ROOT APICAL ORGANIZATION IN MONOCOTYLEDONS—CANNACEAE

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In a previous communication the authors (1961) have described the apical organization in the roots of some members of the family Musaceae of the order Scitamineae. This article embodies their observations on the root apical organization of some members of Cannaceae.

Materials and Methods

The methods used in the study of the members of Musaceae were followed here also. The root-tips of the following species were investigated:—

Canna indica Linn. and *Canna edulis* Ker-Gawl.

Observations

In these root apices also the organization was studied from the structural and cyto-physiological points of view.

A. Structural Organization

The root-tips of these two species show a similar structural organization. The root-cap is separate from the root body. Distinct structural initials are found at the tip of the root body.

(1) *Root-cap and Columella*

In the centre of the cap can be seen distinct longitudinal files of cells constituting the columella. The meristem giving rise to this is not contributing to the rest of the calyptra. It is composed of a few layers of cells across and in longisections is seen fitting into a depression found at the tip of the root body (Text-Figs. 4 and 7). The cells of this meristem divide transversely like a rib meristem and its derivatives elongate to the front and get vacuolated. This meristem has been named the columellogen.

Surrounding the central columella and slanting from the flanks towards it are cells oriented in oblique files. They are located outside the dermatogen. T-divisions, with the capital of the T directed towards the flanks, occur here and these enable the peripheral zone to widen out towards the tip. The meristem is called the "peripheral region" by Allen (1947) and is located outside the dermatogen.

The formation of the root-cap was studied in developing lateral roots of *Canna indica*. Only the endodermal cells are involved in its formation. These cells divide anticlinally first (Text-Fig. 1). Then periclinal divisions are seen at the middle of the row (Text-Fig. 2). These cells appear to continue such periclinal divisions whereas the cells to the flanks exhibit T-divisions. Thus, after the lateral root has developed for some time, but when it is still within the mother root, it is possible to distinguish the two patterns of cell division characteristic of the two regions of the cap. A few cells in the middle exhibit only periclinal divisions (transverse to the axis of the lateral root) constituting the columellogen whereas the cells around this show the T-type of division with the T-head located towards the hind part of the lateral root, *i.e.*, towards the stele of the mother root, constituting the peripheral region (Text-Fig. 3). Thus, the two meristems of the root-cap become separate even very early in the development of the root body.

