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Organization and development of apical root meristem in *Elodea canadensis* (Rich). Casp. and *Elodea densa* (Planck) Casp.

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Analysis of the differences and discrepancies in the views on the types of growth of the apical meristem of roots led some investigators relatively early, already in beginning of the 19th century, to the conclusion that the structure of apical root meristem undergoes, at least in some species, changes in the course of development.

Holle (1876) on the basis of the results of other contemporary authors (Reinke 1872, Janczewski 1874, Eriksson 1876, 1878) and of his own investigations on plant development, particularly on *Pisum*, *Phaseolus*, *Tilia* and *Acer*, reached the conclusion that the main reason for the differences and discrepancies in the prevalent views was the insufficient understanding of the changes occurring in the meristem cell arrangement during ontogenesis. He affirmed "dass ein zum Theil mit voller Bestimmtheit ausgesprochener Modus des Spitzenwachstums im Laufe der Entwicklung des Organs in einen anderen übergeht" (Holle 1876 p. 252). He saw in this secondary type of growth "den extremsten Fall einer Degeneration des typischen Vegetationspunktes" (l.c., p. 251).

Holle further demonstrated that the moment of appearance of "the secondary growth type" during development varies from one plant species to another. For instance in *Pisum*, *Phaseolus* and *Cucumis* the secondary type already appears in the embryo, in *Robinia*, *Vicia* and *Tilia* — soon after germination, and in *Acer* only later, in older roots.

Considering the typical, primary growth type of apical root meristem in roots of various plants, Holle established one type common to all dicotyledonous plants which he termed "Helianthus-Typus" and one type for monocotyledons "Monocotylen-Typus".

Changes in the structure of the meristem in the course of development have been also observed by Schönland (1887/88 quoted after Guttenberg 1940, p. 44). Observing the development of *Eichhornia azurea*, *E. crassipes* and *Pontederia cordata* roots, he established that the apical meristem of the youngest roots in these species had initial cells common to the epidermis and primary cortex. In older roots, the epidermis had its own initial cells arranged in a separate layer. The four-layer structure of the meristem in older roots of *Eichhornia* and *Pontederia* would thus correspond to the structural type described for the first time by Janczewski (1874) in the roots of *Pistia* and *Hydrocharis*.

Also Esau (1953) classes meristems with a four-layer structure to a separate type.

Studies on development performed lately by Guttenberg et al.: Guttenberg (1940, 1947, 1960), Guttenberg, Heydel, Pankow (1954a, b), Guttenberg, Burmeister, Brosell (1955), Guttenberg und Mitarbeiter (1957) also proved, that the meristem structure of apical roots changes, at least in some plants during development.

The discovery by the aforementioned investigators of the single transformation of the root apex structure did not essentially change the views on the stability of the structural pattern. According to the opinion prevailing up to date, accepted only tacitly, apical root meristem would have a stable structure. The changes to which Holle, Schönland and Guttenberg referred would occur only once and only very early in the course of root development. The new secondary structural patterns of the meristem should be considered as stable and characteristic of the given species.

The results of the author's preliminary observations concerning the structure and development of the meristem of apical roots in the order *Helobiae* do not fit the above expounded views. It was namely found that a change of the structural patterns occurs several times in the course of elongation growth of the root. This phenomenon is particularly pronounced in *Elodea canadensis* and *E. densa* as will further be described.

MATERIAL AND METHODS

Adventitious roots of *Elodea canadensis* and *E. densa* served as material for the investigation. The roots of *E. canadensis* were collected in the small river Czechówka in the environs of Lublin and those of *E. densa* were received from the aquarium of the Wrocław Botanical Garden. The roots of both species were so chosen as to obtain a continuous growth series. Primordia of the youngest roots were obtained by taking parts of the stems with leaf and branch nodes. Also roots of 0.5, 1, 4, 7, 10, 15, 20, 30 and 50 cm length were collected. All the roots were fixed in CrAF (0.5—1—20), and after short washing were dehydrated, passed through benzene and embedded in paraffin. The roots embedded in blocks were cut with a microtome in 5μ sections. A number of longitudinal and cross sections were prepared. The sections stuck on microscopic slides with Haupt's glue were stained by several methods. The best results were obtained by staining with tannin with ferric ammonia alum and counterstaining with hematoxylin. A Lumipan microscope was used. Photographs were taken with an Exacta-Varex camera.

GENERAL REMARKS

Formation and structure of adventitious roots in *Elodea*.

Adventitious roots of *Elodea canadensis* and *E. densa* develop as a rule singly in the leaf branch nodes, that is in the nodes from which lateral shoots arise. They grow out of the stem between the latter and an axillary shoot at the level of separation of the branch trace. The initiation of these roots may be distinguished already near the apex of the stem. However not all the root primordia develop further.

Most remain in primordial form within the mother organ. Only few roots attain full development. In *E. canadensis* they reach a length of about 20 cm. The roots of *E. densa* are much longer, attaining sometimes up to 50 cm. The mean thickness of the roots in *E. canadensis* is about 300 μ; in *E. densa* they are somewhat thicker, about 450 μ in diameter.

In the anatomical structure of the *E. canadensis* roots no major differences were found as compared to the description given among other authors by Van Tieghem (1870/71), Schwarz (1883) and Snow (1905) except for the size of the cells. The same was observed by Herrig (1951) in these species at the stem apex.

According to the information reported by Guttenberg (1940) as given by Kroemer (1903) and Wilson (1936), the central cylinder occupies about 1/5 of the entire cross section diameter. It comprises generally vascular bundles both of xylem and of bast, four of each. The centre of the cylinder is occupied by the central metaxylem vessel. The sieve tubes are distinguishable at about a 150 μ distance from the apex; they are distinctly visible in the cross section on Plate V (Photos *6*, *7*). The pericycle consists of a single cell layer and is rather regular. It would seem that under normal conditions it does not form lateral roots which occur in large numbers in other species of the order *Helobiae* e.g. in *Sagittaria*.

The structure of the primary cortex is not homogeneous along the whole root length. In the apical parts of the root it has a radial structure with small intercellular spaces (Plate V, *4*). At a somewhat greater distance from the apex, the primary cortex cells undergo gradually characteristic diagonal divisions (Plate V, *5*). Owing to these divisions closely associated with the occurrence of large intercellular spaces, the radial arrangement of the cells of the central part of the cortex is substituted by an annular arrangement of cells around the tracheae (Plate V, *5—7*). In the two layers of cortical cells adjacent to the endoderm, the radial arrangment persists for a long time. The endoderm contains Caspary's strands, does not undergo suberization and has no secondary thickenings. The exoderm is built of one cell layer. The rhizoderm is differentiated into tricho- and atrichoblasts. *Elodea canadensis* when suspended in water does not produce root hairs, they only appear at the site of contact of the root with soil.

General characteristic of the organization of meristem

The apical meristem of adventitious roots in *Elodea canadensis* and *E. densa* has a similar structure. It has the root cap typical of monocotyledons, a distinct central cylinder and would present no special interest were it not the repeated recurrence of reorganization of the constructional centre of the primary cortex in the course of growth of the root. Apart from the immediate consequences of these changes in the central part of the meristem, no noticeable differences in the remaining parts of the root apex could be detected.

