DEVELOPMENT OF THE ROOT OF *DENDROBIUM KWASHOTENSE* HAY. WITH SPECIAL REFERENCE TO THE CELLULAR STRUCTURE OF ITS EXODERMIS AND VELAMEN*

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ABSTRACT

It has been found in the study of *Dendrobium kwashotense* Hay. that the various root tissues arise in regular sequence from the root apical meristem. The detailed anatomical and histological analysis shows that the adhesive roots, *i. e.*, the roots attached to a solid substrate, are more adapted for the water absorption, since they have root hairs, smaller cells in the velamen and many thin walled passage cells in exodermis. On the contrary, the aerial roots, *i. e.*, the roots developed freely in the air, possess no root hairs and have many thick walled exodermal passage cells which are covered by lignified and suberized secondary walls. The exodermis consists of long and short (passage) cells; they regularly interpose each other. The exodermis is suggested to be the main barrier of the water path in orchid roots and the structure of exodermal cells are considered to play an important role in regulation of water absorption. The exodermal passage cells are compared to the potential root hairs in the root epidermis of angiosperms. The orderly arrangement of endodermal cells in relation to the distribution of protoxylem is described. The sequence of initiation, differentiation and maturation of various tissues in the vascular cylinder is also studied.

INTRODUCTION

A large number of papers have been published on the anatomy of orchid roots. Engard (1944) paid attention to the organization of root apical meristem and the differentiation of velamen. The velamen which is present in both terrestrial and aerial roots has been considered to be the specialized epidermis, being either uniseriate or multiseriate. The velamen is the structure which has received the greatest attention among all the tissues in the orchid roots by early workers (Dycus and Knudson, 1957; Engard, 1944; Gessner, 1956; Mulay and Deshpande, 1959; Mulay and Panikkar, 1956). The velamen is also found in the roots of some other monocotyledons (Mulay and Panikkar, 1956). Earlier workers believed that the aerial roots of orchids was concerned mainly in absorbing water and probably nutrients, whereas Dycus and Knudson (1957) have provided the evidence that little or no water enters the cortical cells from the velamen. The presence of this peculiar structure, or velamen, as well as the related structures in orchid roots interested the present

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author in initiating this work. The aim of this study has been: (1) to trace the sequence of initiation, differentiation and maturation of various tissues in the root, (2) to make a detailed study on both anatomical and histochemical features of some root tissues, (3) to study these structures in relation to the water path from the media into the root.

MATERIALS AND METHODS

The developing roots of *Dendrobium kwashotense* Hay. are used in this investigation. Both aerial roots (developed in the air) and climbing or adhesive roots (attached to a solid object) were fixed in FAA immediately after collection. All collections were made early in the morning in a vinyl house. Both histochemical and anatomical studies were made on paraffin embedded materials which were dehydrated by the tertiary butanol series. Sections for anatomical study were made at the thickness of 8–10 μ in various planes and were stained by either safranin and fast-green (Johansen, 1940) or tannic acid and iron alum with safranin and orange G (Sharman, 1943). For the histochemical study the sections were treated by the appropriate methods described in the text.

RESULTS

Apical organization

As in the roots of some orchids (Engard, 1944) the cells in the apical meristem of *Dendrobium kwashotense* are specialized into three clear zones, or groups of cells. The first group of the meristematic cells which are located at the lowest region of the meristem, these give rise to root cap and protoderm (Figs. 1A, 1B). The second group which is located between the first group and the third group appears as a two or three celled layer. The cortical cells are derived from the second group of cells. The third group which is immediately above the second group gives rise to the central cylinder (Figs. 1A, 1B). Although the boundary between the dermatogen (initial cells of protoderm) and the calyptrogen (initial cells of root cap) is not clear, these group of cells can be interpreted to represent the histogens (Hanstein, 1868; Janczewski, 1874). This cell group, the initials of both root cap and protoderm are 7 to 8 cells in width. The cells in each histogen are not distinguishable from each other cytologically. But all of the root tissues can be traced in definite sequence

Fig. 1.A. Median longitudinal section of a root apical meristem, showing the initiation and differentiation of various root tissues, ×88.

Fig. 1B. Diagram of a median longitudinal section of a root apical meristem, showing the differentiation of various initial zones. Key to labeling: C, cortex; En, endodermis; Ex, exodermis; LEx, long cell in exodermis; P, pore; R, raphide; Rc, root cap; Rh, root hair; SEx, short (passage) cell in exodermis; T, tonoplast; Vc, vascular cylinder; Ve, velamen.

