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Structure of the Shoot Apex in some *Cupressaceae*

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With 5 Figures

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1. Introduction

Earlier interpretations of shoot apical structure in gymnosperms were influenced to a great extent by the apical cell and the histogen theories. These studies emphasized only the structural patterns of the cell-net in interpreting apical organization. It was FOSTER's extensive investigation during the early part of this century that brought out the inadequacy of such an approach. From then on, the emphasis changed to the cytohistological condition of the cells of the shoot apex. FOSTER 1938, described the organization of the shoot apex of *Ginkgo biloba* as consisting of five zones, of *Cycas revoluta* of four zones (FOSTER 1939, 1940) etc. Thus, according to CLOWES 1961, the "zonation theory" came into existence. It still holds sway in investigations on shoot apical organization.

2. Materials and Technique

The shoot apices of *Thuja orientalis* LINN., *Thuja compacta* HORT., *Juniperus chinensis* var. *alba* LINN., and *Callitris robusta* R. BR., were studied.

Shoot apices of *Thuja orientalis* were collected in the first week of every month all the year round from a 4 to 5 year old plant growing in the College Garden. No seasonal study was conducted on the shoot apices of the other three species. All materials were fixed in F. A. A. (cf. BROWNLIE

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1953), washed many times in 70% alcohol, dehydrated, cleared and imbedded in paraffin. Longitudinal and transverse sections were cut at a thickness of 5 to 8 μ. FOSTER's 1934 staining schedule of tannic acid-ferric chloride-safranin was followed. Counterstaining with light green was also done.

Measurements of diameter were taken from median longisections at the level of the adaxial base of the youngest visible leaf primordium and heights from the upper surface of the apices to this basal reference point.

3. Observations

The shoot apical organization in all the four members is basically similar. The shape of the apex varies from a blunt cone at the maximal stage of the plastochron to a pointed one at the minimal stage. In *T. orientalis* no marked seasonal changes are observed in the structure of the shoot apex. Plastochronic variations in size occur throughout the year and the lowest dimensions observed are 70 μ diameter and 39 μ height and the highest values are 105 μ diameter and 70 μ height. The average diameter and height from about 150 apices is 87 μ and 54 μ respectively giving a height to diameter ratio of 1:1.6. Table 1 gives the corresponding values for the other three species. These values compare favourably with those of AL SHERIFI 1952, for some members of the *Cupressaceae*.

Table I

The number of apices examined, the average diameter and height, and the ratio of height to diameter in the shoot apices of members of the *Cupressaceae* *)

Species	No. of apices examined	Diameter in μ	Height in μ	Ratio of hight to diameter
Thuja orientalis	150	87	54	1:1.6
Thuja compacta	20	70	49	1:1.4
Juniperus chinensis var. *alba*	25	105	63	1:1.66
Callitris robusta	25	102	63	1:1.6

3. 1. Zonation of the apex

The zonation agrees with that described by earlier authors for other conifers with the exception of *Araucariaceae*, where a discrete tunica is reported (JOHNSON 1951, PILLAI 1964b). The following zonation is evident at the apex: zone 1 = the surface layer, which is divisible into (a) the apical initials, and (b) the surface layer on the flanks, zone 2 = the sub-apical initials, zone 3 = the flanking zone, and zone 4 = the pith mother cells (Fig. 1).

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*) The above measurments have no statistical value, but they serve to indicate the broad differences in the size of the apices of the species.

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3. 1. 1. The Surface Layer

Based primarily on the plane of division and secondarily on the size and staining reaction of the cells, this layer is divided into the apical initials and the surface layer on the flanks.

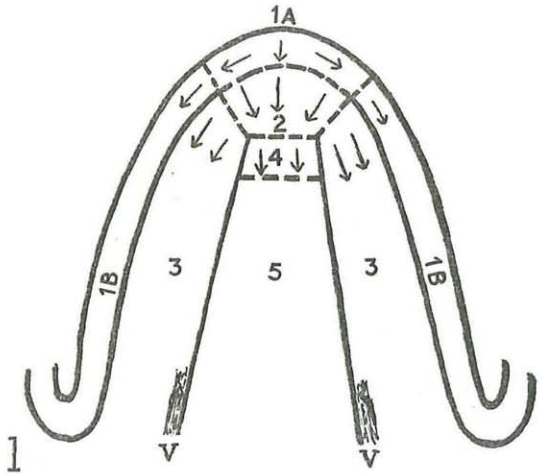

Fig. 1. A schematic diagram of the zonation of the apices of members of the *Cupressaceae*. — 1A = Apical initials; 1B = Surface layer on the flanks; 2 = Subapical initials; 3 = Flanking zone; 4 = Pith mother cells; 5 = Pith; V = procambial elements.

