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ZONATION IN THE ROOT APICAL MERISTEM OF SOME ANGIOSPERMS

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ABSTRACT

Water is one of the most essential natural resource for existence of life on this planet. With increasing
The zonation and behavior of root apical meristem was studied in 8 plant species viz. *Brassica juncea* (L.), *Linum usitatissimum* (L.), *Ziziphus nummularia* (Burm.f.), *Cicer arietinum* (L.*), Pisum sativum* (L.*), Cucumis callosus* (Rottl.*), Coriandrum sativum* (L.) *and Helianthus annuus* (L.) at embroyonal, seedling and mature stages. On the basis of arrangement and behavior of stelar and columella initials and their immediate derivatives at the root pole, the apical organization is broadly categorized into type I with discrete initials for six zones at the root pole and the type II with common group of initials with hemispherical or quadrangular to rectangular shapes of cells. The seedling root apices showed a process of secondary columella formation by the process of "opening out" in all the species. The growing root apices of all the eight species showed lighter stained cells region constituting "quiescent centre".

Key words: Root cap, Secondary columella, Opening out, Columella initials, Quiescent centre

INTRODUCTION

Angiosperms constitute the most diverse group of land plants. The present literature on root apical organization reveals three different approaches and they are (a) analysis and classification of the cell net of the root apex (b) the cytohistological state and (c) the physiological role of the different zones and differentiation of the root apex. Root apical meristems fall into three broad structural classes based on the number of cells or cell layers to which the files of root cells can be traced (Gunning 1982). Clowes (2000) reported that roots of angiosperms differed in the behavior of their apical meristems. In closed meristems inner cell layer of the cap complex formed epidermis and in the open meristems, where cortex and cap are intermittently of common origin linkage between epidermis and the cap predominates. Sharma and Sharma (1988) in some members of Mimosoideae and Negi (2002) in some Cesalpinoideae members reported a common group of initials and supported the conclusion that this type was the most primitive. Schuepp (1917) introduced the concept, the "Korper-Kappe" for the analysis of the cell net in the roots. In Kappe and Korper type cell divisions the "T" or "Y" shape of the cell walls are found at each locus where a longitudinal division followed by a transverse division of one of the daughter cells causing one file of cells to become two. Sharma and Sharma (1987) studied the presence of a quiescent centre in the growing roots of *Polyathia*, based on the comparative values of nuclear to cell area ratios in the centrally and peripherally located cells of the common group of initials. Jiang and Feldman (2005) reported that the establishment of the angiosperm root apical meristem is dependent on the specification of a stem cell niche and the subsequent development of the quiescent centre at the primitive root pole is required for root meristem development and elaboration. Heimsch and Seago (2008) reported in most angiosperm's RAMs, initials for the central region of the root cap or columella are distinct from the lateral root cap and its initials. The present study based on the embryological, developmental and anatomical characterization of root apical meristems of eight species of angiosperms. All the species has valuability on the canvas of commercial, economical and medical importance. Lee (2013) reported that the apical root growth requires inter-relative processes of cell division, elongation and differentiation. Root apical meristem localised at the root tip harbours stem cells that divide asymmetrically and generate initial cells for all the cell types in the root. The quiescent centre maintains stem cells and thereby sustains a constant supply of cells for root growth. Bizet (2014) reported a new non-invasive method that couples infrared light imaging and kinematic analyses and that allows *in vivo* measurements of the RAM length. The study provides a detailed description of the RAM activity, especially in terms of cell flux and cell division rate. Drisch (2015) studied that transcription factors play a central role in root development and are regulated by phytohormones, small signaling molecules, and miRNAs. Lvanov (2017) reported that the cytokinins regulate root growth through it action on meristematic cell proliferation but not transition to differentiation in the angiosperm plants. Dolzblasz (2018) studied the impairment of root meristem proliferation

in *Arabidopsis* plants lacking of mitochondrial protease AtFTSH4.