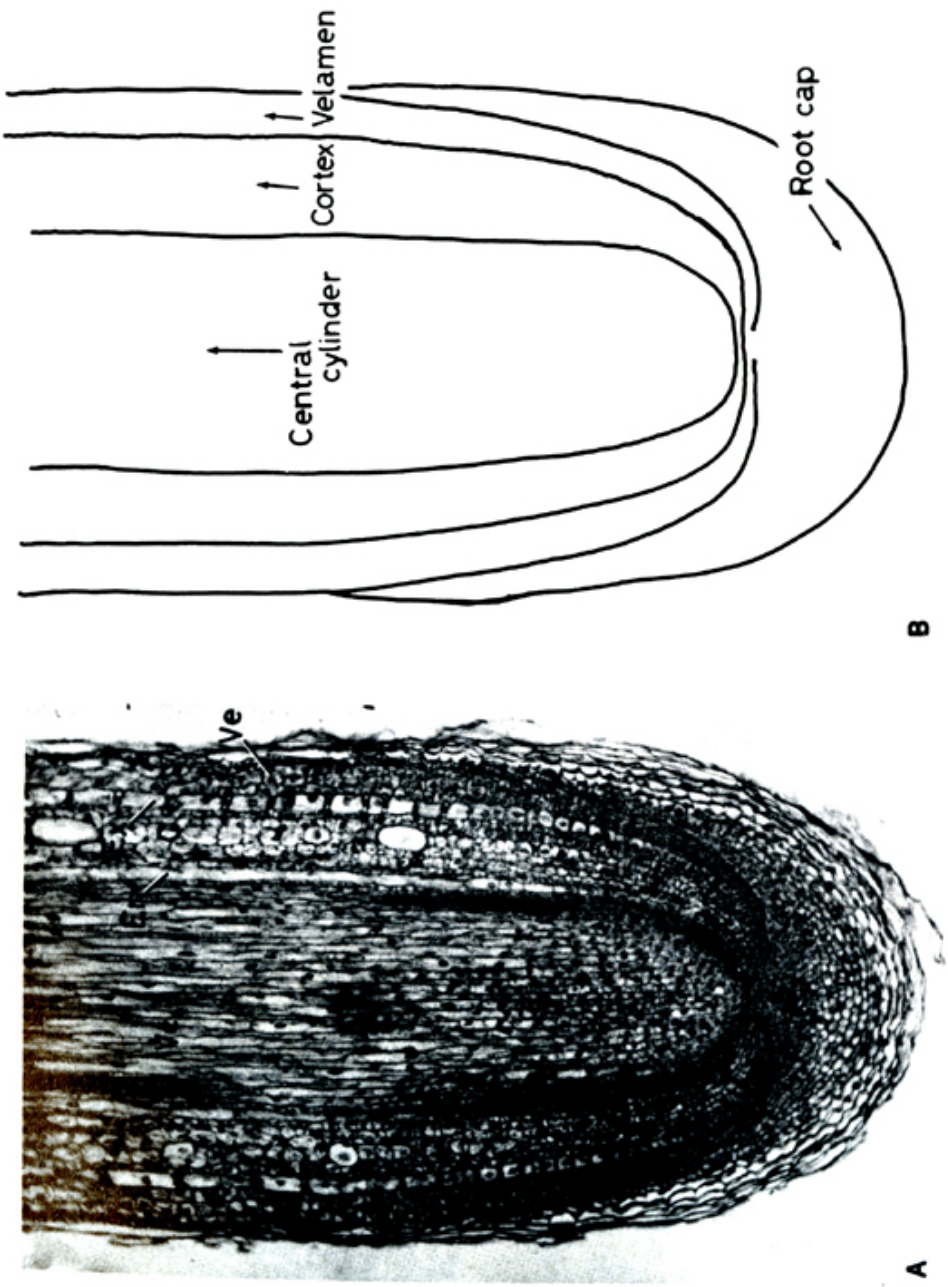
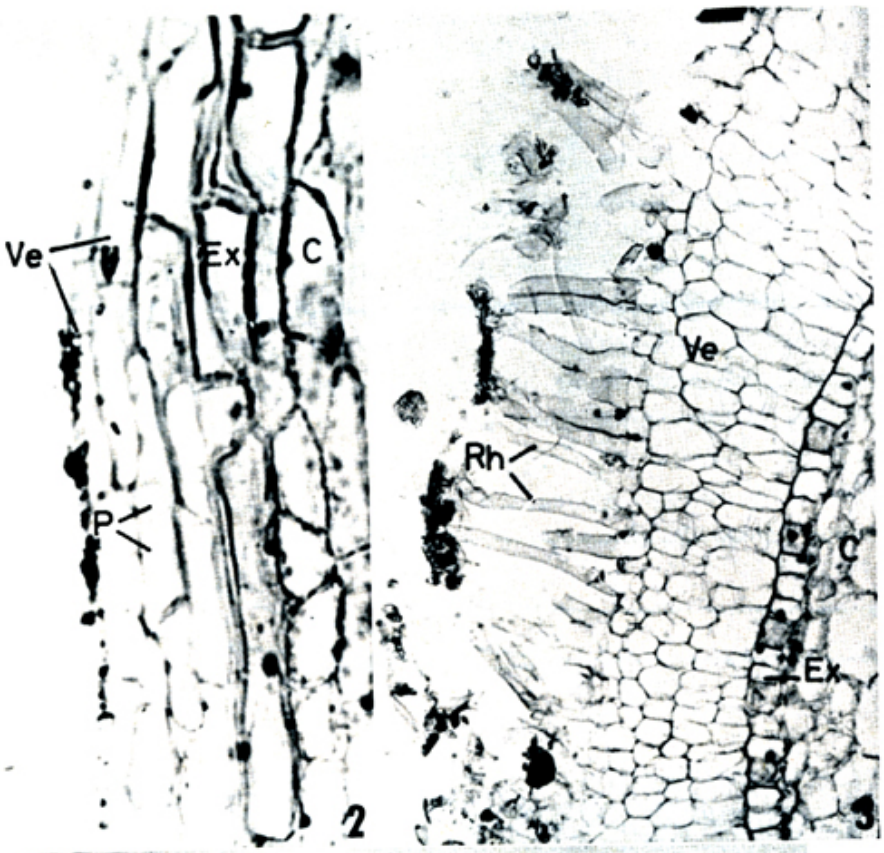


