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DEVELOPMENTAL ANATOMY OF GINGER RHIZOMES - II. ONTOGENY OF BUDS, ROOTS AND PHLOEM[1]

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Abstract

Developmental pattern, growth and branching behaviour of rhizomes of ginger were studied. Axillary buds are present at each node. Secondary and tertiary branches originated from the axillary bud from the adaxial sides of the leaf or scale leaf. Cytohistological zonation of rhizome buds and adventitious roots was studied. The phloem mother cell in ginger originated from the primary thickening meristems. The sieve tubes develop by pycnotic degeneration of nuclear structure. The fragmented multinuclear stages were observed in several sieve tube members. The sieve element has an average length of 76.8 μm and width of 8.76 μm. The sieve plates are transverse to oblique with varying degrees (110-140°) of inclination. Slime body exists only in early stages of development. No definitive callose was observed in mature sieve tube. The number of companion cells per sieve tube member varied from four to eight; these showed dense cytoplasm and prominent nuclei. Phloem parenchyma and fibres were also present.

Key Words : *Zingiber officinale*, ginger, developmental anatomy, ontogeny, sieve tube, companion cells.

To study the developmental morphology of ginger rhizomes it is essential to trace its growth pattern. Earlier histological studies in ginger and allied genera were reported by Solereder & Mayer (1930), Tomlinson (1969), Shah & Raju (1975), Fisher (1978) and Bell (1980). They dealt with only the general morphology, growth and branching pattern of rhizome and comparative studies of root and shoot apices. Tomlinson (1969) indicated that no special study of sieve tube elements had been made and the available information is far too scanty to permit worthwhile comments. The pattern of autolytic break down of the nucleus and cytoplasm at the final stage of the development of sieve tube elements was known and electron microscopic studies were also carried out in many species (Easu & Gill 1971, Evert 1984, Aloni 1987, Van Veenandall & Den Outer 1993). Among dicotyledons the above workers have studied the ultrastructure of sieve element in 20 species from five families, though the process of development was not examined thoroughly enough in all the species.

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Danilavo & Telepova (1978, 1981) investigated the differentiation of the protophloem sieve element in *Hordeum vulgare* and other aspects of phloem development in different plant species belonging to diverse groups.

The present paper describes the detailed study of structure and development of shoot apex, procambialisation, axillary bud initiation, root initiation and ontogeny of phloem in ginger that will fill the existing gap in our knowledge of development of secondary and tertiary branches from the main rhizome and ontogeny of shoots adventitious roots and phloem in ginger, one of the most popular spices used all over the world.

Material and Methods

Materials for this study were collected from the experimental farm of Indian Institute of Spices Research, Peruvannamuzhi. For microtomy, pieces of rhizomes were fixed and then processed in the conventional way (Johansen 1940). Materials were cut at 10 μm and stained separately in Safranine - Aniline blue, Acid fuchsin and Bromophenol blue (Krishnamoorthy 1988). Observations were made with light microscopy.

Observations

Ginger is a herbaceous perennial belonging to the family Zingiberaceae. Rhizomes of ginger bear a leafy shoot above the ground which carries the photosynthetic pseudostem with leaves. The underground rhizomes are highly branched showing nodes and internodes, each node having a dormant bud protected by scale leaves. The main rhizome produces secondary and tertiary branches which do not show positive geotropism. Fully developed branches are up to fourth order.

In a longitudinal section the shoot apex is dome shaped with a single tunica layer. Below which the central mother cell zone is present (Fig. 1A). The flank meristem, as observed in median longisection, is situated on either side of the central mother cell zone (Fig. 1B). Leaf is initiated from the outer tunica layer and from the flank meristem. But the apical zones vary in their size and distinctness in different plastochronic phases. The shoot apical configuration and acropetal differentiation of procambial strands are closely related to the phyllotaxy. At an even lower level basipetally in the rhizome axis, additional inner cortical cells are produced by a lateral primary thickening meristem (PTM) or procambium in which the resulting cells are in radial rows (Fig. 1B).

