. The early stages show striking resemblance to wound reactions (146); under prolonged irritation callus masses of unusual dimensions develop which, however, age and differentiate in various ways, often producing root and shoot primordia. The qualitative character of such forms also appears determined by the type of injury and the mode of growth of the particular plant type rather than by a specific action of the irritant or the inciting organism (95, 117).

Also the spontaneous, hereditary tumors of *Nicotiana* hybrids have close histological relationship to chemically induced overgrowths and to crown-gall, and often arise on wounds, whatever the genetic base of the malformations may be (98, 101).

The organizing and reconstructing tendency in plant tissues, which is characteristic of wound healing and plays a conspicuous rôle in anomalous overgrowths, finally finds still other methods of expression in the products of certain gall-inducing insects (compare 34). Here often normal cell forms and tissue arrangement become specifically modified and controlled to a remarkable extent under the influence of the inciting organism, but our knowledge as regards the interaction in this process of host and parasite is still very meager.

The occurrence of polyploid cells in tumors of hereditary, parasitic or chemical origin has been frequently reported. Comparatively few studies were made of related changes in wound and callus tissue.

Winkler's (192) method of obtaining polyploid shoots from somatic cells by wounding was successfully developed by Jørgensen (89) and has been employed since in horticultural practice.

Kostoff (97) suggested that polyploidy and other irregularities in cell division were due to factors which increase the cytoplasmic viscosity in the callus tissue.

Grafl (66) recently investigated ploidy in the tuber of *Sauromatum guttatum*. She found large 16-ploid nuclei beneath wound surfaces, and noted also dividing large nuclei which were tetra- or octoploid in the normal tissue. These facts suggest that multiplication of chromosomes during the resting stage is probably a general phenomenon of tissue differentiation in higher plants, and this may be demonstrated by wounding.

It is possible that in such cases the nuclear changes may be the result of progressive cell enlargement rather than the cause of it, and similar conditions might apply to cases of polyploidy observed in hypertrophic cells after treatment with indoleacetic acid, also in some galls and root nodules. Such nuclear changes would thus fall into a category somewhat different from the types of atypical growth in which chromosomal aberrations have been suggested as the primary cause of histological anomalies (*e.g.*, 99, 100, 88).

SUMMARY

The research reviewed in the foregoing paper deals with theoretical and practical aspects of wound healing in higher plants, *i.e.*, with the tissue changes which take place adjacent to cells and tissues damaged by various artificial and natural accidents.

Recent work has been particularly concerned with experimentally induced wound repair in different plant types, in so far as such studies are able to throw light on the problem of cellular reactivity and the physiological basis of plant structure.

The study of dedifferentiation, meristem formation and redifferentiation in vacuolate cells has also proved to be a helpful tool in the elucidation of the mechanics of cell division and differentiation.

The first part of this paper reviews more or less related, practical

and theoretical studies on wound healing in plants of different structure and reactivity under different conditions. The results in stems, root leaves, fruits, *etc.*, show that metabolic activities and the quality of the protective tissues formed are correlated with the mode of growth and the manner of distribution of meristematic and potentially meristematic zones and cell layers in the plant.

The age of the plant and seasonal variations affect wound healing. More especially the external conditions (light, temperature, gravity, access of oxygen and humidity), furthermore the internal environment (the presence of leptom elements and vascular ducts, water supply, food distribution, pH, enzymes and growth substances) influence the wound reaction both qualitatively and quantitatively.

In the second part of the paper the phenomena of meristematic activity, dedifferentiation, cell division and growth, and cell and tissue redifferentiation are considered in more detail. Reference is made to the morphogenetic problems involved in these various phases of wound tissue formation.

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. Another type of pathological dedifferentiation is the postmortal breakdown of cells and cell walls under the influence of enzymes from necrobiotic cells.

In spite of the progress made in the analysis of changes in cells abutting on the wound surface, the exact nature of the traumatic stimulus and of the physical and physico-chemical changes in wounded cells is still unknown. Of interest are the necrotic and necrobiotic processes in the surface layers of the wound, such as the infiltration of intercellular spaces with sap and decomposition products, which in their turn seem to affect respiration, cell growth and division in adjacent healthy cells. Water and oxygen seem to play a limiting rôle in these processes.

Recent research on wound hormones has shown that numerous organic and inorganic compounds, some of them occurring naturally in plants, are capable of influencing metabolic processes and inducing meristematic activity, if applied to the exposed surface of the seed cavity of the *Phaseolus* pericarp or to other tissues. Certain heat-stable preparations from tissue extracts were particularly effective.

Cell division is always parallel to the surface of the wound or internal centers 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.

Cell growth becomes more prominent in humid and stagnant atmosphere; it is also more pronounced in the outer zone of the wound meristem, whose intercellular spaces have become injected with liquid after wounding, and it is typical for internal meristematic activity, for example, tyloses.

In developing young organs differentiation may become inhibited in cells abutting on the injury, but it is usually promoted in cells further distant.