Fig. 1.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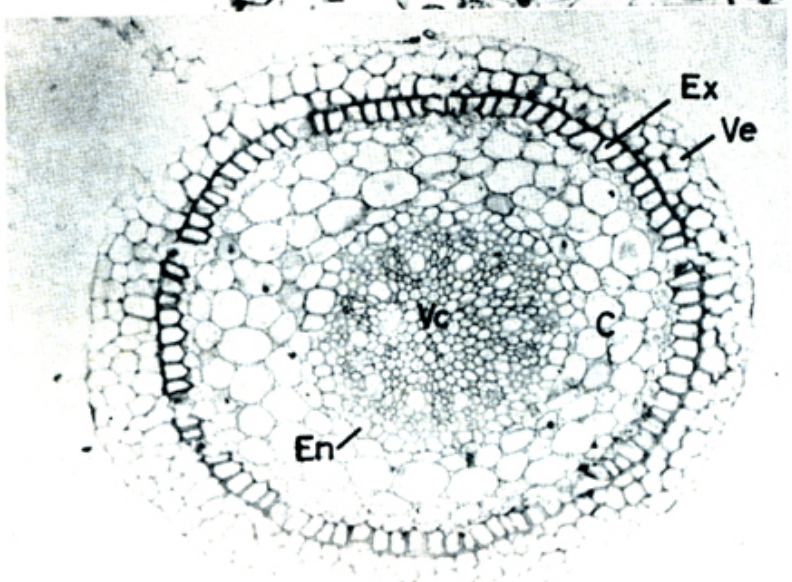
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back to each histogen zone in the apical meristem because of their orderly arrangement, orientation and position.

Velamen

The velamen has been considered to be a peculiar type of epidermis which is definitely present in the outermost part of the root of *Dendrobium kwashotense*. The velamen is derived from the protoderm by both anticlinal and periclinal divisions (Figs. 1, 9). It encloses all the root tissues except the apical meristem which is covered by another type of cells, or root cap. The velamen is derived from the protoderm by both periclinal and anticlinal cell divisions (Figs. 1A, 1B). It is 3–4 layer celled thick. But it has more cell layers where it develops root hairs in its outermost layer (Fig. 3). In roots closely attached to a substrate some of cells in the outermost layer of the velamen, the adhesive surface, grow into root hairs (Fig. 3). The root hair is absent on roots growing freely in the air or when attached loosely to a substrate (Fig. 4). The velamen cells which bear no root hair on their outermost layer are extensively elongated with their long axes parallel to the root axis. They develop lignified and suberized secondary walls except at the many circular or elliptical pores (Fig. 2). This is shown by the deep red in the phloroglucinol-HCl test and by the orange color in sudan III test.

But the velamen cells which bear root hairs on their outermost layer are elongated in the radial direction and the cells are smaller in both diameter and length. They deposit lignified secondary threadlike thickenings instead of the porelike openings (Fig. 3). However, all the velamen cells are alike in the chemical nature of their secondary thickenings and in the absence of living protoplasts at maturity. The outermost layer of the velamen has smaller cells in comparison with the inner layers. No pneumathode, which is present in some other secies (Dycus and Knudson, 1957; Gessner, 1956), has been found in materials examined. All the velamen cells are arranged in a compact pattern with no air spaces. In addition to the porelike and threadlike thickenings no other type of wall pattern has been seen in the velamen cells.

The vacuolation in velamen initials take place before the deposition of the secondary walls. The disintegration of the nucleus in the velamen cell occurs in the later stage of its development. The nucleus still retains its shape in cells which have very thick secondary walls. The completion of the nucleus disintegration and of the wall-thickening takes place at about the same time. The first velamen cells to develop thick walls are close to the exodermis, *i.e.*, the maturation is centrifugal.

Fig. 2. Longitudinal view of the velamen cells in a mature root, ×150.
Fig. 3. Transverse section through the adhesive surface of root, showing the root-hair bearing velamen, ×140.
Fig. 4. Transverse section of an aerial root, ×110.
See Fig. 1 for labeling.

The walls retain their pores mostly on their tangential and radial sides in the cells in which the long axes run parallel with the root axis (Fig. 2). But they possess more pores on their radial and transverse sides in the cells in which the long axes are perpendicular to the root axis (Fig. 3). These velamen cells are filled with air when they are exposed to the dry air but they become filled with water when they are irrigated. Numerous endotrophic mycorrhizal fungi and algae are present in the root hairs and velamen cells which bear root hairs on their outermost layer. But neither fungus nor alga has been found in the velamen cells which bear no root hairs. The root hairs have more abundant fungal hyphae and algae than the velamen cells. These microorganisms probably find their entry to the velamen through root hairs, and not through the velamen cells; and then pass from root hairs to velamen cells through the openings in the cell walls. Neither fungal hypha nor algal cell has been found in the tissues other than the root hairs and velamen. The root hair cells lose their protoplasts soon after the velamen cells become dead. The disintegration of protoplast in the root hair takes place before the maturation of exodermal cells and of the metaxylem (Fig. 3).