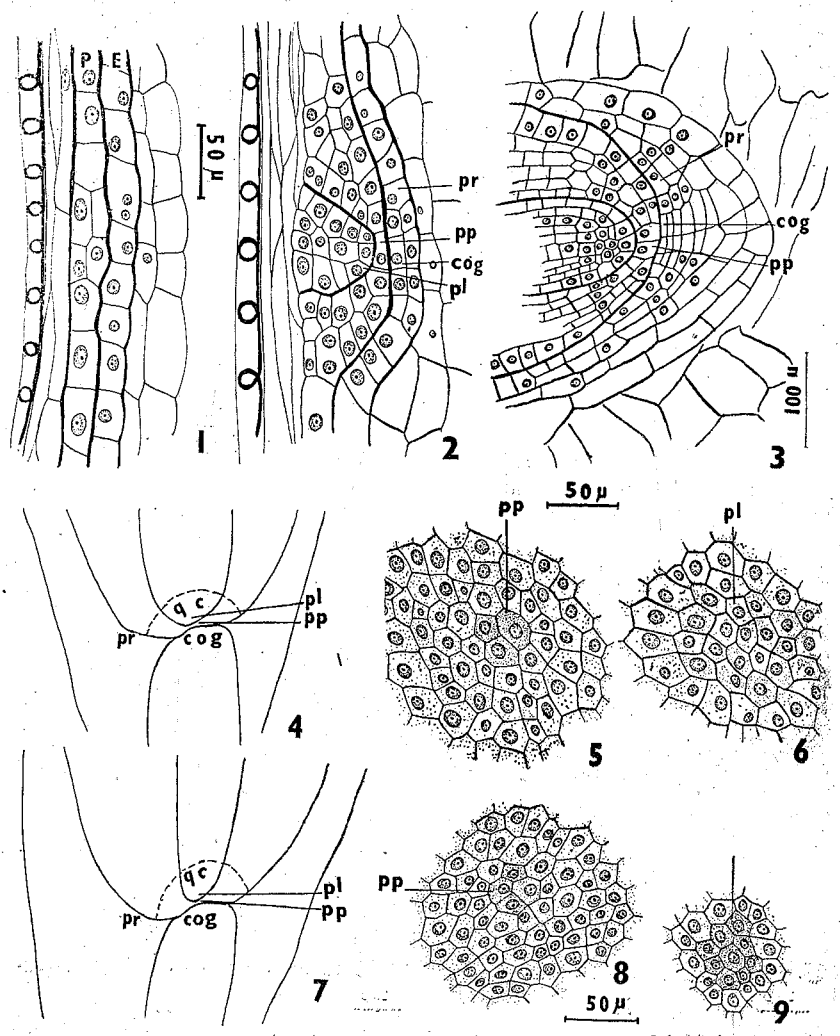
(2) *Histogens of the Root Body*

At the tip of the root body can be distinguished the plerome and outside its dome a single tier of initials which give rise to the cortex and the epidermis, called the protodermperiblem complex (Clowes, 1954; Kasapligil, 1954).

(*a*) *The Protoderm-Periblem Complex.*—As mentioned above, this is composed of one tier of about 1–5 cells (Text-Figs. 5, 8, 10 and 11). These cells undergo T-divisions on the flanks enabling this region to become wider both towards the tip and the body because of which there results a concavity into which the columellogen fits (Text-Figs. 10 and 11). This common initiating zone has been called *Dermoperiblem* by Clowes (1954) and *Protoderm-Periblem Complex* by Kasapligil (1954).

(i) *Dermatogen.*—From the products of division of the outermost layer of the derivatives of the protoderm-periblem complex separates out at some distance, a tier of the cells. This tier divides only anticlinally and gives rise to the epidermis in the older portions. This is referred to as the *dermatogen* here and so the expression is used in a restricted sense.

(ii) *Periblem.*—This includes the originating zones of the hypodermis, cortex and endodermis. In the initial stages all these have a common origin with the dermatogen. Some of the outermost derivatives of the protoderm-periblem complex undergo T-divisions. The inner of the twin daughter cells of such T divisions (Text-Fig. 10, T) by further divisions give rise to the hypodermis. The remaining cells of this complex exhibit many more T-divisions thus making the cortex wider so that oblique files of cells are formed inside the dermatogen which run in the opposite direction to those of the cap cells located outside it. The innermost file of these, bordering on the pericycle, becomes distinct after a few such T-divisions into a separate, uniseriate tissue, the endodermis. The cells of this layer from now on divide



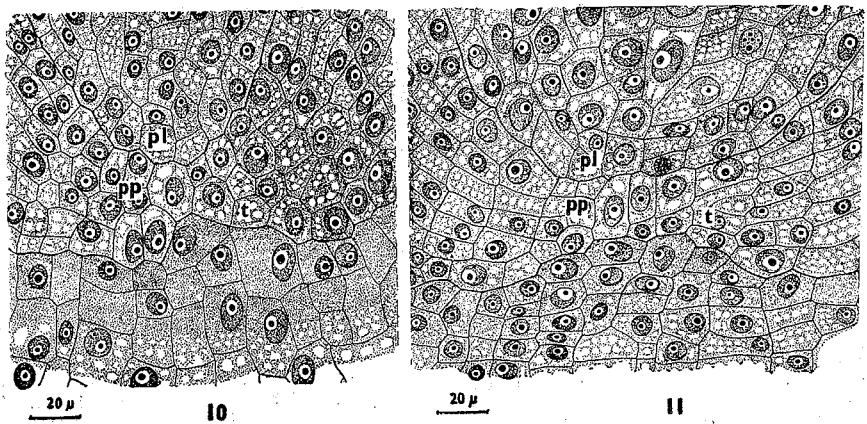
TEXT-FIGS. 1–9. Figs. 1–6. *Canna indica*; Figs. 7–9, *Canna edulis*. Fig. 1. *Canna indica*. Development of lateral root. Pericycle (P) giving rise to the root body and endodermis (E), to the root-cap. Fig. 2. A more advanced stage in the development of the lateral root where the protoderm-periblem (*pp*) and plerome (*pl*) have become clearly differentiated in the body of the root, while with the periclinal division of the middle endodermal cells, the columellogen (*cog*), and the anticlinal divisions of the endodermal cells at the sides, the peripheral region of the cap (*pr*), are formed. Fig. 3. A more advanced stage in development of the lateral root, still within the mother root. The plerome (*pl*) and protoderm-periblem complex (*pp*) are well formed. The peripheral region of the cap (*pr*) can be distinguished by T-divisions and the columellogen (*cog*) by the transverse divisions of the endodermal cells. Fig. 4. A diagrammatic sketch of the median longisection of the root apex showing the structural histogens columellogen (*cog*), peripheral region of the cap (*pr*), protoderm-periblem complex (*pp*) and plerome (*pl*). Note the concavity at the apex of the root body into which the columellogen fits; also, the quiescent centre

