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DIFFERENTIATION AND PATTERN IN *MONSTERA DELICIOSA*. THE
IDIOLASTIC DEVELOPMENT OF THE TRICHOSCLEREIDS
IN THE AIR ROOT¹

Robert Bloch

To THE student of both normal and abnormal cell behavior anything which can be learned about conditions under which cells differentiate (develop different properties during ontogenesis) is of theoretical and practical consequence. At the plant growing point embryonic cells in all likelihood start out as morphologically very similar and genetically identical totipotent units, although probably no two cells in the organism remain exactly alike for long; very soon cells can be distinguished which exhibit specialized combinations of various cellular properties and activities (as to growth, membrane structure, contents, and physiological character). Usually such cells differentiate in association with the formation of specific tissues in typical locations within the plant organ; sometimes, however, they are arranged in less regular fashion, namely, as individuals scattered through the ground tissue, to which Sachs applied the term "idioblasts." Among the latter those cells appear of special interest which occur as solitary, actively proliferating elements among the more static and regularly shaped elements of the fundamental tissue. Notable among these cells, which often combine developmental and structural features of bast fibers, sclerotic parenchyma cells, hairs and other forms (for classification see Tschirch, 1885; Foster, 1944), are certain actively growing, prosenchymatous and branched sclereids which ramify between elements of the ground tissue, such as the well-known astrosclereids of leaves (de Bary, 1884; Solereder, 1908; Foster, 1944). In a number of plants these cells are known to develop by proliferation of internal initials abutting on the intercellular space system, as in the *Nymphaeaceae* and *Menyanthoideae* (Gürtler, 1905), the *Araceae* (van Tieghem, 1866), and *Rhizophora* (de Bary, 1884; Gürtler, 1905); where the lacunae are large, the development of these cells reminds one of that of external hairs from an epidermal surface. The terms "internal hairs" (Meyen, 1837) and "trichoblasts" (Sachs, 1882; Gürtler, 1905) applied to these cells refers to this property; they are also frequently described, together with other kinds of idioblastic sclereids, as "spicular cells" (Solereder, 1908). Both the terms trichoblast and spicular cell are also used, however, to denote other kinds of plant cells; the present writer, therefore, proposes the use of the term *trichosclereid* for such forms as are described in this paper. These cells can be distinguished clearly both morphologically and developmentally from the brachysclereids which are differentiated in the hypodermal region of the cortex of *Monstera* air roots during later development (Bloch, 1944).

Comparatively little is known about the induction and development of trichosclereids and other forms of idioblastic sclereids. Gürtler (1905) studied their development in *Nymphaeaceae* and other plants; Foster (1944, 1945) has recently investigated the development of sclereids in compact tissue of the petiole of *Camellia japonica*, as well as in the more highly lacunate tissue of the lamina and petiole of *Trochodendron aralioides*. Characteristically in all cases the idioblasts developed from small initials which, however, did not occur in any definite pattern; in *Trochodendron*, according to Foster, all spongy parenchyma cells retain the capacity to form sclereid initials. The most outstanding feature of the sclereids in *Camellia* and *Trochodendron* appears to be their capacity to grow under different intercellular conditions. Thus in *Camellia*, cell processes intrude between densely arranged collenchyma or parenchyma cells and cease growth when a large space is entered, while in *Trochodendron*, where sclereid formation occurs over a relatively long period of time, the branches of the sclereids grow through spaces and intervening tissue alike. The potency here of considerable portions of the primary wall to grow out would appear as a property which these cells share with those of the ordinary parenchymatous type which retain the capacity for wall growth for considerable time. It appears significant that in *Camellia*, where the growth is almost entirely intercellular, but in close contact with the parenchyma walls, pit connections are apparently re-established between the walls of parenchyma cells and sclereids, much as in other intrusively growing fibers, while in *Trochodendron* pits are restricted to the central part of the sclereid which remained in contact with parenchyma cells.

The present writer has worked with the long, pointed, fibrous and more or less branched cells which ramify in air spaces of various tissues of *Araceae*, especially the *Monsteroideae*. These have been described several times on account of their very peculiar and variable forms (van Tieghem, 1866; Wiesner, 1875; Lierau, 1888; Gürtler, 1905; Solereder, 1919; Solereder and Meyer, 1928), but relatively little is known about their development. Van Tieghem (1866) mentions their origin from small, parenchymatous initials which form processes into the adjacent intercellular space system. These processes may be seen readily enough in transverse sections through mature regions of the mesophyll of leaves or the cortex of roots and air roots (fig. 8); the early origin of the initials, however, requires more intensive study. The author noticed previously (1944) that in the air root of *Monstera deliciosa* the initials of these sclereids appear very early near the

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apex of the root meristem, and that these initials send out fast growing processes which grow upward and downward between the parenchyma cells. The tissue in which they arise is a rib meristem of considerable symmetry, and such tissue would appear to have certain natural advantages for the study of early intercellular relationships in idioblastic development.