MATERIALS AND METHODS

The root apical meristems were collected at embryonal, seedling and mature stages of plants. The seeds of *Brassica juncea* (L.) *Ziziphus nummularia* (Burm.f.), *Cicer arietinum* (L.), *Cucumis callosus* (Rottl.), *Coriandrum sativum* (L.) were germinated in petriplates lined with moist blotting paper while of *Linum usitatissimum* (L.) in petriplates lined with moist cotton. *Helianthus annuus* (L.) seeds were germinated through tray technique using the coconut hair manure while of *Pisum sativum* (L.) using polybags technique by keeping them in the freezer at 4°C temperature. Root tips of these seedlings were collected during 1st to 7th day after seed wetting. Embryonal root tips were collected from mature embryos dissected out after seed wetting. The root tips were also collected from one month old plants grown in plastic bags. The tips were fixed in Formalin-Acetic Acid alcohol (FAA) for 24 hrs. The fixed materials were preserved in 70% alcohol till required for processing. Samples were washed thoroughly in 70% alcohol, dehydrated through Tertiary Butyl Alcohol (TBA) series and embedded in paraffin. Serial longitudinal sections of roots were cut on automated microtome of Leica RM2255 at 4-5 µm. Haupt's adhesive was used for affixing the paraffin ribbons to the slides. The dried slides than run through the staining series (up and down series). Sections were stained with tannic acid-ferric chloride, safranine and light-green combinations (Johansen 1940). Stained sections cleared in xylol were mounted in DPX. Microphotographs were taken using Leica DFC 295 stereo-microscope.

RESULTS AND DISCUSSION

The organisation and behaviour of root apical meristem in all the plant species was studied at embryonal, seedling and mature stages. On the basis of differences shown in arrangement and behaviour of stelar and columella initials and their immediate derivatives at the root pole, apical organisation is broadly categorized into type I (with discrete initials) and type II (with common initials). Root measurements (Mean ± S.D.) of 8 plant species at different stages of growth are given in Table 1-3.

Type I (Root apices with discrete initials)

Six zones present at the root pole in *Brassica, Linum, Coriandrum, Cucumis* and *Helianthus* showed six zones were; Zone 1 (The initials), Zone 2 (The stele), Zone 3 (The columella), Zone 4 (The cortex), Zone 5 (The epidermis) and Zone 6 (The peripheral part of root cap). The radicular apex of all five species exhibit Zone I having separate initials for stele, columella and cortex and common initials for the epidermis and peripheral part of the cap. The former three types of initials are arranged in three layers at the root pole

Table 1. Measurements (Mean ± S.D.) of roots at different stages of growth

(Plant Name	Stage(µ)	Diameter of root (µ)	Width of peripheral region (one side in L.S.)(µ)	Width of Columella region (µ)	Length of Columella region (µ)	Area of Quiescent Centre (µ) (WxL)
Brassica juncea	Radicular	75.27±1.7559	15.13±0.1312	44.68±0.4265	26.95±0.3386	ND
	2nd day old seedling	63.00±0.1517	12.22±6.5545	37.85±0.2943	38.86±0.2372	ND
	7th day old seedling	43.55±0.4770	9.17±0.2531	24.37±0.3693	33.63±0.4840	ND
	Well established root	50.66±0.5804	12.01±0.2247	26.50±0.4737	38.78±0.3062	±34.64
Linum usitatisimum	Radicular	77.52±1.0688	14.20±48.6066	48.60±0.4452	36.22±0.7578	ND
	2nd day old seedling	57.35±3566	13.56±0.8466	31.23±1.0149	50.38±1.0010	ND
2/7 days old seedling	7th day old seedling	73.23±0.9141	14.20±0.5295	44.11±0.4062	38.98±0.6245	+42.06
	Well established root	51.98±1.4748	12.17±0.5564	26.09±0.4251	50.60±0.4439	ND
Ziziphus nummularia	Radicular	72.11±0.5734	14.13±0.3635	43.32±0.4899	21.28±0.4766	ND
	2nd day old seedling	37.51±0.8099	11.13±0.8165	14.17±0.2644	44.27±0.6064	ND
	7th day old seedling	46.60±0.5336	12.19±0.8428	21.23±0.3569	51.24±0.6894	+43.40
	Well established root	46.56±0.8991	9.22±2.4732	27.56±0.4751	39.23±0.5299	ND