(*qc*) marked out is in the form of an inverted cup. Fig. 5. A transection passing through the protoderm-periblem complex, a tier of a few cells (shown stippled). Fig. 6. A transection passing through the plerome initials (shown stippled) surrounded by the cells of the quiescent centre. Fig. 7. *Canna edulis.* A diagrammatic sketch of the median longisection of the root apex showing the structural histogens columellogen (*cog*), peripheral region of the cap (*pr*), protoderm-periblem complex (*pp*) and plerome (*pl*). Note the concavity at the apex of the root body into which the columellogen fits. The quiescent centre (*qc*) marked out is in the form of an inverted cup. Fig. 8. A transection passing through the protoderm-periblem complex, a tier of a few cells (stippled). Fig. 9. A transection passing through the plerome initials (stippled) surrounded by the cells of the quiescent centre.

(Scales common for Text-Figs. 1 & 2, 5 & 6 and 8 & 9.)

mainly anticlinally. The endodermis, therefore, can be said to arise from an endodermis-periblem complex.

(*b*) *Plerome.*—The dome of this is composed of 4–5 cells across (Text-Figs. 6 and 9). The plerome is distinguishable into an outer single-layered pericycle, the cells of which have densely staining cytoplasm much nearer the dome. The pericyclic cells divide anticlinally. In the centre of the plerome there are some isodiametric cells which divide mainly transversely like a rib meristem and give rise to the medulla in the middle.



TEXT-FIGS. 10 and 11. Fig. 10. *Canna indica.* A portion of the tip of the root body enlarged with the columellogen to the outside of the protoderm-periblem complex (*pp*) and the plerome (*pl*) to its inside. *t*, T-divisions showing the beginning of the hypodermis from the outer layers of the protoderm-periblem complex. The cyto-physiological state of the cells at the tip is brought out. Fig. 11. *Canna edulis.* Details as in Text-Fig. 10.

Histogenesis of the Body of the Lateral Root.—The body of the lateral root is built up from the products of division of the pericyclic cells. These cells become dense with deeply staining cytoplasm and prominent nuclei. In the middle of this group, the cells undergo periclinal divisions (Text-Fig. 1). Even before the calyptra becomes easily distinguishable into the columellogen and peripheral region, the cells

derived from the anticlinal and periclinal divisions of the pericycle are distinguishable into the single-layered protoderm-periblem complex and the plerome (Text-Fig. 2).

Thus, the structural organization of the lateral root is exactly similar to that of the main root. But, all the cells are dense with contents and with prominent nuclei and nucleoli so that cells in a state of repose are not noticed in this early stage.