MATERIAL AND TECHNIQUE.—Tips and mature parts of air roots of *Monstera deliciosa* were killed in C R A F and the development of trichosclereids studied from the youngest stages onward, both in longitudinal and transverse sections, 12–20 μ in thickness, stained with safranin and fast green. Air roots of various sizes, from 1.5 to 15 mm. diameter and of varying length, were studied. Young stages of trichosclereids in hand sections of fresh material may be profitably studied after staining of the young cell walls and cytoplasm with ruthenium red. The form and length of fully grown sclereids were studied after maceration and mechanical isolation.

THE DEVELOPMENT OF THE MOTHER TISSUE AND INTERCELLULAR SPACE SYSTEM.—The development of the sclereids is so closely related to changes in the cortical parenchyma that it is advisable to describe these first. Both transverse and longitudinal sections were studied. At a distance of about 700 μ from the apex of the cone of the meristem the cortical parenchyma cells have begun to vacuolate, and show in longitudinal sections the typical configuration of a rib meristem. In it numerous files of cells may be distinguished, each of which is made up of the derivatives of one meristematic cell of the cortex, now consisting of 3–5 cells (fig. 3). It will be noted that these files are not always exactly continuous, but occasionally stagger or alternate somewhat; as the cells vacuolate and expand longitudinally; however, this discontinuity becomes less distinct.

The intercellular space system begins to develop very early and may be recognized in both longitudinal and transverse sections. A number of channels may be seen to run longitudinally between the files to within a short distance of the apex, and in the longitudinal sections small intercellular spaces may also be seen at the corners where the cell files abut on each other (fig. 3). Both the somewhat tapering shape of each file and the presence of air spaces where the files abut on each other, make it easy to recognize the boundaries of the original cortex cells.

Transverse sections show that the air space systems undergo considerable changes during ontogenesis. Already near the apex three kinds of spaces may be distinguished: triangular, somewhat larger quadrangular, and still larger pentangular spaces (fig. 1 a–c, 2). The number of air channels with more than three sides increases as vacuolation and differentiation of the parenchyma proceed, and is due to various factors, namely (1) some cell divisions which meet an air space (fig. 1 a); (2) cell divisions in opposite position (fig. 1 b); and (3) particularly early and later loss of contacts between cells (fig. 1 c–d). The air spaces finally become much larger

than the diameter of the trichome-like sclereid processes which originally entered them (fig. 1 d, 8), and in the case of later loss of contacts several air spaces containing sclereid branches may coalesce so that finally several branches which belong to different sclereids are seen in the same space (fig. 1 d).

INITIATION OF TRICHOSCLEREIDS AND THEIR GROWTH IN RELATION TO THE INTERCELLULAR SPACE SYSTEM.—In the cortex of young air roots, varying in diameter from 1.5 to 3.0 mm., polar, differential divisions occur, often as near as 700 μ from the apex. These divisions cut off one small cell, and very frequently a pair, at the basal (proximal pole) in many, but not in all cell files (fig. 4, 5). In this manner a distinct difference in cell size results. These last formed small cells may be readily recognized, on account of their dense and more deeply staining cytoplasmic content and their nuclei which are relatively large in relation to the cell volume (fig. 4, 5). In roots with comparatively little meristematic activity often only one small cell is formed in one cell file.

The small cell located at the basal (proximal) end of the cell file becomes a trichosclereid initial or mother cell from which processes develop into the adjacent parenchyma. Generally this cell is the only one which develops into a trichosclereid. If there is a second small cell present, it usually expands somewhat longitudinally, like the cells of the ordinary parenchyma; sometimes, however, both cells develop into trichosclereids (fig. 9). Thus both relative size, resulting from an unequal, differential division, and relative position within a cell file characterize the sclereid initials and make it easy to locate them at their earliest stage, i.e., when the cortical mother cells begin to divide. The foliar sclereids of *Camellia* and *Trochodendron*, according to Foster (1944, 1945), can be recognized only by the larger size of their nuclei, but in the present case a more determined type of idioblastic development occurs, from divisions which are both differential and bear a constant positional relation to the cells of the mother tissue.

