ISSN NO. 2320-5407

Journal homepage: http://www.journalijar.com

INTERNATIONAL JOURNAL OF ADVANCED RESEARCH

RESEARCH ARTICLE

ANATOMICAL SALIENT FEATURES OF SCHEFFLERA STELLATA (FOSTER) WITH REFERENCE TO LEAF ONTOGENY

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Manuscript Info

Manuscript History:

Received: 11 February 2014
Final Accepted: 25 March 2014
Published Online: April 2014

Key words:
Histogenesis, primordium, Adaxial meristem, Araliaceae, Schefflera

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Abstract

A perusal of literature on leaf ontogeny reveals that the early apical growth of the leaf primordium is either by a single apical cell or by a group of subapical cell initials. But in *Sechefflera t*he early growth in rather diffused. The shoot apical meristem of *Schefflera* does not deviate from the structure of other angiosperms. The cytohistological zonation with a single layer of tunica and a subjacent corpus without pith region, rib meristem is evident. This particular character probably is related to much crowding of leaves without internodal region. In this current study of *Schefflera stellata* , the leaflets are formed from most adaxial side of the leaf primordium resulting in the formation of leaflets around a central axis.

INTRODUCTION

The ontogenetic studies in angiosperm plant species are restricted to a very few morphological forms which do not deviate from prevalent forms. For proper understanding of the evolution of the leaves, in addition to the study of prevalent forms, the ontogeny of the leaves which exhibits morphological peculiarities should also be investigated. Most of the authors consider the dicot leaf to be the basic type from which the monocot leaf forms are derived. However, a few authors construed the monocotyledons as primitive forms from which the dicotyledons arose. To resolve these controversies, extensive leaf ontogenetic studies are highly needed. For proper elucidation of the evolution of the leaves, it is also necessary to investigate the ontogeny of the leaves which exhibits the architecture of both monocot and dicot. Among many plants in which both monocot and dicot leaf characters are discernible, the genus *Schefflera* of *Araliaceae* is peculiar in many respects. Considering the factor into account, the leaf ontogeny of *Schefflera stellata* is presently investigated to see how far its ontogeny is in accord with the ontogeny of prevalent forms.

Cytohistological zonation first described by Foster (1938) in *Ginkgo biloba*, has been extended to Angiosperms also (Clowes,1961).There are mainly three zones based on the degree of differentiation:

1). A distal zone giving rise to other zones.

2). A Central mother cell zone and its derivatives from the ribmeristem.

3). The peripheral zone from which the leaf primordia and procambium arise through division of the small cells of denser protoplasm.

According to Swamy and Krishnamoorthy (1977,1978) the quiescent center is a necessary pre- requisite for effective function of both shoot and root apical meristems and in the shoot apex, it is derived from epiphysis of embryo. Usually the initiation of the leaf commences with the periclinal division in the hypodermal layer at the flanks of shoot apex(Avery, 1933; Foster, 1935: Ramji, 1968) Sharman,(1942,1945) and Thieke (1951) have reported leaf intiating periclinal division in grasses, in the cells of the layer immediately below the hypodermis. As a result of continued cell division, the leaf primordium protrudes from the shoot apex as a buttress which as the form of a small papilla on crescent (Girolami, 1954; Ramji,1968; Kaplan,1970; Merril,1970). The early apical growth may take place by the activity of a single apical cell (Avery, 1933) or by a group of sub apical initials (Boke,1940;

Ramji,1968). The procambial initiation takes place as early as the primordium reaches a height of 60µ (Maksmowych, 1973).The apical growth of the primordium ceases very early in Angiosperms. Further growth of the primordium is intercalary. In *Xanthium*, Maksymowych and Erickson (1960) have demonstrated periclinal division in the plate meristem contributing to the increased thickness of lamina. Denne (1966) has also reported periclinal divisions in the plate meristem lamina in *Trifolium* leaves.

The ontogeny of dicot compound leaves has been described by many authors.(Foster, 1935; Hagemann, 1970; Kaplan,1970a; Meril,1979, Denne, 1966) if leaf has a terminal leaflet,it is formed from the apex of the leaf axis (Foster,1936). Each leaflet primordium after its iniation under goes apical and intercalary growth in the same way as the primordium of the simple leaf and produces lamina by the activity of marginal meristem in *Colophospermum* and *Hymenaea*, the leaf begins as a trifoliate structure but matures as bifoliate leaf as the terminal leaflet primordium fails to develop further. With the commencement of the development of lamina, the procambial strands of the large lateral veins begin to form gradually (Avery, 1933). In almost all monocotyledons, the first procambial strands to develop is the median vein (Stevenson, 1973; Periasamy 1986). The direction of differentiation of procambium of the median vein is always acropetal (Avery, 1933; Foster, 1936; Ramji, 1961; Pray, 1955a).The procambium of the secondary vein is multiseriate and is initiated from the mid-vein procambium and proceeds towards the lamina margin (Ramji, 1961; Merril, 1979; Franck, 1979.) According to Slade(1957&1959) the blind vein endings are caused by the rupture of minor vascular network as a result of leaf enlargement.

