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ROOT APICAL ORGANIZATION IN GYMNOSPERMS

ROOT APEX OF *EPHEDRA FOLIATA*, WITH A SUGGESTION ON THE POSSIBLE EVOLUTIONARY TREND OF ROOT APICAL STRUCTURES IN GYMNOSPERMS

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Summary. The roots of *Ephedra foliata* have a long cap. The root apical meristem can be distinguished into (1) a discrete layer of stelar initials, (2) the columella and its initials, and (3) a common initiating region for the cortex and the peripheral region of the cap. The study of the cell lineages brings out that the first zone and its derivatives show a "Körper"complex of cells, the second and its derivatives divide in a transverse plane, and the third zone exhibits the "Kappe" complex.

This organization resembles the "gymnospermous" type mentioned in the older literature in the discreteness of the "plerome."

A possible line of evolution of the root apical structures of gymnosperms is suggested.

A perusal of the literature reveals that the root apical organization of gymnosperms was studied during the last century by VAN TIEGHEM (1870, 1891), STRASBURGER (1872, 1879), BOWER (1882), DE BARY (1884), and VAN TIEGHEM and DOULIOT (1889). In recent years only a few more have added to this list (ALLEN, 1947a, b; SPURR, 1949; WILCOX, 1950, 1954, 1962). The recent publications of GUTTENBERG (1961) and CLOWES (1961) also do not mention any more significant additions to this. The author undertook a comprehensive study of the root apical organization of about 38 species of gymnosperms. The results are being presented in a series (PILLAI, A., 1963, 1964). This article deals with the root apical organization of *Ephedra foliata* BOISS. var. *ciliata*.

Material and Methods

Root tips of mature plants were dug out carefully and fixed immediately. In the laboratory, seeds were germinated in petri dishes and the roots collected when 1 to 2 cm long. Root tips from 1, 2, 3 and 4 week old seedlings grown in earthenware pots were also fixed in separate lots. These materials were in active growth at the time of fixing (i.e.) they were not exhibiting any dormancy which some gymnospermous roots exhibit (cf. A. PILLAI, 1964). Embryos in various stages of development, including mature ones, were dissected out of seeds and fixed. All materials were fixed in BUCHHOLZ's variation of F.A.A. (cf. BROWNLIE, 1953) and processed by the alcohol-xylol method as described previously (A. PILLAI, 1963).

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Observations

The apical organization in the roots and in the radicular tips of the embryos at the different stages of development, is similar (Figs. 1—5). The most prominent feature in the mature root is the great length of the root cap (Fig. 4). It is about 1,200 μ long and comparatively narrow, being only 210 μ at its broadest region at the proximal end of the columella.

The cap shows two distinct regions — the columella and the peripheral region. The stele has discrete initials. The cortex and the peri-

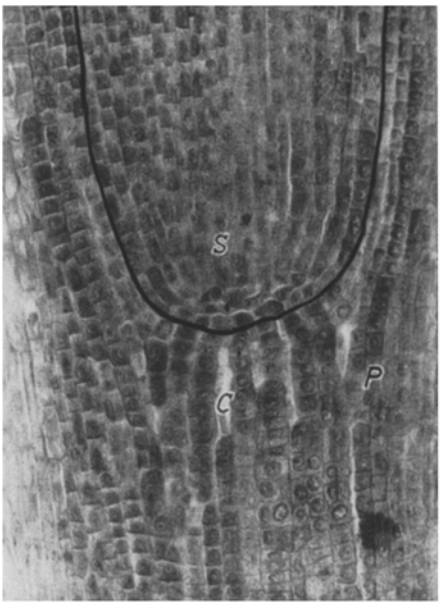

Fig. 1

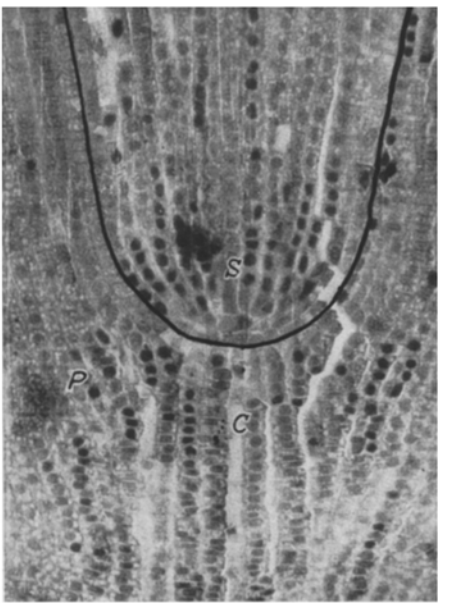

Fig. 2

Fig. 1. Median longisection of a mature root apex showing the three initiating zones. (× 175)