PROCAMBIAL DIFFERENTIATION — The peripheral or flank meristem divides periclinally and produces parenchyma cells. Some of the cells can be distinguished from the rest by deeper stainability, and smaller size (Fig. 1B). The cells are compact, less vacuolated and their nuclei stain darkly (Fig. 1C). The longisections show some rectangular cells with densely stained prominent nuclei - round in early stages but later becoming oval to elliptical in shape. Such procambial groups contain 15-20 cells. Later on further elongation of the cell and nucleus takes place; vacuolation of the cell also increases (Fig. 1D). These are early stages of sieve tube cell differentiation. Protophloem differentiation preceded that of proto-xylem. The collateral differentiation of phloem and xylem with parenchymatous bundle sheathes becomes distinct after an intermediate stage of random differentiation of the bundles.

TABLE 1 — PHLOEM ELEMENTS OF GINGER RHIZOME

Diameter of Rhizome	Sieve Tube		Companion Cell		Phloem Fibre			Phloem Parenchyma	
	Length	Width	Length	Width	Length	Width	Wall Thickness	Length	Width
10 mm (90-d-old)									
Range	57.5-103.5	5.29-10.35	18.3-32.5	7.3-10.8	123-168.3	10.3-14.3	1.5-4.8	4.8-71.3	6.21-21.2
Mean	76.82	8.76	23.3	7.3	138.3	12.3	3.2	59.94	17.6
Sd	13.82	1.662	3.238	0.810	10.86	0.42	0.01	7.86	3.39
20 mm (160-d-old)									
Range	60.7-120.5	16.2-12.35	20.3-35.5	16.5-18.6	123-198.83	12.3-18.83	2.5	52-1.5	7.32-22.2
Mean	80.25	10.86	28.3	16.32	156.8	14.3	4.9	67.94	18.4
Sd	10.32	1.87	4.23	0.910	11.23	0.89	0.23	7.86	3.28

Value average of 10 samples each. (Sd. standard deviation, Measurements in μm).

Ultimately the vascular bundles are found scattered in parenchymatous ground tissue (Fig. 2A). During development an endodermoidal layer is seen in transverse section of rhizome (Fig. 2B).

