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WOUND HEALING IN HIGHER PLANTS. II[1]

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INTRODUCTION

The organizing principle in living things controls, in some way, not only the production of many different patterns and specific individual forms but also their maintenance and regeneration under changing or adverse conditions. An expression of this is the capacity, possessed by both plants and animals, to repair injuries of different kinds and to restore certain lost portions.

In the previous review (8) the general phenomena of wound healing in higher plants have been discussed with reference to organ structure, to external conditions and to specific morphogenetic problems. These are, in particular, dedifferentiation, meristem formation, redifferentiation and tumor formation (compare 8, summary pp. 135–137). In the decade which has elapsed since, additional information has become available on practically every aspect of wound healing. There have been relatively few papers dealing with experimental work on wound hormones; the problems of cellular reactivity and specificity in plants have, on the other hand, gained wider interest. Researches in atypical growth forms and tissue cultures have attained major importance, and workers in these fields are recognizing the significance of reactivity studies for their particular materials. It is becoming increasingly obvious that many of the phenomena and atypical growth forms encountered must be interpreted in the light of experience gained from studies of regenerative processes and certain "pathologic-anatomical" tissue structures.

Strictly speaking, of course, the concept of wound healing would not seem to imply much more than the closing and scarification of a wound by means of strictly local cellular changes involving cell division, cell growth and cell differentiation, or, as in the majority

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of cases, a combination of these. As it is, however, the actual processes can be neither adequately described nor properly interpreted without reference to plant structure and development and to the general phenomena of differentiation and regeneration. On the one hand, wound healing is concerned with the induction and growth of individual meristems. It poses problems of a general morphogenetic nature, for one may ask: What is it that knits together the various developmental phases in the healing of a wound in such a way that structures emerge which resemble or are even identical with those originally present?

Thus in an injured terminal meristem the original cell and tissue pattern may become fully reconstituted. Wound healing is here identical with true or direct regeneration. In other parts of the axis, but in the same plant, there may be areas in the cortex or pith which react to the stimulus of wounding by formation of wound cork or callus, or more specific cell patterns. These areas differ from the apical regions in their anatomical and physiological properties. The differences are related to the stage of development of cells located in these various areas and to their reactivity or developmental potency. Many injuries even lead, in addition to local responses, to growth reactions in places that are rather distant from the wound. They may lead to compensatory development of organ primordia, and in this manner they may involve the entire system of the plant. These reactions are of great theoretical and also of practical significance, but are usually discussed in a separate category dealing with regeneration (compare 68*a*).

Emphasis, on the other hand, will be laid on the aforementioned relationships of wound tissues to atypical growth. Familiarity with various types of wound calluses is essential for the interpretation of artificially induced and often seemingly more complicated deviations from the typical tissue pattern, as observed in tissue cultures and various kinds of plant tumors.

ORGAN STRUCTURE AND WOUND RESPONSE

STEMS. Wound repair in terminal meristems has the character of regeneration. The self-reconstituting capacity of these specific regions is well known and has been experimentally analyzed by a series of operative treatments on shoot apices. The latter have been subdivided artificially into smaller tissue units than those studied by previous workers. Wardlaw (75, 76) demonstrated techniques by which the shoot apex of a leptosporangiate fern, *Dryopteris aristata* Druce, may be divided into four segments instead of two by making two longitudinal incisions in lieu of one. In other experiments the apical cell was punctured, or central parts of the meristem were damaged. Similar operations were subsequently performed on a higher plant, *Lupinus albus* L. (Ball, 5, 6). In some of these experiments the central part of the apical meristem remained without direct vascular connection with the main system of the shoot; nevertheless it retained high regenerative ability. Additional information was obtained with regard to the developmental potencies of other regions of the growing point.

Previously cases had been noted in which the callus of grafted woody stems was derived from tissues other than the cambium. Juliano (39) reported similar behavior for various species of *Nothopanax;* in cleft-grafted stems callus was first formed in the gap from parenchyma cells of the cortex and pith and from ray cells. From the callus a cambial bridge subsequently joined the cambial regions of the stock and scion.

Various forms of periderm formation have been studied. Klinkenberg (41) made a careful histological study of cork formation in herbaceous stems, such as *Pelargonium tetragonum* L'Hérit and *Begonia Seemanniana* A.D.C., paying special attention to processes of necrosis and the reactivity of different cell types. Brauner et al. (12) reported that potato tubers do not form wound cork at all if kept under anaerobic conditions, thus confirming earlier workers. De Zeeuw (81) investigated the influence of exposure on the time of deep cork formation in three northeastern trees, red ash (*Fraxinus pennsylvanica* Marsh), tulip poplar (*Liriodendron tulipifera* L.) and white pine (*Pinus strobus* L.). Exposed trees formed deep cork earlier than those which had been protected from direct insolation. The discrepancy was six years for red ash, five years for tulip poplar and fifteen for white pine.