The cells of the wound meristem often redifferentiate in a manner characteristic for the particular plant, but the derivatives of dedifferentiated cells may redifferentiate in a fashion distinctly different from the parent cell. In older organs and certain plant types, differentiation, *e.g.*, thickening and impregnation of the wall, may be the only wound response. The process of differentiation and of restoration of anatomical features near the wound surface appears often to be largely a result of metabolic and microchemical changes, and of oxidation and condensation processes in the cells similar to those occurring under normal differentiation of the organ.

A part of the recent literature on growth substances has been concerned with anomalous tissue structures induced by the application of growth substances to wounds. These, as well as other plant tumors of chemical and bacterial origin, are discussed and reference is made to their developmental and histological relationship to wound structures. Recent reports on polyploidy in wound tissues are reviewed.

* * * *

DEFINITIONS

Differentiation: Appearance of differences in the physiological and morphological character of cells.

Dedifferentiation: Process by which mature or specialized cells lose their differentiated character and rejuvenate.

Redifferentiation: Physiological and structural differentiation of dedifferentiated cells.

Necrosis: Rapid, atrophic death of cells.
Necrobiosis: Gradual, degenerative death of cells, characterized by abnormal metabolic changes and postmortal activity of enzymes.
Phragmosome: Cytoplasmic diaphragm, formed early during division of vacuolate cells in the position of the future division wall.

Bibliography

1. Alexandrov, W. G., and Alexandrova, O. G. Ist die Verholzung ein reversibler oder irreversibler Vorgang? Planta **7**: 340–346. 1928.
2. ————, and ————. Über Thyllenbildung und Obliteration bei Spiralgefässen. Beitr. Biol. Pflanz. **17**: 393–403. 1929.
3. ————, and Djaparidze, L. I. Über das Entholzen und Verholzen der Zellhaut. Planta **4**: 467–475. 1927.
4. Artschwager, Ernst. Wound periderm formation in the potato as affected by temperature and humidity. Jour. Agr. Res. **35**: 995–1000. 1927.
5. Audus, L. J. Mechanical stimulation and respiration rate in the cherry laurel. New Phytol. **34**: 386–402. 1935.
6. Avery, G. S., Jr. La notion des phytohormones. Leurs rapports avec les stimulants et l'irritabilité des plantes. Études et recherches sur les phytohormones. Inst. Int. Coop. Intell. Soc. Nations. 49–54. 1938.
7. Badian, J. Ueber Zellteilungen in verwundeten Keimblättern. Acta Soc. Bot. Pol. **14**: 87–115. 1937.
8. Bannan, M. W. Seasonal wounding and resin-cyst production in the hemlock, *Tsuga canadensis* (L.) Carr. Ann. Bot. **48**: 857–868. 1934.
9. Barker, J. A note on the effect of handling on the respiration of potatoes. New Phytol. **34**: 407–408. 1935.
10. Beal, J. M. Bud development in *Lilium harrisii* following treatment with indoleacetic acid. Proc. Nat. Acad. Sci. **23**: 304–306. 1937.
11. ————. Histological responses of three species of *Lilium* to indoleacetic acid. Bot. Gaz. **99**: 881–911. 1938.
12. Beth, K. Untersuchungen über die Auslösung von Adventivembryonie durch Wundreiz. Planta **28**: 296–343. 1938.
13. Birkholz, E. Wundreiz und Kernveränderung. Protoplasma **13**: 282–321. 1931.
14. Bloch, R. Umdifferenzierungen an Wurzelgeweben nach Verwundung. Ber. Deut. Bot. Ges. **44**: 308–316. 1926.
15. ————. Zum Problem der Korkentstehung. Ber. Deut. Bot. Ges. **44**: 316–321. 1926.
16. ————. Observations on the relation of adventitious root formation to the structure of air-roots of orchids. Leeds Phil. Soc. Proc., Sci. Sec. Vol. 3, Part 2: 92–101. 1935.
17. ————. Wound healing in *Tradescantia fluminensis* Vell. Ann. Bot. **49**: 651–670. 1935.
18. ————. The natural wounds in the leaves of *Araucaria imbricata* Pavon. The Naturalist (North of England): 193–199. Sept. 1936.
19. ————. Wound healing and necrosis in air roots of *Phoenix reclinata* and leaves of *Araucaria imbricata*. Am. Jour. Bot. **24**: 279–287. 1937.
20. ————. Anatomical changes in *Tradescantia fluminensis* Vell. after treatment with growth substances. Boyce Thomp. Inst. Contr. **9**: 439–454. 1938.
21. Boehm, J. Über Function und Genesis der Zellen in den Gefässen des Holzes. Sitz. Ber. K. AK. Wiss. Wien, Abt. II. **55**: 851–866. 1867.