* Radicular - Embroyonal Root; ND-Not Detected

Table 2. Measurements (Mean ± S.D.) of roots at different stages of growth

Plant Name	Stage	Diameter of root (µ)	Width of peripheral region (one side in L.S.)	Width of Columella region (µ)	Length of Columella region (µ)	Area of Quiescent Centre(µ).Mean+ S.D. (WxL)
Cicer aerientinum	Radicular	91.64±0.9275	14.25±0.4926	62.02±0.7421	23.04±0.3595	ND
	2nd day old seedling	51.46±0.6393	8.53±0.3704	34.97±0.6529	23.43±0.3235	ND
	7th day old seedling	45.26±1.0268	8.04±0.1084	29.74±0.4954	37.25±0.8649	ND
	Well established root	16.70±0.6001	3.63±0.4108	10.63±0.3819	13.51±0.052	±50.01
Pisum sativum	Radicular	76.91±0.2760	15.38±0.3470	45.25±0.8340	36.28±0.2978	ND
	2nd day old seedling	46.261±0.3702	9.60±0.3718	27.48±0.3802	36.97±0.9361	ND
	7th day old seedling	66.04±0.3769	13.20±0.2654	39.52±0.1936	36.54±0.4215	ND
	Well established root	63.09±0.0857	10.44±0.3476	41.20±0.1798	40.92±0.1651	±42.06
Coriandrum sativum	Radicular	41.56±0.4243	9.44±0.3706	21.37±0.3242	27.20±0.4943	ND
	2nd day old seedling	44.32±0.4654	9.25±0.3164	26.31±0.3024	58.19±0.4339	ND
	7th day old seedling	41.63±0.4605	9.05±0.0778	21.31±0.3024	55.22±0.4459	±43.9
	Well established root	25.49±0.3767	2.76±0.0294	20,29±0.2160	13.21±0.2453	ND

Table 3. Measurements (Mean ± S.D.) of roots at different stages of growth

Plant Name	Stage	Diameter of root (µ)	Width of peripheral region (one side in L.S.)(µ)	Width of Columella region (µ)	Length of Columella region (µ)	Area of Quiescent Centre(µ) (WxL)
Cucumis callous	Radicular	43.47±0.3937	7.13±0.1512	29.10±0.1080	23.32±0.3765	ND
	2nd day old seedling	34.51±1.9462	6.39±0.2127	19.44±0.0648	18.55±0.0571	ND
	7th day old seedling	37.04±0.0778	9.29±0.4665	17.15±0.1857	29.32±0.2885	±48.01
	Well established root	25.65±0.0697	5.04±0.1067	14.69±0.0736	29.51±0.0579	ND
Helianthus annuus	Radicular	55.15±0.1268	13.98±0.0974	27.07±0.1993	18.56±0.0535	ND
	2nd day old seedling	45.65±0.2927	10.00±0.0408	25.05±0.0.1607	26.48±0.2201	ND
	7th day old seedling	60.11±0.0974	15.68±0.2494	27.51±0.1247	33.67±0.0883	+61.15
	Well established root	28.21±0.1693	5.41±0.2483	17.76±0.0787	19.52±0.1319	ND

(Figs. 1, 6, 25, 28). The stelar initials are in form of innermost (on proximal side) plate made up of 3-4 densely stained smaller isodiametric cells. The peripherally located cells divide by vertical divisions whereas centrally located cells divide by transverse and occasional vertical divisions (the korper type of divisions). The plate of cortical initials is present subjacent to the stelar initials. It consists of 4-5 densely stained isodiametric cells. The outermost (distal side) plate of cells subjacent to the cortical initials constitutes layer of initials for columella. It is present at the head of columella and stained lighter than the former two tiers. The isodiametric to quadrangular cells of this tier divide by repeated transverse divisions and add new cells distally. Proximal to root pole is a complex of densely stained rectangular initials present on its periphery. This group of initials shows two types of division patterns. The proximally located cells divide continuously by transverse divisions whereas distal cells divide by transverse and occasional longitudinal divisions (Kappe divisions). It is termed as root cap epidermis complex. Zone 2 is represented by the stelar initials dividing by repeated transverse divisions and occasional longitudinal divisions in the immediate derivatives. This forms an ' ⊥' pattern i.e. Korper pattern of divisions and helps in broadening of cylinder due to increase in number of longitudinal cell files proximally. These are central cylinder precursor cells which are small densely stained cells. Zone 3 consists of quadrangular to rectangular and highly vacuolated cells of columella (the distal most tier of initials at the root pole) dividing by transverse divisions only. The columella cell files are slightly curved and show continuity with the cell files of peripheral part of root cap. There is no demarcation between boundaries of columella and peripheral region of the root cap. Zone 4 is represented by the cortex initials (in between stelar and columella initials) showing only longitudinal (anticlinal) divisions whereas Zone 5 consists of proximally located initials of the root cap - epidermis – complex dividing repeatedly by transverse divisions that gradually differentiate into the mature epidermal cells proximally and become the outermost layer of the root body. Zone 6 is the peripheral part of the root cap consisting of the distally located initials of the root cap-epidermis complex dividing by Kappe pattern of divisions. The epidermis and peripheral part of root cap originate from the peripherally located epidermis root cap complex of initials.