The bark of aspen (*Populus tremuloides* Michx.) normally consists of a smooth persistent periderm. According to Kaufert (40), rough fissured bark may occur as a result of mechanical injury, fungi and lichens. *Macrophoma tumefaciens* Shear appears to be the most common cause of rough bark, the mycelium penetrating the layers of periderm and stimulating formation of new layers below. Mechanical injuries are apparently caused by hail, sleet or whipping of brush.

Injuries to trees caused by vines are of a different kind. Muller (63) noted that in *Celtis mississippiensis* Bosc. the vines of *Menispermum canadense* L. cause the formation of spiral lines of constriction on the bark of the host tree, along which peridermal excrescences or tumors subsequently appear. These are due to meristematic activity of small areas of phloem. The causative factor is apparently some chance mechanical injury.

Other vines which cause conspicuous injuries to stems and branches of young trees are bittersweet (*Celastrus scandens* L.) and grape (*Vitis aestivalis* Michx., *V. vulpina* L., *V labrusca* L., and *V. bicolor* Le Conte). The injuries resulting from spiral coiling of bittersweet, for example, around the stems of *Sassafras albidum* Nutt., produce constriction of the phloem with ensuing accumulation of substances. Considerable increment takes place of radial growth above the constricting vine. However, the trees are rarely killed by bittersweet vines, since new conductive tissues are formed whose elements become oriented parallel to the spiral constrictions (Lutz, 52).

Thoennes (69) described effects on the later growth of trees of injuries caused by the cicada *Magicicada septendecim*. The egg-laying activities result in injury, apparently destruction or modification of xylem tissue.

Gilbert (31) described traumatic effects in the young stems of oaks in which there were definite signs of " reversion " to the diffuse porous condition as the result of the hypertrophy produced. Whatever the physiological conditions affecting the growth processes in the wounded areas may be, there seem to be good indications " that in this case there is definite reversion to the ancestral type of vessel arrangement ". Different types of tyloses in two oak subgenera, *Erythrobalanus* and *Leucobalanus,* have been described by Williams (80).

Interxylary cork as well as formation of cork in other locations were studied by Moss (61) in various species of *Artemisia;* reference was made to their taxonomic significance.

ROOTS. Klinkenberg (41) studied periderm formation and necrotic processes in roots of various Crassulaceae and Cactaceae, and also made a detailed histological investigation of tomato plants affected with corky root. She also studied the necrotic virus spots of roots of lupine that had been affected by sore shin or Lupinenbräune. Numerous figures of stages of internal and external cork formation and illustrations of necrotic cell areas are given.

Fourcroy (25), in an extensive paper, described experiments with roots of *Vicia Faba, Ricinus communis* and *Lupinus albus* that had been injured by pricking, cutting or dipping into acids. Particular attention was paid to the way in which differentiation of the vascular system was affected by a wound near the tip of the root. As in this worker's previous communications, inhibiting effects as well as accelerating ones on the differentiation of xylem cells were observed, the former with reference to elements to be formed first in the ontogeny of the root, the latter with regard to elements normally differentiated later. This latter effect is carried to a considerable distance from the wound, and the author compares this pathological acceleration with "precocious aging", similar to the normal basifugal acceleration or progress of differentiation. Effects of the injury on tissues other than vascular systems were also studied, such as the formation of protective layers of cork meristem and of necrotic centers. The gradual reappearance of the normal structure of the root was also examined in detail. This paper also contains a study of the anatomical changes that are produced at the base of the hypocotyl of *Brassica oleracea* by a gall-forming species of *Ceuthorrhynchus.*

Continuing his studies on the roots of monocotyledons, Bloch (9) studied wound healing in the air roots of *Monstera deliciosa.* Roots injured at a sufficient distance from the meristematic apex react to the stimulus of wounding by formation of a repair tissue which is formed from older cortical cells and shows a characteristic surface-interior pattern. This pattern consists of successive layers of suberized cells toward the surface, thick-walled lignified cells beneath, and parenchymatous cells in the innermost region. Such a pattern is commonly found in plant tissues adjacent to external or internal surfaces. In *Monstera* it could also be made to form in internal locations simply by experimentally creating internal "centers" or surfaces of necrotic cells.

LEAVES AND PETIOLES. Cork spots on the leaves of various species of Crassulaceae and on leaves of non-succulent plants, such as *Gnetum Gnemon* L., *Camellia japonica* L. and *Clivia* sp., were studied histologically by Klinkenberg (41).

In leaves and in petioles of *Monstera deliciosa* wound tissues show characteristic patterns quite analogous to those in the air roots of this plant (Bloch, 9). Welch (77) studied the progress of cicatrization in leaves and petioles of *Bryophyllum calycinum*. Sections were made immediately after wounding, after four hours, after three, four and six days, and after ten weeks. In leaves that had been removed from the plant the layers of pseudocicatrice were less developed than in those that remained attached to the plant.