Fig. 2. Median longisection of the radicular apex of a mature embryo showing the three initiating zones. (× 175)

pheral region of the cap form a continuous tissue (Figs. 1, 2 and 5). Thus, three zones occur in the root apical meristem.

Zone 1. The Stelar Initials. Discrete stelar initials can be clearly distinguished from the columella. As seen in longitudinal section, these initials lying immediately proximal to the columella, form a single row of about 4 to 7 isodiametric cells at right angles to the long axis of the root (Figs. 1 to 5). "*Körper*"divisions of these initials contribute to the stele, enabling it to broaden out.

In *Ephedra foliata* Deshpande and Bhatnagar (1961) have reported a uniseriate transverse layer of "root initials" below which the linear rows

of the columella arise. They have not mentioned whether these initials contribute to the stele as well as to the columella. In the present study it is observed that the initials for these two regions form two superimposed tiers (Figs. 2, 3 and 5). An examination of about 50 mature root tips and 150 embryonic ones in different stages of development failed to reveal a single instance where divisions of these initials contributed to the columella distally. Nor do they contribute to the cortex. Such clearly delimited stelar initials were absent in the Cycad and Conifer root apices reported earlier (A. PILLAI, 1963, 1964).

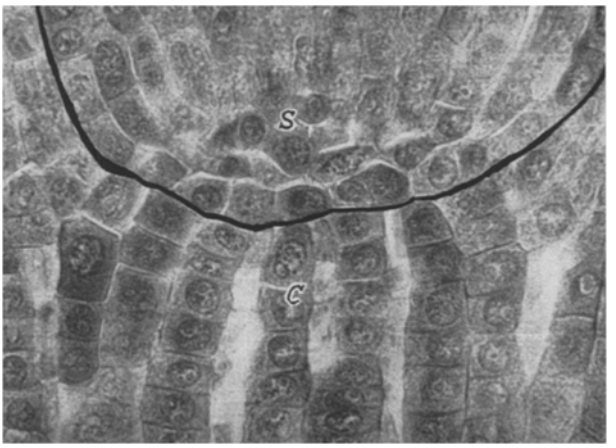

Fig. 3. The initiating region of the mature root apex shown in Fig. 1 enlarged to show the stelar and columella initials in superimposed tiers. (× 430)

Zone 2. The Columella Initials. The columella is composed of regular files of cells and its initials form a plate of about 5 to 6 cells when observed in longitudinal section (Fig. 5). The plane of division of the initials is transverse, and the daughter cells retain their capacity to divide even after slight vacuolation. Occasional longitudinal divisions add to the width of the columella.

Zone 3. The Initiating Zone for the Cortex and the Peripheral Region of the Cap. This zone surrounds the stelar pole and the proximal end of the columella. The exact extent of this initiating region is vague because the cells show the same cytological features for some distance proximally and distally. In longitudinal sections, only 6 to 7 cell-layers of this zone occur on either side of the stelar and columella initials (Fig. 2 and 5). This zone gradually narrows proximally and so the mature cortex is narrower than its initiating region (Fig. 4). The cells around the stelar and columella initials exhibit the "Kappe"type of divisions as mentioned for the Conifer roots (A. PILLAI, 1964). Such divisions bring about an increase in the number of cell rows distally. Continuous cell rows can be

traced from the cortex into the peripheral part of the root cap, interrupted here and there by "Kappe"divisions (Figs. 2 and 3).