B. Cyto-physiological Organization

As in the apices of the roots of the members of Musaceae, here also could be distinguished two zones on cyto-physiological grounds. A group of cells at the tip of the root body, *i.e.*, excluding the root-cap, shaped like a cup with the broader part towards the cap, could be distinguished by their lightly stained and vacuolated cytoplasm (Text-Figs. 10 and 11), comparatively smaller nuclei and nucleoli (Table II) and lesser frequency of mitotic figures (Table I). This is the quiescent centre (Clowes, 1956 *a*). The size of the quiescent centre is found to vary, being smaller in thin and young roots and bigger and more pronounced in thick and mature roots (Table I). It includes cells of the

TABLE I

The total number of cells constituting the quiescent centre and the meristematic zone and the number and percentage of dividing cells in them (as observed in one transection each of five roots)

Species	Quiescent Centre			Meristematic Zone		
	Total no. of cells	No. of dividing cells	Percentage	Total no. of cells	No. of dividing cells	Percentage
Canna indica ..	66	2	3·03	98	17	17·34
	25	1	4·00	98	18	18·36
	45	2	4·44	97	17	17·45
	50	2	4·00	100	19	19·00
	40	1	2·50	97	17	17·45
Canna edulis ..	25	1	4·00	101	25	25·00
	67	4	5·97	115	25	21·73
	60	3	5·00	100	20	20·00
	62	3	4·90	103	23	22·33
	70	4	5·71	100	24	24·00

various structural histogens of the root body. It gradually transcends into a region behind as seen in longisections and around as seen in transections, where the cells have densely stained cytoplasm, lesser vacuolation, comparatively bigger and more prominent nucleoli and nuclei (Table II) and much greater frequency of division figures (Table I). This zone, named as the meristematic zone, also includes all the structural histogens of the root body.

The sizes of the cell, nucleus and nucleolus and the nucleolus/nucleus and nucleus/cell ratios in these two regions were calculated (Table II). These show that the cells in the latter region are synthesizing more nucleic acids and are in a better state of preparation for division. The meristematic nature of the cells is supported by the appearance of the cells of the dermatogen in the two zones. In the quiescent centre they are longer whereas in the meristematic zone they are short and densely packed one above the other like a stack of coins. This meristematic zone appears to be the actual site of initiation of new cells in such roots.

TABLE II

The areas in sq. μ of the cell, nucleus and nucleolus in the quiescent centre and meristematic zone and the respective nucleolus/nucleus and nucleus/cell ratios

(Mean of 20 determinations)

Plant species	Quiescent Centre				
	Cell	Nucleus	Nucleolus	Nucleolus / Nucleus	Nucleus / Cell
Canna edulis ..	35·42± 7·64	8·317± 1·812	0·4265± 0·0608	5·12	23·48
Canna indica ..	75·84± 28·70	14·509± 5·102	0·8038± 0·2719	5·54	19·13

Plant species	Meristematic Zone				
	Cell	Nucleus	Nucleolus	Nucleolus / Nucleus	Nucleus / Cell
Canna edulis ..	49·34± 15·53	12·219± 2·396	1·509 ± 0·0442	12·35	24·76
Canna indica ..	65·38± 22·36	14·969± 3·827	2·4845± 0·7296	16·60	22·89

Hence, though a distinct structural organization is recognizable at the apices of these roots, the cells at the extreme tip go into quiescence as the root matures and appear to be merely carried forward and to play a comparatively minor part in histogenesis.

The distances of the first appearance of the vascular elements and the first appearance of the mature phloem elements were measured in the roots of these species also and it can be seen from the values in Table III that the latter is about 200–500 μ behind the tip of the root body.

TABLE III

The levels of origin of metaxylem, protoxylem and phloem and the level of appearance of mature phloem elements from the tip of root body

Species	Level of origin of			Level of appearance of mature phloem μ
	Metaxylem μ	Protoxylem μ	Phloem μ	
Canna indica ..	160	390	310	500
Canna edulis ..	45	85	70	200

DISCUSSION

The structural organization at the root apices falls under type 2 of Janczewski (1874), Treub (1876), Haberlandt (1914), Hayward (1938), Popham (1952) and Esau (1953). This type, according to them, is found mainly in grass-root apices. But, investigations by the authors show that this is found in the members of Cannaceae being reported here and in the members of Zingiberaceae and Marantaceae to be reported later. Esau (1953) does not mention this type of organization as occurring among Monocotyledons at all, whereas Popham (1952) mentions it as the principal monocotyledonous type, although the examples that he quotes are mainly from among the Gramineae. It appears that this is an important type of structural organization among Monocotyledons.