22. Bonner, J. and English, J., Jr. Purification of traumatin, a plant wound hormone. Science **86**: 352–353. 1937.
23. ———, and ———. A chemical and physiological study of traumatin, a plant wound hormone. Plant Physiol. **13**: 331–348. 1938.
24. Borthwick, H. A., Hamner, K. C., and Parker, M. W. Histological and microchemical studies of the reactions of tomato plants to indoleacetic acid. Bot. Gaz. **98**: 491–519. 1937.
25. von Bretfeld. Über Vernarbung und Blattfall. Jahrb. Wiss. Bot. **12**: 133–160. 1880.
26. Brieger, A. Untersuchungen über den Wundreiz. I. Ber. Deut. Bot. Ges. **42**: (79)-(90). 1924. II. Die Ätiologie der Thyllen. Ber. Deut. Bot. Ges. **43**: 443–449. 1925.
27. Brockhuizen, S. Wondreacties van hout. Het ont staan van thyllen en wondgom, in het bizonder in verband met iepenziekte. Diss. Utrecht. 1929.
28. Brown, A. B. Activity of the vascular cambium in relation to wounding in the balsam poplar, *Populus balsamifera* L. Canad. Jour. Res. **15**: 7–31. 1937.
29. ———, and Carmack, R. G. H. Stimulation of cambial activity, locally in the region of application and at a distance in relation to a wound by means of heteroauxin. Canad. Jour. Res. **15**: 433–441. 1937.
30. Brown, N. A., and Gardner, F. E. Galls produced by plant hormones, including a hormone extracted from *Bacterium tumefaciens*. Phytopath. **26**: 708–713. 1936.
31. ———, and ———. Indoleacetic acid galls of a secondary type. Phytopath. **27**: 1110–1113. 1937.
32. Brown, W. The physiology of host-parasite relations. Bot. Rev. **2**: 236–281. 1936.
33. Bünning, E. Untersuchungen über die Koagulation des Protoplasmas bei Wundreizen. Bot. Arch. **14**: 138–164. 1926.
34. Carter, W. Injuries to plants caused by insect toxins. Bot. Rev. **5**: 273–326. 1939.
35. Chauveaud, G. L'appareil conducteur des plantes vasculaires et les phases principales de son evolution. Ann. Sci. Nat. Bot. IX. **13**: 113–436. 1911.
36. Collins, J. F. Treatment and care of tree wounds. U. S. Dept. Agr. Farmers Bull. 1726. 1934.
37. Conard, A. Sur un nouveau mode de formation de la membrane dans les tissus cicatriciels d'une feuille. Bull. Classe Sci. Acad. Roy. Belgique V. **8**: 531–541. 1922.
38. Coutant, M. W. Wound periderm in certain cacti. Bull. Torr. Bot. Club **45**: 353–364. 1918.
39. Crüger, H. Einiges über Gewebeveränderungen bei der Fortpflanzung durch Stecklinge. Bot. Zeit. **18**: 369–374. 1860.
40. Cunningham, H. S. Histology of the lesions produced by *Sphaceloma Fawcettii* Jenkins on leaves of Citrus, and A study of the histological changes in leaves by certain leaf-spotting fungi. Phytopath. **18**: 539–545; 717–751. 1928.
41. Dauphiné, A. Recherches sur les variations de la structure des rhizomes. Ann. Sci. Nat. Bot. IX. **3**: 317–368. 1906.
42. Dufrénoy, J. Cellular immunity. Amer. Jour. Bot. 23: 70–79. 1936.
43. Eglits, M. Der Einfluss der Infektion auf die Temperatur und die Kohlensäureabgabe bei Kartoffeln. Phytopath. Ztschr. **5**: 343–379. 1932.
44. English, J., and Bonner, J. The wound hormones of plants. I. Traumatin, the active principle of the bean test. Jour. Biol. Chem. **121**: 791–799. 1937.