3. 1. 1. 1. The Apical Initials

This refers to a single tier of one to three self-perpetuating cells (as seen in longisections), situated at the summit of the apical cone. They differ from the surface cells on the flanks in their larger size, lighter staining capacity and the plane of division. They divide anticlinally as well as periclinally and so a typical tunica layer is absent (Fig. 2). The origin of all cells of the shoot apex can ultimately be traced to this tier of apical initials. Anticlinal divisions predominate (Table II) and the derivatives form the surface layer on the flanks. The outer derivatives of the periclinal divisions continue as apical initials and the inner ones augment the subapical initials zone (Fig. 2).

In *Thuja orientalis* the percentage of periclines in the apical initials is more in the apices collected during the spring and summer months (Table II). Comparable observations regarding the increased frequency of periclinal divisions during seasons of more active growth were made by many workers on conifer shoot apices (Kemp 1943, Al Sherifi 1952, Jackman 1960, Singh 1961, Cross 1941).

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GUTTENBERG 1955 has reported a single-layered tunica in the shoot apex of *Cupressus sempervirens*. PILLAI 1964a, has reported apical initials and no tunica in the same species. In this respect the present study supports the observations of PILLAI 1964a, and AL SHERIFI 1952, on *Cupressaceae* and CROSS 1939, 1940, on *Taxodiaceae*.

Table II

Percentage of periclines in the surface layer of the shoot apex of *Thuja orientalis* in the different months of the year

Month of year	Percentage
January	nil
February	,,
March	,,
April	17
May	25
June	21
July	26
August	23
September	16
October	14
November	15
December	8
Annual average	10,4

3. 1. 1. 2. Surface Layer on the flanks

The cells in this zone divide strictly anticlinally. This layer is marked off from the underlying tissues by a thick, darkly staining wall (Fig. 3). Cells are small and deeply staining as compared to the apical initials. Even during leaf initiation, no periclines occur and hence this layer forms only the epidermis of the leaves. AL SHERIFI 1952 is of the opinion that "...since the surface layer augments itself by anticlinal divisions only and produces epidermal tissues of the shoot, it may be regarded as a protoderm".

3. 1. 2. The Sub-apical Initials

This zone is situated at the summit of the apical cone just below the apical initials. The inner derivatives of the periclines in the apical initials augment this zone. All the tissues of the shoot, excepting the epidermis, originate from the subapical initials. A similar zone is reported in *Taxodiaceae* and *Abietaceae*. The "corpus initials" of *Araucaria* (GRIFFITH 1952, PILLAI 1964b) also are comparable to this in position and function.

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Divisions occur here in the cells in all planes and consequently their arrangement is irregular. The peripheral derivatives form the beginning of the flanking zone and the basal ones the pith mother cells. The cells are larger than those forming the flanking zone and show slight vacuolation. Once a derivative cell is contributed to the flanking zone further divisions follow a regular pattern. Similarly, once a basal derivative forms a pith mother cell, it enlarges, gets more vacuolated, divides further mainly transversely, and so, such cells are distinguishable from the cells of the subapical zone.