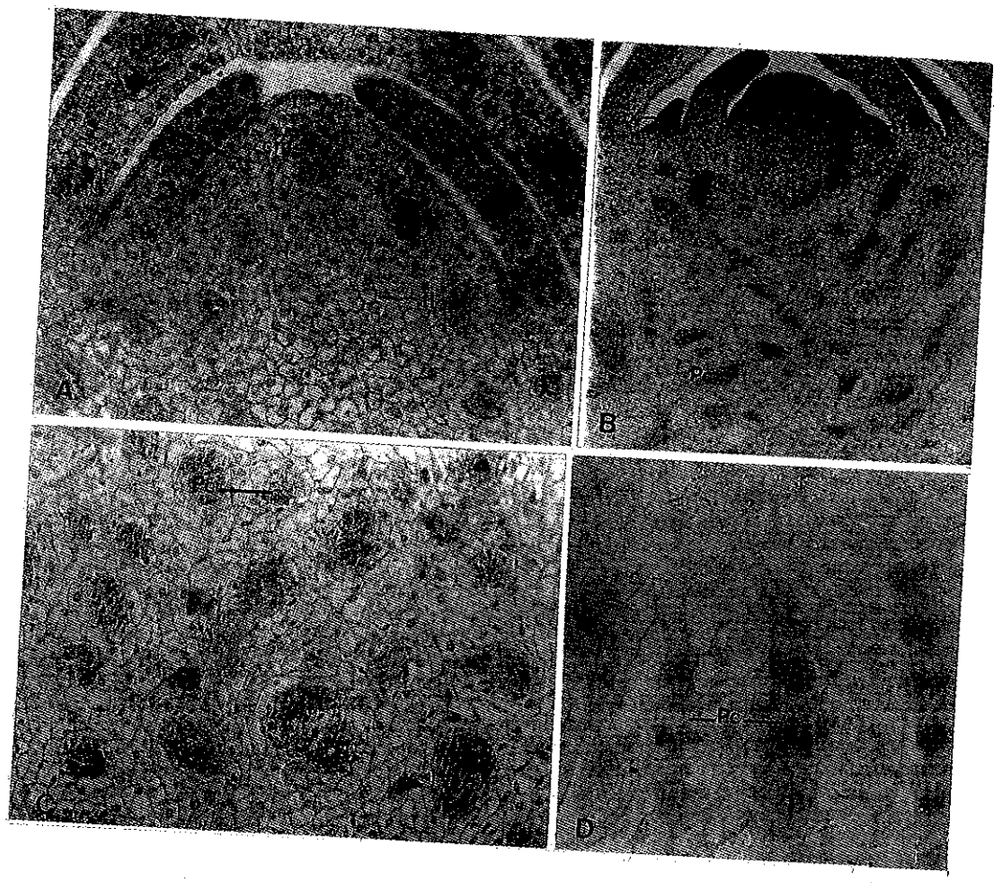

Fig. 1A-D — (*t*, tunica; *cm*, central mother cell; *fl*, flank meristem; *ax*, axillary bud' *bm*, bud meristem; *Pc*, procambium). **A,B** L.s of shoot apex **A.** x 200. **B.** x 40. **C.** T.s of rhizome showing procambium x 200. **D.** L.s of rhizome showing procambial groups x 200.

Fig. 2A-D — (*vb*, vascular bundles; *ed*, endodermoidal layer; *Ph*, phloem; *x*, xylem; *ax*, axillary bud; *n*, nucleus; *q*, quiescent centre; *P*, protoderm; *rc*, root cap). **A.** T.s of rhizome x 40. **B.** T.s showing endodermoidal layer x 200. **C.** L.s showing axillary bud x 400. T.s showing root initiation x 200.