The sclereid initials abut on several longitudinal air channels, usually one of them being a larger four- or five-sided space (fig. 2, 4, 8). After very little longitudinal expansion of the initial, tubular processes begin to grow out from it which enter the four-sided intercellular channel (fig. 2, 6). At this stage the growth of the invading branch thus appears free, like a root hair, or a tylosis pushing into a vessel. The originally small branches grow with great rapidity and also expand somewhat and thus often reach the end of an intercellular channel (fig. 7). Throughout their growth the trichosclereids are thus characterized by the fact that they closely follow the developing intercellular system and by their ability to change their direction of growth, to branch and to fork at their ends when obstacles of various kinds are encountered. In this manner forms are produced which closely resemble certain fibers, such as those found in *Cannabis* and *Luffa* (Sinnott and

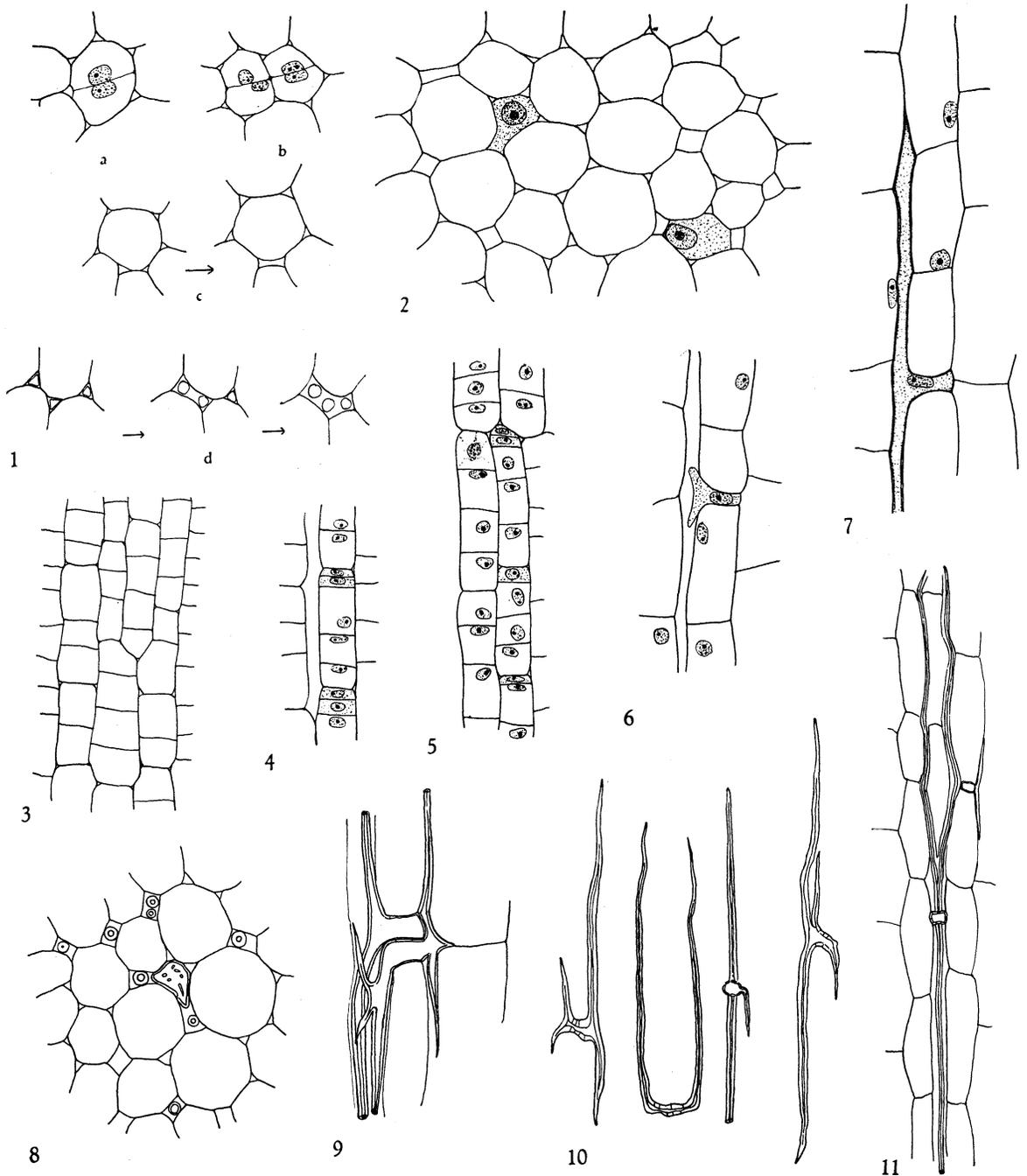


Fig. 1-11.—Fig. 1. Transverse sections through cortical parenchyma of air root, showing origin of quadrangular and pentangular air spaces by early cell divisions (a and b), by early loss of cell contacts (c), and by later loss of cell contacts (d).—Fig. 2. Transverse section through cortical parenchyma, showing two trichosclereid initials, one of which sends out a process into a quadrangular air space. $\times 450$.—Fig. 3. Longitudinal section through root meristem 500μ from apex, showing files of cells. $\times 240$. (In all longitudinal sections the root apex is toward the bottom of the page.)—Fig. 4. Similar section, showing formation of trichosclereid initials at basal (proximal) end of two cell files abutting on longitudinal intercellular space. 700μ from apex. $\times 240$.—Fig. 5. Similar section; one nucleus (upper left) is in prophase. $\times 240$.—Fig. 6. Similar section, 2200μ from apex, showing the formation of processes into an intercellular space (compare fig. 2). $\times 240$.—Fig. 7. More advanced stage, in which the basal end of the process has reached the end of an intercellular space; 2200μ from apex. $\times 240$.—Fig. 8. Transverse section similar to figure 2, showing both the initial part of the trichosclereid and several processes in the thickened mature stage. The initial part is pitted. $\times 195$.—Fig. 9. Longitudinal section, showing parts of two mature trichosclereids which have developed from divisions as in figure 4. $\times 240$.—Fig. 10. Four comparatively short trichosclereids from macerated material, showing diversity of branching and distribution of pits; the walls are somewhat swollen. $\times 105$.—Fig. 11. Trichosclereid, the upper process of which has formed two branches around a parenchyma cell. $\times 105$.