45. ———, ———, AND HAAGEN-SMIT, A. J. The wound hormones of plants. II. The isolation of a crystalline active substance. Proc. Nat. Acad. Sci. **25**: 323–329. 1939.
46. ———, ———, AND ———. Structure and synthesis of a plant wound hormone. Science **90**: 329. 1939 (see also Jour. Am. Chem. Soc. **61**: 3434–3436. 1939).
47. FIEDLER, H. Die pflanzliche Gewebe- und Organkultur. Ztschr. Bot. **33**: 369–416. 1938.
48. FISCHER, H. Grössenveränderungen von Kern und Nucleolus im Blattgewebe. Planta **22**: 767–793. 1934.
49. FISCHNICH, O. Weitere Versuche über die Bedeutung des Wuchsstoffes für die Adventivspross- und Wurzelbildung. Ber. Deut. Bot. Ges. **57**: 122–134. 1939.
50. FITTING, H. Untersuchungen über die Auslösung von Protoplasmaströmung. Jahrb. Wiss. Bot. **64**: 281–388. 1925.
51. ———. Untersuchungen über den Protoplasmaströmung auslösenden Reizstoff der Pflanzen. Naturwiss. **21**: 489–495. 1933.
52. ———. Über Auslösung von Protoplasmaströmung bei *Vallisneria* durch einige Histidinverbingungen. Jahrb. Wiss. Bot. **82**: 613–624. 1936.
53. ———. Beiträge zur Physiologie der Protoplasmaströmung in den Blättern von *Vallisneria spiralis*. Ber. Deut. Bot. Ges. **55**: 255–261. 1937.
54. ———. Die Hormone als physiologische Reizstoffe. Biol. Zentralblatt **56**: 69–86. 1936.
55. FOURCROY, M. Action indirecte des traumatismes sur l'évolution de l'appareil conducteur. Compt. Rend. Acad. Sci. **196**: 210–212. 1933.
56. ———. Reconstitution de la structure normale dans des racines traumatisées. Rév. Gén. Bot. **45**: 159–170. 1933.
57. FRANK, B. Über die Veränderung der Lage der Chlorophyllkörner in der Zelle und deren innere und äussere Ursachen. Jahrb. Wiss. Bot. **8**: 216–303. 1872.
58. FRITZ, F. Über die Kutikula von *Aloë* und *Gasteria*arten. Jahrb. Wiss. Bot. **81**: 718–746. 1935.
59. FUNK, R. Untersuchungen über heteroplastische Transplantationen bei Solanaceen und Cactaceen. Beitr. Biol. Pfl. **17**: 404–468. 1929.
60. GARDNER, F. E., MARTH, P. C., AND BATJER, L. P. Spraying with plant growth substances to prevent apple fruit dropping. Science **90**: 208–209. 1939.
61. GARMS, H. Untersuchungen über Wundheilung an Früchten. Beih. Bot. Centralbl. I. **51**: 437–516. 1933.
62. GODWIN, H. The effect of handling on the respiration of cherry laurel leaves. New Phytol. **34**: 403–406. 1935.
63. GOLDBERG, E. Histological responses of cabbage plants grown at different levels of nitrogen nutrition to indole-3-acetic acid. Bot. Gaz. **100**: 347–369. 1938.
64. GOODWIN, R. H., AND GODDARD, D. R. The oxygen consumption of isolated woody tissues. Amer. Jour. Bot. **27**: 234–237. 1940.
65. GORE, U. R., AND TAUBENHAUS, J. J. Anatomy of normal and acid injured cotton plants. Bot. Gaz. **92**: 436–441. 1931.
66. GRAFL, I. Kernwachstum durch Chromosomenvermehrung als regelmässiger Vorgang bei der pflanzlichen Gewebedifferenzierung. Chromosoma **1**: 265–275. 1939.
67. GÜRTLER, F. Über interzellulare Haarbildungen. Diss. Berlin. 1905.
68. HABERLANDT, G. Culturversuche mit isolierten Pflanzenzellen. Sitz. Ber. K. Akad. Wiss. Wien. Math.-nat. Classe. **111**. I: 69–91. 1902.
69. ———. Zur Physiologie der Zellteilung. Zweite Mitteilung. Sitz. Ber. K. Pr. Akad. Wiss. Phys.-math. Classe. **46**: 1096–1111. 1914.