Type II (Root apices with common initials)

In older seedlings and mature roots of all the eight species, stele, columella and cortex arise from a common group of initials. In *Cicer* and *Pisum* the common group of initials is slightly regularly arranged in transverse layers of cells forming a so called transversal meristem (Figs. 15, 17, 19, 21) whereas in the remaining six species it is a broad group of cells at the root pole.

The common group of initials (Hemispherical)

The common group of initials is seen in older seedling and mature roots of *Brassica, Linum, Coriandrum, Cucumis* and *Helianthus* (Figs. 2,4,8,22,27,30) and all roots (embryonal, older seedling and mature roots) of *Ziziphus, Cicer* and *Pisum* (Figs.11,12,14,15,17,21) Cells are uniformly densely stained in the proximal region of this group whereas distal and centrally located cells are slightly lesser cytoptasmic. The proximal (stelar initials) and peripherally (cortical initials) located initials divide by transverse and occasional longitudinal (Korper) divisions and contribute precursors to the stele and cortex respectively, which by further divisions and differentiation contribute to the stele and cortex proximally. The lateral peripheral cells of the hemispherical group are densely stained and divide to form precursors of the cortex proximally. The precursors of stele and cortex with Korper divisions are distinguishable clearly on the basis of relative size of cells as cortical precursor cells are broader than the stele precursors cells. Outermost cells of the differentiating cortex also contribute cells to the epidermis.

Ontogenetic changes

The seedling roots during second to fifth day (after seed wetting) showed oblique divisions in the peripheral cortical and columella initials. This results in formation of a "knee" like structure at the root pole in *Brassica, Linum, Coriandrum, Cucumis* and *Helianthus* (Figs.3, 9, 24, 26, 29). The closed configuration becomes an open structure with a common group of initials for the stele and columella during the following 1-2 days. Formation of secondary columella starts around the top of the primary columella in *Brassica, Linum, Coriandrum,* and *Helianthus* (Figs. 4, 7, 22, 30).

Formation of secondary columella and "knee" structure is also seen in the seedling roots of *Ziziphus, Cicer* and *Pisum* during third to fifth days of seedling growth (Figs. 12, 16, 18, 19). In all seedling roots and in some samples of mature roots, outermost few layers of root body and root cap are seen as being removed. The diameter of the root apex gradually decreases from radicular to seedling and mature roots in *Brassica* and *Linum* (Figs.5, 8).

Quiescent centre

The root apices in growing (seedling) roots of *Brassica, Linum, Ziziphus, Cicer, Pisum, Cucumis, Coriandrum* and *Helianthus* showed lighter stained cells at the root pole which include centrally located cells of the initiating zones. These cells are broader, vacuolated and lightly cytoplasmic as compared to their surrounding cells (Figs.5, 10, 13, 17, 20, 23, 29).