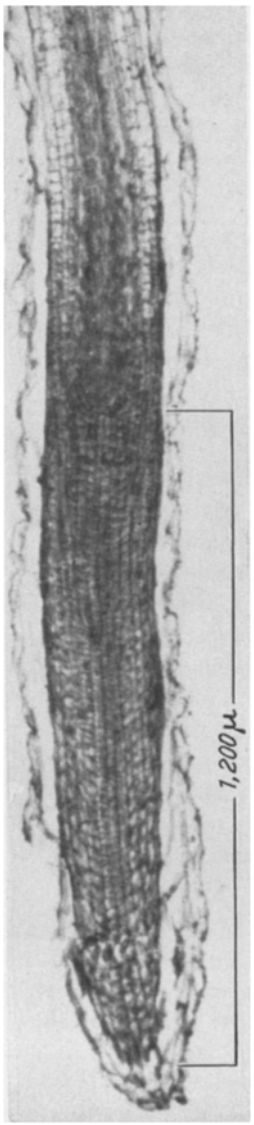

Fig. 4. Longisection of the mature root apex showing the extraordinarily long root cap. (× 50)

According to CLOWES (1950), groups of cells derived from a single cell "represent cell complexes". The cell-rows in this zone exhibit a fairly constant pattern and constitute a genetically related cell complex. The cell-rows of the peripheral region of the cap are arranged almost parallel to the root axis and they do not curve inwards towards the columella cylinder as observed in the majority of Conifer root reported upon earlier. This may be due to the columella in this root being almost as broad as the stelar cylinder (70 μ), whereas in Conifer roots it is narrower than the stele.

The changeover from the meristematic to the mature cortical cells proximally is a

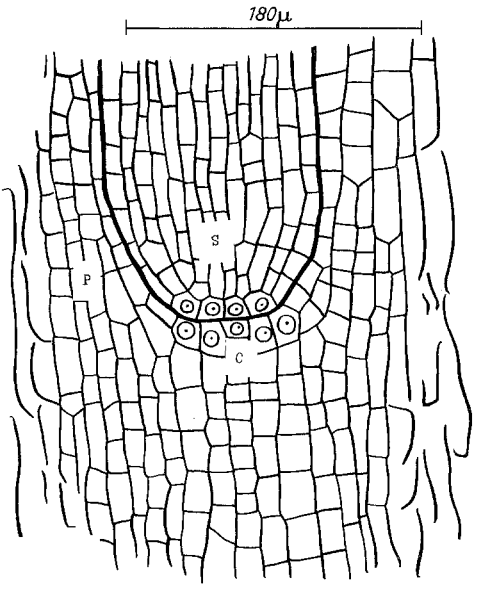

Fig. 5. Median longisection of the apex of a mature root showing the three initiating regions

gradual process. The permanent increase in cell-rows distally due to "Kappe"divisions cannot continue without a compensating mechanism, which may be the sloughing off of the outer cells. Unlike in the Conifer roots, the peripheral part of the root cap is devoid of any coloured contents.

Discussion

The root apical organization in this species resembles the "gymnospermous" type mentioned by earlier authors like JANCZEWSKI (1874) in the presence of a discrete "plerome". The latter describes a common initiating region for all the other zones, whereas here separate initials for the columella and a common initiating region for the cortex and peripheral part of the cap could be shown. DESHPANDE and BHATNAGAR (1961) have reported that the "initials are arranged in a single, transverse layer", but do not trace the fate of the resulting files.

GUTTENBERG (1960) classifies the apical structures of the root into two major types, the "closed" one with discrete initials for the different regions, and the "open" one with common initials for all the regions of the root. As the structure of the root apex of *Ephedra foliata* falls into neither of the above types, it may be designated as partially open. In the Cycads and Conifers the root apical structures are of the open type (A. PILLAI, 1963, 1964).

Relation between the columella and the peripheral region of the root cap

Even from the time of SCHACHT (1853) the two regions in the gymnospermous root cap — the columella and the peripheral region — have been recognized. TIEGS (1913) was the first to report separate initials for these two component parts of the root cap. Later investigators disagree regarding the relation between the columella and the surrounding region. SCHOPF (1943), ALLEN (1947a) and WILCOX (1954) hold that the more lateral cells of the column shift polarity abruptly and grow out obliquely upward and radially from the axis alignment, thus contributing to the rest of the cap. SPURR (1949), while tracing the cell lineages in the embryo of *Pinus strobus*, reports cells in the outer and upper flanks of the root cap assuming an oblique orientation forming the peripheral part of the cap by further divisions.