70. ———. Zur Entwicklungsphysiologie des Periderms. Sitz. Ber. Pr. Akad. Wiss. Phys.-math. Klasse 317–338. 1928.
71. HAGEMANN, A. Untersuchungen an Blattstecklingen. Gartenbauwiss. **6**: 69–195. 1932.
72. HAMMETT, F. S. AND CHAPMAN, S. S. A correlation between sulfhydryl, mitosis, and cell growth in length in roots of *Phaseolus vulgaris*. Growth **2**: 297–302. 1938.
73. HAMNER, K. C. Histological responses of *Mirabilis jalapa* to indoleacetic acid. Bot. Gaz. **99**: 912–954. 1938.
74. ———, AND KRAUS, E. J. Histological reactions of bean plants to growth promoting substances. Bot. Gaz. **98**: 735–807. 1937.
75. HARRISON, B. F. Histological responses of *Iresine Lindenii* to indoleacetic acid. Bot. Gaz. **99**: 301–338. 1937.
76. HEITZ, E. Das Verhalten von Kern und Chloroplasten bei der Regeneration. Zeits. Zellf. **2**: 69–86. 1925.
77. HEMENWAY, A. F. An anatomical study of traumatic and other abnormal tissues in *Carnegiea gigantea*. Amer. Jour. Bot. **21**: 513–518. 1934.
78. HITCHCOCK, A. E. AND ZIMMERMAN, P. W. Unusual physiological responses induced on intact plants by capping with black cloth. Boyce Thompson Inst. Contr. **10**: 389–398. 1939.
79. ———, AND ———. Effects obtained with mixtures of root-inducing and other substances. Boyce Thompson Inst. Contr. **11**: 143–160. 1940.
80. HOLDEN, H. S. Some wound reactions in Filicinean petioles. Ann. Bot. **26**: 777–793. 1912.
81. ———. On the occurrence of cavity parenchyma and tyloses in ferns. Jour. Linn. Soc. Bot. **47**: 141–153. 1925.
82. ———. Observations on some wound reactions in the aerial stem of *Psilotum triquetrum*. Ann. Bot. **44**: 285–296. 1930.
83. ———. Some observations on the wound reactions of *Ankyropteris corrugata*. Jour. Linn. Soc. **48**: 643–655. 1931.
84. HOWARD, H. W. Possible action of phytohormones as root-determiners. Ann. Bot. **2**: 934–942. 1938.
85. JAKEŠ, E. AND HEXNEROVÁ, H. Über den Einfluss der Wuchsstoffe auf Wundgewebebildung bei Obstbäumen. Gartenbauwiss. **13**: 83–93. 1939.
86. JEFFREY, E. C. The comparative anatomy and phylogeny of the coniferales. Part I. The genus *Sequoia*. Mem. Boston Soc. Nat. Hist. **5**: 441–459. 1903.
87. JOHNSTONE, G. R. Effect of wounding on respiration and exchange of gases. Bot. Gaz. **79**: 339–340. 1925.
88. JONES, D. F. Nuclear changes affecting growth. Amer. Jour. Bot. **27**: 149–155. 1940.
89. JØRGENSEN, C. A. The experimental formation of heteroploid plants in the genus *Solanum*. Jour. Genet. **19**: 132–210. 1928.
90. JOST, L. Wuchsstoff und Zellteilung. Ber. Deut. Bot. Ges. **53**: 733–750. 1935.
91. ———. Zur Physiologie der Gefässbildung. Zeits. Bot. **35**: 114–150. 1940.
92. JUMP, J. A. Wound responses of *Ficus australis*. Bull. Torr. Bot. Club **63**: 477–481. 1936.
93. KAAN, ALBEST A. VON. Anatomische und physiologische Untersuchungen über die Entstehung von Siebröhrenverbindungen. Zeits. Bot. **27**: 1–94. 1934.
94. KEIL, R. Über systolische und diastolische Veränderungen der Vakuole in der Zelle höherer Pflanzen. Protoplasma **10**: 568–597. 1930.
95. KISSER, J. Über die Wirkungen carcinogener Substanzen bei Pflanzen. Ber. Deut. Bot. Ges. **57**: 506–515. 1939.

96. Kny, L. Über den Einfluss von Zug und Druck auf die Richtung in sich theilenden Pflanzenzellen. Ber. Deut. Bot. Ges. **14**: 378–391. 1896.
97. Kostoff, D. Protoplasmic viscosity in plants. II. Cytoplasmic viscosity in callus tissue. Protoplasma **11**: 184–189. 1930.
98. ———. Tumor problem in the light of researches on plant tumors and galls and its relation to the problem of mutation. Protoplasma **20**: 440–456. 1933.
99. ———. Abnormal mitosis in tobacco plants forming hereditary tumors. Nature **144**: 599. 1939.
100. ———. Studies on atypical growth in plants from a cytogenetic point of view. Jour. Genet. **39**: 469–484. 1940.
101. ———, and Kendall, J. Studies on plant tumors and polyploidy produced by bacteria and other agents. Arch. Mikrobiol. **4**: 487–508. 1933.
102. Kraus, E. J., Brown, N. A., and Hamner, K. C. Histological reactions of bean plants to indoleacetic acid. Bot. Gaz. **98**: 370–420. 1936.
103. ———, and Mitchell, J. W. Histological and physiological responses of bean plants to alpha naphthalene acetamide. Bot. Gaz. **101**: 204–225. 1939.
104. Krenke, N. P. Wundkompensation, Transplantation und Chimären bei Pflanzen. 1933.
105. Krieg, A. Beiträge zur Kenntnis der Kallus- und Wundholzbildung geringelter Zweige und deren histologische Veränderungen. Diss. Würzburg. 1908.
106. Kümmel, K. Elektrische Potentialdifferenzen an Pflanzen. Planta **9**: 564–630. 1930.
107. Küster, E. Histologische und experimentelle Untersuchungen über Intumeszenzen. Flora **96**: 526–537. 1906.
108. ———. Pathologische Pflanzenanatomie. 3. Aufl. 1925.
109. ———. Pathologie der Pflanzenzelle. I. Protopl. Monogr. 1929.
110. Laird, D. G., and West, P. M. The influence of bios on nodule bacteria and legumes. A. The influence of bios on legume seedlings. Canad. Jour. Res. **15**: 1–6. 1937.
111. LaRue, Carl D. Intumescences on poplar leaves. I. Structure and development. II. Physiological considerations. III. The rôle of plant hormones in their production. Amer. Jour. Bot. **20**: 1–17; 159–175. 1933. **23**: 520–524. 1936.
112. ———. Intumescences on leaves of *Eucalyptus cornuta, E. coccifera, Hieracium venosum, Mitchella repens,* and *Thurberia thespesioides.* Phytopath. **23**: 281–289. 1933.
113. ———. The part played by auxin in the formation of internal intumescences in the tunnels of leaf miners. Bul. Torr. Bot. Club **64**: 97–102. 1937.
114. ———. Cell outgrowths from wounded surfaces of plants in damp atmospheres. Papers Mich. Acad. Sci. **22**: 123–139. 1937.
115. ———, and Avery, G. S., Jr. The development of *Zizania aquatica* in seed and in artificial culture. Bull. Torr. Bot. Club **65**: 11–21. 1938.
116. Lepeschkin, W. W. Zell Nekrobiose und Protoplasmatod. Protopl. Monogr. 1937.
117. Levine, M. Plant responses to carcinogenic agents and growth substances; their relation to crown gall and cancer. Bull. Torr. Bot. Club **67**: 199–226. 1940.
118. Link, G. K. K., Wilcox, H. W., and Link, A. D. Responses of bean and tomato to *Phytomonas tumefaciens, P. tumefaciens* extracts, β-indoleacetic acid, and wounding. Bot. Gaz. **98**: 816–867. 1937.