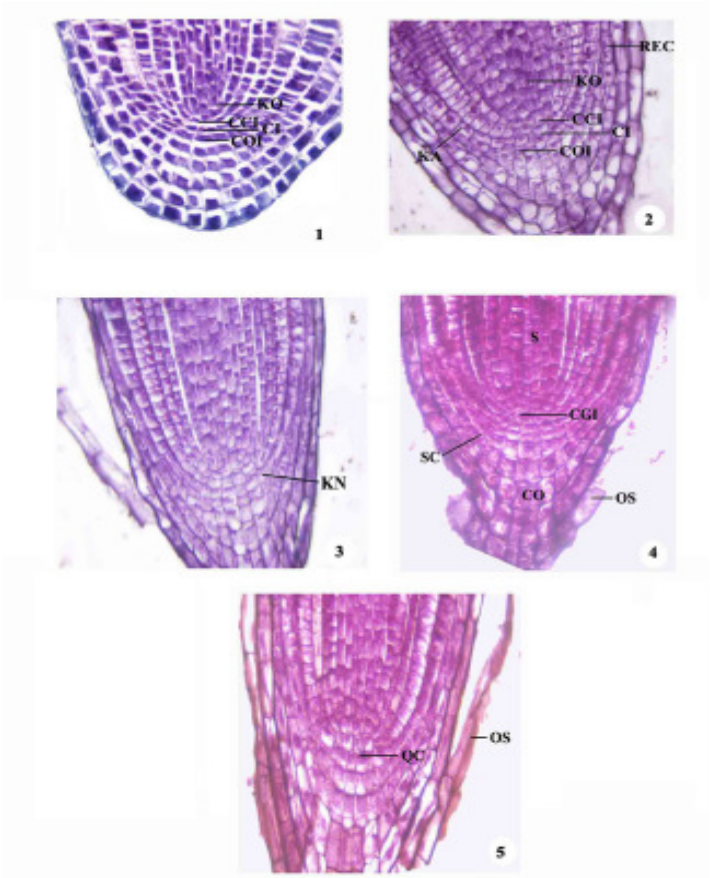

Fig. 1-5 *Brassica juncea* : L.S. of radicular – mature root apices

1. Radicular apices X 400, 2. 5 day old seedling root apices X 400, 3-4. Seedling root apices, 5. Mature root apices Quiencnt centre X 400.