The zone of dividing cells in the meristem is relatively high. Mitotic figures in the basal parts of the meristem can be observed even at a distance greater than four times the height of the cap, at a distance of 3000 μ from the border of the plerome (Plate III, *1*). Mitoses in this zone occur, however, chiefly in the protoderm and

Plate I

Central longitudinal sections through the adventitious root primordia of *Elodea canadensis* before their emergence from the cortex of the mother organism

Fig. 1 — The youngest primordium examined in this paper
Fig. 2 — Cell of the cortex constructional centre, in which the periclinal division is terminated
Fig. 3, 4 — Primordia with a primary four-layer growth pattern of the meristem
Fig. 5, 6 — One of the cells now situated in the constructional centre of the protodermis has divided periclinally

Plate II

Central longitudinal sections through young roots of *Elodea canadensis*

Fig. 1, 2 — Young root emerging from the cortex of the mother organism. All cells situated in the constructional centre of the protodermis have just periclinally divided
Fig. 3, 4 — Root of 1.5-cm length from the surface of the mother organism
Fig. 5, 6 — A root of a length of 2 cm
Fig. 7, 8 — The longest root length, about 20 cm, which I have ever found in *Elodea canadensis*.

Plate III

Central longitudinal sections of roots of *Elodea densa*

Fig. 1, 2 — Roots of about 20-cm length
Fig. 3, 4 — Roots of 20—30-cm length

Plate IV

Central longitudinal sections of roots of *Elodea densa* of 30—50 cm length

Plate V

Cross sections through root of *Elodea canadensis*. The figures on the right refer to the sequence of the pictures in the plate the left side figures give the distance between the section and the border of the root cap

Plates VI, VII

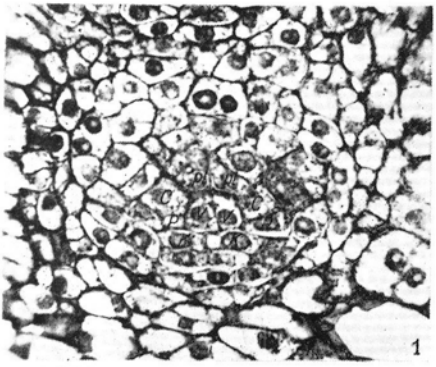
Scheme showing the successive reorganization of the apical root meristem in the course of development

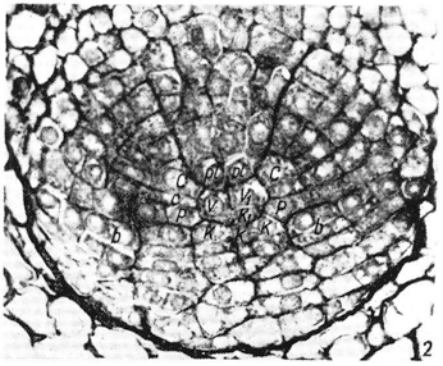
Legend to plates

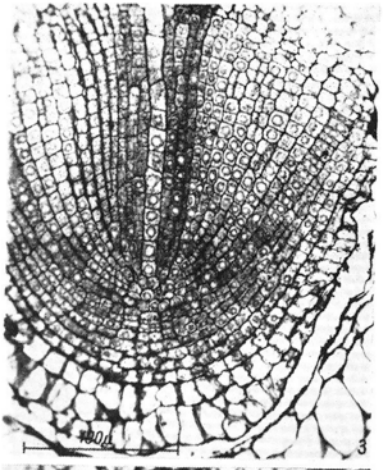
pl — Constructional centre cells of the vascular cylinder; *v* — cells of the constructional centre of the protoderm-cortex zone found in the youngest adventitious roots primordia; v_1, v_2, v_3 — cells of the cortex constructional centre arising from *v* cells as a result of successive periclinal divisions; *p* — initial cells of protodermis in the youngest primordia; p_1, p_2, p_3 — cells corresponding to the protodermis owing to their situation in relation to the cells of the cortex constructional centre; *k* — initial cells of the primary columella; k_1, k_2, k_3 — initial cells of the secondary, tertiary and quaternary columella; *c* — primary cell complexes of the cortex; c_1 — secondary cell complexes of the cortex; *b* — initial complexes of the lateral parts of the root cap; *pc* — pericycle; *e* — endodermis; *egz* — exodermis; trichobl. — trichoblast; *mk* — central vessel of the metaxylem; *pk* — protoxylem; *f* — phloem

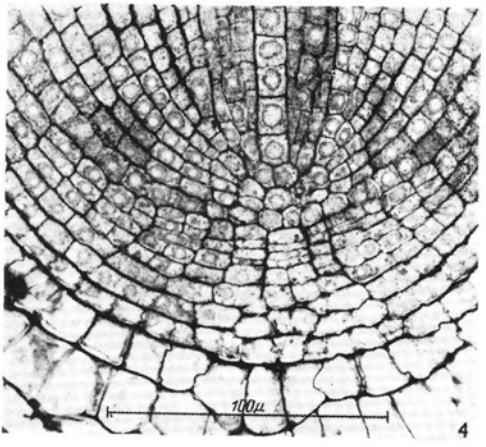
Thick lines show the border between the central cylinder and the primary cortex and the primary cap border; interrupted lines correspond to the border of the secondary columella; dotted lines show the cell complexes of the tertiary columella

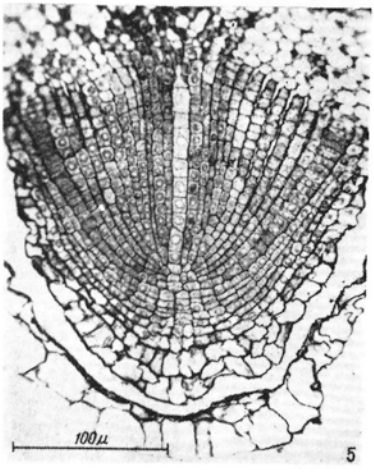
Plate I











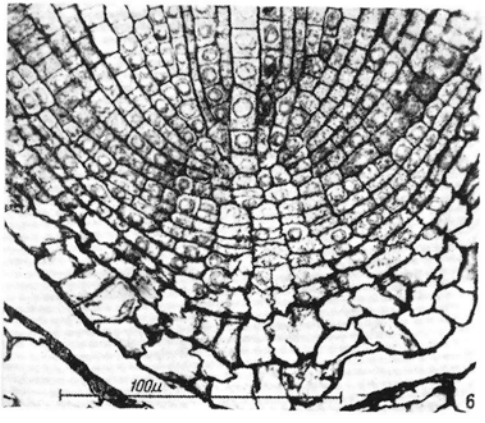
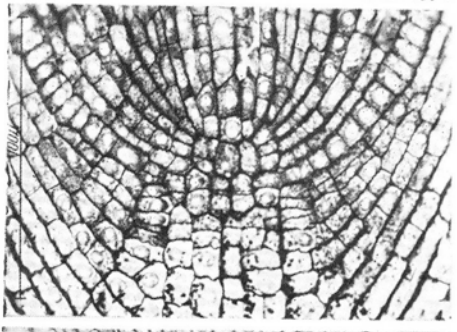
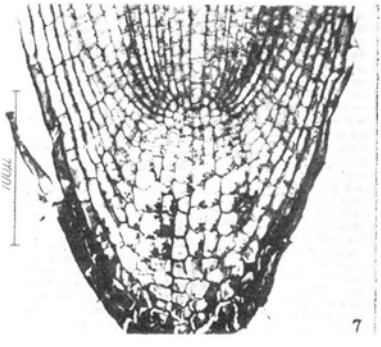