Again, a number of workers have investigated various anatomical types of abscission. The process of separation of leaves and other plant organs has received much attention in the past, since it has various important theoretical and practical implications. Hilpert (37) described the processes of abscission and the closing of the ensuing wounds in flowers and fruit stalk of *Ricinus communis*. Anatomical and chemical aspects of abscission of apple fruits were studied by McCown (57), and the anatomy of leaf abscission in guayule and of experimental defoliation by means of flash-drying by Addicott (1).

Facey (24) investigated abscission of leaves in *Fraxinus americana* L., studying in particular the progressive chemical changes in the cell wall before and during abscission. It is concluded that some of these changes are associated with a natural lowering of pH in the leaves and could be induced artificially by treatment with dilute hydrochloric acid. On the other hand, retention of leaves occurred in branches which had been exposed to ammonia vapor that produced an alkaline reaction in the cells and prevented the change from calcium pectate to pectic acid.

The histological changes associated with leaflet abscission in *Phaseolus vulgaris* were studied by Brown and Addicott (13). Explants consisting of the terminal leaflet, including pulvinus and ten millimeters of the subtending leaf stalk, were used. The progressive changes were observed until abscission took place which reached its maximum on the third day. A variety of anatomical and physiological changes in pulvinus and stalk were noted, in addition to cell division and other changes in the abscission zone proper. The effects of chemicals, such as 2,4-D, were also studied. Livingston (47) described leaf abscission in the Valencia orange.

A discussion of the numerous papers dealing with different physical and chemical factors or agents, accelerating or inhibiting the abscission of leaves and other plant organs, would exceed the scope of this review. A study by Gawadi and Avery (27) is of interest here, however. These workers carried out experiments of a physiological nature in order to determine to what extent cell divisions occurred within the zone of separation and were causally related to the process of abscission. The authors used several species of herbaceous plants, representing three types. In the first type the process of separation of the leaf is preceded by cell division in the separation zone (*Poinsettia,* cotton and pepper); in the second (*Impatiens*) there is no preformed layer of dividing cells; in the third, the leaf of tobacco, there is evidence of occasional cell division, although the leaves do not abciss naturally. It is significant that in the first group leaf fall can be induced experimentally, for example, by treatment with vapor of carbon tetrachloride or ethylene chlorohydrin, before cell divisions have made their appearance in the separation zone. On the other hand, in type II, which lacks these divisions, abscission occurs both normally and after experimental induction. It is obvious that the presence of a layer of dividing cells in the separation zone at the base of the petiole of abscissing leaves is not essential for abscission to take its regular course. This layer should thus be interpreted as of the nature of periderm, ultimately forming the protective tissue of the leaf scar, a view held by many previous workers. There remains the problem of the factors normally instrumental in the induction as well as the location of these divisions in definite positions. To this reviewer it would appear that they must be related to those which control the analogous formation of superficial or internal cell divisions in tissues which later become typical periderm.

FRUITS. An anatomical examination of the brownish cork spots in the flesh of the fruit of apple varieties was made by Klinkenberg (41). These well known spots, which occur both superficially and internally, consist of small areas of necrotic cells adjacent to which normal cell groups assume the character of callus or cork.

The present reviewer made a histological examination (unpublished) of wound tissue formation in fruits of various lines of *Lagenaria vulgaris.* Both young and fairly grown fruits showed excellent regenerative ability, as demonstrated by the fact that circular plugs of fruit tissue that had been removed with a cork borer and promptly reinserted would generally fuse and subsequently reach maturity along with the rest of the fruit. This was also the case when the plugs were replaced after having been rotated into a position differing from the original. Tissues were thus made to coalesce that originally had not been in contact with one another, indicating that there is little polarity in such fruits.

PHYSIOLOGICAL CHANGES ASSOCIATED WITH WOUND HEALING

The physiological basis of normal development and of regenerative growth and differentiation must be, of course, closely related. However, there is still relatively little known as to how sudden disturbances of the "correlative" and internal environmental equilibrium express themselves in physiological or physico-chemical terms.

Ulrich and Lafon (74) studied respiratory intensity in tomato fruits at different stages of development, as well as its increase and variations in wounded fruits of this plant. Their data confirm those reported by previous authors, and it was also found that wound respiration becomes reduced as fruits approach maturity.

It is known that mechanical manipulation increases respiration in leaves and other plant organs. Audus (4) studied, in detached leaves of cherry laurel, the role in this effect of intermittent stimulation and of leaf turgidity. Arceneaux (3) reported on the accumulation of sugar in the stalks of sugar cane that had been damaged by wind. Combes (18), supplementing his previous work on leaves, studied the effects of incisions in petals and sepals of *Lilium croceum;* transport of nitrogenous material from the perianth became accelerated. The general effects of wounding on the nitrogen metabolism of various fruits have been discussed by Ulrich (70); his paper contains, in addition to his own experiments, a review of literature in this field. The same author (71) studied similar effects in the leafy shoot of *Pisum sativum* and reported for the same material (73) on the effect of wounding on carbohydrate metabolism. He has also, in a résumé of wound reactions in higher plants (72), discussed some of the general problems of wound healing.