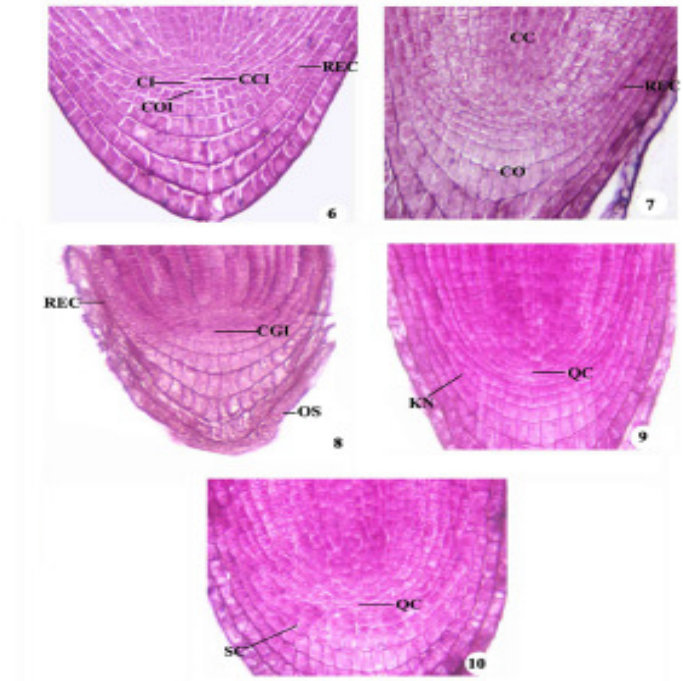

Fig. 6-10 *Linum usitatissimum* L.S. of radicular – mature root apices

6. Radicular apices X 400, 7-8. Seedling root apices X 400, 9-10. Root apices with Quiencnt centre X 200, 400.

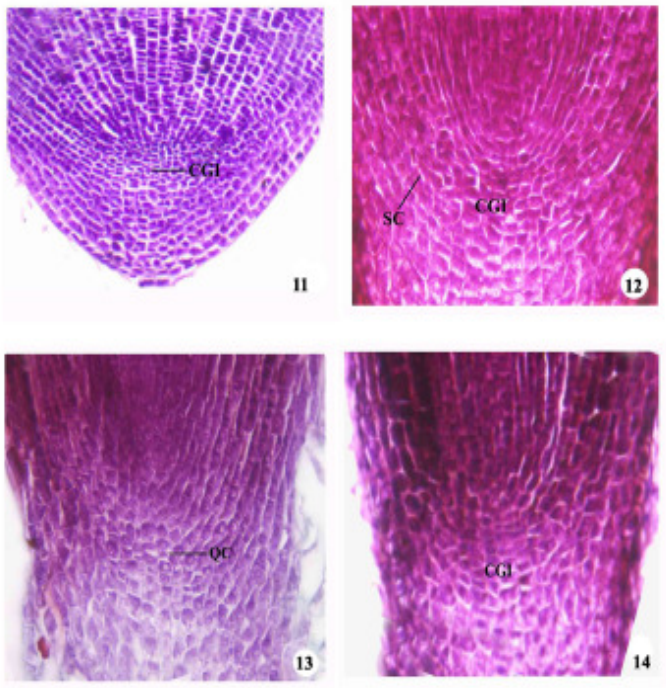

Fig. 11-14 *Ziziphus nummlaria* L.S. of radicular – mature root apices

11. Radicular apices X 200, 12. 1 Day old root apices X 400, 13. Seedling root apices X 400, 14. Mature root apices with Quiencnt centre X 400.

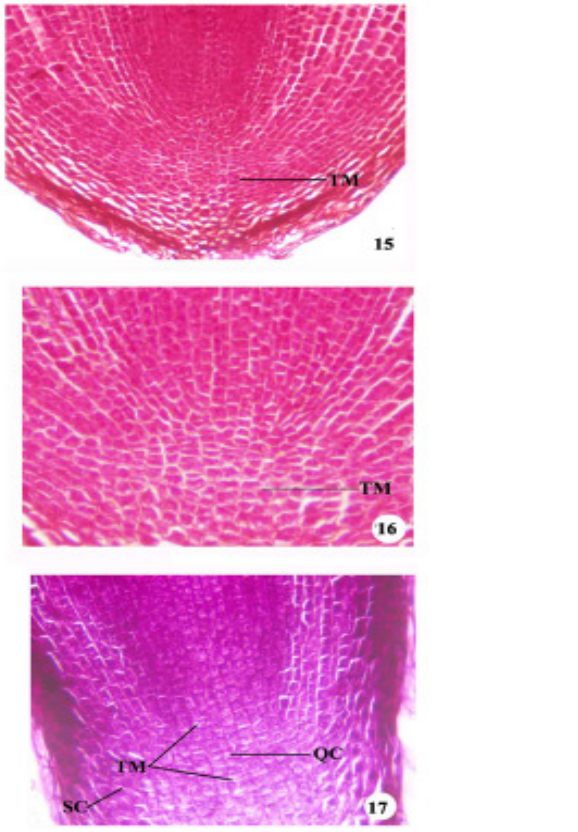

Fig. 15-17 *Cicer arietinum* L.S. of radicular – mature root apices

15. Seedling root apices X 200, 16. Seedling root apices X 400, 17. Mature root apices with Quiencnt centre X 400.

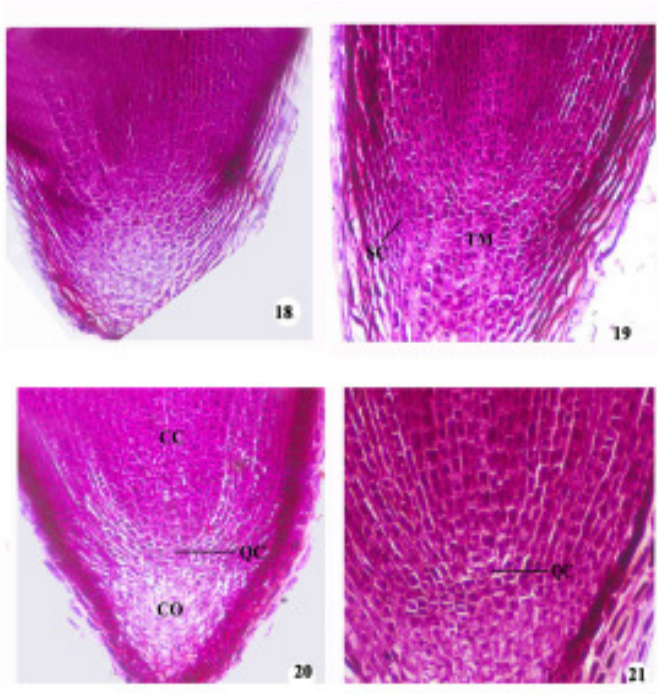

Fig. 18-21 *Pisum sativum* L.S. of seedling – mature root apices

18. Seedling root apices X 200, 19. Seedling root apices X 200, 20-21. Mature root apices with Quienent centre, X 200 X 400.