Plate II





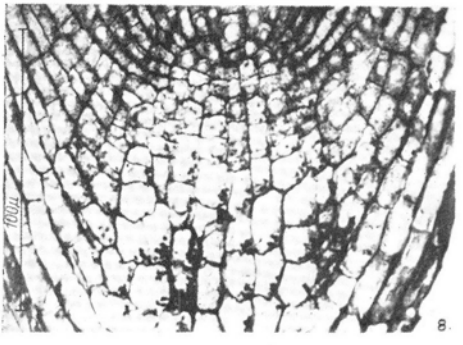
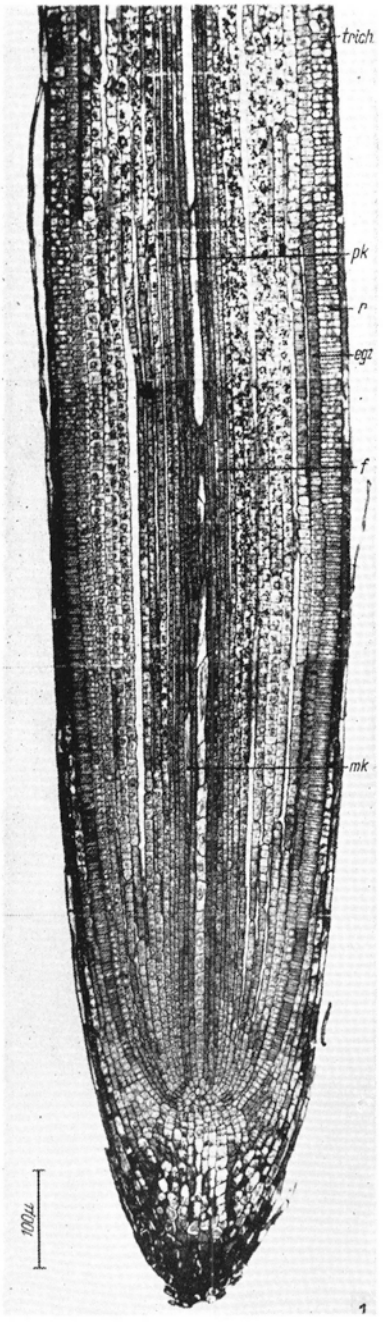
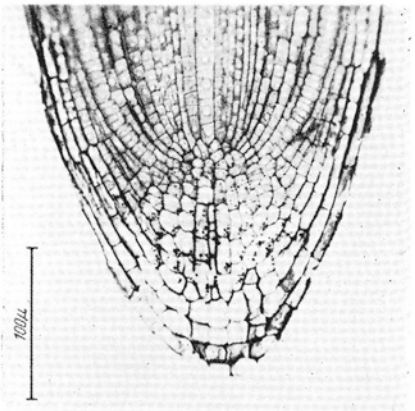
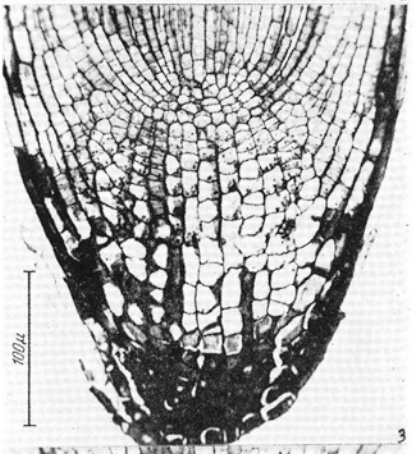


Plate III







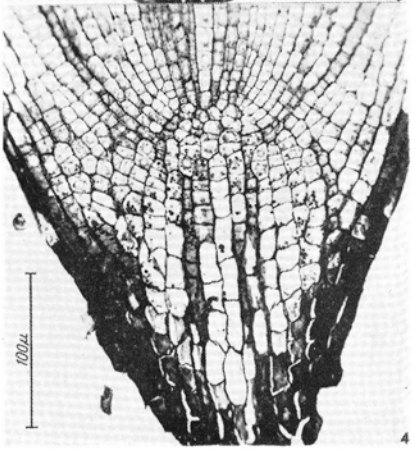
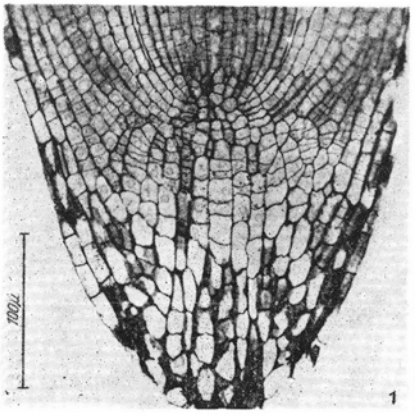
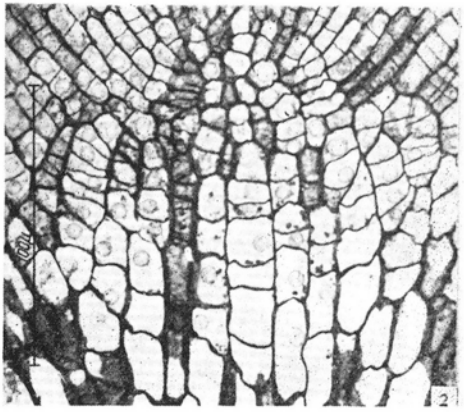
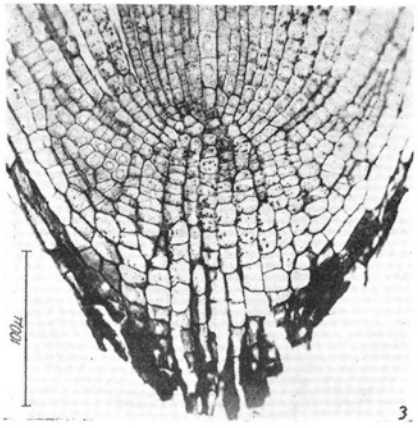
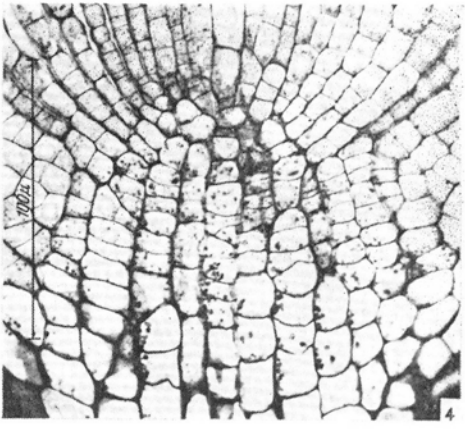