Marshall, Childers and Brody (55) reported that several species of apple leaf hoppers and the potato leaf hopper cause injuries in apple leaves (Stayman Winesap variety) that are accompanied by a more or less marked reduction in apparent photosynthesis and transpiration. Apple leaf hoppers generally removed the contents of the palisade cells.

Among the numerous physiological traumatic reactions, changes of a necrobiotic kind and chemical changes of a hormonal nature appear particularly significant.

WOUND HORMONES AND NECROTIC CHANGES

WOUND HORMONES. The complex mechanism and the physiology of wound healing and regenerative growth are by no means better understood now than when the previous review was written. Like typical growth, organized wound repair consists of many components: dedifferentiation, cell division, cell growth and differentiation, as well as formation of orderly patterns. These involve a multitude of factors and processes intricately woven together. The initial phases of wound tissue or callus formation, namely, cell division and growth, are usually associated with decomposition processes in cells and with the formation of necrotic and autotoxic products, and may be related to them causally (compare 8). Such a relationship, probably of a specific chemical nature, has long been suspected, and wound substances have been isolated, termed " wound hormones " (compare 8 and 64, pp. 76–83). One of those substances previously purified, traumatic acid, is possibly an oxidation product of substances normally present in the cells and may, besides auxin, stimulate the growth and division of cells.

English (22) reported additional synthesis of a number of dicarboxylic acids other than traumatic acid which are all active to varying degrees as wound hormones.

Hemberg (34) found that in cut discs or slices of potato tubers that had been exposed to air for three hours there are formed two kinds of growth substances (*Avena* test). The first one is acid in nature and probably identical with indoleacetic acid or one of its homologues. Presumably this is formed from decomposition products of injured cells. Possibly this decomposition product serves as activator for the formation of auxin or a wound hormone of the type suggested by Haberlandt. The second substance has a neutral reaction and may possibly be indoleacetaldehyde (35).

It is known that the rooting of certain cuttings may be enhanced not only by treatment with growth substances, but also by additional wounding of the base or side of the cutting. LaRue (45) found that petioles and stems of herbaceeous cuttings that had their bases repeatedly sliced showed increased rooting as compared with uninjured controls. Extracts presumably containing wound hormones were effective also.

Davis (21) tested wound healing activity in sugar maple (*Acer saccharum* Marsh) for traumatic acid, glutathione, and four growth substances, using different concentrations in talcum as a carrier. In these experiments only glutathione was found to stimulate wound healing.

Loofbourow and collaborators have continued their studies of the formation of proliferation-promoting intercellular hormones in injured yeast cells (48, 49, 50, 51), and Cook and Cronin (19, 20) have compared extracts from such cells with known bios components and amino acids.

NECROTIC CHANGES. Characteristic physiological and structural changes commonly occur in cells adjacent to wounds. The study of these changes is of considerable interest, since they are closely linked with the stepping up of metabolic activity and the resumption of division and growth in adjacent healthy cells. The formation of cork barriers, " suberized deposits ", wound gum, lignin, phlobaphenes or phenolic compounds have been studied by various investigators. Often these changes render the tissue more or less resistant or immune to parasitic infection and thus form an important part of the natural defense reactions of the plant to the presence of pathogens and their toxins (compare 8 and 25*a*).

As has been previously pointed out (8, page 122), there are often difficulties in the interpretation of the microchemical reactions of necrotic deposits, and care has to be exercised in determining, for example, whether a certain chemical change in the cell wall is due to the presence of true lignin or of other necrotic compounds which may give a similar microchemical color reaction.

Klinkenberg (41) has illustrated a number of typical cases of tissue necrosis which occurred as a result of wounding or other pathological conditions, such as virus infection. Included is an anatomical study of those well known small necrotic " gummy " areas or " centers " which frequently make their appearance at a certain distance from the main wound surface. In sugar beet (42) it has been possible to differentiate between *Verticillium* disease, virus-yellows and an etiologically obscure necrosis, merely anatomically on account of differences in the internal necrotic changes. In *Verticillium* disease there appear dark substances first in xylem elements which then spread to surrounding tissue and to the surface of the petiole. Beets afflicted with virus-yellows show gummosis of the sieve tubes, following a generally diseased condition of the phloem. The necrosis of unknown cause is not easily distinguishable from virus-yellows microscopically. In this disease there appear, however, very darkly staining necrotic compounds in the wood vessels.

The effects on differentiation of internal necrotic areas in parenchymatous tissues in air roots and petioles of *Monstera deliciosa* were studied by Bloch (9).

Hill (36) has made a comparative study of suberin and " suberized deposits " of lesions in potato tubers affected with different diseases. Simonds (65) investigated phloem necrosis, deposition of tannin-like material and other pathological changes in raspberry canes. These occurred as the result of winter-injury or of artificial injuries such as freezing, alternate freezing and thawing, or desiccation above freezing temperature. Esau (23), in studying the anatomical changes in the phloem of *Nicotiana Tabacum* affected with curly top, described degenerative changes that occurred in the apices of shoot and root; these started to appear in the cells adjacent to the first differentiated sieve tubes. Cell divisions subsequently lead to formation of hyperplastic atypical phloem. Tomato and sugar beet show the same degenerative changes as tobacco.