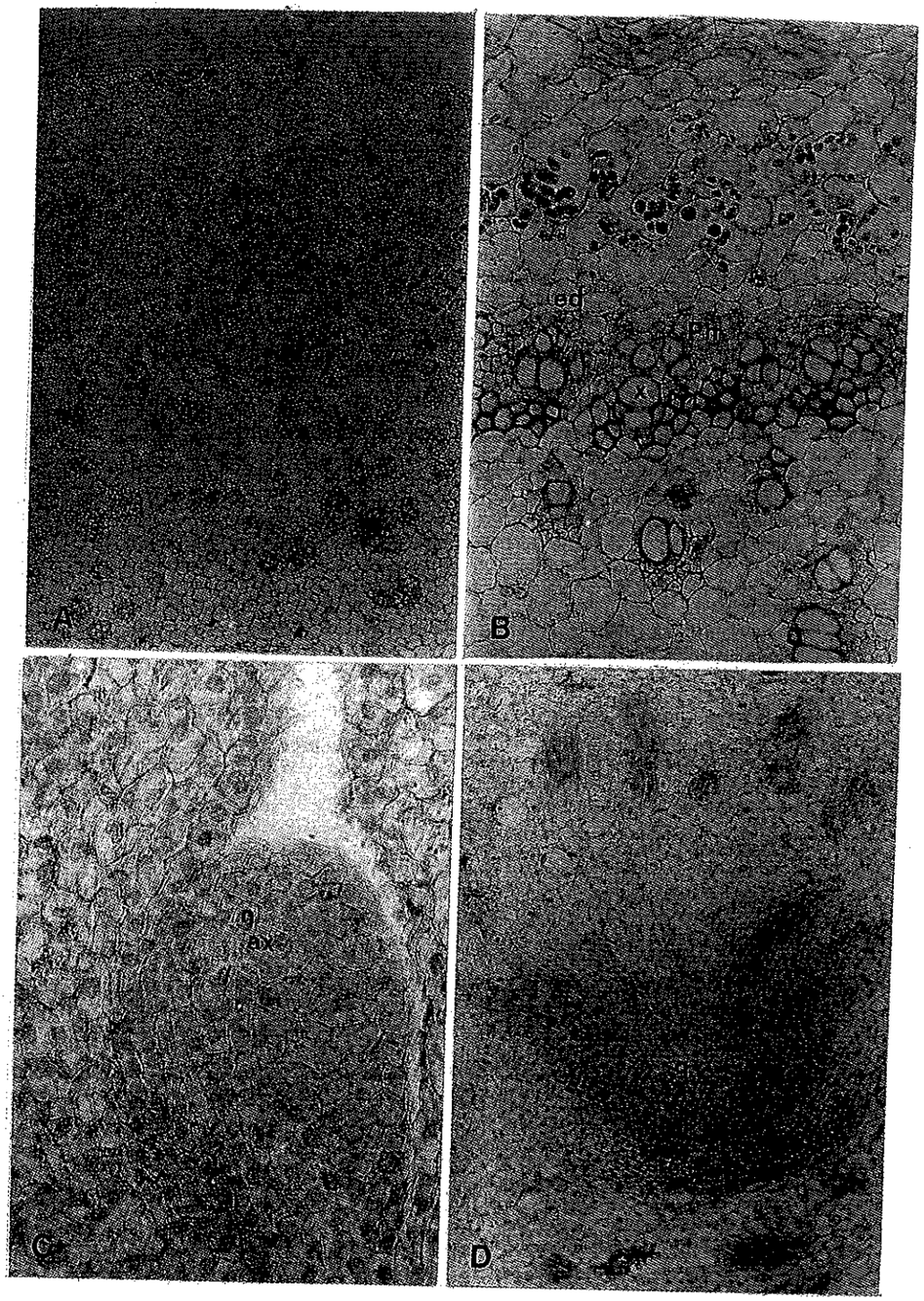

Fig. 2A-D

DEVELOPMENT OF AXILLARY BUD — The development of leaves and scale leaves in ginger rhizomes are clockwise directions and it encircled the shoot apex. The axillary bud meristem is first discernible in axillary position on adaxial sides of the third leaf primordium from apical meristem as a distinct zone by the stainability of the constituent cells and multi-plane division of the cells in the concerned peripheral meristem sectors (Figs 1B, 2C). The axillary buds thus originate as cellular patch in the adaxial side of leaf or scale leaf of the node (Figs 1B, 2C). The axillary buds thus originate as cellular patch in the adaxial side of leaf or scale leaf of the node (Fig. 1B). Dormant axillary bud is present in each node, its origin may vary from axillary to foliar position (Fig. 2C). Ultimately, in a fully developed axillary bud the cytohistological zones akin to main shoot apex could be distinctly observed. The development of new rhizome is by the enhancement of dormant axillary bud which acts just like the main shoot apex. The procambial cells and the ground meristem cells divide and produce parenchyma as well as vascular tissues, adding thickness to the newly enhanced axillary bud. Likewise many dormant buds become active during favourable conditions, each of which produces secondary and tertiary rhizomes. The axillary buds show vascularization by the activity of procambial strands of the mother rhizome and procambial cells originated by the dedifferentiation of parenchyma cells.

DEVELOPMENT OF ROOT — The adventitious root primordia become differentiated endogenously from the endodermoidal layer of rhizome. The roots always develop just below the nodal regions. The position of roots are lateral or opposite to axillary shoot bud. The transection of rhizome reveals that the endodermoidal layer and the pericycle become meristematic and undergo periclinal and anticlinal divisions resulting in a group of root initials (Fig. 2D). This is in direct connection with the vascular ring situated beneath the endodermoidal layer. The root primordia are of open type, having common initials for the cortical meristem, root cap and protoderm.

A group of cells revealing less number of mitotic divisions form a root apical quiescent centre (Fig. 2D). The actively dividing and prominently staining central cylinder shows vascular connections with the rhizome vasculature. As the enlarging root primordia emerge through cortex, the cortical cells get crushed and torn apart. Thus the roots pierce the epidermis of the rhizome to emerge out. Normally one to three roots are originated from the lateral or opposite side of the axillary bud and scale leaf.

PHLOEM — Normally there is no secondary differentiation in monocot. However, the rhizome structure of ginger gives evidence of both primary and secondary growth having well developed endodermoidal layer and cambium. The vascular bundles are collateral, closed and scattered in the ground parenchyma (Fig. 3A). The phloem elements consist of sieve tube, companion cells, parenchyma and fibre.

DEVELOPMENT OF SIEVE TUBE — Phloem cells originate from a group of actively dividing procambial cells of primary thickening meristem. These cells can be distinguished from the surrounding cells by their meristematic activity, stainability and size of the nucleus (Fig. 3C). The procambial cells are less vacuolated in early stages. During development, a procambial cell elongates and becomes thick-walled with cytoplasm and a prominent nucleus (Fig. 3D); this is the sieve tube mother cell. It undergoes a longitudinal unequal division, and the resulting smaller cell, which gives rise to companion cell. It continues to have cytoplasm and nucleus and later undergoes transverse divisions forming four to eight cells (Fig. 3B,F).

