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ABSTRACT – The primary body of the root of *Cyclamen persicum* Mill. is described. The rootcap consists of two components of separate origin. Cells of the columella are derived from the dermatocalyptrogen by periclinal wall formation. Further growth of the columella is due primarily to the increase in size of existing cells. Cells of the lateral rootcap arise from the protoderm by periclinal wall formation. Continued growth in this region is due to both increase in cell number and increase in size of existing cells. Proximal to the dermatocalyptrogen is the presumptive quiescent center. Around the periphery of this zone are located the initials of the ground meristem and procambium.

It would not be an exaggeration to say that organization of the root apex, with reference to site of initials, orientation of divisions, and derivatives, is one of the least studied and least understood aspects of plant anatomy. The classical descriptions of Janczewski (1874) and Schüepp (1917) were considered to be sufficiently comprehensive to discourage further study. Recent workers, notably Clowes (1961) and Guttenberg (1968) have again taken up the study of the root. They have shown that patterns of development in the root are complex and vary markedly from taxa to taxa.

For an understanding of the relationships between cells, lineages, and initials, a complete ontogenetic study of the root is necessary. Guttenberg and his associates (1955), and several other recent workers, among them Seago and Heimsch (1969) and Seago (1971) have demonstrated that dramatic changes in growth patterns often occur subsequent to germination. This is especially true of those plants described by Guttenberg (1968) as having an open structure, lacking clearly defined initials. In plants with a closed structure, the cell patterns of the apex furnish information concerning the previous history of the meristem (Clowes, 1961).

The root apex of *Cyclamen*, up to the present, has not been examined critically. It is both an interesting and useful material. The taproot (derived from the radicle of the embryo) its four lateral roots, and adventitious roots arising from the base of the corm are readily available for study.

At this writing work is being done in the Department of Horticultural Science, University of Minnesota, to determine the effect of various soil temperatures on floral initiation and development. An understanding of the typical organization of the root will be a useful tool in assessing the effects of experimental conditions. Hagemann (1959, 1960) has made an extensive study of the morphology, anatomy, and ontogeny of *Cyclamen*. However, the organization of the primary body of the root is completely ignored. It is the purpose of this paper to describe this basic component of the plant body.

Flowering material, seedlings and plants

Flowering material of five cultivars of *Cyclamen persicum* Mill., cvs. Hallo, Improved Bonfire, Penningsfeld Red, Zuiver Wit, and Donkerzalmenrood was furnished by Loren Stephens of the Department of Horticultural Science, University of Minnesota. In addition, three-week old seedlings and four-month old young plants of cv. Mayer Reinweiss were provided. Observations were made on forty root tips including taproot and lateral roots of seedlings and adventitious roots of older plants. 2-5 mm root tips were killed and fixed in either Craf III, Craf V, or FAA, dehydrated in the t-butyl alcohol series of Sass (1958) and embedded in "Tissuemat", m.p. 56.6 C. Median longitudinal sections were cut at 5 u, 8 u, and 10 u, and serial transverse sections were cut at 10 u. These were mounted on slides with Haupt's medium and stained with iron-hematoxylin, safranin-fast green, or Conant's Quadruple Stain (Sass, 1958). For the study of the pattern of cell divisions in the root apex, 5 u thick longitudinal sections fixed in FAA and stained with safranin-fast green proved most satisfactory, while 8 u sections stained with iron-hematoxylin was preferred for observing mitotic activity. Microscopic observations and drawings were made using a Wild M 20 equipped with a drawing tube.

Approach and terminology

The approach used in this paper is principally topographic, analyzing the cell patterns in the distal portion of the root. None the less, it is understood that the living root is a dynamic system and that the patterns evident in sections are not necessarily indicative of the actual growth process. It is because of this, that much confusion has arisen in the past, and is perpetuated in the present. In the absence of a comprehensive and synthetic study to clarify the processes involved, the following nomenclature will be employed.