These two regions of the cap exhibit different types of complexes. The columella files divide in the transverse plane and are arranged in vertical files which are aligned for a long distance. The cells of the peripheral region show the "Kappe"type of divisions to form files which increase in number distally. Moreover, histogenetic studies on nearly 150 early embryos and about 50 mature root apices show no evidence of the columella initials contributing to the peripheral region of the cap. If, as SCHOPF (1943), ALLEN (1947a), and WILCOX (1954) mention, the columella initials contribute to the peripheral region by "shifting polarity," the cell lineage around the columella cannot continue to represant the "Kappe"complex as exhibited by this root and widen distally.

Theories of apical organization and their application to the interpretation of the root apex of Ephedra foliata

NÄGELI'S (1845) apical cell and GUTTENBERG'S (1941) central cell theories are not suitable for the interpretation of the organization met whith in this root. HANSTEIN'S (1868) histogen theory, though still useful for the interpretation of the root apical meristems of angiosperms (CLOWES, 1961), is of little utility here. Here, the root apex is divided into zones for descriptive purposes. SCHÜEPP'S (1926) "Körper-Kappe"concept has been used in interpreting the cell lineages and the organization of the root apices of this and other gymnosperms (A. PILLAI, 1963, 1964).

A Probable Evolutionary Trend in the Root Apical Structures of Gymnosperms

Literature on root apical meristems in general does not discuss much the evolutionary lines in their apical organization. The earliest of the

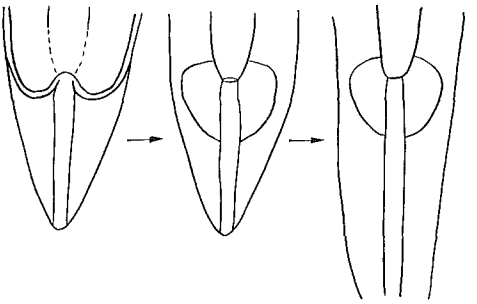

Fig. 6. Diagrammatic representations of the initiating zones at the root apices of the Cycads, Conifers and *Ephedra foliata* to show the suggested evolutionary trend.
S Stelar initials, *C* Columella initials, *P* Common initiating region for the cortex and peripheral region of the root cap

few references concerning this aspect is by HABERLANDT (1914) where he traces a line of advance from the root apices showing distinct stratification to those with a common unstratified group of initials for all the tissues of the root. In contrast, ESAU (1960, p. 180) discussing VORONIN'S (1956) work, says "The type of apical meristem with the common initials may be phylogenetically primitive". S. K. PILLAI (1963) and S. K. PILLAI et al. (1961, 1965) have suggested such an evolutionary trend in the roots of members of the *Scitaminales*, *Palmae* and *Compositae*, i.e. from those having a common group of initials to one with separate initials for the different tissues.

The author's studies on the root apical organization of gymnosperms (A. PILLAI, 1963, 1964) lend support to the latter suggestion. The most primitive group, viz. the Cycads, exhibit a common or undifferentiated type with a cup-shaped promeristem from which all the tissues of the

root originate. The next advance appears in the Conifer root apices where the stele and columella arise from one set of initials, and the cortex and the peripheral part of the root cap from another. This is the most prevalent type. The organization met with in the root apex of *Ephedra* described here shows an advance over the Conifer type in having distinct initials for the stele, another set for the columella and a third set for the cortex and the peripheral part of the root cap. This may possibly show the culmination of the phylogenetic trend within the gymnosperms. This line of advance is shown in Fig. 6.

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References

ALLEN, G. S.: Embryogeny and the development of the apical meristems of *Pseudotsuga*. II. Amer. J. Bot. **34**, 73—80 (1947a).

— Embryogeny and the development of the apical meristems of *Pseudotsuga*. Amer. J. Bot. **34**, 204—211 (1947b).

BARY, A. DE: Comparative anatomy of the vegetative organs of the phanerogams and ferns. Oxford: Clarendon Press 1884.

*BOWER, F. O.: The germination and embryogeny of *Gnetum gnemon*. Quart. J. micr. Sci., N.S., **22** (1882).

BROWNLIE, G.: Embryogeny of the New Zealand species of the genus *Podocarpus*, section *Eupodocarpus*. Phytomorphology **3**, 295—306 (1953).

CLOWES, F. A. L.: Root apical meristems of *Fagus sylvatica*. New Phytologist **49**, 248—268 (1950).

— Apical meristems. Oxford: Blackwell Sci. Publ. 1961.