Cortex

The cortex can be divided into three regions: the exodermis, or the outermost layer next to the velamen; the cortex proper, or the middle tissue; and the endodermis, or the innermost layer surrounding the central cylinder (Fig. 4).

Exodermis. The exodermis in this plant extends as an uniseriate layer which consists of two kinds of cells: long cells and short cells, or exodermal passage cells. In longitudinal view long cells are elongated along the root axis and the short cells are approximately isodiametric. The long cells and short cells are arranged in vertical rows and regularly interpose each other (Figs. 5, 6, 7, 8). The sequential observation has been made on the transverse section of the serial sections of the root tip from the meristem. The vacuolation of long cells occurs about the same time as that of the cortex proper and it is easy to identify the exodermal initials because of their topographical arrangement in the root tissues (Figs. 1A, 9). The vacuolation of the long cells and cortex proper occur the earliest among all the tissues in the root meristem.

After the vacuolation and enlargement, the long cells develop secondary walls which show a positive reaction in phloroglucinol-HCl test for lignin and also show the presence of suberin with the sudan III test. The short cells still retain their dense protoplasmic contents and their thin wall nature when the long cells at the same level have already developed secondary thickenings (Fig. 6). Soon after the lignified secondary wall formation in the long cells, some of the short cells develop thick secondary walls as well.

A careful measurement was made of the tangential view of the exodermis which

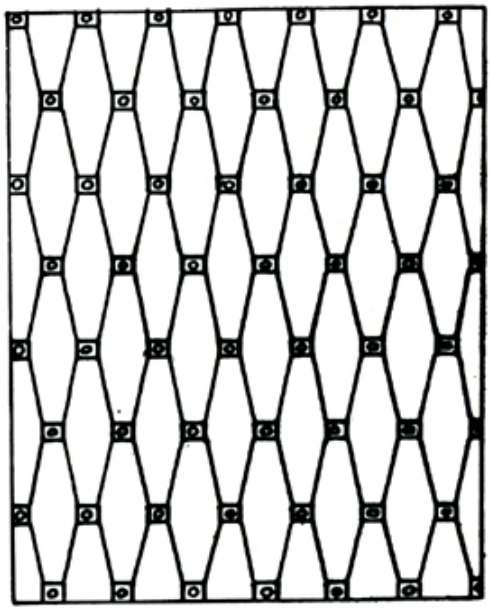


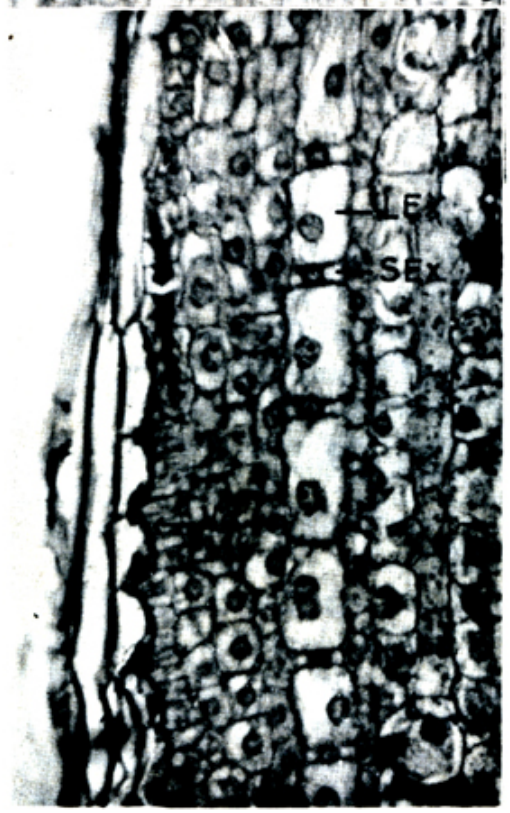
Fig. 5. Diagram showing the arrangement of exodermal cells and the associate passage cells (indicated by the presence of nuclei) in tangential view.

is located on the adhesive side of a particular root which is more or less epiphytic on the substrate and its apical meristem has ceased its development because of damage. This root has a free surface completely exposed to the air and an adhesive surface loosely attached to the substrate. The results of this measurement are shown in Table 1. The measured area of the exodermis surface in tangential view, 128.28×10^{-3} mm^2 is occupied by 100 cells, *i. e.*, 50 long cells and 50 short cells. All the long cells and two thirds of the short cells in this area develop lignified and suberized thick walls. About one third of the short cells are surrounded by thin walls. Thus, as shown in Table 1, of about 7.06 percent of the surface in the uniseriate exodermis is occupied by the thin walled cells and 92.94 percent by the thick walled cells. Both long and short cells of the exodermis which is next to the freely exposed root surface develop thick secondary walls.