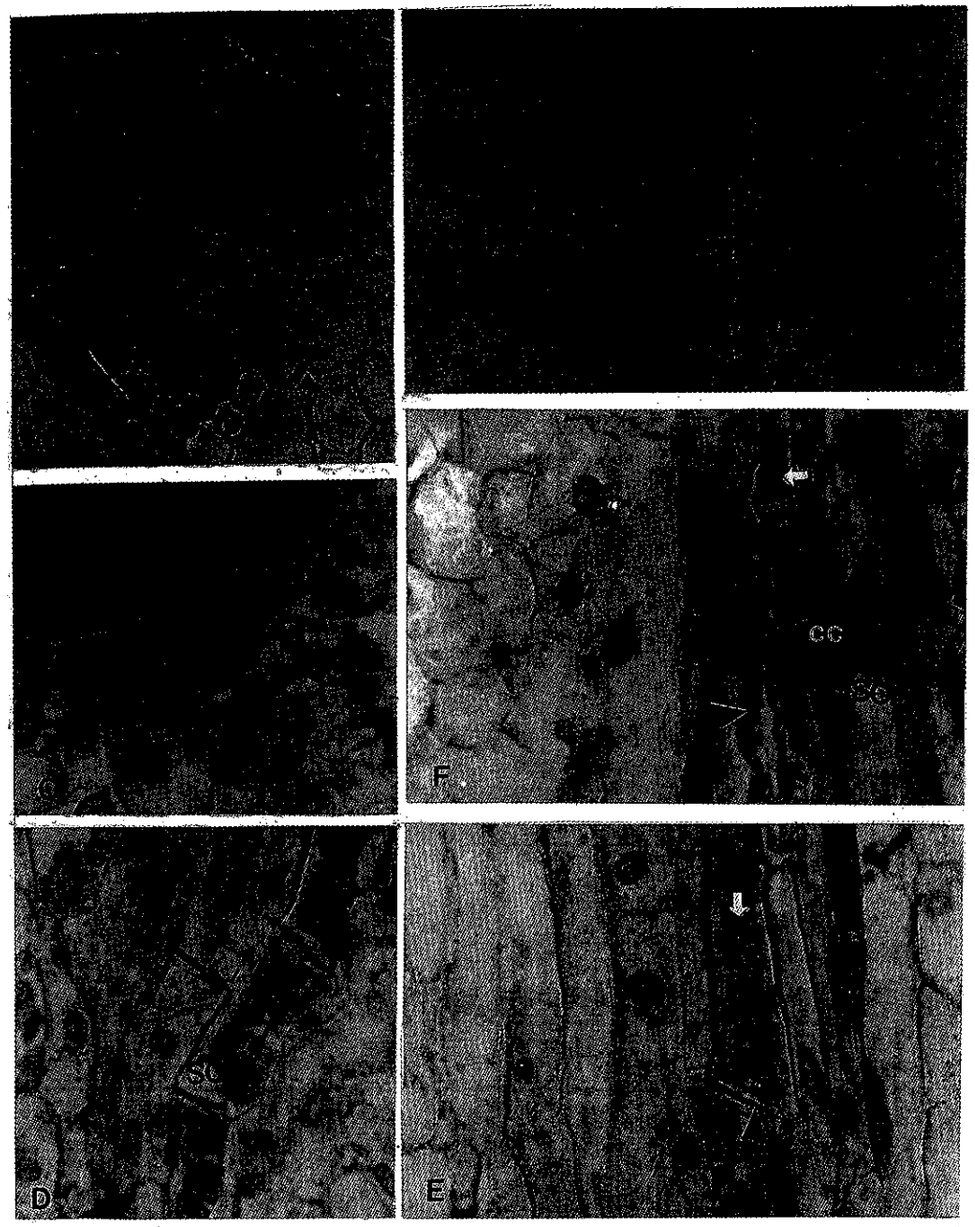

Fig. 3A-F — (*x*, xylem; *ph*, phloem; *cc*, companion cell; *sc*, sieve cell; *pc*, procambium) **A.** C.s of ginger rhizome showing endodermis and vascular bundles. **B.** L.s of phloem elements. **C.** Procambial cell. **D.** Arrow shows the sieve tube mother cells. **E.** Arrow head indicating sieve plate and white arrow shows the reduction of cytoplasm. **F.** Disintegration of cytoplasm and nuclear fragmentation. White arrow indicates slime body.