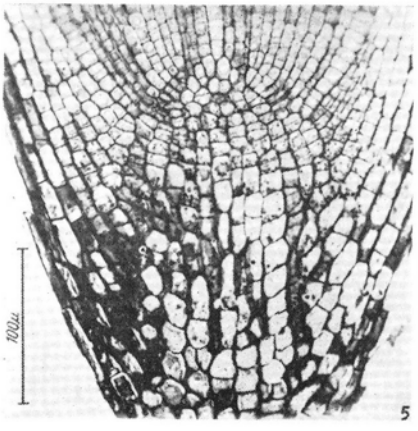
Plate IV











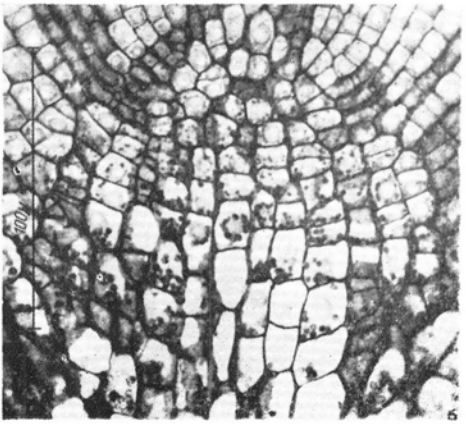
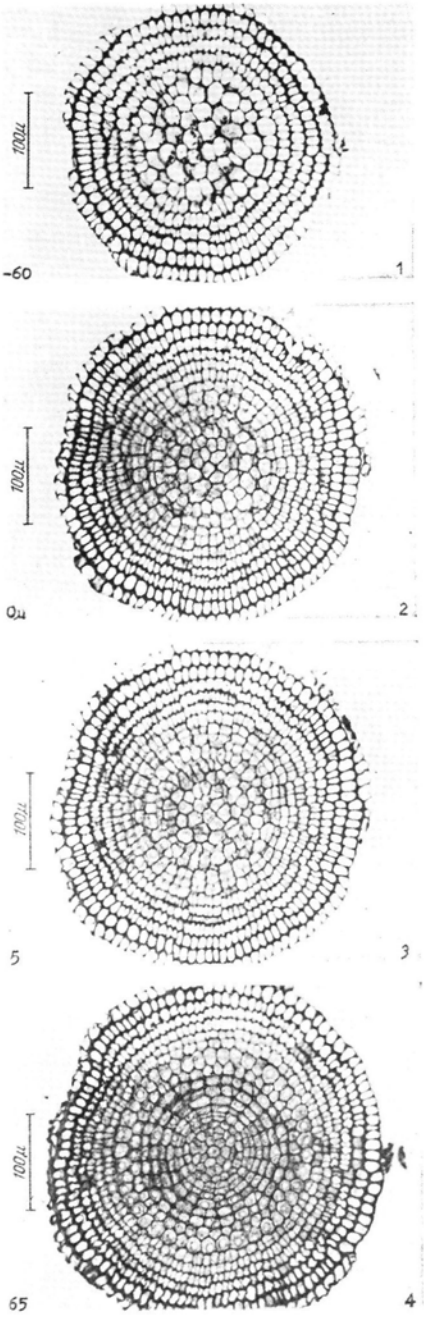


Plate V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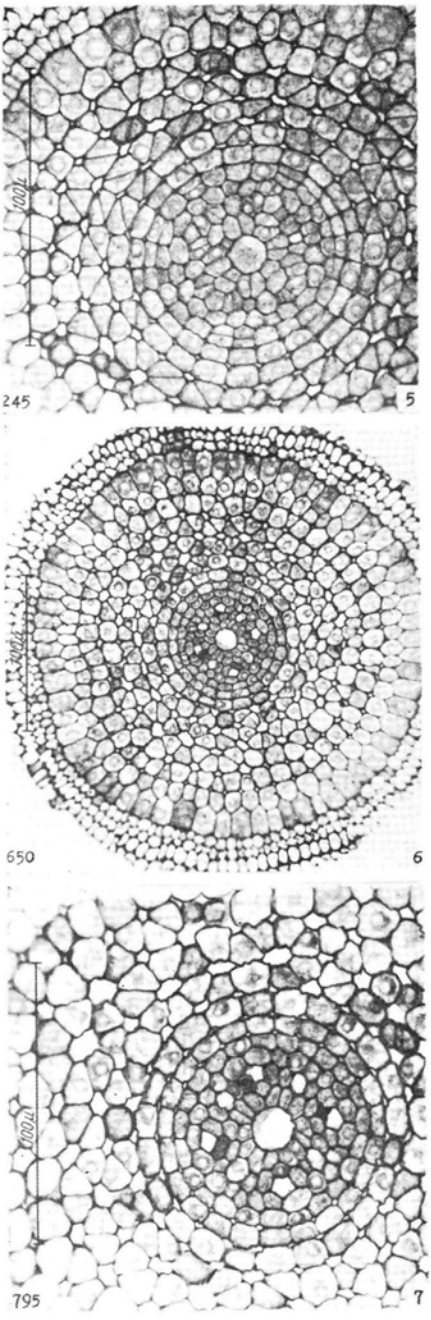
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Plate VI

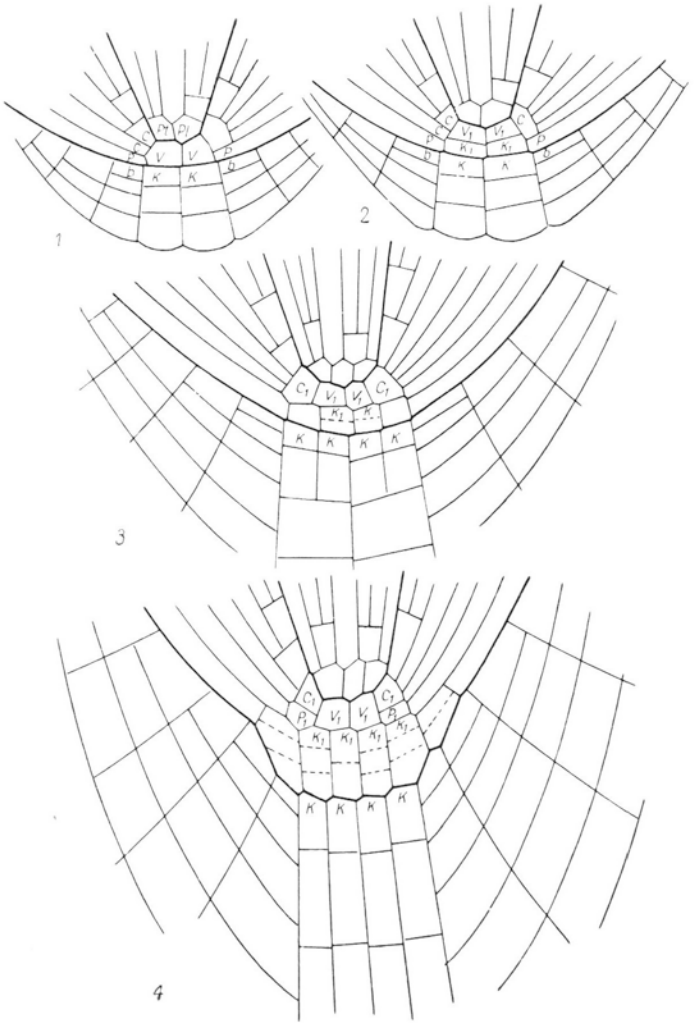
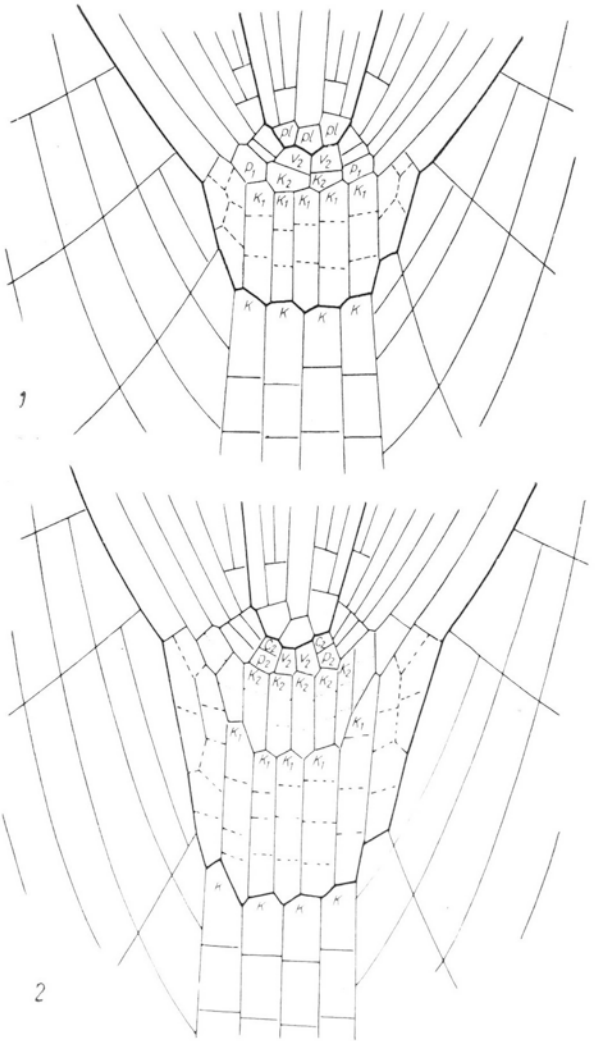