Table 1. The area* of exodermis in tangential section, in mm^2

	long cell**	short cell*** (passage cell)	total	percentage
thick wall cell	93.70×10^{-3}	16.68×10^{-3}	119.23×10^{-3}	92.94
thin wall cell	—	9.05×10^{-3}	9.05×10^{-3}	7.06
total	93.70×10^{-3}	25.73×10^{-3}	128.28×10^{-3}	100.00

*Consists of 100 cells in a mature root.
**Consists of 50 cells.
***Consists of 50 cells.



Figs. 6, 7, 8. Photographs showing the arragement of long exodermal cells and short passage cells.

Fig. 6. Tangential section of exodermis near the apical meristem, ×300.

Fig. 7. Tangential section of exodermis from a mature root, ×150.

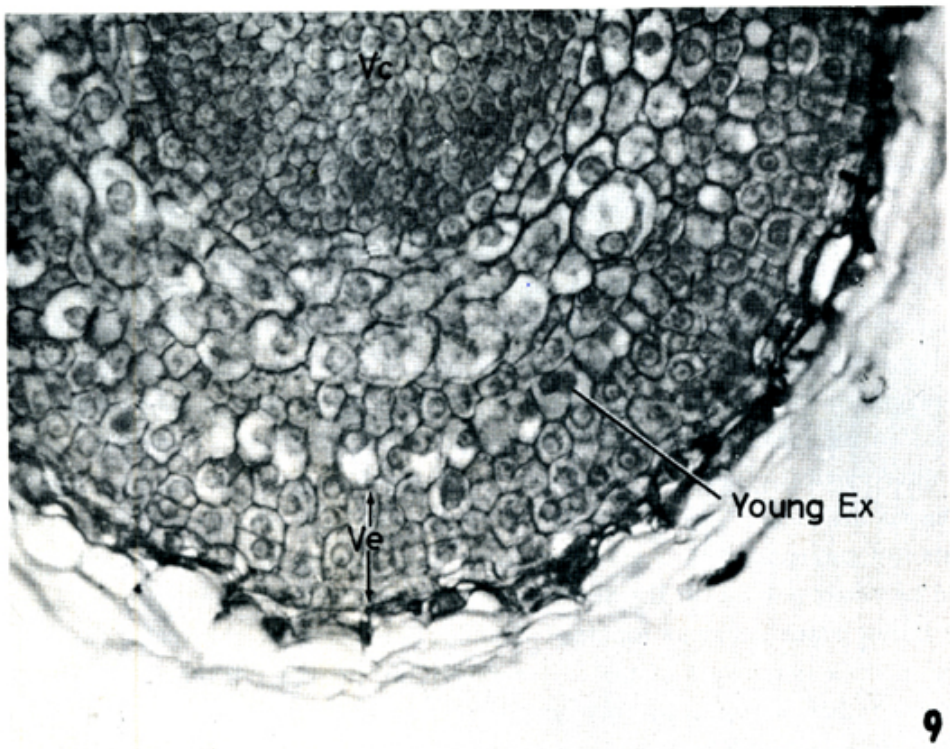
Fig. 8. Radial section of a root near the apical meristem, ×480.

Both long and short cells in the exodermis contain conspicuous nuclei. Each cell contains one nucleus. There are many pits on the inner tangential walls of the thick walled exodermal cells, *i. e.*, the wall in contact with cortex proper (Fig. 11). But few pits have been found on the outer tangential wall, *i. e.*, the wall in contact with velamen.

Cortex proper. As mentioned above, the cortex initials are one of the tissues which vacuolate very early in the root meristem. The cortex proper is approximately six cells thick in transverse section in the mature root (Fig. 4). It consists of enlarged cells except the layers which are located next to the exodermis and the endodermis. Numerous intercellular spaces are present except in the outermost layer, *i. e.*, the layer in contact with the exodermis. The raphide-containing idioblasts can be recognized in the region very near the apical meristem because of the unequal rate of enlargement of the cells. The idioblast initials enlarge at a faster rate than the other cortical cells. But their size is comparable to the remaining cortical cells in the mature root. The idioblasts develop raphides very early. The raphide is constantly surrounded by a tonoplast in its young stage (Fig. 10), but the tonoplast could be destroyed due to the development of the raphide. The cortex proper is the only tissue which develops raphide-containing idioblasts in the root. They usually occur in the outer layers of the cortex rarely in the inner layers. All the cortical cells are rather uniform in their contents except the idioblasts which contain a bundle of crystals. The cytoplasm of the cortical cells including the idioblasts are thin with numerous chloroplasts. No mucilagenous-like substance, which is present in the raphide-containing idioblast in some other plants (Esau, 1961), has been seen in these idioblasts. The cells of the outermost and innermost layers are smaller than those in the central portion. The cells in both the outermost and innermost layers are also uniform in their protoplasmic contents. No special types of cells, termed complementary and cover cells by Mulay and Deshpande (1959) have been found. No lignified banded cortical cells are present in this plant even in the later stages of development. The cells in the cortex proper are elongated in the mature root. Their long axes run parallel to the root axis.