119. LINSBAUER, K. Betrachtungen zum Problem der Sprossregeneration. Planta **9**: 334–338. 1929.
120. LOHSE, R. Entwurf einer Kritik der Thyllenfrage mit Ergebnissen eigener Versuche. Bot. Arch. **5**: 345–380. 1924.
121. LOOFBOUROW, J. R., COOK, E. S., DWYER, C. M., AND HART, M. J. Production of intercellular hormones by mechanical injury. Nature **144**: 553–554. 1939.
122. LUTMAN, B. F. Respiration of potato tubers after injury. Bull. Torr. Bot. Club **53**: 429–455. 1926.
123. MAGER, H. Die Endodermis als Grenze für Stoffwanderungen. Planta **19**: 534–546. 1933.
124. MARSHALL, R. P. The relation of season, of wounding and shellacking to callus formation in tree wounds. U. S. Dept. Agr. Tech. Bul. 246. 1931.
125. MASSART, J. La cicatrisation chez les végétaux. Mém. Cour. Acad. Roy. Sci. Belg. **57**: 2–68. 1898.
126. MENDEL, KURT. The anatomy and histology of the bud-union in *Citrus*. Palestine Jour. Bot. & Hort. Sci. **1**: 13–46. 1936.
127. MERRY, J. Formation of periderm in the endosperm of *Crinum asiaticum*. Papers Mich. Acad. Sci. **22**: 159–164. 1937.
128. MEYEN, F. Phytotomie. 1830.
129. MIRSKAJA, L. Über Regenerationsvorgänge an Vegetationspunkten von *Tradescantia guianensis*. Planta **8**: 27–35. 1929.
130. MOHL, H. VON. Über den Vernarbungsprozess bei der Pflanze. Bot. Zeit. **7**: 641–652. 1849.
131. MOLISCH, H. Zur Kenntniss der Thyllen, nebst Beobachtungen über Wundheilung in der Pflanze. Sitz. Ber. K. AK. Wiss. Wien. I. **97**: 264–299. 1888.
132. ————. Beiträge zur Mikrochemie der Pflanze. Nr. 17. Über ein bei den Kakteen vorkommendes, einen roten Farbstoff bildendes Chromogen. Ber. Deut. Bot. Ges. **46**: 205–211. 1928.
133. MRKOS, O. Über den Einfluss des Wuchsstoffes auf die Regeneration und Wundgewebebildung. Planta **21**: 206–210. 1933.
134. NAKANO, H. Untersuchungen über Kallusbildung und Wundheilung bei Keimpflanzen I. II. Ber. Deut. Bot. Ges. **42**: 261–267; 267–272. 1924.
135. NEEFF, F. Über Zellumlagerung. Zeits. Bot. **6**: 465–547. 1914.
136. NOMMENSEN, R. Beiträge zur Kenntnis der Anatomie der Cacteen, insbesondere ihres Hautgewebes. Diss. Kiel. 1910.
137. NUTMAN, P. S. Studies in vernalization of cereals. VI. The anatomical and cytological evidence for the formation of growth-promoting substances in the developing grain of rye. Ann. Bot. **3**: 731–757. 1939.
138. OLUFSEN, L. Untersuchungen über Wundperidermbildung an Kartoffelknollen. Beih. Bot. Centralbl. **15**: 269–308. 1903.
139. ORSÓS, O. Untersuchungen über die sogenannten Nekrohormone. Protoplasma **26**: 351–371. 1936.
140. ORTH, H. Die Wirkung des Follikelhormons auf die Entwicklung der Pflanze. Zeits. Bot. **27**: 565–607. 1934.
141. PATERSON, A. The occlusion of pruning wounds in Norway spruce (*Picea excelsa*). Ann. Bot. **2**: 681–698. 1938.
142. PETRI, L. Experienze sulla formazione del sughero delle ferrite. Boll. Staz. Patol. Veg. (Florence) **9**: 328–352. 1929.
143. PILKINGTON, M. The regeneration of the stem apex. New Phytol. **28**: 37–53. 1929.
144. POULTER, R. W. Problems of wound healing in red clover stems. Science **90**: 108–109. 1939.
145. REICHE, H. Über Auslösung von Zellteilungen durch Injektion von Gewebesäften und Zelltrümmern. Zeits. Bot. **16**: 241–278. 1924.