Plate VII



exoderm. They are observed much less frequently in the internal cortex cells. None could be found in the cells of the differentiating column of the central metaxylem vessel. This column stands off within the constructional centre of the central cylinder. The zone of divisions within the central vessel is relatively low. The elongation of the members of the vessel is already noticeable at a seven-cell height.

The pericycle is also distinct within the parts of the constructional centre (Plate III). It differs from other layers at first only by its localization. On longitudinal sections it is difficult to distinguish the pericycle from other layers in the basal parts of the meristem (Plate III). It is visible as a distinct layer only on cross sections (Plate V, *5—7*). The central cylinder presents generally on longitudinal sections eight cellular columns. It is often possible to distinguish among them the protoxylem mother cells, *pk*, and the cells of the future sieve tubes, *f* (Plate III, *1*).

The central cylinder is always set off. However, the border between the cells of the constructional centre of the cylinder and the cells of that of the primary cortex is only distinct in very young roots. During growth of the root, the border between the cells of these two layers is obliterated, owing to shifts of cells and their parenchymization, to such an extent that it is difficult to distinguish it without recurring to detailed analysis.

The primary cortex is arranged in columns which converge towards the cell layer of the cortex constructional centre below the limit of the cylinder. In the columnar arrangement of the cortex, features of a segmented structure may frequently be observed. The segmented complexes are generally noticeable only in the vicinity of the constructional centre (Plate I, *3—6*). In the course of development of the root, the layer of the constructional centre cells of the primary cortex splits repeatedly. In consequence of this, the protoderm and outer columns of the cortex become independent of the cortex constructional centre and the columella is renewed.

The root cap in *Elodea* root is relatively large and has a columella standing out distinctly against the lateral parts of the cap. No traces of desquamation of the outer cells are visible on the root cap. Its lateral sides are grown together with the protoderm and persist in the basal parts of the root beyond the zone of elongation (Plate III, *1*).

Organization of meristem in the course of root development.

The apical meristem of the youngest root primordia in which the first elements of the future root tissues are already distinguishable, has a highly differentiated structure.

All the cells of these primordia on longitudinal sections (Plate I, *1*) are arranged in cell complexes which constitute the rudiments of the growth pattern of the future root meristem. In photo *1* (Plate I), the centre of this pattern is occupied by a group of cells arranged in three superposed sharply set off layers. It is easily noticed that these cells are the constructional centre of the meristem, which in these primordia consists of three cell groups commonly known as initial cells Guttenberg (1960), Esau (1961), Clowes (1961) (Plate I, *1*).

The constructional centre cells of the central cylinder denoted *pl* are the innermost group. At this developmental stage they are almost the only structural element of the differentiating cylinder, since at this moment it is difficult to find any symptoms of separation of the first elements of the pericycle or the central metaxylem vessel.

The primary cortex is somewhat more advanced in development. Its constructional centre consists generally of three cells, of which on longitudinal sections usually two and sometimes one or three are visible. These cells (*v*) in young primordia often differ from the remaining cortex cells by their much larger dimensions. To these cells the youngest elements of the primary cortex, *c*, and protoderm, *p*, adhere on both sides. They are adjacent to the cells of the cortex constructional centre forming a *T* in horizontal position. It is easily seen, however, that this arrangement is not the result of some productive activity of the cells of the cortex constructional centre, as might be concluded, e.g. from the studies of Wagner (1939) or of Clowes (1954, 1959 and 1961).

No doubt we are dealing here with the same typical way of separation of adventitious root primordia out of the meristem, as has been described by Van Tieghem and Duoliot (1888), Steffen (1952) and Guttenberg (1960).

All the characteristic features of the primary three-layer organization of the meristem are visualized in photo *2* (Plate I). This organization is extremely regular reminding of the meristem organization in the roots of grasses. The central cylinder is sharply set off, the cells of the constructional centre of the cylinder, *pl*, constitute the group of its future initial cells. Under them lie the cells which so far have not played the role of initial cells: those of the structural centre common for the cortex and protoderm, *v*. Under the *v* cells are the future initial cells of the primary columella columns. The letter *b* denotes the initial complexes of the lateral parts of the root cap.

The absence of genetic connection between the cells of the meristem constructional centre and the youngest elements of their corresponding histogens proves that the cells of these centres have not so far contributed to the development of the root. It would result therefrom that the structural pattern of the root primordium developed independently of the cells of the constructional centres which, in the first stage of root development, do not play the role of initial cells.

The three-layer organization occurs, however, in *Elodea* only in very young root primordia. It still can be detected in such primordia as the one just described (Plate I, *2*). However, even in this meristem the beginning of transformation of the growth pattern is observable. It starts at the moment when periclinal cell division occurs in one of the cells of the cortex constructional centre. Similar periclinal divisions occur successively in all the cells of this centre. Owing to these divisions, the protoderm layer which in the youngest primordia was structurally linked with the cells of the cortex constructional centre, now separates as a distinct layer also in the parts of the meristem constructional centre (Plate I, *3*, *4*). This layer is sharply set off from the cells of the cortex constructional centre, v_1, by a sharply delimited border similar to that between the protoderm and the root cap. New cells of the constructional centre v_1 of the cortex preserve a close structural connection only with the cortex cells.

The differentiation of the protoderm as a separate layer changes the growth pattern of the meristem fundamentally. The new pattern with the independent layer of cells of the protoderm constructional centre becomes almost identical with that of the apical meristem of roots in various species which used to be classified as a separate growth type with four layers of initial cells. To this type distinguished for the first time by Janczewski (1874) have been classified the roots of *Pistia*, *Hydrocharis*, *Linum* and some species of *Potamogeton* (Treub 1876, Schuepp 1926, Guttenberg 1940, 1960 and Esau 1953).

The four-layer organization of the apical meristem in *Elodea* roots develops in root primordia when they still remain in the primary cortex of the mother organ. The above described organization appeared at this stage of development in all the specimens examined. In older root primordia within the mother organ, on the 50 slides examined, the author did not find one meristem with three-layer organization.