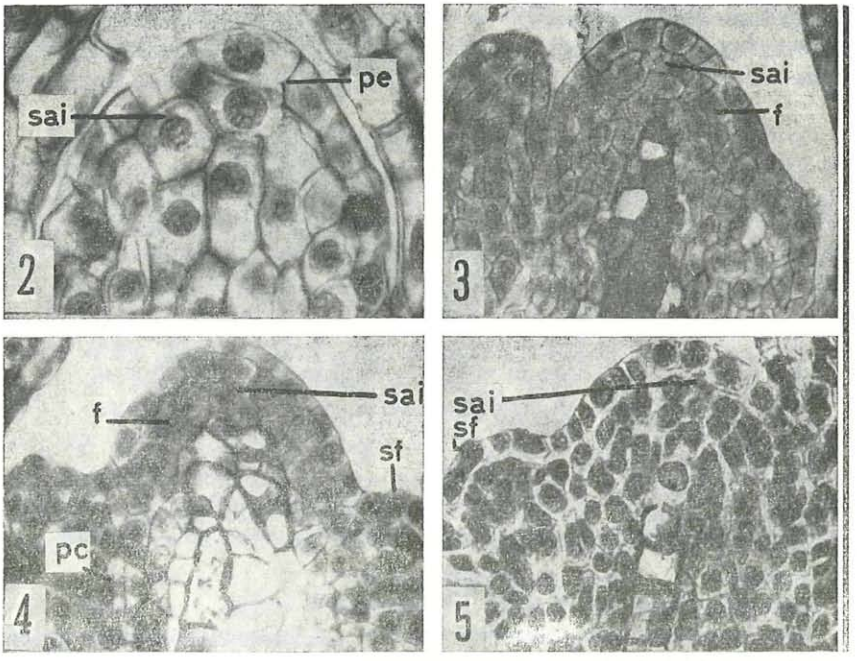

Fig. 2. *Thuja orientalis.* L. S. of a shoot apex showing a pericline in the apical initial, smaller cells on the flanks and the shallow subapical zone (× 900).

Fig. 3. *Callitris robusta.* L. S. of shoot apex exhibiting corner thickenings in the cells of the subapical zone, stratified flanks and dark wall beneath the surface layer (× 585).

Fig. 4. *Thuja orientalis.* L. S. of shoot apex with procambial tissue and maturing cells close to the summit of the apex and the discrete surface layer covering the leaf primordia (× 460).

Fig. 5. *Juniperus chinensis,* var. *alba.* L. S. of shoot apex showing stratified flanks, pith maturing close to summit of the apex and discrete surface layer covering the leaf primordia (× 585).

pe = Pericline; sai = Subapical initials; sf = Surface layer on the flanks; pc = Procambium; f = Flanking zone.

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As seen in longisections, the vertical extent of this zone ranges from one to four cells. In some apices (probably during winter months) it is only one cell deep (Fig. 4). In *Callitris robusta* irregular wall thickenings at cell junctions are observed in this zone (Fig. 3). This feature is comparatively less evident in *Thuja orientalis* and *T. compacta* (Figs. 2, 4). Al Sherifi 1952 has reported "...in some of the species studied, heavy deposits of intercellular substances may sometimes be clearly noticed at the interstices of subapical mother cells" in some *Cupressaceae*. In the present study, these appear more like thickenings than intercellular deposits. In *Callitris robusta*, a structure akin to blocks of genetically related cells, as reported by Johnson 1950 in *Gnetum gnemon* and by Cross 1942 in *Cunninghamia* is observed (Fig. 3). This is absent in *Thuja*, probably due to the reduced extent of this zone.

3. 1. 3. The Flanking Zone

This forms a hollow cylinder of meristematic tissue covering the pith mother cells and pith. As seen in longisections, the flanks are of about two to four cell layers. The peripheral derivatives of the subapical initials give rise to this zone by further transverse and vertical divisions. The predominance of anticlinal over oblique and periclinal divisions results in a rather well-stratified cellular pattern (Fig. 3). Procambial tissue formed of long, narrow cells is recognisable very high in the apex (Figs. 3, 5).

The predominance of anticlinal divisions and the consequent stratification, the uniformly smaller size of the component cells and also the denser staining helps in demarcating it from the subapical initials zone and pith mother cells. The cortex and the vascular tissue of the shoot and all the tissues of the leaf excepting the epidermis, arise from this zone.

3. 1. 4. The Pith Mother Cells

The basal derivatives of the subapical initials zone enlarge and vacuolate to form the pith mother cells. A pith rib meristem is absent. Johnson 1951 pointed out the necessity to check this feature in strong leading shoots also. The results of the present study confirm that even in strong leading shoots, a pith rib meristem is absent. This zone is about one to three cells in depth and two to three cells broad. Periclinal or transverse divisions predominate, though a few anticlinal or longitudinal divisions add to the width of the zone occasionally. But, usually the pith mother cells enlarge abruptly within three or four cells beneath the summit of the apical meristem and mature into pith cells with or without any further divisions (Figs. 3, 4, 5). Consequently, mature pith cells with or without coloured (tanniferous) contents occur high on the apical cone. A similar condition has been reported by earlier investigators (Cross 1939, 1941; Al Sherifi 1952; Jackman 1960) and seems to be widespread in conifers, especially in the

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Taxodiaceae and *Cupressaceae*. On account of the high degree of vacuolation and the tanniferous contents, this zone is clearly demarcated from the flanking zone surrounding it. The cells retain their capacity to divide even after vacuolation. Occasional oblique divisions obscure to some extent the regularity of the vertical files in the pith. Pith is narrow varying from about two to five cells across. The central cell row matures first.