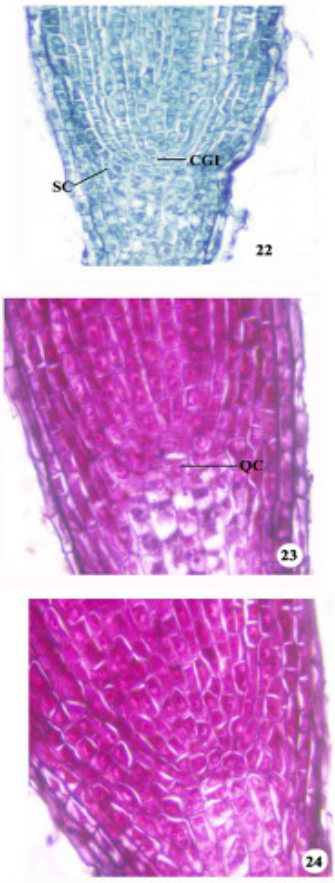

Fig. 22-24 *Coriandrum sativum* L.S. of seedling – mature root apices

22. Seedling root apices X 200, 23. Seedling root apices Quiencnt centre X 400, 24. Root apices X 400.

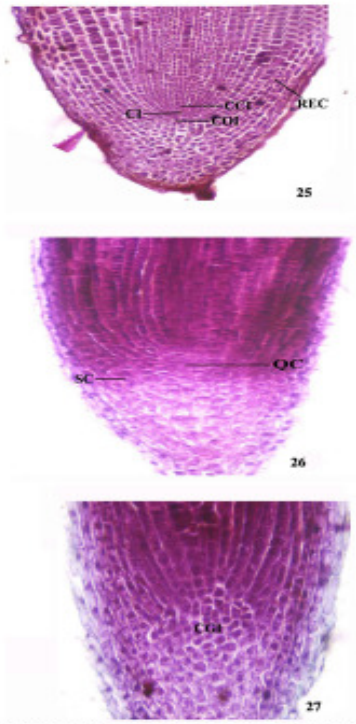

Fig. 25-27 *Cucumis callosus* L.S. of radicular – mature root apices

25. Radicular apices X 200, 26. Seedling root apices with Quienent centre X 200, 27. Mature root apices X 400.

literature reveals that Hanstein's (1968) histogen theory attracted attention of several workers. Janczewski (1874) and Pillai and Pillai (1961a) added a fourth histogen to the three identified by Hanstein. The data presented here also have used these two concepts to be broadly suitable for cell net analysis at the root pole. The present data reveal that not a single concept can give a clear picture of the root pole structure. While broadly classifying the roots studied here, into open and closed, there is a typical root cap- epidermis complex at the periphery. Popham (1955) describing zonation of primary and lateral roots of *Pisum sativum* classified angiosperm roots into different types based on arrangement and functions of cells at the root pole. Guttenberg et al. (1955) and Guttenberg (1960) classified roots into open and closed types. This concept of classification of roots into open and closed is broadly followed in the present treatise. Accordingly the roots of mature embryos in *Brassica, Linum, Coriandrum, Cucumis* and *Helianthus* were described under type I root apices with discrete initials (seedling and mature roots in *Brassica, Linum, Coriandrum, Cucumis* and *Helianthus*) and all roots (radicular, seedling and mature) in *Ziziphus, Cicer* and *Pisum* were described under type II i.e. root apices with common initials. The common group of initials in the later two species is almost a quadrangular group of cells where regular files of cells are present. Popham (1955) called this type of arrangement of initials as transversal meristem. The data reveal that while growing roots exhibited open configuration, the majority of radicular apices had closed