146. RIKER, A. J. Cytological studies of crown gall tissue. Amer. Jour. Bot. **14**: 25–37. 1927.
147. RIPPEL, K. Über Teilungs- und Streckungswuchsstoffe. Planta **26**: 164–166. 1937.
148. ———. Zur Frage der pflanzlichen Zellteilungs- und Zellstreckungshormone. Planta **26**: 812–815. 1937.
149. ———. Über den Gehalt von Zellteilungshormonen in Samen und Keimlingen von *Pirus malus, Prunus domestica* und *Prunus avium*. Planta **29**: 1–10. 1938.
150. ROACH, W. A. Plant injection as a physiological method. Ann. Bot. **3**: 155–226. 1939.
151. RODGER, E. A. Wound healing in submerged plants. Amer. Mid. Nat. **14**: 704–713. 1933.
152. ROGENHOFER, G. Wirkung von Wuchsstoffen auf die Kallusbildung bei Holzstecklingen I. II. Sitz. Ber. AK., Wiss. Wien. Math.-Nat. Kl. I. **145**: 81–99; 179–193. 1936.
153. RUHLAND, W., UND RAMSHORN, K. Zur Steuerung der Pflanzenatmung durch Hormone. Naturwiss. **27**: 391. 1939.
154. SARAN, A. B. Note on wounding of the leaves of *Anacardium occidentale* Linn. at different stages of their development and its effect on respiration. Jour. Indian Bot. Soc. **17**: 1–4. 1938.
155. SASS, J. E. Formation of callus knots on apple grafts as related to the histology of the graft union. Bot. Gaz. **94**: 364–380. 1932.
156. SCHELLENBERG, H. Beiträge zur Kenntnis der verholzten Membranen. Jahrb. Wiss. Bot. **29**: 237–266. 1896.
157. SCHENK, H. Beiträge zur Biologie und Anatomie der Lianen. 1892.
158. SCHILLING, E. Über hypertropische und hyperplastische Gewebewucherungen an Sprossachsen verursacht durch Parraffine. Jahrb. Wiss. Bot. **55**: 177–258. 1915.
159. ———. Ein Beitrag zur Physiologie der Verholzung und des Wundreizes. Jahrb. Wiss. Bot. **62**: 528–562. 1923.
160. SCHINDLER, H. Untersuchungen über eine an *Cereus grandiflorus* Mill. beobachtete Gewebenekrose. Ang. Bot. **19**: 505–508. 1937.
161. SCHWARZ, W. Die Strukturänderungen sprossloser Blattstecklinge und ihre Ursachen. Ein Beitrag zur Kausalanalyse der Gewebebildung. Jahrb. Wiss. Bot. **78**: 92–155. 1933.
162. SEIFRIZ, W. Pathological changes in protoplasm. Protoplasma **32**: 538–550. 1939.
163. SHARPLES, A., AND GUNNERY, H. Callus formation in *Hibiscus Rosa-sinensis* L. and *Hevea brasiliensis* Müll. Arg. Ann. Bot. **47**: 827–839. 1933.
164. SIMON, S. V. Transplantationsversuche zwischen *Solanum melongena* and *Iresine Lindeni*. Jahrb. Wiss. Bot. **72**: 137–160. 1930.
165. SINNOTT, E. W., AND BLOCH, R. Changes in intercellular relationships during the growth and differentiation of living plant tissues. Amer. Jour. Bot. **26**: 625–634. 1939.
166. ———, AND ———. Cytoplasmic behavior during division of vacuolate plant cells. Proc. Nat. Acad. Sci. **26**: 223–227. 1940.
167. SMITH, E. F. Mechanism of tumor growth in crown gall. Jour. Agr. Res. **8**: 165–186. 1917.
168. SORAUER, P. Handbuch der Pflanzenkrankheiten. 6. Aufl. **1**. 1933.
169. SPITZER, K. Über das Vorkonnen eines Dioxyphenylderivates und eines spezifischen Fermentes in Apfel und anderen Fruchtarten. Bioch. Zeits. **231**: 309–313. 1931.
170. STEWARD, F. C., WRIGHT, R., AND BERRY, W. E. The respiration of cut discs of potato tuber in air and immersed in water, with observations upon surface-volume effects and salt accumulation. Protoplasma **16**: 576–611. 1932.