4. Discussion.

Johnson 1951: 201 states "the apices of all investigated gymnosperms are similar in possessing a superficial zone of initiation, a group of subapical mother cells, and a flanking zone". The above mentioned zones cannot be regarded as histogens because of their interdependence.

A distinct tendency toward the elimination of periclinal divisions in the superficial zone (especially on the flanks) is noted. Kemp 1943 in *Torreya californica* and Singh 1961 in *Cephalotaxus drupacea* have reported periclines on the flanks of the superficial layer also. In *Podocarpus gracilior* Pillai 1963 has reported that the surface layer shows rare periclinal or oblique divisions on the flanks and slightly more at the summit of the flanks. Even these, according to him, occur only during the actively growing periods in the annual growth cycle. In the *Cupressaceae* members reported upon here, periclines are confined to a small group of one to four cells at the summit of the apex (designated here as the "apical initials"). The investigations of Cross 1939, 1941, 1942, 1943a, b and Al Sherifi 1952 on *Cupressaceae* lend support to these observations. The flanks of the surface layer can be considered here as a discrete "protoderm" according to Strasburger's earlier description. But, Cross 1941 suggests that the surface layer on the flanks of the apical meristem even as seen in *Cryptomeria* could scarcely be regarded as a protoderm but may represent a significant stage in the evolution of a tunica. Even within the apical initials, a tendency toward the elimination of periclinal divisions is noted in the present study. In the cold and unfavourable months of the year, the surface layer including the apical initials shows a tendency to become more stabilized and simulate a tunica. This leads to the occurrence of a discrete surface layer during some months of the year. This is evident in *Thuja orientalis* (Table II). Cross 1939 has reported a discrete surface layer in the permanent shoots of *Taxodium* and Guttenberg 1955 in those of *Cupressus sempervirens*. Pillai 1964a reports a condition similar to that reported here in *Thuja* where periclines occur in the apical initials during the spring and summer months and almost none during the winter months. This tendency toward the elimination of periclines from the surface layers emphasizes Foster's 1941 idea of a "potential tunica" in gymnosperms. The discreteness of the superficial layer on the flanks is maintained during leaf initiation also in

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Thuja etc. In *Araucaria* shoot apices GRIFFITH 1952 and PILLAI 1964b have reported one to two layers of tunica. It stands to reason that the members of *Cupressaceae* reported upon here occupy a position between the shoot apices of *Pinus* etc., which show periclines throughout the surface layer, and *Araucaria*, *Gnetum* and *Ephedra* where a tunica is established.

The subapical initials zone, as met with in most gymnosperms is poorly developed and is made up of a few irregularly arranged cells. In the Cycads, this zone seems to be the largest and in *Cupressaceae*, *Taxodiaceae* and *Ephedraceae*, the smallest. JOHNSON & TOLBERT 1960: 174, 175 have used a new expression "metrameristem" for "the central part of the shoot apex which maintains itself, contributes peripherally to the growth and organization of the apex, but exhibits little or no evidence of tissue segregation". "In gymnosperms the metrameristem consists of the surface initials and the central mother cell zone when present". JACKMAN 1960 designates this zone (metrameristem of JOHNSON) as the "apical cells" even in shoots showing a discrete tunica. PAOLILLO & GIFFORD 1961 include the subapical initiation zone and the tunica directly above it together under the "distal zone". In the present study, it is deemed better to separate the apical and subapical initials. In the first place, the planes of division are different in the two regions (periclinal and anticlinal in the former and irregular in the latter). Secondly, the former gives rise to the latter. The tendency toward elimination of periclines in the surface layer leading to the formation of a tunica also warrants the consideration of the surface layer as separate from the subapical zone.

The pith is described as arising either from pith mother cells or from a pith rib meristem. JOHNSON 1951 mentions that the Cycads, *Ginkgo*, *Gnetum* and *Araucaria* "represent a third condition where the pith rib meristem arises from the base of the central mother cell zone which generally has not been thought of as pith mother cells, although the term could be applied here". The early maturation of pith from the pith mother cells (without a rib meristem) is reported in *Taxodiaceae* (CROSS 1939) and *Cupressaceae* (AL SHERIFI 1952, PILLAI 1964a) as is observed in the present study. According to STERLING 1958, the eumeristem gives rise to the pith mother cells which form a rib meristem and in turn, the pith. He observes that in smaller apices the pith mother cells and pith rib meristem are absent and mature pith occurs directly below the apical initials.