Metcalfe (58) reported that the watermark disease of willows is characterized by pathological changes in the cells of the wood, consisting in accumulation of oil, polyphenolic compounds, and oxidation of these to brown substances; probably this is the result of a greatly disturbed physiology caused by the presence of bacteria. That such substances frequently render the cells and thus the plant resistant to parasitic infection or penetration, has previously been shown in a number of cases. Phenolic compounds play a significant part in many instances of cellular resistance. Greathouse and Rigler (33) tested 45 phenolic and related compounds upon the growth of *Phymatotrichum omnivorum* (Shear) Duggar in pure culture and have listed the compounds in order of their toxicity.

Behr (7) reported that potato tubers which had been treated with different alcohols or with chloroform did not develop periderm, although the cells remained alive. Subsequently the tubers showed little resistance to species of *Phytophthora* and *Fusarium*.

McClure and Robbins (56) made a study of damping-off in cucumber seedlings and found that resistance to infection by *Pythium* depended on a change in the walls of the cells surrounding the areas of infection, described by them as deposition of lignin.

SPECIFIC PROBLEMS

The technique of artificially induced wound healing is a useful tool for the study of specific morphogenetic problems, for example, those which have to do with the mechanism and plane of cell division, cell growth and cell dedifferentiation and differentiation. Compared with the original meristems of the plant, wound meristems generally possess much larger, easily recognizable cells with well developed walls. Such cells are much less sensitive to experimental manipulation than the small, densely cytoplasmic, thin-walled cells at the growing points.

CELL DIVISION. As is well known, the plane of cell divisions in a wound meristem is usually parallel to the surface of the wound, or vertical to a gradient in wound hormone concentration or some other factor. Other directions may also occur, especially in the later stages of wound tissue formation and in special locations (compare 8, page 128). One interesting property which characterizes early divisions in a wound meristem is the relative position in adjacent cells of cell walls which are frequently laid down exactly opposite each other (Sinnott and Bloch, 66). Commonly, in plant tissues a new wall does not meet an old one at a point directly opposite the point of insertion of an adjacent partition wall. In the majority of plant tissues the walls thus alternate or " break joints ", and only three walls meet at a point. But in certain tissues, for example, in many types of roots whose cortical tissue cells show a " radial concentric " arrangement, as seen in cross section, exactly the reverse condition occurs. In early development each new wall is laid down exactly opposite the point of insertion of a previous one so that four walls meet at one point. The same occurs frequently in normal and regenerative periderm, and has, for example, been induced artificially in wounded stems and petioles of *Bryophyllum, Kalanchoe, Tradescantia fluminensis* and other plants. An understanding of the factors which control the insertion of cell walls opposite each other in wound tissues may therefore throw light on an important general character in the normal tissue pattern.

Bünning (15) has also studied the plane of cell division in wounded roots of *Sinapis alba.* In the cells of the cortical parenchyma and the rhizodermis the plane of division is such that it can be related logically to a characteristic path of transport of wound hormones from the wound surface.

In the somatic tissues of a considerable number of angiosperms there occur not infrequently cells which possess a multiple of the set of chromosomes typical for the plant. Such cells, that have long since stopped dividing, are characteristic for certain tissues or regions, particularly the periblem of roots. This phenomenon and the process of internal somatic doubling have been called rather loosely and interchangeably, polysomaty, endopolyploidy or endomitosis. The occurrence of such polyploid cells has been noted not only in normal tissues but also in wound tissues and calluses, and in certain plant tumors. In some cases the condition may be inferred from the size of nuclei and other criteria in the resting cells of the vegetative tissues. Mostly, however, some special technique, such as wounding, is required in order to induce mitotic divisions artificially and observe the number of chromosomes present in the cells. Grafl (32) demonstrated in this manner that in *Sauromatum guttatum* certain mature tissue cells were tetraploid, octoploid and 16-ploid. Geitler (28, 29) reported similar conditions from evidence in induced wound tissues in succulent leaves of *Rhoeo discolor,* and Geitler and Lauber (30) and Lauber (46) in fruits of *Liliaceae, Loasaceae* and *Solanaceae.*

DEDIFFERENTIATION AND REACTIVITY. Typical dedifferentiation of cells has been frequently described for plants, but it is less generally encountered in animals. Plant cells may lose, not only in wound and in regenerative tissues but also during the course of normal development, their differentiated character and become more embryonic and less specialized. They, at the same time, show changes in metabolic activity and protoplasmic character. Resumption of cell division and wall growth are frequently followed by functional and structural metaplastic changes which indicate that the cells have undergone a process of redifferentiation. The concept of totipotency or pluripotency has long been familiar to botanists (compare 8). The rather unstable determination of cellular character in plants, as compared with those of animals, has also not entirely escaped the attention of experimental plant morphologists, although it has been mentioned only rarely. A statement made by Küster in 1903 (44, page 299) appears significant in view of the recent revival of interest in this field. Referring to the fact that in atypical growth any kind of tissue may give rise to any other type of cell or tissue, the view was expressed that in plants there is no " specificity of tissues ", such as seems to occur in animals. At the same time Küster recognized that the different behavior of plant and animal tissues may be explained on the ground that the differentiation of the latter is predominantly determined by internal factors and relatively little affected by those changes in external factors with which we operate in our experiments.