While the large cell is the sieve cell, has cytoplasmic and nuclear contents in the early stages but later their disintegration occurs, leading to the development of the sieve tube elements is by pycnotic degeneration of the nuclear structure.

The young sieve cells appear considerably elongated in longisections (Fig. 3D). Simultaneously, small vacuoles start appearing in the cytoplasm and gradually spread in the entire cell (Fig. 3D,E). The vacuolation increases and the cytoplasm shrink considerably and eventually restricting themselves along the cell wall (Fig. 3F). Another important feature is inconsistency regarding the time of disorganization of the nucleus with reference to the various developmental phases of the sieve tube element. In the early stages, the nucleus shape varies from round to elliptical. When elliptical, the nucleus measures 14.74 - 15.50 μm along the long axis and 8.2 - 15.5 μm in the mid-short axis. During differentiation of the sieve tube,

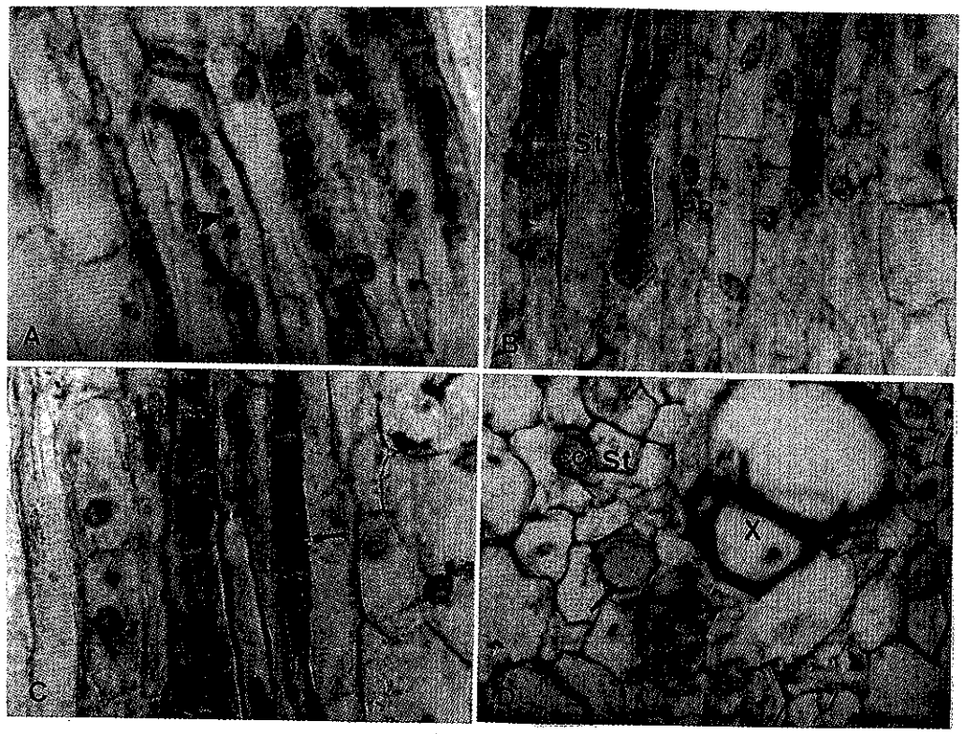

Fig. 4A-D — (*st*, sieve tube; *pp*, phloem parenchyma; *cc*, companion cell; *x*, xylem) **A.** L.s of sieve-tube mother cell with multinucleated stage. **B.** Formation of enucleated sieve tube. **C.** L.s of sieve tube with companion cells. **D.** C.s of rhizome showing xylem, phloem, arrow indicate the sieve plate with many pores.

their nuclei become elongated, show constrictions (Fig. 3E), and become lightly stained though the nucleolus and chromatin threads stain more deeply. Successive development leads to the dispersion of chromatin materials almost throughout the nucleoplasm and some deeply stained distinct nuclear fragments are also visible (Fig. 3E). The number of distinct fragments varies from two to five, giving the appearance of a multinucleated condition (Fig. 4A).