Endodermis. The innermost layer of the cortex, endodermis, is one cell in thickness, and is also derived from the same origin as that of the cortex proper and of the exodermis (Fig. 1A). In the course of development in the apical meristem, one of the most conspicuous features is the elongation of endodermal initials in the axial direction (Fig. 1A). The elongation of the cells occurs earliest in endodermal initials among the cells of cortex and velamen. The young endodermal cells are also distinguishable from the vascular cylinder because of the small size of the pericyclic cells which form the outermost layer of the vascular cylinder.

In the transverse section of a mature root, the uniseriate endodermis forms a sheath around the vascular region (Figs. 12A, 12B). They are uniformly thickened



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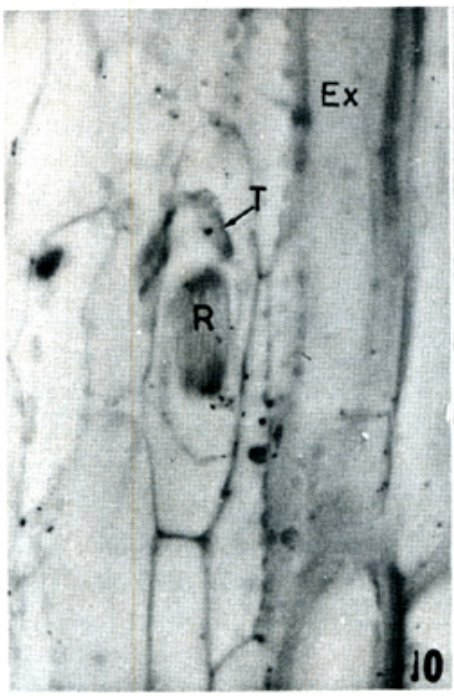

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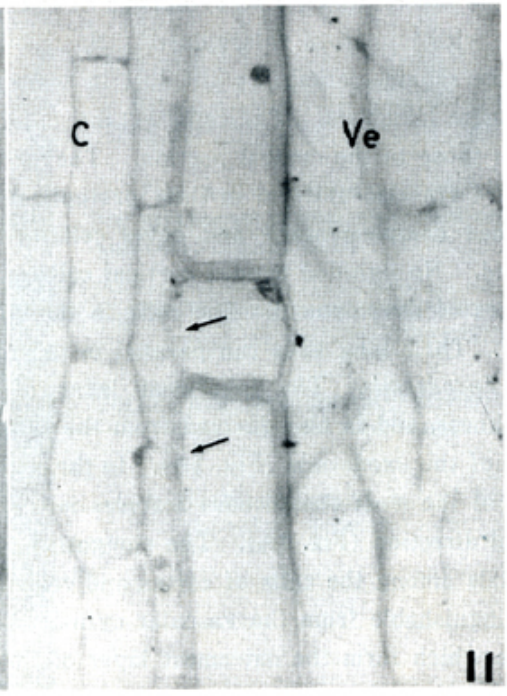

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and lignified except the cells which are located opposite to the protoxylem poles. One to three cells, termed endodermal passage cells, are located opposite to each protoxylem pole and are smaller in size and have thin walls. Three to six cells which occur opposite to each phloem group are larger with uniformly thickened lignified walls. Both thick walled-and thin walled-cells possess nuclei in the mature portion of the root (Figs. 12A, 12B).

During the course of development, the typical Casparian strip has not been seen in any stage. As in some other plants (Van Fleet, 1942; Guttenberg, 1943), the endodermal cell does not develop a thick walled layer in all directions at the same time. The successive stages of the secondary wall development first appears at the inner tangential wall and spreads towards the radial-, transverse-, and the outer tangential walls. The secondary thickening of endodermal cells does not occur simultaneously in all the endodermal cells in the same level of the root. The secondary thickening is laid down first opposite to each phloem group and then spreads towards the enodermal cells which are opposite to the protoxylem poles. But the endodermal cells (endodermal passage cells) which lie opposite to each protoxylem pole retain their thin wall natures even in the very old root (Figs. 4, 12A, 12B).

Vascular cylinder

The central cylinder has its independent origin in the promeristem (Figs. 1A, 1B). It possesses a pith in the center and typically 9 to 12 groups of phloem and the same number of xylem groups. They are arranged alternately in the periphery of the central cylinder (Figs. 12A, 12B). Each xylem group is located opposite to the endodermal passage cells. The outermost row of cells of the vascular cylinder, the pericycle, in the mature root are sclerified except the cells located between each group of protoxylem and the endodermal passage cells (Figs. 12A, 12B). Only primary tissues are found in the root.

The sequence of differentiation and maturation of the various tissues in vascular cylinder was examined in six roots. These roots show a similar sequence of initiation, differentiation and maturation of root tissues. They are indicated by the distance from the base of the promeristem in a particular root as follows: the pericycle is recognizable as the continous cylinder approximately 0.07 mm; metaxylem differentiates before the other cells at about 0.27 mm and matures at 4.04 mm; protophloem can be identified at 0.28 mm and matures at 0.38 mm; the lignification of the

Fig. 9. Transverse section through the young root showing the vacuolation of cortical cells and of exodermal cells, ×300.
Fig. 10. Longitudinal section through the cortex showing the raphide-containing idioblast, ×250.
Fig. 11. Longitudinal section through the exodermal cells, showing the pits on the inner tangential walls (arrows), ×250.