Bloch, 1943), although these grow in much closer morphological and physiological contact with the adjacent parenchyma cell walls. The type of growth observed in the *Monstera* trichosclereids appears to be that formerly described as "intrusive," in which growth occurs mainly at the tips of proliferating portions of the cells, with no appreciable shifting or sliding of larger portions of cell walls (Sinnott and Bloch, 1939, 1943). In the inner cortical regions trichosclereids occur whose processes follow closely the course of the intercellular canals in zig-zag fashion (fig. 12). The diameter of these intercellular channels changes at regular intervals owing to the curved surface of the adjacent longitudinal parenchyma walls, and the trichosclereid processes show corresponding wider portions. It was found that this relation had not changed after maturation and sclerification of the processes (fig. 11, 12) which would indicate that there had been no slipping or sliding of large portions of the processes within the intercellular canal, any possible sliding occurring only at the tip. Furthermore, small lateral branches and outgrowths, which protrude into the adjacent parenchyma, are never subsequently torn out of place.

The growth of the sclereid processes is free within an intercellular space or in rather close contact with parenchyma membranes, but wherever an obstacle in the form of a cell wall is encountered, the processes are easily deformed and deflected from their course. In the early stages the advancing arms can frequently be seen in close contact with the middle lamella (intercellular substance) of the parenchyma cells at the end of an intercellular space (fig. 7), and in fully differentiated trichosclereids the very narrow and pointed tips of long processes may occasionally be seen in close contact with the parenchyma walls. It is difficult, of course, to say whether and to what degree the sclereid might actively contribute to the separation of the primary membranes of the cortex cells. In *Monstera* this process seems to take place relatively easily, and the intrusive growth of the processes may be considerably facilitated by the fact that it proceeds along the course of natural air space formation. The wall of the processes seems never to be in very intimate connection with the parenchyma walls since it separates most readily under various treatments.

Branching of the trichosclereid may be associated with the formation of new air spaces adjacent to it, or may be induced by obstacles encountered by the processes, such as cell contacts, or by growing parts of other trichosclereids. Mostly two or four processes are seen to develop from one initial (fig. 10); H-shaped cells, known to occur in many species, are common (fig. 15). Branching and bending of processes around intervening cells are frequent (fig. 11), and very irregular forms were figured by van Tieghem (1866) from the leaves of *Spathiphyllum lanceaefolium* and *Torneia fragrans*. The tip of the growing sclereid process may be induced to branch by even a slight obstacle such as the young tip of

another process, growing in the same air space, but in the opposite direction (fig. 14). Branching of processes within an air space, however, does not seem to occur as readily as in other types of freely growing hairs, for example in some of the internal hair cells described by Gütler (1905).

Sclereid initials may remain dormant for some time until suitable conditions for their further development arise. They then may grow into a space full of other more mature sclereid processes.