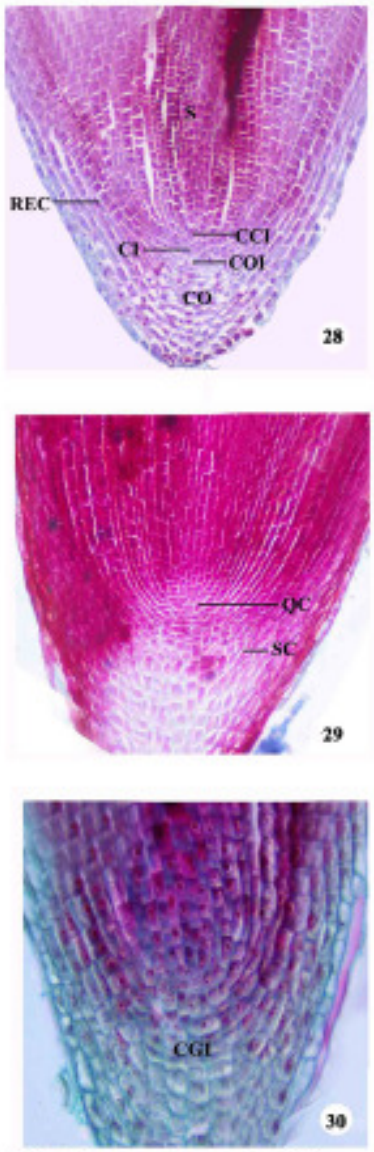

Fig. 28-30 *Helianthus annuus* L.S. of radicular – mature root apices

28. Radicular apices X 200, 29. Seedling root apices with Quiencnt centre X 400, 30. Mature root apices X 400.

configuration. This is in broad agreement with Guttenberg et al.'s (1955) observations in *Helianthus.* Guttenberg et al. (1955), while studying histogenesis in the embryos and seedlings of *Helianthus annuus* reported the process of "opening out" and "knee formation". They observed discrete tiers of initials for stele, cortex and common group of initials for the epidermis and peripheral part of the root cap surrounding a columella in the early stages of root apex. As embryo matures gradually into the seedling, cortical initials in the pericolumnar region exhibit oblique and transverse divisions forming "knees" resulting in curving files of cells proceeding distally and forming secondary columella. The root apices at embryonal stage in *Brassica, Linum, Coriandrum, Cucumis* and *Helianthus* studied in the present investigation showed discrete initials at the root pole with separate tiers of initials for the stele and columella. This is in accord with the observations made by Dubey (1986), Shekhawat (2001), Negi (2002) and Parashar (2003). During first to five days of seedling growth there are oblique divisions seen in the peripheral cortical and columella initials resulting into formation of "knees" at the root pole. In the remaining three species (i.e. *Ziziphus, Cicer* and *Pisum*) a common group of initials is seen at the root pole at embryonal stage. But in these species also orientation of cells forming "knees" is observed. This process is followed by formation of secondary columella around the head of primary columella in all the species. The data reveal that the Guttenberg's observations are fully supported by the five species (with discrete initials) and partially by the remaining three species. It seems that formation of secondary columella is a general feature during seedling growth in angiosperms. The development of root as an integral part of root body or a separate entity has been discussed since long. Holle (1876) categorized roots of all plants to two categories (i) where root cap originate from an apical cell (ii) where root cap originate from the periblem but the data presented here indicate double origin of the root cap i.e. the central part originated from the columella initials and the peripheral part from the root cap-epidermis complex. The data indicate that root cap is not an integral part of root body and tend to become an independent entity. These support Sharma and Sharma's (1988), Khorwal (2004) suggestions that the columella is ontogenetically, morphologically and anatomically separates from the peripheral region of the cap. Clowes (1971, 1984) interpreted lower mitotic activity in the quiescent centre. The present study reveals appearance of quiescent centre as the lighter stained, large, vacuolated cells in all the four species. The data presented here support earlier studies of legumonosae plants by Kaur (2010) and Saini (2012). The present report showed a discrete initials type of organisation at the embryonal stage as the embryo germinates and radicular apex starts growing, the closed root becomes open and all the mature roots showed a common group of initials for all the regions of root body and root cap excepting epidermis and peripheral part of root cap which arise from a separate complex of initials. The data are in support of Haberlandt's conclusions where both root body and root cap arise from common group of initials.

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