In normal ontogeny the different histological character of cells in different positions in the plant body is in many ways tied up with factors in the environment. It is therefore not surprising to find that many potentially meristematic cells will exhibit considerable pluripotency whenever inhibiting correlative influences can be removed and external factors may once more conspicuously affect the physiological state of the cell and regulate its growth activities in a variety of ways. Most effective experimental methods which will bring about such changes are wounding and isolation of tissues or organs, culture of tissues, and growth substance treatment.

There are, however, differences in the reactivity of plant cells to the stimuli which induce dedifferentiation, and wounding is a convenient method with which to demonstrate this differential behavior of plant cells in relation to their age, position within the plant body and their histological type (9). There are differences in their readiness for division and renewed wall growth, although both are very commonly seen in cells of the parenchymatous and collenchymatous type. Relatively differentiated cell walls may resume active growth in surface and in thickness. During the process they sometimes lose their impregnated character. To the present reviewer there appears little doubt that the study of the fine structural changes of such extending cell walls in wound meristems and calluses can provide valuable information about the processes of cell wall growth in general and about certain aspects of wall nomenclature in particular. It is in itself a remarkable fact that the walls of cells which have long ceased growing and dividing should be able to undergo reversible changes or renewed growth under the altered conditions that prevail in wound meristems. This is not surprising, however, when one considers that, for example, in the normal development of collenchyma cells the major part of extension in the young wall actually occurs long after the onset of wall thickening. According to the old nomenclature the thickened part of the wall is " secondary wall ", and its formation was believed to follow the primary phase of extension and growth in surface (Majumdar and Preston, 54; Majumdar, 53).

The method by which the growth in surface of the wall of cells takes place within the callus or wound tissue is most probably one of active intussusception in which the protoplasm itself plays an active role. Often this growth is limited to certain parts of the cell, for example, its ends. This general concept of surface growth of walls has been supported by electron-microscopical evidence in primary cell walls (Mühlethaler, 62).

Cytological aspects of cell and tissue dedifferentiation have been studied by Buvat (16). In an extensive paper there are surveyed cases of dedifferentiation in normal and regenerative development, augmented by new investigations. These deal in part with adventitious root formation in the stem of tomato and with vegetative propagation of leaves of *Brimeura amethystina* L. Besides histological development of regenerating organs, various phases of dedifferentiation have been studied, with emphasis on nucleus, plastids and chondriosomes within different cell types. Another part of the paper describes dedifferentiation in parenchymatous tissue cultures of *Daucus carota* L. and in tissue cultures of the tuber of *Cichorium intybus* L., also including similar cytological studies. Finally changes were studied in stems of tomato that had developed crown gall. This investigation fully confirms those observations of previous investigators who had noted that in processes of regeneration cells of very different origin, type and location may dedifferentiate. The author gives numerous details of the changing cytological structures of cells, especially of the chondriom, in the various phases of regressive development. He concludes that, in contrast to animal cells, no plant cell is irreversibly determined. In his opinion every cell in an angiosperm, unless degenerated, can more or less dedifferentiate under the proper conditions. " Elle est toujours capable de se remettre à proliférer, de perdre ses caractères structuraux de spécialisation et dė se spécialiser différemment par la suite " (16, II. pp. 103/4).

The conclusion of this investigation thus supports the previous one reached by Küster and other workers. Whether it would be tenable in such a generalized form, however, will, in the reviewer's opinion, depend on further comprehensive experiments with a greater variety of physiologically different types of cells. Certain observations of developmental as well as experimental nature seem, at least at the present stage of our knowledge, to suggest that some caution may be indicated. It appears, for example, rather remarkable that there are no clear and convincing observations available which would show that the various types of physiologically specialized cells of so-called idioblastic type undergo full dedifferentiation in wound tissues. Many of these cells contain oil, tannin or other secretory material, such as crystals. A study to ascertain the behavior of one type of such cells has been made in *Ricinus communis* (10, 11). In the stem of this plant there occur secretory cells whose contents give the reactions of unsaturated fats and tannins. These cells acquire the specialized cytoplasmic character very early in development and transmit it to their daughter cells. In wound tissues, as well as in tissue culture, cells of this type, which have stopped dividing within the mature zone of the internodes or nodes, resume both division and growth along with the rest of the cells of the ground parenchyma. They do not, however, lose their special cytoplasmic character during this process. Apparently the properties which distinguish them from the rest of the parenchyma arise originally as a result of so-called differential divisions, that is, they are, in the last analysis, determined internally. It appears only natural, therefore, that secondary changes in external conditions or in the intercellular correlative position of the cells within the plant body do not easily affect their cytoplasmic character. Nevertheless, under proper conditions the cells still reveal the potentiality of division and growth along with the rest of other living tissue elements.