The four-layer type of organization of the meristem occurs, however, only in primordia still resting within the cortex. With their further development successive changes are observed in the cell arrangement. These changes occur in the previously differentiated layer of cells of the protoderm constructional centre. They are initially manifested only in periclinal division of the cells of this layer (Plates I, *5*, *6*; II, *1*, *2*).

Soon, however, generally immediately after the emergence of the root primordium from the cortex, elongation growth starts in the cells of the protoderm constructional centre, towards the cap tip (Plate II, *3*, *4*). After some time, the cells dividing once more, transform gradually into several-cell complexes of the secondary columella, which penetrate into the root cap (Plate II, *5*, *6*). In the cap, these cells shift the border existing so far between the cap and the axial part of the root towards the tip of the cap. Owing to these processes, the new border of the cap forms above the cell complexes of the secondary columella (Plate II, *5*, *6*).

Under the influence of these transformations, the four-layer growth pattern in meristem is completely obliterated. The new pattern has again all the characteristics of a three-layer organization which is so distinct that it may be observed in all preparations without difficulty at this stage of root development.

The cell arrangement with features of secondary three-layer organization occurs, however, only in roots much shorter than 15 cm. Longer roots have a different cell pattern.

In Plate II (*7*, *8*) the place of v_1 cells is occupied by two-cell complexes of common origin which are the product of priclinal divisions of the earlier single v_1 cells. Owing to these divisions the lower-lying sister cells which are now on the side adjacent to the cap, adhere to the layer of cells under the protoderm forming with them one continuous subprotodermal layer closed also on the axis of the meristem constructional centre (Plate II, *7*, *8*).

As the independent layer of cells of the subprotoderm constructional centre separates, the cell arrangement in the meristem transforms back to the four-layer pattern.

If we compare the four-layer meristem organization in the youngest primordia with that in older roots, we observe differences between them which are particularly well visualized by comparison of Plates I (*3*, *4*) and I (*7*, *8*).

The secondary four-layer structural pattern in the apical root meristem remained unchanged to the end of development of the *Elodea canadensis* roots.

The transformations of the meristem growth pattern in the development of roots in *Elodea densa* run an almost identical course as in *E. canadensis*. The secondary four-layer growth pattern in *E. densa*, appears, however, somewhat later, when the root has reached a length of about 20 cm (Plate III, *2*).

The pattern does not, however, persist in *E. densa* to the end of development. It undergoes further changes analogous to the previous transformations.

In this way once more a three-layer pattern arises wh'ch is the second secondary three-layer pattern (Plate IV, *1*, *2*).

In the course of this transformation the cells of the subprotodermal constructional centre transform to columnar complexes of the tertiary columella penetrating into the root cap (Plate IV, *1*, *2*).

This transformation in *E. densa* is probably not the last in the course of root development. The two-cell complex in Table IV (*3*, *4*) in the cortex constructional centre indicates the beginning of a subsequent reorganization.

A common feature of both of *Elodea* species examined is the formation of a secondary columella from the cells of the protoderm constructional centre. Transformation of these cells into multicell columns of the secondary columella brings in consequence a correlated growth of the adjacent protoderm cells along the root axis. These cells give rise to the lateral columns of the columella. Owing to this, a renewal in the course of root development of the lateral parts of the cap by cells of protodermal origin seems possible. In the roots of *Elodea canadensis* examined by the author this did not occur. In older *E. densa* roots the lateral parts of the cap are formed of cells of protoderm split in a way strikingly similar to that observed in the dermocaliptrogen of dicotyledons (Plate IV, *3*, *4*).

Thus there exists a basic similarity in the meristem organization between the meristem of older *Elodea* roots and that in dicotyledonous plants as has been pointed out by Janczewski (1874).

DISCUSSION

The results of the present investigation prove that in the apical meristem of *Elodea* roots, several different growth patterns occur. The differences between these patterns are of the same order as those which so far served as fundamental criteria for establishing growth types of apical root meristem (E.g. Kroll 1912).

It has already been pointed out in the description in detail that these patterns are connected with development and they have been presented as successive stages of development of the meristem. This conclusion resulted from the developmental method applied in the investigation. Roots of different lengths were, namely ana-

lyzed separately. The foregoing interpretation is further supported by the following arguments:

1) The youngest root primordia all grow according to one pattern.

2) Roots of similar length have the same pattern of meristem growth.

3) In the cellular arrangement in meristems with a definite organization, there persist traces of the earlier arrangement which allow to reconstruct the history of the successive growth patterns.

It would, therefore, seem that the occurrence of different growth patterns in the apical root meristem of *Elodea* may be considered as the result of developmental changes in the cell arrangement in the meristem. These changes will further be referred to as meristem reorganization.

The youngest root promordia have a three-layer organization with common cells for the primary cortex and protoderm constructional centres (v) (Plates I, *1*, *3*; VI, *1*).

The first reorganization of the growth pattern starts by the periclinal division of cells of the cortex constructional centre, v. Division of these cells leads to the differentiation of a separate cell layer of the protoderm constructional centre (Plate I, *2*, *3*; VI, *2*). The new pattern becomes almost identical to that in roots of species which were classified to a different growth type with four layers of initial cells. To this type were classified the roots of *Pistia*, *Hydrocharis*, some species of *Potamogeton* and *Linum* (Janczewski 1874; Treub 1876; Schuepp 1926; Guttenberg 1940, 1960 and Esau 1953).

According to Guttenberg (1960) in *Linum* all the growing roots have a four-layer organization. The situation is different in *Elodea*. The four-layer pattern of meristem growth subsists only for a short time. It begins to change even before the apex of the adventitious root emerges. The transformation starts by a change in the direction of growth of the protodermal constructional centre cells. The periclinal division of these cells is the consequence of the change in the direction of growth. This splitting gives rise to the development of cell complexes which penetrate into the cap area forming a secondary columella (Plate VI, *3*, *4*). They push back the complexes of primary columella cells, that is the primary border of the cap towards its apical part. The new secondary border of the cap forms above the cell complexes of the secondary columella. Simultaneously with the appearance of the secondary cap border, a separate cell layer, v_1, appears in the cortex constructional centre (Plate VI, *4*), and a three-layer meristem organization becomes visible.

Young adventitious roots growing from the stem to a length of at least some dozen centimeters or more exhibit such an organization. At this stage, in the middle layer of the meristem no symptoms of longitudinal or transverse growth can be seen. This layer separates the parts of the root growing in opposite directions: the central cylinder, and the columella. The distribution of growth in the middle part of the meristem is thus the same as in the closed-type meristem organization distinguished by Guttenberg.

During further growth of the *Elodea* root, the cortex constructional centre cells,

v_1, begin to grow along the axis. This leads to a periclinal splitting of the cells and separation of a secondary four-layer organization (Plate VII, *1*).

This secondary four-layer structural pattern of the apical root meristem subsisted without further change to the end of root development in *Elodea canadensis*.

In *E. densa* the pattern undergoes further changes analogously as in the preceding transformations. In this way another three-layer pattern is formed, transforming in turn into a four-layer one (Plate VII, *2*).

Owing to the successive reorganizations in the course of apical meristem development in *Elodea canadensis* roots, there occur four growth patterns, whereas in *E. densa* there are as many as six.