MATERIALS AND METHODS

Materials of Schefflera stellata a tropical genus of Araliaceae were collected as fresh specimen. The Shoot tips and leaves at various stages of development were fixed in FAA (85 Parts of 70% ethanol, 10 parts glacial acetic acid and 5 parts of 40% formaldehyde) at the field itself. After fixing in FAA for 24 to 48 hours, the specimens were transferred to 70% ethanol for storage.The specimens were dehydrated in ethanol series and embedded in paraffin wax. Sections of materials at various stages of development were cut at 10-12µ using a rotary microtome.The sections were triple stained with tannic acid, Haematoxylin and erythrosine. For the study of vein development, leaves and shoot apices were cleared using 5-10% potassium hydroxide solution (Foster, 1970). For computing the height of the leaf primordial the section thickness was multiplies with the number of sections.The scanning was done in the Laboratory, Department of Biological sciences, Madurai Kamarajar University. Microphotographs were taken using Pen tax Camera.

RESULTS

Organography

The plant produces many branches which in turn produce small branches bearing leaves (Fig.1). The terminal bud remains dormant during the winter and grows actively with the onset of the spring. The leaves are produced in alternate phyllotaxy with 120 angle of divergence between them. The leaf is regionally differentiated into an open sheath, elongated rachis and a compound lamina consist of six to twelve leaflets and each leaflet has a petiole. These leaflets radiate from the tip of the rachis. However, the leaflets are of different sizes. The median one is the biggest and the leaflets lateral to this are smallest. The first formed leaflets have larger area with longer petiole while the later formed leaflets have smaller area with shorter petioles (Fig.2). When a bud produces leaves, the number of leaflets varies. Thus, the leaf architecture of *Schefflera* shows a perfect blending of monocot and dicot leaf characters. The sheathing leaf base is a monocot character whereas the elongate rachis, petiole and lamina with reticulate venation are shown as dicot characters. The younger leaves are tightly enclosed within the sheath of preceding leaf base. Axillary buds are seen at the place where the leaf sheath joins the stem.

Apical organisation

The shoot apex is dome shaped. It is about 300µ-350µ in width and about 90µ in height, during the maximal phase. In transverse section the shoot apex has a more or less a biconvex shape. The shoot apical meristem shows cytohistological zonation (Fig.4). The cell division frequency is very low in this region. This region probably represents the central mother cell zone. At the peripheral region of the shoot apex, the cells are smaller, thin walled and deeply stained with higher rate of cell division frequency. (fig 5)

Leaf initiation

The leaf initiation starts with periclinal division in the hypodermal layer of the shoot apex at the peripheral region of the shoot apical meristem. As the hypodermal cells divide anticlinally, the cells of subjacent corpus divide in all planes to form a protuberance. This protuberance grows in height rather by diffuse growth. As the primordium

grows in height simultaneously its basal region spreads around the apex. When the primordium is about 200µ in height, there is no evidence of the leaflet initiation. At this stage the sheath formation is not complete. However six procambial strands can be seen(fig.6) . At the upper region of the basal half of the primordium, periclinal divisions appear in one or two layers below the adaxial protoderm. This marks the initiation of adaxial meristem. The repeated periclinal divisions mark the activity of the adaxial meristem (Fig.7). As the growth further proceeds, three morphogenetic processes take place simultaneously. The initiation of the leaflet primordium take place when the leaf primordium reaches the height of 500µ, the first pair of leaflets gets initiated at the adaxial side, 200µ below the distal end of the leaf primordium (Fig.8).

During the initiation of the leaflet primordium two layers of the cells below the protoderm on either adaxial side below 200µ from the tip of the primordium divide predominantly periclinally to form a protruberance. This protruberance performs longitudinal growth just like the leaf primordium (Fig.9). In a leaf primordium of 700µ height six leaflet primorida are seen. Of these, there is a median one and of the remaining five, 4 are seen in two pairs and the fifth one remains as single (Fig.10). The median leaflet is formed from the distal portion of the leaf primordium. The first pair gets initiated 220µ below the distal end of the primordium. During the initiation of the first pair, the hypodermal cells on either adaxial of the primordum below 220µ divide periclinally which is followed by the division of the cells below the same in all planes. This results in the formation of protruberance on either side of the leaf primordium.The second pair of leaflets get initiated more or less 10-15µ below the first pair. It also initiated from the hypodermal cells adaxial to the first pair. The sixth leaflet is initiated 10µ below the second pair. As a result, all the leaflet primordial radiate around a central mass of tissue. (Fig.11,12,13&15).This precociously differentiated procambium is continuous from the tip of the leaflet primordium to the base of the leaf primordium.