During further development of sieve cell, the vacuolation increases and the cytoplasm shrinks to appear as a thin thread-like band along the walls (Fig. 4B,C). At the same time nucleus also disintegrates completely and attains the features of enucleated sieve tube element. The transverse wall of the sieve tube changes to simple sieve plates with many pores (Fig. 4D) having very little callose depositions and they differ a great deal in width and are placed at varying degrees of inclination (110-140°) (Figs 3E, 4D). Callose deposition on the sieve plate in a mature sieve tube element is very meagre in ginger (Figs 3E, 4A). The first sieve tube element could be distinguished at a distance of 720-920 μm from the shoot apex (Fig. 4B).

In ginger rhizome, the four to eight companion cells per sieve tube element are arranged in vertical files with transverse end walls (Figs 3B, 4C). They may vary from 18-32 μm in length and 7-19 μm in breadth (Table 1). The sieve tube elements are arranged end to end to form columns of sieve tubes. The length of a sieve tube element varies from 57.5-103.8 μm, average being 76.82 μm. Width varies from 5.29-10.35 μm, the average being 8.76 μm (Table 1).

At early stages of development slime body is present in the sieve tube which appears amorphous but homogenous in the cell (Fig. 3F). Later the slime body stretches and extent up to the sieve plate in opposite directions and finally accumulates near the sieve plate; later, however, the slime body gets dispersed (Fig. 4B). No stage was observed even at maturity of rhizome, where the sieve tube element is completely blocked by definite callose as in the case of dicots.

PHLOEM PARENCHYMA — The phloem parenchyma cells are comparatively larger than the companion cell and smaller than normal cortical parenchyma cells (Fig. 2B). The length of phloem parenchyma cell varies from 48-71.3 μm with an average of 59.94 μm and the width varies from 6.21-21.2 μm the average being 17.6 μm (Table 1). The size increase of the phloem element is proportional to the growth of the rhizome. Some older phloem parenchyma cell become secondarily lignified and thick walled phloem fibres. The dimensions of phloem fibre length and width are 138.3-158.8 μm and 12.3-14.32 μm respectively and the wall thickness varies from 3.2-44.9 μm (Table 1).

Discussion

Ginger rhizome is sympodial by the successive addition of new rhizome buds and bear a aerial shoot system, whose growth pattern is distinct from that of the rhizome. Many previous publications presented static description of anatomical and morphological features without much consideration given to development. The development of a meristematic zone, peripheral to the vascular cylinder in stems and rhizomes of certain monocotyledons has held interest to developmental biologist (Gifford & Bayer 1995). Such persistent meristematic zone outside the primary vascular cylinder as a detached meristem in certain monocotyledons has

been known. Guillard (1878) referred to it as meristemiforme. Shah & Raju (1975) studied the morphology and branching behaviour of rhizome of *Zingiber officinale*, *Curcuma domestia* and *C. amada*. The root apical organisation of ten Zingiberaceae was studied by Pillai & Pillai (1961).

In many monocotyledons Mangin (1882) reported that adventitious roots originate from a special meristem formed at the periphery of the central vascular cylinder, he termed it as 'couche dictyogene'. Sargent & Arber (1915) observed that the roots originated from the intermediate zone; they proposed a new term for the layer, the root plate. Gifford & Bayer (1995) reported the origin of rhizome primordia from the axil of leaves. The present authors found that the branched development of ginger rhizome is mainly through axillary bud development situated in axils of scale leaves. The rhizome primordia are initiated in the axils of the leaves and becomes vascularized by the interconnecting procambial strands. These strands are attached to the vascular bundle networks of the main rhizome and the new branch.

In one group of monocotyledons, the meristem ceases activity after root initiation, in a second group, meristem does not lose its activity after the initiation of root but retains it for varying period (Gifford & Bayer 1995). Ginger belongs to the second group, here the meristematic activity is continued ever after root initiation.

De Mason (1979, 1980) described the details of primary thickening meristems in monocotyledons. Rudall (1991) reported that the lateral meristem is responsible for shoot growth and stem thickening in monocotyledons. Gifford & Bayer (1995) reported that primary thickening-meristem, may be responsible for the stem thickening and the production of shoot and root. Increase in number of cells in the cortex and central cylinder of ginger is brought about by the meristematic procambial cells and the division of parenchyma present in the ground meristem. That cambium beneath the endodermoidal layer is also responsible for the growth of ginger rhizome was reported by Remashree et al. (1997). Bendixen (1973) stated that roots originated in the pericycle while in *Cyperus* Wills et al. (1980) reported their origin from the endodermis. Gifford & Bayer (1995) interpreted the primary thickening-meristem as the endodermoidal layer, and that the root primordia are initiated early in primary thickening-meristem the precise cell layer uni- or multilayered, is difficult to determine. Ginger root primordia, originating lateral or opposite to axillary bud, are formed in position of the endodermoidal and the pericycle layers which became meristematic and gave rise to a group of root primordial initials.