The term *apical meristem* will be used to indicate that portion of the root distal to a distinct mature epidermis which is usually identified by the presence of root hairs. The most distal part of the apical meristem, excluding the rootcap, will be referred to as the *protomeristem*. This is a somewhat more restricted definition of the protomeristem than that given by Esau (1965) which includes the initials and their derivatives. Protomeristem in this sense could be closely equivalent to the minimum construction center of Clowes (1961). Within the protomeristem are the classical histogens of Janczewski (1874); the plerome, associated with the vascular cylinder, and the periblem, associated with the cortex. An additional histogen, the dermatocalyptrogen (Guttenberg,

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1968), is associated with both the roopcap and the epidermis. It must be borne in mind, that the histogens are not necessarily centers of intense meristematic activity, but may be quite inactive, indicating only the previous history of the meristem. The region adjacent to the protomeristem will be collectively designated the *primary meristem* and consists of the *procambium, ground meristem,* and *protoderm. (Esau, 1965). Subepidermal layer* designates that single cell layer directly beneath the epidermis and continuing beneath the protoderm. *Columella* refers to the central cells of the rootcap, while lateral rootcap consists of cells different in origin from those of the columella. A *small root* is one less than 200 u, while a *large root* is greater than 250 u in diameter at the level of the procambium. For a graphical summarization, see Fig. 1.

Columnar cells observed

Upon examing a longitudinal section of the root tip of *Cyclamen persicum* Mill., one is immediately struck with the peculiar appearance of the peripheral row of cells, the protoderm. These cells are more or less columnar and have thick, deeply staining walls. In primary roots (Fig. 2) it can be seen that although there is a distinct tendency toward a columnar shape, many cells appear nearly cuboidal. The same is true for the most distal portion of later roots. Cell diameter ranges from 7-11 u tangentially and 11-19 u transversely. Each cell contains a relatively large nucleus, centrally located within the cell, and suspended by protoplasmic strands. The outer and radial walls are distinctly thicker than the inner wall. In adventitious roots, both large and small, these cells form a dense, columnar layer (Fig. 3). Their anticlinal walls, 30-40 u long, are much thinner than their periclinal walls, 8-15 u long, and their nuclei often appear to be slightly compressed between the former. In most cases the extensive vacuome is very prominent, taking the form of vacuoles on both sides of the nucleus. Most new alls form anticlinally. Various stages of mitosis can be observed.

In large roots, the protoderm often is not a homogeneous, single-layer tissue as would ordinarily be expected (Fig. 3). Periodically, and apparently at random, a group of two to five cells can be seen where presumably columnar cells have divided periclinally to give a two-layed tissue. In such cases, each cell appears to be nearly cuboidal and resembles those cells described for the primary root. Occasionally in large roots, and occurring more proximally, a third layer may be discerned. In transverse section (Fig. 4) the appearance of the protoderm is remarkably similar, columnar in appearance with the radial walls longer than the tangential. As in longitudinal sections, occasional perclinal walls may be seen so that the protoderm consists of two layers.

The rootcap (Fig. 1) consists of large, highly vacuolated cells with relatively thin walls. The cells of the columella are quite regular being cuboidal to slightly elongate, 12-30 u on a side. The cells of the lateral rootcap, however, are often considerably elongated, often up to 80 u, and those on the periphery have rounded external walls. On extremely large roots the cells on the flank of the cap are greatly contorted and crushed. The nuclei of most rootcap cells stain rather lightly.

Directly beneath the protoderm and extending beyond into the mature regions is the subepidermal layer (Fig. 1). In both, longitudinal and traverse sections this layer is very distinct and can be used as a reference point when analyzing the protoderm. These cells are cuboidal in shape, 8-12 u on a side when in the primary meristem, and elongate considerably in the more mature regions where their diameter is comparable to that of the epidermis. In general, it can be said that the cells of the protomeristem are lighter staining than those of the adjacent primary meristem, however, in the case of the subepidermal layer, the staining is uniformly lighter throughout. Each cell contains a large nucleus and an occasional mitotic division may be seen.

The subepidermal layer forms the outer boundary of the ground meristem, while the inner boundary is formed by the presumptive pericycle. The cells of the ground meristem are uniform staining and have quite prominent nuclei. As one progresses from the distal to the more proximal region, the cells remain similar in size and shape to those of the subepidermal layer, and many of the cells become distinctly vacuolate. The walls of these cells are moderately thick, the anticlinal walls being more so then the periclinal. The ground meristem is the region of greatest mitotic activity, with new walls being predominantly anticlinal. Like the ground meristem, the cells of the procambium stain uniformly, but darker. The cells of this region are rectangular in outline, even in the most distal parts.