Lamina initiation begins when the leaf primordium is 800µ in height.The lamina is initiated first in the median leaflet then in the other leaflets in the order of the formation of the leaflets. The extreme distal end of the leaf primordium lacks lamina and the cell maturation occurs precociously in this region. At the extreme distal end of the leaflet primordia, there is much crowding which results in the irregular development of marginal meristem (fig.14). But at the middle region the marginal meristem development shows a regular tendency where as the lamina develops in a centripetal manner.

The adaxial and the abaxial layers are formed by the activity of the submarginal initial. However, the behaviour of the submariginal initial is not regular. The middle layer is formed either directly from the submarginal initial or by the periclinal division of the adxial or abaxial layers. After the establishment of the plate meristem by the activity of the marginal meristem the middle layers undergo periclinal divisions which results in the increase of the number of middle layers. The veins are produced from the middle layers. In regions where there are no veins, the number of middle layers is four. The mature leaf is dorsiventral (Fig.16) with palisade parenchyma on the adaxial side and the spongy parenchyma in the abaxial side.

Venation

In a mature leaf, each leaflet has a midrib and 3-5paris of lateral veins. The leaflet show pinnately open reticulate venation(fig 3). The lateral veins do not branch from the median vein but they run along with the median vein for some distance and diverge in to the lamina. In the petioles of leaflets, below the lamina the vascular strands are not in the form of a ring but they are present in the form of a compressed ring. This ring-like arrangement is maintained at the abaxial side whereas it is flattened at the adaxial side. So the petiole has dorsiventral distribution of the vascular strands rather than the radial distribution. This radial distribution is maintained throughout the petiole even at the basal region. The vascular strands are distributed in two rows in the form of 'C'.

In *Schefflera* the leaflets are formed from the most adaxial side of the primordium resulting in the formation of leaflets around a central point. In *Schefflera,* the distal end of the leaf primordium becomes the median leaflet and the formation of other leaflets in a basipetal sequence. These are characteristics of palmately compound leaves. In the rachis region the vascular strands are arranged in the form of a ring. Even in this ring-like arrangement definite groupings are seen. Each group enters a particular leaflet.

Ontogeny of vasculature.

Even before the leaf primordium is 100µ in height the first vascular bundle enters the leaf primordium and extends acropetally. This vascular bundle is present at the abaxial median position. This ultimately becomes the median bundle of the median leaflet. Then two other strands one on either side of the median bundle develops. Next two other strands get differentiated. Before the leaf primordium reaches a height of 200µ, six vascular strands can be differentiated (Fig.17) Even though there is differentiation of six well marked vascular strands; there is no evidence of leaflet initiation at this stage. Each of these primarily developed vascular strands, become the median vein of the leaflets.The secondarily formed strands are present adaxial to the first formed abaxial row (Fig.18) at higher levels, each of these strands split further and occupy an adaxial position . The strand formed from a common bundle entered a single leaflet.