During growth of the primordial roots in *Helianthus* and *Anoda*, Guttenberg, Burmeister and Brosell (1955) observed a change in the growth pattern. According to these authors, the change consists in the transformation of the three-layer closed type (geschlossener Typus) of the meristem to what is called the open type (offener Typus) with a common layer of initial cells for the cortex, epidermis and root cap. The "binding" cells (Verbindungszellen) would be these common initial cells. By the respective divisions of the border binding cells, the primary cortex and lateral parts of the cap together with the epidermis would be renewed. The centrally situated binding cells dividing periclinally form the secondary columella of the cap. Such a cellular arrangement remains in *Helianthus* to the end of root development.

Authors studying *Anoda* call attention to the occurrence of two layers of binding cells. From the lower layer, the secondary columella is formed by perclinal divisions. The upper layer situated between the plerome and the secondary columella undergoes in turn periclinal division transforming to a tertiary columella. The borders between the primary, secondary and tertiary columella are completely obliterated during development.

Further investigations of Guttenberg and his followers demonstrated that in various representatives of mono- and dicotyledonous plants similar changes occur in the organization of the meristem as in *Helianthus*. Generalized conclusions based on these investigations are contained in Guttenberg's (1960) monograph "Grundzüge der Histogenese höherer Pflanzen".

According to this author, the development of the root primordia always leads to the formation of three layers of initial cells. In the closed-type meristem this organization persists without change during further growth of the root, whereas in the open type it undergoes reorganization. Owing to the particularly intensive activity of the middle layer, a two-layer pattern is formed or even only one layer common to all histogens.

In the apical meristem of *Elodea* roots no two-layer organization is observed. Changes in the cell arrangement in the meristem during root growth occur according to two fundamental patterns: the three- and the four-layer one. Both these patterns alternate but the following ones are never quite identical with the earlier ones.

Such structural changes in the development of apical root meristem have so far not been reported.

A four-layer structure of the meristem structural centre in growing root has been described in several species, however as a distinct type.

Only Schönland (1877/78) reports that the four-layer organization with a separate and independent "dermatogen", occurring in older roots of *Eichhornia* and *Pontederia* arises in the course of development of the roots from a three-layer organization with common initial cells for the "periblem and dermatogen".

Guttenberg (1960) interpreted in a similar way the organization of the apical meristem of *Linum* roots.

In view of the recurring changes in the organization of the growth pattern in *Elodea*, the roots of these species can hardly be classified to any definite type of those earlier distinguished. The apical meristem organization in *Elodea*, according to the author's opinion, cannot be assigned without reservations to the type described by Guttenberg (1960) as open.

Of course the apical meristem of *Elodea* roots cannot be considered as closed according to Guttenberg's definition. They are open since the original three-layer structure undergoes repeated reorganization leading several times to the renewal of the columella of the cortex constructional centre cells. However, in *Elodea*, no immediate genetic binding of various histogens by the intermediary of common initial cells exists, what, according to Guttenberg, is the basic feature of the open type. The cortex constructional centre cells play but a minor role in the initiation of the primary cortex. As found by the present author, these cells only once in the course of the root development, in the early period of the stage of primary four-layer organization give rise to secondary cortex complexes.

In the further development of the root, the cortex constructional centre cells only renew the columella.

A significant feature of the development of apical root meristem in *Elodea* is the formation in older roots of dermocaliptrogens renewing the lateral parts of the cap similarly as in dicotyledons.

In the primary three-layer stage, the cortex constructional centre and protoderm cells, *v*, contact on the periphery the primary cortex complexes, *c*, and protodermal cells, *p*. After their periclinal division into v_1 and k_1 (4-layer stage) the initial protodermal cells, *p*, contact directly the mother cells of the secondary columella, k_1, which at this moment constitute the constructional centre of the protoderm (Plate VI, *2*).

The formation of the secondary columella results in the correlated growth of the protodermal cells along the root axis and their transformation to dermocaliptrogen. In this way in the *Elodea* root development two independent histogens: dermatogen and caliptrogen are substituted by dermocaliptrogen formed from the protoderm cells. This kind of genetic linkage has not been described by Guttenberg.

The preserved traces of the primary border of the cap persisting in its apical part to the end of development of roots, even when they reach their maximum length, allow to calculate with certainty that the total number of cells shifted to

the cap from the cortex constructional centre does not exceed 12. From this it is easy to calculate that the growth increment in this part of the root tip varies within the limits of some dozen microns.

More precise analysis of the cell arrangement adjacent to the cortex constructional centre proves that the cells of this centre also take part in the initiation of secondary cortex complexes.

The small number of cells comprised in these complexes, however, even in the longest roots, e.g. 30 cm long *Elodea* roots (Plate III, *2*) indicates that the contribution of these cells to the initiation of secondary cortex complexes is also negligible. Analysis of the formation of these complexes seems to indicate that the cortex constructional centre cells which so far were considered as the initial cells of the cortex only once fulfill the initiating function in the course of root development.

Manifestations of this initiating activity appear, however, only in root primordia with a four-layer organization. The lack of genetic connection in the youngest root primordia between the cortex constructional centre cells and its youngest elements is understandable only if we assume that meristem growth in the youngest primordia occurred without the participation of the cortex constructional centre cells.

It would seem, therefore, that so small a number of cell divisions as that exhibited over the whole root development period in *Elodea* by the cortex constructional centre cells and their sister cells justifies the assumption that the mitotic activity of this centre is negligibly low as has been suggested by Clowes (1961), Jensen (1960) and others.

The cortex constructional centre cells in *Elodea* roots, exhibit, however an unquestionable morphogenetic activity manifested in the cyclically occurring reorganization of the meristem growth pattern.

The results of the present investigation support in a certain sense the view advanced by Guttenberg and col. ascribing to the cells of the meristem constructional centre an active role in the development of the root.

Changes in the organization of the cell arrangement in the cortex constructional centre in *Elodea* seem also to confirm the conclusions of Brumfield (1943) based on analysis of the changes in cell nuclei in roots previously exposed to X-rays. They also would bear out the results obtained by Kadej (1963) by segmental analysis of the apical meristem structure in *Cyperus* roots.

Analysis of the apical meristem development in *Elodea* roots allows to reconcile the seemingly contradictory concepts of Guttenberg and Clowes.

SUMMARY AND CONCLUSIONS

The present paper gives a description of the organization and development of the apical meristem in adventitious roots of *Elodea canadensis* and *densa*.

In both these species the occurrence of several different growth patterns in the apical meristem of the root was demonstrated.

The meristem constructional centre in the youngest root primordia is differentiated into three cell layers: constructional centre cells of the plerome, *pl*, of the cortex and protodermis, *v*, and the primary columella cells, *k*.

In the first stage of development of the root promordia, that is in the period of development of the entire meristem, the particular histogens spread over the whole area in a way characteristic of them without the participation of initial cells.

In primordia more advanced in growth, the meristem constructional centre, already within the mother organ, has a four-layer structure with a separate cell layer, k_1, exhibiting structural connections with the protodermis. This layer forms as the result of periclinal divisions of the cells belonging to the *v* layer of the constructional centre common to the cortex and protodermis.

At this stage of root development, the cells of the constructional centres of the particular histogens begin to manifest an initiating activity. In the central cylinder, the *pl* cells act as initial cells in the entire course of root growth. The function of initial cells in the protodermis is taken over by *p* cells contacting on the periphery the k_1 layer which constitutes the constructional centre of the protodermis. The primary columella arises from the complex of *k* cells. The lateral parts of the root cap are initiated for a long time period by initial *b* complexes. The cortex constructional centre cells, *v*, on the contrary, only once, at this stage of root development take part in the initiation of secondary cortex cell complexes. Further development of the cortex occurs owing to the growth of primary cortex complexes with the cooperation of new secondary complexes c_1.