SECONDARY THICKENING OF THE TRICHOSCLEREIDS.—In the mature stage the walls of the sclereid arms are considerably thickened and the lumina reduced; the cells possess pointed, tapering tips, much like bast fibers, and the thickness of the secondary layers decreases gradually toward both the tip and the initial (fig. 13, left). The basal or central initial portion of the cell is usually less thickened (fig. 13, 16), a fact already mentioned by Wiesner (1875) for sclereids of the mesophyll. The same author noted an irregular thickening of the wall the external contour of which, similar to the bast fiber of jute, is not always parallel to the inner one. In the present investigation the same irregularities were noted. Wiesner also found that the secondary wall of the arms shows some spiral striation, but no pits. In the present study it was found that pits occur in the initial portion of the cell which contains the nucleus, but no pits were found in the branches. Obviously the initial part of the cell retains from the beginning close morphological and physiological contact with the neighboring cells, similar to the sclereid of *Trochodendron*.

As the air spaces grow wider, the growth in width of the processes does not keep pace with them. In *Raphidophora decursiva*, another species of the *Monstera* family, however, the branches fill almost the entire space, even in the mature, sclerotic stage, showing the imprint of the outlines of the parenchyma on their walls (fig. 17). Van Tieghem noted the same in *Raphidophora pinnata* (1866; p. 153).

The mature walls of the *Monstera* sclereids are impregnated with suberin, but not truly lignified. They stain readily with Sudan III and safranin, but do not give the lignin reaction with phloroglucin and hydrochloric acid, unlike the sclereids in other members of the *Araceae*.

Final thickening and suberization of the wall do not take place until a considerable distance from the root tip. This distance varies with the type of air root and with its diameter; in a thick air root, 80 cm. long and 15 mm. wide at its base, the sclereids at 20 mm. from the tip and 7 mm. diameter were still thin-walled.

Striking differences in the onset of wall thickening and chemical impregnation occur, not only between individual sclereids, but also between the various parts of the same cell. At the same root level sclereids are found which are fully mature, while others may be still thin-walled or occasionally even beginning to develop (fig. 13). Furthermore, parts of the long arms of one cell, often the tip or a portion some