Fig 1.Habit of *Schefflera stellata*- A branch showing leaves

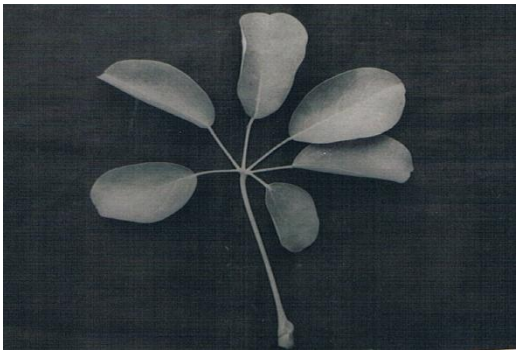


Fig 2.Structure of leaf showing lamina,petiole,rachis and sheath

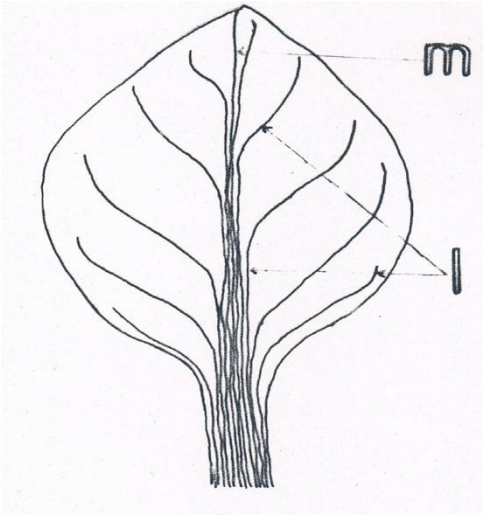


Fig :3 Venation pattern of mature lamina m-median vein, l - Lateral vein,

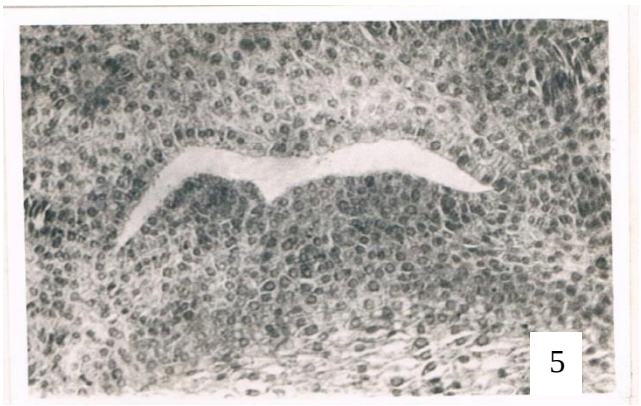
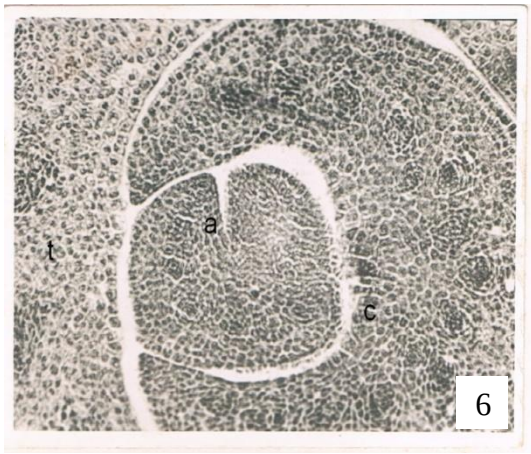


Fig 4 : T.S. of young terminal bud showing axillary bud: ax - axillary bud

Fig 5 : L.S. of the shoot apex with tunica and corpus:



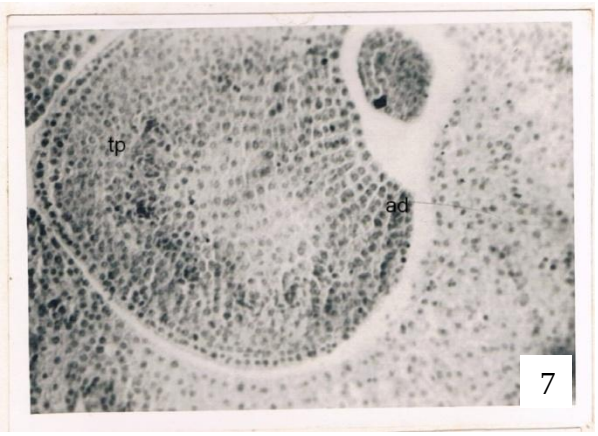
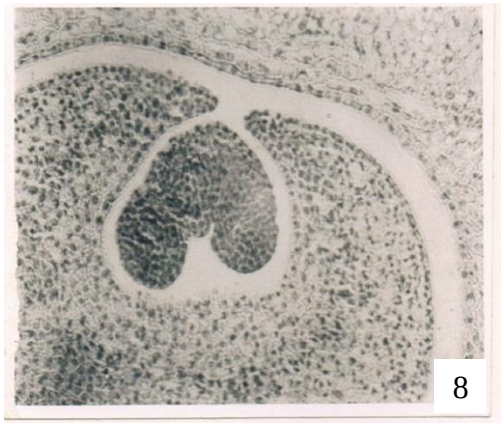