Another example of cells undergoing early functional segregation from the rest of the tissue cells has been reported by Meyer (59). In the leaf of *Urtica dioica* the cystolith cells are rather stably determined. In leaves affected with galls caused by *Perrisia Urticae* these cells undergo modifications according to their new position in an atypical location. In the hair-bearing region of the stomatal openings hair-shaped cells are found which contain, however, cystoliths. On the other hand, in the region of growth, rows of cystolith cells occur; these arise by transverse and especially by longitudinal divisions which are characteristic for the epidermal layer. Here, as in other cases, the character of cells may be considerably modified by cecidogenesis, but the potency for the differentiation of cystoliths is determined in these cells at an early stage and is not lost. It is significant that cystoliths are formed only in those daughter cells that have arisen as a result of longitudinal divisions, for only then does each daughter cell obtain a part of the external cell wall in which the potency for crystal formation resides.

There are other indications that the various forms of cellular and tissue determination and of modification which occur during the course of normal differentiation within a plant differ in degree of stability and reversibility; this has been suggested also by Bünning (14). Of those modifications initiated by external agents at least one is well known that appears irreversible under conditions of regeneration and tissue culture, namely, the secondary tumor cell type attributed to the action of *Bacterium tumefaciens*.

DIFFERENTIATION. The accelerating effect of wounding on metabolic activity and on visible cell and tissue differentiation has been previously discussed (8). Fourcroy (25) studied these processes, especially as they affect differentiation of the vascular system.

One phase in the redifferentiation or reconstitution of the original tissue pattern is the thickening of the walls in cells or specific layers of cells near the wound surface. Many examples are known. In the development of the periderm of potato the first histological change of this kind is apparently a slight thickening in the outer walls of cells located in the third or fourth layer below the wound surface. Brauner et al. (12) noted that the thickened wall is present as early as 24 hours after wounding, that it stains with Sudan III and Safranin, and soon resembles an " internal epidermis ".

In the roots, stems, petioles and leaves of *Monstera deliciosa* reconstitution of more complex dermal tissue patterns is common. Generally these patterns have a relation to the developmental potency of the tissue cells at the time of wounding (Bloch, 9). One remarkable feature is the differentiation of thick-walled " hypodermal " sclereids. These sclereids always differentiate below a surface in a characteristic position where special external conditions must be effective.

Redifferentiation of vascular strands in wounded organs has also been investigated by several workers. Jost (38) studied regeneration of xylem bridges in *Fittonia argyromeura, Saintpaulia ionantha* and *Elatostemma sessile.* He confirmed the older observations of Simon and Freundlich and noted that the regenerating strand formed mostly in a polar fashion from the upper margin toward the lower part of the cut; sometimes it followed the outline of the wound. This process was studied also by Sinnott and Bloch in several herbaceous plants, especially in the stem of *Coleus hybridus* (67, 68), from the point of view of the finer but still microscopically visible changes within the protoplasm and cell wall. The new bundle connections which developed across the pith included both phloem and xylem strands. The latter consisted in part of elongate tracheids and vessels formed from procambial divisions parallel to the course of the new strands, and in part of vacuolate and nearly mature parenchyma cells which differentiated directly into spiral and reticulate xylem elements without previous division. In these cells the configuration of the lignified bands had a definite orientation relative to the axis of the new strand, and this reorientation became evident first in the cytoplasm of the cells. This cytoplasmic pattern of bands and its final manifestation in the lignified thickenings are not independent configurations in each cell, but form a harmonious coherent pattern extending across a group of cells, the bands in one cell being directly continuous with those in adjacent ones. The evidence suggests that histological differentiation, both normally and in regeneration, frequently involves the establishment and operation of such intercellular fields or patterns in the cytoplasm of groups of contiguous cells.

This reviewer has always been impressed by the relative ease with which fundamental parenchyma cells can be made to differentiate into tracheid-like elements. This may be observed in many instances of regenerative as well as of pathological growth. This type of cellular metaplasia very commonly observed in calluses, tissue cultures and tumors, requires relatively little change in the fundamental character of the cell, involving only deposition of specifically arranged " secondary " wall material.

From a discussion of this phase of research in regenerative differentiation the significant observations made by Camus (17) should not be omitted. In order to analyze the promoting influence of buds on the formation of roots, grafts were carried out in which the buds acted as organizing centers. These induced processes of dedifferentiation and subsequent redifferentiation of vascular strands in the stock tissue onto which they had been grafted. That an organizing principle from the buds is able to pass through the region of the graft could be demonstrated even more strikingly by placing a bud on an isolated piece of tissue taken from the root of *Cichorium intybus* L. These tissue fragments consisted of old cells of vascular parenchyma only, and it was found that under the influence of the bud such old parenchyma cells would dedifferentiate and redifferentiate into groups of conducting elements. The presence of considerable potentialities in cells normally at rest is here quite evident.