The specialization trends in the size and shape of the sieve tube elements and the arrangement of sieve areas have been very well investigated in monocotyledons by Cheadle & Whitford (1941) and Parthasarathy (1968). The specialization involves the following trends: (i) gradual localization of highly specialized (the connecting strands are very thick) sieve area to the end walls, (ii) gradual changes in the positions of the end walls from very oblique to horizontal, (iii) gradual changes from compound sieve plate to simple one, and (iv) gradual reduction of the sieve areas on the side walls of the element (Fahn 1990). The presence of protophloem sieve cells in mature organs of vascular cryptogams is normally identified from the size and obliterated condition of the sieve tube (Easu 1969). The problem of nuclear structure transformation during sieve element differentiation has been widely discussed. In majority of investigated angiosperms and gymnosperms, intact nuclei are absent in mature sieve elements (Easu 1969). Degenerative changes in nuclei of differentiating sieve elements takes place by two ways : (i) first one is characterized by the gradual loss of nuclei and

chromatin, decrease in the density of nucleoplasm and the rupture of the nuclear envelope and (ii) the second path is the so called pycnotic degeneration, featured by the extreme degree of chromatin condensation and nuclear fragmentation (Easu 1969). Easu & Gill (1973) reported pycnotic degeneration of the nucleus in the case of protophloem sieve elements of *Allium cepa*. Buvat (1968) studied the development of phloem in *Hordeum vulgare* root and Danilavo & Telepova (1978, 1981) in *Hordeum vulgare* stem. Melaragno & Walsh (1976) reported details of the ultrastructure of sieve elements in *Lemna minor*.

In the case of ginger, the development of sieve tube is pycnotic and is similar to the second type of degeneration of the nucleus reported by Easu (1969) and Evert (1984). The sieve element passes through "fragmented multi-nucleated stage" - a unique feature in the ontogeny of multinucleated sieve tube as reported by Easu (1938). In ginger rhizomes also, the sieve plates are simple and the end walls are oblique. In sieve elements, the disintegration and loss of content and final disappearance of the stainable nuclear membrane was reported by Thorsch & Easu (1981) and Eleftheriou (1987) which closely resemble the present findings. Our observations also confirm that the slime body is non- persistent but persistent slime body is reported by Evert & Derr (1964) in *Robinia*. The number of companion cells in a vertical row is relatively high in ginger rhizomes as compared to the early reports (Evert 1984, Aloni 1987). Zimmermann & Broen (1971) reported that in arborescent monocotyledons the most remarkable aspect of phloem is its longevity in general and sieve tube in particular. This part of phloem does not go through a dormant stage as in the case of dicots and conifers. The sieve tube element of dicots develop callose plug during the onset of winter and autumn. By the return of summer, the callose plug is dissolved away by enzymatic action. This is 'a walve mechanism' of nature provided to dicots according to Zimmermann & Broen (1971). In the present case ginger rhizome revealed that definitive callose is not formed at the end walls of sieve tube elements even when the rhizome is at full maturity. Probably this is to function as another kind of 'walve mechanism' in perennial rhizomatous crop like ginger.

In conclusion it may be mentioned that although we have now relatively much information about the cytohistological zonation of the apical meristems, development of procambial cells from the meristematic regions, ontogeny of axillary bud initiation and root initiation. Development of phloem takes place before xylem from procambium. Increase in growth is directly proportional to the increase in size and number of phloem elements. The number and groups of phloem and xylem are higher in the rhizome than in the pseudostem. The elements of phloem contains typical parenchyma cells as well as specialized parenchyma i.e. the companion cells, in which reserve substances are stored. In ginger rhizome, the number of companion cells are more and these act as storage cells. Most of the parenchyma cells nearer to the phloem elements contain carbohydrates stored in the form of starch grains. We do not know how to various zones related to the morphogenetic events occurring just behind them and exact mechanism of the relationship between the increase of phloem elements and starch accumulation can be explained with further biochemical studies.

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