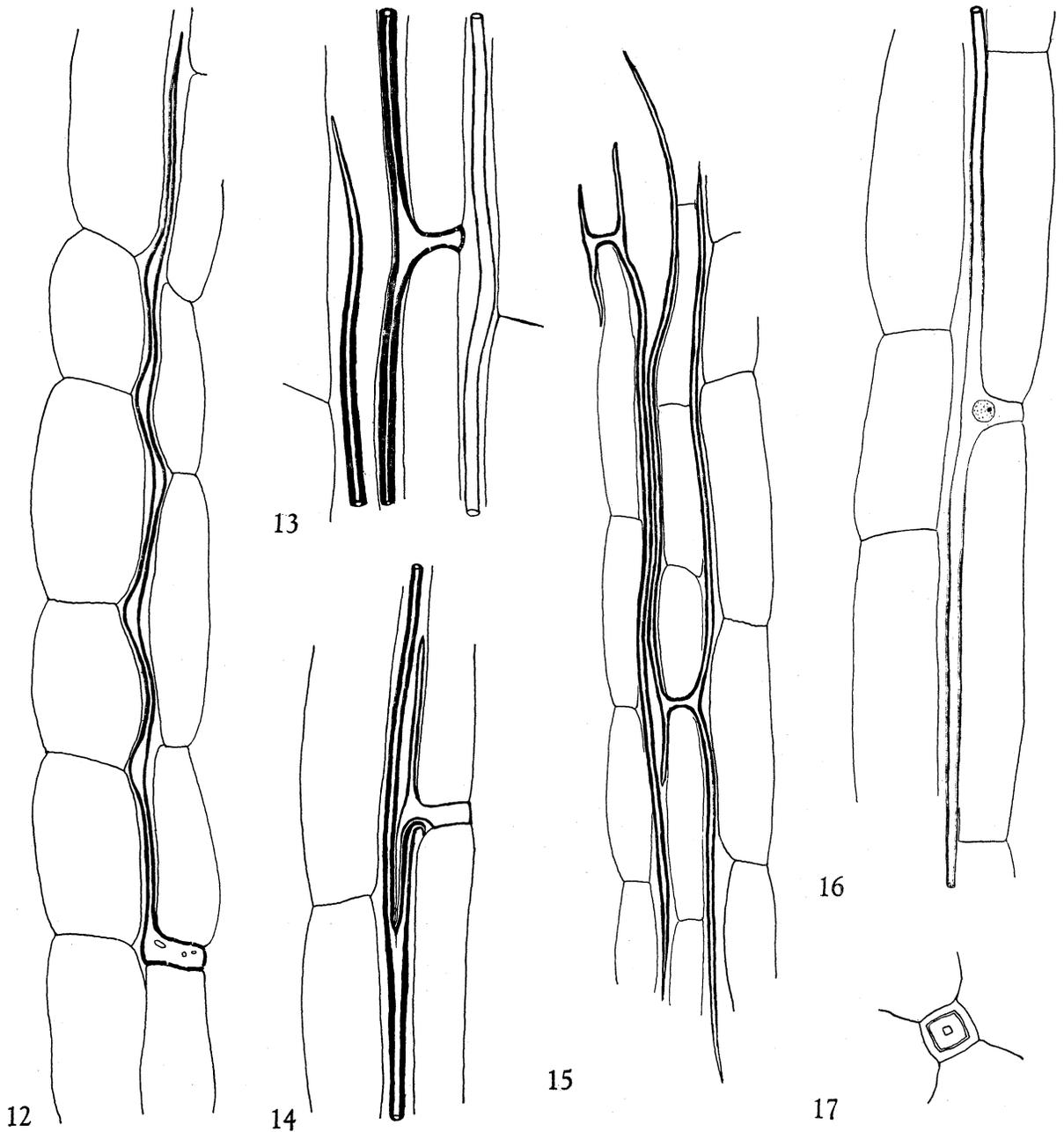


Fig. 12-17.—Fig. 12-16 showing later stages of growth and differentiation of trichosclereids. $\times 290$.—Fig. 12. Trichosclereid, showing relation between regions of lateral expansion in process and width of intercellular canal.—Fig. 13. Three trichosclereids which have developed close to each other, the two at left are fully differentiated, the one at right still thin-walled. Note that the secondary layers of the wall become thinner toward the tip and toward the initial part of the cell.—Fig. 14. Two trichosclereids in the same intercellular canal, one process grows upward and has split in two where it encountered the small process growing downward.—Fig. 15. Two H-shaped sclereids.—Fig. 16. Trichosclereid showing beginning of secondary thickening of the wall. The central initial portion is still thin-walled and shows the nucleus.—Fig. 17. Transverse section, through process of mature trichosclereid is air root of *Raphidophora decursiva*, showing collenchymatous thickening of parenchyma cells around original air space, quadrangular trichosclereid process which fills the air space completely, and small quadrangular lumen of process. $\times 360$.

distance from it, may begin to thicken and change chemically, while other parts are still thin-walled, and this may account for the subsequent variation in the thickness of the secondary layers at maturity which were noted by Wiesner and the writer. In

fibers, such as those of *Luffa*, the growing tip is generally the last to lignify; in the present case the central, initial parts and adjacent areas of the branches mature last (fig. 16).

The diameter and lumen of the trichosclereid

arms may also vary considerably, not so much because of differences in the thickness of the secondary layers, but on account of the previously described expansion of the processes in regions where the intercellular channels naturally widen. Especially in the inner cortical region this occurs frequently, and a peculiar zig-zag-shaped course of the branches results. In the regions where these expand laterally the secondary layers are frequently, but not always, somewhat thinner (fig. 12).

All these observations seem to indicate that both growth and differentiation are more variable and irregular in sclereids than in fibers, bast cells, parenchyma cells, etc. The process of wall differentiation seems not to be entirely controlled by a gradient which affects all cells at the same level evenly, but rather to be an individual reaction of the cell in relation to local conditions. Such conditions must vary considerably, since the cells are of considerable length; cells 2–3.5 mm. long are not rare. Environmental conditions would thus determine to some degree not only the growth reactions in various parts of the same cell but also the ultimate differentiation of its wall.

DISCUSSION.—The trichosclereids in the air root of *Monstera deliciosa* are interesting in several respects. The most striking feature is their origin from mother cells near the apex, formed by late, polar and differential divisions, analogous to those occurring in the hypodermis, at the basal ends of cell files of the cortical parenchyma. The position and origin of these “idioblasts” are thus not accidental, random ones, but have a definite relationship to the cell pattern in the mother tissue from which they arise. A difference between sclereid initial and ordinary parenchyma in cell size and in the relation of the nucleus to the cell volume results, and highly embryonic initials are formed adjacent to cells somewhat more advanced in maturation, comparable to the trichoblasts of the surface layer of grass roots, which also form a characteristic pattern in the mother tissue. The root hair cell, however, later undergoes considerable longitudinal expansion, but the sclereid initial grows very little, its expansion being limited almost entirely to the tubular branches. Developmentally the trichosclereids of *Monstera* can best be understood if one remembers that they are formed as densely cytoplasmic cells at a time when their neighbors are already in the vacuolating and expanding stage. Like the trichoblasts of the epidermis they are located on surfaces abutting on air, under conditions which apparently favor specific expansion, growth and subsequent differentiation of the wall.