DESHPANDE, B. D., and P. BHATNAGAR: Apical meristems of *Ephedra foliata*. Bot. Gaz. **122**, 279—284 (1961).

ESAU, K.: The anatomy of seed plants. New York: John Wiley 1960.

GUTTENBERG, H. v.: Der primäre Bau der Angiospermenwurzel. In: LINSBAUER, Handbuch der Pflanzenanatomie. Berlin: Gebrüder Borntträger 1940.

— Grundzüge der Histogenese höheren Pflanzen. I. Die Angiospermen. In: LINSBAUER, Handbuch der Pflanzenanatomie. Berlin: Gebrüder Borntträger 1960.

— Grundzüge der Histogenese höheren Pflanzen. II. Die Gymnospermen. In: LINSBAUER, Handbuch der Pflanzenanatomie. Berlin: Gebrüder Borntträger 1961.

*HANSTEIN, J.: Die Scheitelzellgruppe im Vegetationspunkte der Phanerogamen. Festschr. Niederrhein Ges. Natur und Heilkunde 109—143 (1868).

*JANCZEWSKI, E.: Recherches sur l'accroissement terminal des racines dans les phanerogames. Ann. Sci. natur. Bot. **20**, 162—201 (1874).

*NÄGELI, C.: Wachstumsgeschichte der Laub- und Lebermoose. SCHLEIDEN: In Nägelis Z. für wiss. Bot., H. 2, 138—210 (1845).

PILLAI, A.: Root apical organization in gymnosperms. — Some Cycads and *Ginkgo biloba*. Proc. Indian Acad. Sci. B **57**, 211—222 (1963).

— Root apical organization in gymnosperms. — Some conifers. Bull. Torrey bot. Club **91**, 1—13 (1964).

PILLAI, S. K.: A tentative suggestion on the evolutionary trend in the root apical structures of members of the Scitaminales. Phyton **10**, 253—258 (1963).
—, and A. PILLAI: Root apical organization in Monocotyledons-Palmae. Proc. Indian Acad. Sci. B **54**, 218—233 (1961).
— O. M. GEORGE, and P. VIJAYALEKSHMY: Apical organization in the roots of dicotyledons-III. Root apices of some members of the Compositae. Proc. Indian Acad. Sci. B **61**, 296—308 (1965).
*SCHACHT, H.: Beitrag zur Entwicklungsgeschichte der Wurzel. Flora (Jena) **36**, 257—266 (1853).
SCHOPF, M.: The embryology of *Larix*. Illinois biol. Monogr. **19**, 3—97 (1943).
SCHÜPP, O.: Meristeme. In: LINSBAUER, Handbuch der Pflanzenanatomie. Berlin: Gebrüder Borntträger 1926.
SPURR, A. R.: Histogenesis and organization of the embryo of *Pinus strobus*. Amer. J. Bot. **36**, 629—641 (1949).
STRASBURGER, E.: Die Coniferen und die Gnetaceen. Jena: Hermann Dabis 1872.
— Die Angiospermen und die Gymnospermen. Jena: Hermann Dabis 1879.
*TIEGHEM, P. VAN: Recherches sur la symmetrie de structure des plantes vasculaires. Ann. Sci. natur. Bot. **13**, 1—314 (1870).
— Traite de botanique, Paris: Librairie F. Savy 1891.
—, et H. DOULIOT: Recherches comparatives sur l'origine des members endogenes dans les plantes vasculaires. Ann. Sci. natur. Bot. 8, 1—656 (1888).
*TIEGS, E.: Beiträge zur Kenntnis der Entstehung und des Wachsthums der Wurzelhauben einiger Leguminosen. Jb. wiss. Bot. **52**, 622—646 (1913).
*VORONIN, N. S.: Of evoliutsii Kornei restanii — Obshch Isp. prioridy, otd. biol. biul. **61**, 47 (1956) [in Russian].
WILCOX, H.: The regeneration of the injured root system in noble fir, *Abies procera*. Ph. D. Thesis Univ. California 1950.
— Primary organization of the active and dormant roots of noble fir, *Abies procera*. Amer. J. Bot. **41**, 812—821 (1954).
— Growth studies of the root of incence ceder, *Libocedrus decurrens*. Amer. J. Bot. **49**, 221—236 (1962).

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