In many roots there are two kinds of cells in the superficial layer, those that develop root hairs and those that do not. It is known that under a variety of conditions all cells can be made to form root hairs. Bünning (15) has shown that in *Sinapis alba* the root hair cells readily divide as a result of wounding and that the cells which do not normally bear root hairs may develop them if the superficial layer of the root is partly isolated by short longitudinal incisions.

The preceding examples of redifferentiation strikingly demonstrate the pluripotency of parenchyma cells which may undergo metaplastic changes either directly or after dedifferentiation. However, as previously discussed, there are exceptions. These are, on the one hand, highly differentiated cells in which wall incrustation and other cellular characters are very pronounced and a physiological state of senescence is present. On the other hand, there are those cells of idioblastic type in which physiological specialization is rather stably determined, as in the secretory cells of *Ricinus* or the cystolith cells of *Urtica*.

ATYPICAL GROWTH. When tissue patterns arise which, either spontaneously or in reaction to traceable causes, differ conspicuously from the normal, or when even a lack of pattern is encountered, we speak of atypical growth. Examples are some large calluses, tumors of various kinds and forms obtained in tissue cultures. The interest in the study of such atypical growth forms in plants has greatly increased, mainly in relation to the pressing problem of malignant growth (compare de Ropp, 21*a*; Gautheret, 26; White, 78, 79).

Aside from this, the study of wound tissues and regenerative wound calluses, on the one hand, and the study of bacterial and chemical plant tumors and tissue cultures, on the other hand, are related in more than one way, and the results obtained in these fields mutually supplement each other. Thus in plant tumors and in cultured tissues certain histological changes differing conspicuously from the normal can often be interpreted on the basis of similar structures formed in ordinary wound calluses and under simpler growth conditions. On the other hand, there is hope that the techniques of growth under experimentally controlled conditions of isolated cells and pieces of tissue may bring some of those problems nearer solutions which have to do with the processes of proliferation, differentiation and organized growth in normal and regenerative development. It is very difficult to analyze in the intact plant the physiological and physicochemical events which lead, for example, to cellular diversity. In tissue cultures the experimental approach to this problem appears in certain respects more simplified, and at least some of the factors which may channel the differentiation of cells and tissue into certain directions are now being analyzed by varying the conditions in the culture medium.

In the numerous discussions on atypical neoplastic growth forms that have been compared in some way with malignant " cancerous " growth, it has become customary to employ both physiological and morphological criteria. More or less spontaneous but subsequently persisting changes in the physiology, the growth rate and the histological pattern of plant tissues would seem to indicate a fundamental alteration in cellular behavior and in the typical tissue organization. Such change has by some workers been compared with those alterations in cellular reactivity and specificity which are encountered in animal cancer. Occasionally the diagnosis " plant cancer " is based predominantly on anatomical features, involving alterations in the histological pattern, such as differentiation of centers of tracheids, formation and irregular distribution of organ primordia, or other kinds of abnormal arrangement of tissue constituents, suggesting a loss of the typical organization. It is here that a critical evaluation of the observation becomes indispensable, for the anatomical changes that are encountered in tumors formed by various chemical treatments, by virus or bacterial infection, are often strikingly similar to those seen in wound calluses and related structures. In many instances, therefore, the pathological-anatomical character of the tumors may be interpreted as merely a so-to-speak "exaggerated" manifestation of the same histological changes that occur in ordinary wound calluses. As a matter of fact, not infrequently a relatively simple change in external factors may modify the process of wound healing in such a way that quite substantial atypical tissue proliferations result.

Similarities and analogies between calluses, tumors and cultured tissue forms occur in various developmental phases. In healthy plants hyperhydric conditions may produce formation of intumescences and tissue proliferations which closely resemble those changes that occur in the first phases of tissue cultures. After infection with *Bacterium tumefaciens,* the first stage in the formation of crown gall tumor are cell divisions resembling localized wound reactions. Isolated nests of twisted tracheids as well as irregularly located cambial activities associated with differentiation of vascular strands are often seen in large-sized regenerative calluses of herbaceous and woody plants. They have been reported also for many tumors of etiologically quite different origin, and in tissue cultures. It is known that some plants, when wounded, form cambia whose activity becomes atypical in that they produce xylem toward the outside and phloem toward the inside. Such inversion of cambial activity has been observed also in tissue cultures of the same material, for example, in *Vitis* species (compare Krieg, 43; Morel, 60).

It will not be easy, therefore, to diagnose, on mere histological evidence, a conversion from one type of growth to another one which might be called "unrestrained", since the different forms, as we have seen, are rather closely related in anatomical respect. Additional criteria, physiological and morphogenetic, are obviously required.

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