Compared with the other cells of the cortical parenchyma the development of the trichosclereids would seem to indicate a highly specific nature as a result of differential reactivity. A similar difference in behavior occurs between the root hair cells (trichoblasts) and the ordinary cells in the surface layer of roots, but in this case the distinction is frequently not very sharp, and ordinary epidermis cells

may be induced to form root hairs also. In the present case it was never observed that other cortical cells were capable of developing into a trichosclereid, while previous regeneration experiments showed (Bloch, 1944) that, at a later stage of general differentiation and developmental potency of the ground tissue, any cortical parenchyma cell in the air root of *Monstera* becomes able to differentiate into a hypodermal brachysclereid, if the conditions for their differentiation are experimentally created which in a certain position exist adjacent to an external or internal surface.

In other cases of idioblastic development of sclereids similar patterns and intercellular relationships may exist, but may not always be as pronounced and easily recognizable as in the case here described. Foster (1945) in his description of sclereid development in the spongy parenchyma of *Trochodendron* has emphasized that all parenchyma cells appear to retain the capacity to enlarge and to ramify, and that “the entire career of development of an idioblastic sclereid is marked by a ‘rugged individualism’ which suggests that the normal correlative forces operative during the differentiation *en masse* of parenchyma elements have been replaced locally by new and unique factors.” It is significant in this connection that the definition of the term “idioblast” used by Sachs and other authors for these and similar cells does not refer to any rules or factors which might control their distribution in the mother tissue. Their scattered distribution makes them often appear less typical a part of the general tissue pattern than other more compact tissue systems. Adding to this feature the characteristic “invasive” or rather long-continued character of their growth, which distinguishes them so sharply from their neighbors, the impression may be gained that these cells possess capacities specifically different from the majority of plant cells in closely correlated cell aggregates. However, the distribution and development of the idioblastic trichosclereids of *Monstera*, which have a close genetic relationship to a pattern of cell divisions in the mother tissue, would appear to be as much under organized control as other types of solitary cells, such as stoma cells, certain external hair cells, and other forms which have not been considered to be of idioblastic nature, since more was known about their developmental history. In the growth of the trichosclereids no phenomena were observed which would be fundamentally different from those already known to occur generally in the growth of plant cells, various methods and possibilities of which have been discussed in previous papers (Sinnett and Bloch, 1939, 1943). It is known that many plant cells are able to grow in several ways in response to changing external conditions. A parenchyma cell may show very restrained growth in most types of tissue, under certain conditions its membrane may exhibit considerable differential growth, or may grow freely, for example as a tylosis, into an adjacent lacuna. The trichosclereids of the *Monstera* air roots arise from densely cytoplasmic initials

formed in the meristem by relatively late divisions and in a position abutting on lacunae which are already present or fast developing. These facts are obviously related to the subsequent growth of the sclereids, which is not shared by their neighbors, and should be taken into account in its further analysis. Such "individualistic" behavior, especially emphasized by Foster (1945), appears as a natural concomitant in this extreme type of differentiation in which cells in different stages of development and therefore of different reactivity and developmental potency are exposed to probably very similar, if not the same, external conditions. It is not, in the writer's opinion, an instance of morphogenetically uncontrolled, independent, or pathological growth. The phenomenon of idioblastic development of this kind in plants rather appears as part of the more general problem of differentiation and pattern.

All histological differentiation can be interpreted as a process in which cells become individually different from each other. During this process they go through different stages of reactivity or developmental potency (Bloch, 1944) upon which varied local conditions have differential ways of "control"; thus many individual characteristics are developed. How this is achieved in a specifically and well coordinated manner within the pattern of a given genotype is a major problem of organized development.

The trichosclereids in the air root of *Monstera* offer still another interesting aspect. It has been suggested that their function may be a mechanical one, somewhat comparable to a network of fibers. It appears of interest to compare the pattern in *Monstera* with the mechanical system in the air roots of some orchids, for example *Cattleya*, the so-called "Réseau de Soutien." While in the cortex of air roots of *Monstera* and other Araceae a mechanical system is achieved by a formation of a pattern of fiber-like, sclerotic hairs, in the "Réseau de Soutien" of the cortex of orchid air roots, a continuous network is formed in a whole group of cells by branching bands of thickened and lignified walls, comparable somewhat to the Casparian strip in the endodermis or the thickening in xylem elements (Sinnott and Bloch, 1945). One natural consequence of these differences is that in the air root of *Monstera* a branch root could readily make its way through the cortex, simply pushing aside the sclerotic processes which form no continuous mechanical system and therefore offer little resistance. In the air root of orchids, however, the continuous network would form a real obstacle, and it was found (Bloch, 1935) that here sectors of the root in which branch roots are being formed from the beginning remain free of the lignified thickenings.