The four-layer growth pattern in *Elodea* perists but for a short time. Even before the root apex emerges from the cortex, the pattern begins to transform. The transformation begins by a change in the direction of growth of the cells of the protodermis constructional centre k_1. This results in periclinal divisions of these cells. The division yields cell complexes penetrating into the root cap region and forming a secondary columella.

Simultaneously with the setting off of a secondary border in the cap above the cell complexes of the secondary columella, a secondary three-layer organization forms in the meristem. At this stage, in the middle layer of the meristem, v_1, no symptom of longitudinal or transversal growth can be detected. This cell layer separates the parts of the root growing in opposite directions: the central cylinder and the columella.

In roots of about 10 cm length, in the full course of growth the cortex constructional centre cells, v_1, start to grow along the axis. This leads to a periclinal splitting of these cells which gives a secondary four-layer organization.

This secondary apical meristem pattern in the root persists without further change to the end of root development in *Elodea canadensis*.

In *Elodea densa*, the pattern undergoes further changes analogous to the preceding transformations.

Owing to these successive reorganizations in the course of apical meristem development in *Elodea canadensis*, there occur four different growth patterns, and in *E. densa* as many as six. The formation of the secondary columella brings as

consequence the correlated growth of initial protodermal cells along the root axis. These in turn give rise to initial dermocaliptrogen complexes which grow similarly as in dicotyledons. In this way the two independent histogens, dermatogen and caliptrogen are replaced by dermocaliptrogen.

The low number of mitoses exhibited in *Elodea* by the cortex constructional cells and their sister cells in the course of root development, leads to the assumption that mitotic activity of this centre is negligible.

The cortex constructional centre cells in *Elodea* roots have, however, been found to exert an unquestionable morphogenetic activity manifested in a periodic reorganization of the meristem growth pattern.

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Organizacja i rozwój merystemu wierzchołkowego korzenia *Elodea canadensis* (Rich.) Casp. i *Elodea densa* (Planck) Casp.

Streszczenie

W pracy niniejszej podałam opis organizacji i rozwoju merystemu wierzchołkowego przybyszowych korzeni *Elodea canadensis* i *Elodea densa*.

U gatunków tych stwierdziłam występowanie w merystemie wierzchołkowym korzenia kilku odmiennych wzorów wzrostu.

Konstrukcyjne centrum merystemu w najmłodszych zawiązkach korzeni jest zróżnicowane na trzy piętra komórek: komórki konstrukcyjnego centrum pleromu *pl*, kory i protodermy *v* oraz komórki pierwotnej kolumelli *k*.

W pierwszym okresie rozwoju zawiązka korzenia, to jest w okresie rozrastania się całego merystemu, poszczególne histogeny rozrastają się na całym obszarze w sposób dla nich charakterystyczny bez udziału komórek inicjalnych.

W bardziej zaawansowanych w rozwoju zawiązkach, jeszcze wewnątrz organu macierzystego, centrum konstrukcyjne merystemu ma budowę czteropiętrową, z odrębnym piętrem komórek

k_1 wykazujących powiązanie strukturalne z protodermą. Piętro to powstaje w wyniku peryklinalnych podziałów komórek konstrukcyjnego centrum kory i protodermy *v*.

W tym stadium rozwoju korzenia komórki centrów konstrukcyjnych poszczególnych histogenów zaczynają przejawiać działalność inicjalną. W walcu środkowym rolę komórek inicjalnych spełniają komórki *pl* przez cały czas wzrostu korzenia. Inicjalną rolę dla protodermy spełniają komórki *p* stykające się na obwodzie z piętrem k_1 stanowiącym centrum konstrukcyjne dla protodermy. Pierwotna kolumella powstaje z kompleksu komórek *k*. Boczne części czepka są inicjowane przez długi okres czasu przez inicjalne kompleksy *b*. Natomiast komórki konstrukcyjnego centrum kory *v* tylko raz jeden, właśnie w tym okresie rozwoju korzenia biorą udział w inicjacji wtórnych kompleksów komórkowych kory. Dalszy rozwój kory odbywa się dzięki wzrostowi pierwotnych kompleksów kory przy współudziale nowych, wtórnych kompleksów c_1.

Czteropiętrowy typ wzrostu u *Elodea* utrzymuje się tylko przez krótki okres czasu. Jeszcze przed wydostaniem się wierzchołka korzenia na zewnątrz, wzór ten zaczyna ulegać przekształceniom. Zapoczątkowuje je zmiana kierunku wzrostu komórek konstrukcyjnego centrum protodermy k_1. Konsekwencją nowego kierunku wzrostu są peryklinalne podziały tych komórek. W wyniku tych podziałów powstają kompleksy komórkowe wnikające na terytorium czepka, tworząc wtórną kolumellę.

Równocześnie z wyodrębnieniem wtórnej granicy czepka powyżej komórkowych kompleksów wtórnej kolumelli powstaje wtórna trzypiętrowa organizacja merystemu. W tym okresie w środkowym piętrze merystemu v_1 nie ma żadnych przejawów wzrostu podłużnego ani poprzecznego. Piętro to rozdziela rosnące w przeciwnych kierunkach części korzenia: walec środkowy i kolumellę.

W korzeniach znajdujących się w pełni wzrostu, o długości mniej więcej 10 cm, komórki konstrukcyjnego centrum kory v_1 zaczynają rozrastać się wzdłuż osi korzenia Doprowadza to do peryklinalnego rozszczepienia tych komórek i do powstania wtórnej, czteropiętrowej organizacji.

Ta wtórnie, czteropiętrowa organizacja merystemu wierzchołkowego korzenia utrzymuje się bez dalszych zmian do końca rozwoju korzenia *Elodea canadensis*.

U *Elodea densa* układ ten ulega jeszcze dalszym, analogicznym do poprzednich przekształceniom.

W wyniku tych kolejnych reorganizacji w rozwoju merystemu wierzchołkowego korzenia *Elodea canadensis* występują 4 odmienne wzory wzrostu. W rozwoju merystemu wierzchołkowego korzenia *Elodea densa* występuje aż 6 odmiennych wzorów.

Powstanie wtórnej kolumelli pociąga za sobą współuzależniony wzrost wzdłuż osi korzenia komórek inicjalnych protodermy. Dają one początek inicjalnym kompleksom dermokaliptrogenu, które rosną podobnie jak u dwuliściennych. W ten sposób w rozwoju korzenia u *Elodea* dwa niezależne histogeny: dermatogen i kaliptrogen zostają zastąpione przez dermokaliptrogen.

Nieznaczna ilość podziałów komórkowych, jaką u *Elodea* wykazują podczas całego rozwoju korzenia komórki konstrukcyjnego centrum kory i ich komórki siostrzane, upoważnia nas do przyjęcia tezy o znikomej aktywności mitotycznej tego centrum.

Komórki konstrukcyjnego centrum kory wykazują jednak w korzeniach *Elodea* nie budzącą wątpliwości aktywność morfogenetyczną. Przejawia się ona w cyklicznie występujących reorganizacjach wzoru wzrostowego merystemu.

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