171. SWARBRICK, TH. The healing of wounds in woody stems. Jour. Pomol. & Hort. Sci. **5**: 98–114. 1926.
172. SWINGLE, C. F. A physiological study of rooting and callusing in apple and willow. Jour. Agr. Res. **39**: 81–128. 1929.
173. ————. Regeneration and vegetative propagation. Bot. Rev. **6**: 301–355. 1940.
174. TAUBENHAUS, J. J., AND EZEKIEL, W. N. Acid injury of cotton roots. Bot. Gaz. **92**: 430–435. 1931.
175. THORNTON, N. C. Oxygen regulates the dormancy of the potato. Boyce Thompson Inst. Contr. **10**: 339–361. 1939.
176. TIMMEL, H. Über die Bildung anomaler Tracheiden im Phloem. (Beiträge zur experimentellen Anatomie der Wurzel.) Flora **22**: 203–241. 1927.
177. TRÉCUL, A. Accroissement des végétaux dicotylédonés ligneux, reproduction du bois et de l'écorce par le bois décortiqué. Ann. Sci. Nat. Bot., III. **19**: 157–192. 1853.
178. ULRICH, R. Réactions des fruits aux blessures expérimentales. Rev. Gén. Bot. **48**: 354–375; 427–440; 494–504; 539–561; 621–632; 676–694; 725–759. 1936. **49**: 36–65; 124–140. 1937.
179. ————. Mécanisme et conditions de la chute des fruits chez le lierre. (*Hedera Helix* L.) Rev. Gén. Bot. **49**: 601–618. 1937.
180. UMRATH, K., AND SOLTYS, A. Über die Erregungssubstanz der Papilionaceen und ihre zellteilungsauslösende Wirkung. Jahrb. Wiss. Bot. **84**: 276–289. 1936.
181. VÖCHTING, H. Untersuchungen zur experimentellen Anatomie und Pathologie des Pflanzenkörpers. 1908.
182. WARBURG, O. Über den Einfluss der Verholzung auf die Lebensvorgänge des Zellinhaltes. Ber. Deut. Bot. Ges. **11**: 425–441. 1893.
183. WATKINS, G. M., AND WATKINS, M. O. A study of the pathogenic action of *Phymatotrichum omnivorum*. Amer. Jour. Bot. **27**: 251–262. 1940.
184. WEHNELT, B. Untersuchungen über das Wundhormon der Pflanzen. Jahrb. Wiss. Bot. **66**: 773–813. 1927.
185. WEISSENBÖCK, K., AND STERN, A. Wuchsstoffinjektionen bei Pflanzen. Bot. Arch. **39**: 315–331. 1939.
186. WENT, F. W. Auxin, the plant growth-hormone. Bot. Rev. **1**: 162–182. 1935.
187. WERNER, H. O. Wound healing in potatoes (Triumph variety) as influenced by type of injury, nature of initial exposure, and storage conditions. Univ. Neb. Agr. Exp. Sta. Res. Bul. 102. 1938.
188. WHITE, PH. R. Plant tissue cultures. Bot. Rev. **2**: 419–437. 1936.
189. WIESNER, J. Die Elementarstruktur und das Wachstum der lebenden Substanz. 1892.
190. WILHELM, A. F. Untersuchungen über das Chromogen in *Vicia Faba*. Jahrb. Wiss. Bot. **72**: 203–253. 1930.
191. WILLISON, R. S. Fall spray injury to peach trees. Sci. Agr. **19**: 670–672. 1939.
192. WINKLER, H. Über die experimentelle Erzeugung von Pflanzen mit abweichenden Chromosomenzahlen. Zeits. Bot. **8**: 417–531. 1916.
193. WOIT, M. Über Wundreaktionen an Blättern und den anatomischen Bau der Blattminen. Mitt. Deut. Dendr. Ges. **35**: 163–187. 1925.
194. WOODHEAD, N. Studies in growth and differentiation. V. Histological and metabolic changes during wound-healing in *Kleinia articulata* Hand. Ann. Bot. **48**: 467–480. 1934.
195. WRAY, E. M. The structural changes in a woody twig after summer pruning. Proc. Leeds Phil. Soc. Sci. Sect. **2**: 560–570. 1934.
196. WRIGHT, R. C., PEACOCK, W. M., AND WHITEMAN, T. M. Effect on subsequent yields of storing cut seed potatoes at different temperatures and humidities. U. S. Dept. Agr. Tech. Bul. 394. 1934.

197. WYLIE, R. B. Leaf structure and wound response. Science **65**: 45–50. 1927.

198. ————. Cicatrization of foliage leaves. I. Wound responses of certain mesophytic leaves. II. Wound responses of certain broad-leaved evergreens. Bot. Gaz. **90**: 260–278. 1930; **92**: 279–295. 1931.

199. ————. Concerning the conductive capacity of the minor veins of foliage leaves. Amer. Jour. Bot. **25**: 567–572. 1938.

200. ZIMMERMAN, P. W., AND HITCHCOCK, A. E. Adventitious shoots and roots induced by natural influences and synthetic growth substances. Boyce Thompson Inst. Contr. **11**: 127–141. 1940.