SUMMARY

In the air root of *Monstera deliciosa* trichosclereids are formed early in the cortical rib meristem, which proliferate between parenchyma cells like hairs, sending out long processes which are prosenchymatous like those of astrosclereids or fibers. The

cells are thus clearly distinguished from the brachysclereids of the same root which differentiate at a much later stage from non-specialized cortical ground parenchyma cells of the hypodermal region or adjacent to internal surfaces.

The trichosclereids originate from late, differential, polar divisions of cortex cells near the root apex, analogous to those which give rise to passage cells in the hypodermis. These special divisions occur at the basal (proximal) ends of cell files in the rib meristem, and the trichosclereid initials can be recognized by their position, small size, dense content and large nucleus. Their subsequent specific activity, which distinguishes them from their differently reactive neighbors, consists in the formation of prosenchymatous processes which grow rapidly into the intercellular space system as it develops between the cortical parenchyma cells. This behavior appears to be correlated with their late appearance as "embryonic" cells and with the presence of air spaces. Their subsequently long-continued growth is comparable to that of the external trichoblasts of the grass root epidermis and other plants. The distribution of trichosclereids in the air root of *Monstera* can thus be traced back to a pattern of differential cell divisions in the fundamental tissue which precedes it, and later idioblastic development appears as the outcome of specific differentiation rather than uncontrolled growth of solitary cells.

The growth of the processes of the trichosclereids resembles that of other intrusively growing fibers and sclereids and bears a close relationship to changes in the intercellular space system; later differentiation of the wall of the sclereids is comparable to that of ordinary fibers or sclerenchyma cells, although somewhat more irregular. Pit canals occur only in the initial, central portion of the sclereid, and secondary thickening and suberization are not always initiated uniformly over the entire length of the long tubular branches of a sclereid, but are apparently often subject to variable local conditions.

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GROWTH OF TOMATO ROOTS AS INFLUENCED BY OXYGEN IN THE NUTRIENT SOLUTION¹

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THE GROWTH of many species of plants in water culture is greatly improved by bubbling compressed air through the nutrient solution. This response suggests that the same factors important in soil aeration, *i.e.*, oxygen and carbon dioxide (*cf.* Clements, 1921; Cannon, 1925; Conway, 1940), are involved in water cultures also.

In spite of the large number of accounts written on the benefits of aeration in water cultures there is meager information in the literature concerning the concentrations of oxygen and carbon dioxide that occur in aerated and non-aerated solutions. The result has been that some investigators attribute the aerational responses of the plants to oxygen while others attribute them to carbon dioxide. Also, there is little information on the effect of oxygen tension on root structure, although data are available on the influence of various concentrations of oxygen on the absorption of ions and the production of organic acids.

This paper presents the results of an investigation of the influence of oxygen content in the nutrient solution on the growth of tomato roots. The aims were to determine the concentrations of oxygen and carbon dioxide occurring in aerated and non-aerated water cultures during a period of several weeks and to interpret the growth responses of the plants on the basis of experiments in which these factors were controlled. In a later paper the influence of oxygen concentration on root structure will be considered.

REVIEW OF LITERATURE.—The recognition of aeration as a factor in the water culture of plants was made at the time this method of growing plants was undergoing its first rapid development. Sachs (1860) recognized that a certain amount of air,

in addition to the minerals, must be present in the water for the best growth of the plants.

Arker (1901) made an intensive study of the effects of aerating water, soil, and mud cultures of *Lupinus albus* and *Helianthus annuus* and found that the roots of both of these species made more rapid growth when air was bubbled through the cultures.

Hall, Brenchley, and Underwood (1914) noted a superior growth of barley and lupins in cultures of coarse sand over those in water, fine sand, or silt. While the root systems of plants in kaolin and coarse sand developed freely, those of fine sand and silt were restricted. The authors suspected aeration as the disturbing factor and tested that assumption by arranging comparative water cultures in which one series was not aerated whereas in the other bottles a continuous current of air was bubbled through the solutions. Both the barley and lupins made the greater growth in the aerated solutions, as indicated by the dry weights.

Free (1917) found that passing oxygen, nitrogen, or air through the solutions had no appreciable effect on buckwheat, when compared with open or sealed controls, but that in cultures treated with carbon dioxide the plants wilted within a few hours and died within a few days.

Stiles and Jörgensen (1917) obtained significantly better growth of barley and balsam by aerating the culture solution, but no response was obtained in buckwheat, which was in accord with the finding of Free. Stiles and Jörgensen recognized several possible factors as operating in their experiments and therefore refrained from correlating the beneficial effects of aeration with oxygen supply, removal of carbon dioxide, and other causes.

Pember (1917) did not obtain beneficial effects from daily aerations of barley.

Beals (1917) grew two *Zea Mays* plants in water culture and aerated the solution in one of the con-

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