The cells of the protomeristem are quite similar to each other in size, shape, and intensity of staining. Most of the cells are small, 8-12 u, and cuboidal in shape. Cell divisions are infrequent. In all the material examined only one mitotic figure was seen in the periblem (in a small root), three figures in the dermatocalyptrogen (in large roots) and one in the plerome (in a small root). The cell walls are uniformly thin. The dermatocalyptrogen consists of two layers of five or more cells each, depending on the size of the root. In several instances, cells of the outer layer were observed to divide, producing periclinal endwalls and presumably adding to the adjacent column of cells in the columella of the rootcap. The plerome consists of an indeterminate number of cuboidal cells at the distal margin of the procambium. The periblem consists of two to three layers of four to eight cells, depending on the size of the root. The most distal layer is contiguous with the cells of the subepidermal layer, while the remaining layer(s) is (are) in contact with the ground meristem.

Discerning a common pattern

When determining relationships between cells, a diagram of cell lineages, the Körper-Kappe concept of Schüepp (1917) is useful (Fig. 5b,c). This type of representation does not mean to imply that the active initials for a tissue region are necessarily located at the head of a lineage, but only that this was the case at some time during the past history of the root. Using this approach, a common pattern can be discerned. The rootcap consists of two components of separate origin, the columella and the lateral rootcap. The columella is initiated by periclinal wall formation in the dermatocalyptrogen (Fig. 5a). It appears that growth of the columella is due almost entirely to addition of new cells at the base and increase in size of existing cells. This view is supported by autoradiographic work done on similar roots containing columellas (Clowes, 1961; Phillips and Torrey, 1971). The

lateral rootcap arises from periclinal divisions of the protoderm (Fig. 3, 5a). The work of Clowes, and Phillips and Torrey shows that the cells of the lateral rootcap do undergo further divisions. If production of the lateral rootcap were by anticlinal wall formation by the cells of the columella, the later cells would have to remain meristematic, which appears not to be the case. In addition, one would not expect the cells of the lateral rootcap and protoderm to intergrade in such an orderly manner. This general pattern of rootcap development has been described by Guttenberg et. al. (1955) in *Helianthus* and *Anoda,* Guttenberg (1960) in *Casuarina,* Esau (1965) in *Nicotiana,* Seago and Heimsch (1969) in Convolvulaceae, and Seago (1971) in *Ipomoea* (Convolvulaceae).

Clowes' concept of the quiescent center and minimal construction zone, demonstrated most convincingly by autoradiography, has come to to an accepted phenomenon when dealing with root apices. He has mentioned several histological criteria which seem to correlate well with the more sophisticated technique (Clowes, 1959). Among these are the occurrence of smaller, less densely staining nuclei and the absence of mitotic divisions. The quiescent center, at least in roots with a columella, develops soon after germination (Wardlaw, 1968) and increases to considerable size in large root apices. This zone is positioned like an inverted cone over the root apex so that the active initials of the root come to lie around the periphery, in the case of the cortical inital some distance from the periblem. Fig. 6 shows the presumptive quiescent center in a large root of *Cyclamen.* This zone is bordered on the base by the dermatocalyptrogen and possibly the most distal portion of the protoderm. The periblem is contained entirely within the presumptive quiescent zone, so that the meristematic initials eventually forming the cortex are located in the ground meristem. The plerome, like the periblem, lies within the quiescent zone so that the vascular initials are located in the procambium.

In any more intensive investigation of the root of *Cyclamen,* the ontogeny of the primary root, beginning with the radicle, should be followed up through the mature patterns observed in this paper. This would elucidate embryonic patterns and test the assumption that the cell patterns of the protomeristem are indeed indicative of the past history of the root. The adventitious roots of the corm should not be ignored because, as observed by Hagemann (1959), their vascular arrangement is different from that of the primary root and its laterals, and there may be significant differences in their early meristematic organization. Finally, autoradiography should be employed to confirm the presentce and extent of the quiescent center.

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