Van Tieghem and Douliot (1888) noted a one-layered condition from where the dermatogen and periblem arose, which they named *epistele*. Such a tier of initials which is common to the two histogens has been referred to by Schade and Guttenberg (1951) and Clowes (1954) as the "periblem-dermatogen complex" and by Kasapligil (1954) as the "protoderm-periblem complex".

Root-Cap Formation

Hanstein (1868) and Haberlandt (1914) considered the cap to be a proliferation of the dermatogen and do not attribute its origin to the activity of any separate histogen. In these roots the cap has an inde-

pendent origin. Holle (1876) assigned roots of all plants to two categories on the basis of the mode of root-cap formation:—

(i) those whose root-caps originate from an apical cell, and

(ii) those whose root-caps arise from the 'periblem'.

The possibility of an independent histogen for the formation of this portion has not been visualized by Holle. In these two species of *Canna*, the cap arises from a separate meristematic layer which has no genetic connection with the main body of the root. This is distinguishable into a central columella and a peripheral zone.

The central columella has been distinguished from the rest of the cap even from very early times. Holle (1876) and Eriksson (1878) called it the ' saule' and the 'kolonne' respectively. Schüepp (1926) also called it the 'saule'. Zirkle (1932) calls it the 'core'. Neumann (1939) and Guttenberg (1941) call it the 'kolumella'. Johansen (1941) proposed a new term, the 'stalace' for this region. Recent investigators like Schopf (1943), Allen (1947), Spurr (1949), Kasapligil (1954) and others also recognize the columella in the cap.

As to the meristem which gives rise to the columella, no particular mention is made by most of these authors. The assumption seems to be that the calyptrogen gives rise to the columella also and fundamentally this can be considered to be its mode of origin. Tiegs (1913) seems to be the first to recognize separate initials for the columella from the rest of the initials for the cap. Later authors like Schopf (1943), Allen (1947), Spurr (1949) and Kasapligil (1954) all recognize the cap to have two separate regions of initials, one set for the columella in the centre and the other for the region around it which Allen (1947) has termed the 'peripheral region'. Wagner (1939) and Clowes (1954) have brought out that the formation of the columella in broad root apices is independent of the rest of the cap. But they too have not mentioned the histogen which gives rise to the columella. Since it has been found by most investigators that from a structural point of view a modified histogen theory can be applied, and since the initial zone appears to be concerned with the formation of the columella files only, the authors venture to give it the name 'columellogen' and adopt the terminology of Allen (1947) for the rest of the cap initials namely the 'peripheral region'. When the origin of the histogens of the root-cap is traced in the lateral roots, the two histogens of the root-cap become distinguishable very early in development by the patterns of their cell division, one transversely and the other by T-divisions. Therefore, it appears justifiable to designate the two regions as two separate histogens and to use terms also to distinguish them.

Histogens of the Root Body

Dermatogen.—This arises from the protoderm-periblem complex and this term is used in a restricted sense only as reported earlier by the authors in the case of members of Musaceae (1961). According to

Hanstein (1868) dermatogen and protoderm are not synonymous terms. Protoderm refers to the outermost layer of the apical meristem and may give rise to the epidermis only or to the subepidermal layers also, whereas the dermatogen has its own initials and generates the epidermis only. So, protoderm comprehends something more than the epidermis and is used in the expression 'protoderm-periblem complex' in that sense.

Esau (1953) states that in roots "the dermatogen is supposed to be the outermost layer of the cortex". In these roots this layer separates out from the same initials as for the cortex, which type has been called by Clowes (1953) as arising from the cortex complex.