POPHAM 1951 has classified the shoot apices of vascular plants and includes all the gymnosperm shoot apices from *Abies* to *Cryptomeria*, *Gnetum* and *Ephedra* in one type. This grouping seems unnatural as it puts into one type shoot apices which differ from each other in several respects. This is evident from the observations of KEMP 1943, SACHER 1954, CROSS 1939, 1940, 1941, 1942, STERLING 1945, 1946, 1958, AL SHERIFI

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1952, GUTTENBERG 1955, JOHNSON 1951, JACKMAN 1960, SINGH 1961, and PILLAI 1963, 1964a, b. The shoot apices of *Gnetum* and *Ephedra* (JOHNSON 1950; GIFFORD 1943; PAOLILLO & GIFFORD 1961; DESHPANDE & BHATNAGAR 1961) have attained the tunica-corpus organization and hence should not find a place along with conifers showing another type of apical organization.

JOHNSON 1951 has classified gymnospermous shoot apices into four types on the basis of structure, viz. (I) Cycadophyta type, (II) Ginkgophyta type, (III) Coniferophyta type, and (IV) the tunica-corpus type. According to SACHER 1954 the *Coniferales* show three types of apical organization (a) the Ginkgoid type (*Pinaceae*), (b) the Taxoid type (*Taxodiaceae*, *Cupressaceae*, *Taxaceae*), and (c) the Araucaroid type (*Araucaria* etc). The *Cupressaceae* members reported upon here agree with the Taxoid type of SACHER. Though JOHNSON's "Coniferophyta type" shows variations as regards the discreteness of the surface layer, conformity is observed in other features. Therefore, these types are very useful provided a little flexibility is practised in applying them to different genera.

5. Seasonal Variations

A monthly study of the shoot apices of *Thuja orientalis* revealed no definite seasonal growth phases. Similar observations have been made by AL SHERIFI 1952 on five species of *Cupressaceae*.

Variations occur in the size of the shoot apices during the different seasons of the year. The frequency of periclines in the apical initials also differ during the winter and summer months. The discrete surface layer on the flanks and the perceptible fall in the percentage of periclines in the apical initials in the *Cupressaceae* on the one hand, and the reported tunica-corpus organization in *Araucaria* etc. on the other, seem to suggest that *Cupressaceae* occupies, in this respect, a position intermediate between *Podocarpaceae* (*P. gracilior*, PILLAI 1963) and *Araucariaceae*. Even as early as 1872 STRASBURGER had concluded that *Taxodiaceae* and *Cupressaceae* possess shoot apices intermediate between the *Abietaceae* and *Araucariaceae*.

In view of the fact that apices of the same plant may or may not exhibit a tunica (in resting and active periods of growth in terminal and lateral buds), STERLING 1958 has cautioned us against over-emphasizing the importance of shoot apical structure to determine lines of intra-ordinal phylogeny or intra-familiar ranking. But, it cannot be denied that these tendencies may serve as pointers towards the general trends during evolution and may reveal fresh trends which might otherwise be overlooked.

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to her husband and co-worker, Dr. S. K. Pillai, Reader in her Department, for his constant help and invigourating discussions.

6. Summary

The organization in the shoot apices of *Thuja orientalis*, *T. compacta*, *Juniperus chinensis* var. *alba*, and *Callitris robusta* of the *Cupressaceae* is fundamentally similar. The shoot apex exhibits four zones, viz. the surface layer, which is divisible into the apical initials and the surface layer on the flanks, the subapical initials, the flanking zone and the pith mother cells. A seasonal study conducted on the shoot apex of *Thuja orientalis* shows no marked seasonal variations in the shoot apical structure. There is no discrete tunica, but the surface layer on the flanks is discrete, dividing only anticlinally. This and the fall in the percentage of periclines during some months of the year thereby simulating a tunica, suggest a general trend towards the establishment of a discrete tunica covering the shoot apex. Based on the results of the present study as well as on those of previous authors, *Cupressaceae* is suggested to occupy a position intermediate between *Podocarpaceae* and *Araucariaceae*. But, shoot apical structure should be used with great caution as a tool in phylogenetic relationships. It is no doubt of help in suggesting fresh lines of thought by revealing new trends in evolution.

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