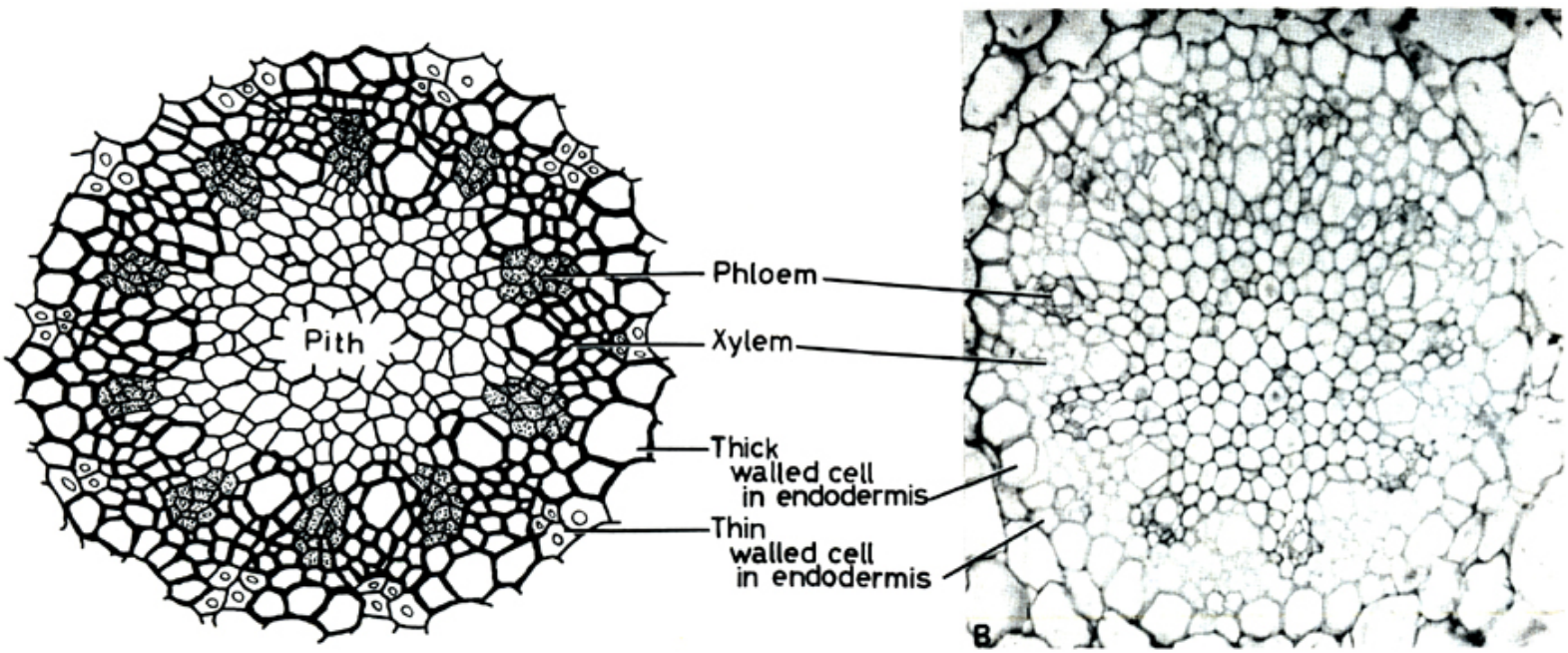

Fig. 12. A, Diagram and B, microphotograph of central cylinder in transverse section, showing the various tissues, ×335.

cell wall in the protoxylem is about at 0.55 mm; endodermal cell wall first develops secondary thickening at 2.96 mm; pericyclic calls start to deposit secondary wall at 3.40 mm. The cells in the pith develop thickened walls soon after the maturation of the metaxylem. The successive stages of the secondary wall development in the pith cells first appear at the periphery of the pith and spreads centripetally towards the center. Both protoxylem and protophloem are found occurring outside the metaxylem and metaphloem respectively (Figs. 12A, 12B). They differentiate and mature progressively from the peripheral position toward the center (exarch). The phloem matures earliest among all of the root tissues. The formation of lignified walls in velamen cells occur only next to the phloem maturation and before the protoxylem maturation. It is measured at 0.50 mm in this particular root.

Root cap

The apical meristem of the root is definitely closely covered by a root cap of closely packed parenchyma cells. The root cap cells are derived from the same origin as that of protoderm in the promeristem, *i.e.*, the most distal part of root meristem (Figs. 1A, 1B). The root cap cells are usually in 25 to 28 celled layers the region in front of the promeristem and in successively fewer celled layers in the region away from the promeristem. The old cap cells are constantly sloughed off and the new cap cells are formed by both anticlinal and periclinal divisions occurring in the cells which are located in distal part of the promeristem. The cell divisions occur in about 15 to 20 layers of the younger root cap cells, (*i.e.*, the cells located near the promeristem and they are in the earlier stages of development), they are both anticlinal and periclinal. But they divide mainly by the formation of anticlinal walls in the later stage. Therefore the root cap cells in the older part, are orderly arranged in layers (Fig. 1A). Of about 15 to 18 layers of the younger root cap cells including most of the meristematic cap cells retain rather complete cell figures and cell contents. But in the cap cells located in the outer part of the root cap they are apparently in the process of sloughing off, the anticlinal walls get out of their shape and degenerate before the disintegration of the nuclei. The periclinal walls of the old root cap cells keep their shape even to the end of the sloughing off process (Fig. 1A). Since in the sloughy cap cells the periclinal walls separate from their adjacent periclinal walls layer by layer by the disappearance of their connecting anticlinal walls (Fig. 1A).