Endodermis.—Haberlandt (1914, pp. 391–92) states "the ontogenetic origin of the endodermis is quite as variable as its phylogenetic development". He has demonstrated the procambial origin of the endodermis in Juncaceae and Cyperaceae. Eames and MacDaniels (1947, p. 160) also mention that the endodermis has been considered as both the innermost layer of the cortex and the outermost layer of the stele. However, it has not been described as arising from an independent histogen like the uniseriate dermatogen for the epidermis. In these plants the endodermis arises from the cortex complex. Near the plerome dome the innermost layer of periblematic cells exhibit T-divisions, from the products of which separates out the endodermis. If we consider this meristem as the one concerned with the formation of the endodermis, then the cells are cut off not only to form the endodermis but also to form the periblem. Williams (1947) and Beckel (1956) have reported this type of meristematic activity and consider the endodermis to be meristematic in the early stages. But, the endodermis arises from a common initial zone for the periblem and endodermis like the one for the dermatogen and periblem towards the outside and so it may be said that it arises from an endodermis-periblem complex.

Plerome.—Initials for this are normal in their activity giving rise to the pericycle, vascular elements and pith.

Histogenesis of the Lateral Root

The pericycle is exclusively concerned with the development of the histogens of the body of the lateral root. Eames and MacDaniels (1947, p. 163) say that "the initials of the lateral roots and of adventitious roots commonly arise in the endodermis". Esau (1953, p. 499) states "that apical meristem (of the lateral root) has not necessarily the same architecture as that of the parent root, but it may develop such with further growth". The authors find that in the roots of *Canna indica* there is no difference in the architecture of the lateral and parent roots.

Cyto-physiological Organization

In these roots also it is found that the cells, at the extreme tip of the root body in the shape of a cup, are in a state of repose exhibiting

(i) lightly stained cytoplasm, (ii) vacuolation (Text-Figs. 10 and 11), (iii) smaller nuclei and nucleoli (Table II), (iv) lesser frequency of division figures (Table I) and (v) smaller nucleolus/nucleus and nucleus/cell ratios as compared with the cells around them. In these roots where the root-cap is separate, it is possible to distinguish clearly that this region, the quiescent centre (Clowes, 1956 *a*, *b*; 1958 *a*, *b*), does not extend to the root-cap unlike that in Musaceae, where such a clear distinction was not possible. The region behind it as seen in longisections and around it, as seen in transections, is the meristematic zone which appears to be the real site of histogenetic activity. This also recalls the similarity with the postulation of the *meristeme d'attente* and *anneau initial* by the Plantefol school (Plantefol, 1947; Buvat, 1952) which was pointed out before.

These studies indicate that the cyto-physiological state of the cells of these two regions at the apex appears to have more importance on histogenesis at the root apices than the structural organization.

In these roots also the distances behind the tip of the root body at which the phloem elements mature was measured (Table III). This is found to be 200–500 μ behind. This supports the suggestion that the cells of the quiescent centre go into that state because of the lack of sufficient nutrients.

Lateral root.—From the cyto-physiological point of view there is no difference in the various cells constituting the extreme tip of the lateral root, all the cells being active. It appears that a quiescent centre develops as the roots grow older and mature. Also the size of the quiescent centre is found to increase as the roots grow thicker (Table I).

Summary and Conclusions

The root apices of two species of *Canna* exhibit a structural organization with discrete initials for cap and plerome and a common initial zone for the protoderm and periblem.

The initials of the root-cap can be distinguished into two regions. The one in the middle fits into a depression at the tip of the root body and is characterised by cutting off cells only transversely to the front to form the columella. The name columellogen which was given earlier is continued to be applied to this. The other, characterised by T-divisions, is concerned with formation of the sides of the cap, called the peripheral region.

The origin of the endodermis is traced to an initial zone common with the periblem named here as the endodermis-periblem complex.

The cyto-physiological state of the cells at the root apices has been studied which brought out that there is a quiescent centre at the extreme tip of the root body and around and behind it is the real histogenetic zone called the meristematic zone. The characteristics of the cells composing these two zones are described. The importance of the cyto-physiological state of the root apices in histogenetic studies is stressed.

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* Originals not seen.