DISCUSSION

Velamen is one of the peculiar structures of the orchid root in which the students of orchid roots are most interested. There are many reports which have dealt with the velamen (Dycus and Knudson, 1957; Engard, 1944; Gessner, 1956; Mulay and Panikkar. 1956). Velamens are also present on some aerial and terrestrial roots of

monocotyledons (Engard, 1944: Mulay and Panikkar, 1956). Although the function of the velamen has been widely discussed (Dycus and Knudson, 1957) no general agreement has been reached on it. The number of cell layers in the velamen of *Dendrobium kwashotense* is not as constant as that of some other orchids (Dycus and Knudson, 1957) in which the number of cell layers and size of velamen cells are affected by media. In the root of *Dendrobium kwashotense* it was found that the number of cell layers. the structure of velamen cells and the presence or absence of root hairs are affected by the substrate on which the roots grow. It develops more cell layers of velamen, smaller velamen cells and produces root hairs on its outermost layer if the root is tightly attached to a substrate (Fig. 3). On the contrary, it develops no root hairs, less cell layers and larger cells in the velamen if it grows in the free air or is loosely attached to the substrate (Fig. 4). This peculiar pattern of root hair distribution gives an additional characteristic to the velamen. Besides, the exodermis which is located in contact with the root hair bearing velamen has more thin walled exodermal passage cells than those which are located in contact with the non-root hair bearing velamen. This anatomical evidence could support the idea of Dycus and Knudson (1957) that the velamen on aerial roots is a liability rather than an asset to the plant. The root hair is generally considered to be the absorbing structure of the root whereas there is some doubt about the absorbing ability of the velamen. But the root hairs die soon after the degeneration of the cytoplasm in velamen cells. Root hairs can then only act as structures for anchorage. So at a later stage the velamen together with its associated root hairs can no longer take part in absorption.

Another evidence found in this plant that the adhesive root rather than the aerial root is engaged in the absorption, is the peculiar distribution of thin walled and thick walled exodermal passage cells. The root of *Dendorbium kwashotense* has more thin walled exodermal passage cells on the side which is laid down next to the velamen with the adhesive surface rather than that on the side which is laid down next to the velamen with a freely exposed surface. Apparently it is easier for water to penetrate through the thin walled exodermal passage cells to the cortical cells rather than through the thick walled exodermal passage cells especially when they are covered by suberized walls. The suberized wall is commonly considered to the barrier of water passage. There is no way for water to flow from the velamen to the cortical cells except through the exodermis. Most of the exodermal cells possess highly lignified and suberized walls (Table 1). Only some of the exodermal passage cells have thin walls. Like that in the root of the epidermis of angiosperms, the root hair initials are smaller in size and are filled with denser cytoplasm in the young stage (Cormack, 1949). In the mature root of this plant, the exodermis rather than the velamen and root hairs plays an important role in water absorption. The exodermal passage cells may be considered to be a special kind of

potential root hairs. Therefore, the existence of many thin walled exodermal passage cells on the adhesive side of the root supports the view that the adhesive root may be the only structure for water absorption. Thus, the present author, like some other workers (Dycus and Knudson, 1957) suggest that the orchid growers should direct the aerial roots so that they become attached or penetrate the substrate.

The sequence of differentiation and maturation of tissues in the root of *Dendrobium kwashotense* agrees with that of some dicotyledonous roots (Esau, 1943, 1965a; 1965b; Peterson, 1967; Popham, 1955), and the roots of some ferns (Chiang, 1967; Conard, 1908). The results of the present work clearly show that, at one level, one kind of tissue may be mature, while another is still in the process of differentiation and another still in the phase of cell division. The sequence of the differentiation and maturation of each tissue is strictly constant in all the roots examined. Further detailed studies of other monocotyledons should assist in the formulation of a general picture of differentiation and maturation of tissues in the root tips of monocotyledons.

As mentioned above, the sloughy root-cap cells separate from their adjacent periclinal walls, layer by layer by the disappearance of their connecting anticlinal walls (Fig. 1A). A considerable number of layers of separating cap cells remain on the outer surface of the living cap cells for a rather long period. Apparently the cap cells act as a protecting structure of the root tip after their death. Or they may remain attached to the root tip simply because of their aerial nature. The aerial roots, which grow in free air have less chance to meet with obstacles, (such as soil particles, water current and other substrates) than those growing in the soil or water. These obstacles prevent the root cap from remaining on the root surface for a longer time. Studying *Acer saccharinum*, Richardson (1955) related the rooting medium to the structure and development of root cap. Further studies of other roots should give a better understanding of the general relationship between the structure of the root cap and its environmental conditions.

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