Fig 6 : T.S. of Terminal bud showing youngest leaf primordium and shoot apex

t - tunica, c - corpus, a - apex

Fig 7 : T.S.of lower region of leaf primordium showing adaxial meristem

tp - tip of primordium, ad - adoxial meristem



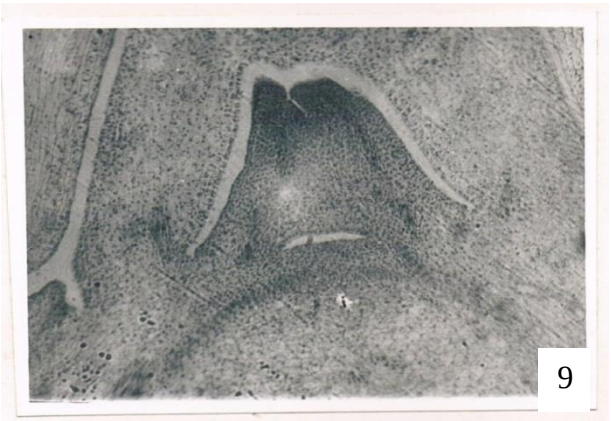


Fig 8 : T.S. of leaf primordium showing the origin of second pair of leaflets

Fig 9 : L.S.of primordium showing the terminal and lateral leaflets

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Fig 10 : T.S.of primordium showing six leaflets arranged in the form off a ring
Fig 11,12 and 13 : Scanning Electron Micrograph (SEM) Showing the tip of the leaf with six leaflets

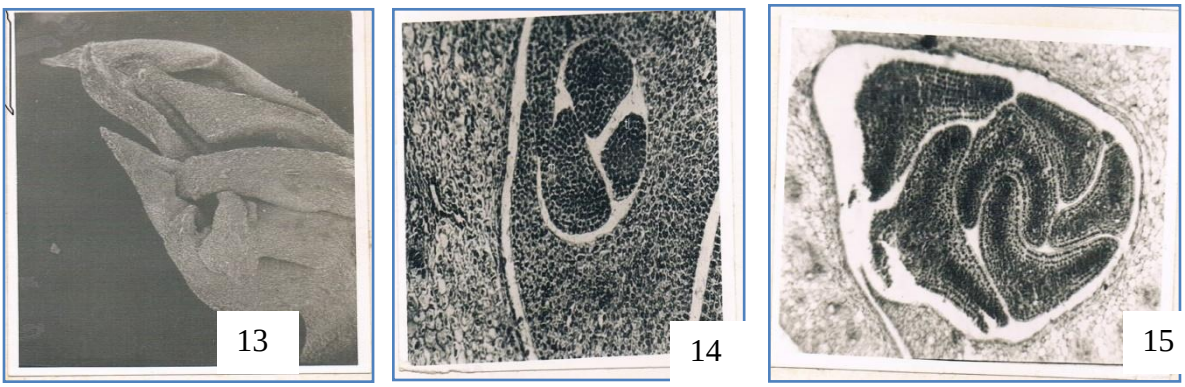

Fig 14: T.S.of the leaf primordium with marginal meristem in the terminal leaflet
m - marginal meristem, tl = terminal leaflet

Fig 15:T.S. of the primordium showing the laminal margin of one leaflet gets interlocked into the laminal margin of another leaflet .

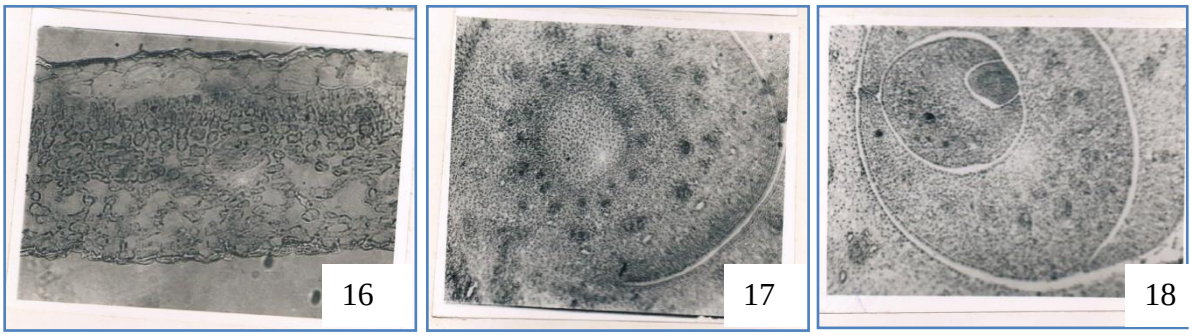

Fig 16: T.S.of mature lamina
Fig 17 : T.S.of rachis showing multilacunar type of node
Fig 18 : T.S.of leafsheath showing adoxial position of the secondarily formed strands

DISCUSSION

The leaf of *Schefflera stellata* is peculiar in having both dicot and monocot characters with reference to leaf origin. The leaf which is characteristic of monocots is perfectly blended with the rachis and the petiole, which are dicot characters. In addition it has the leaflets radiating from a central point. Because if the presence if the radiating leaflets from a common point it could be compared to the structure of peltate leaves where the lamina is entire while it is dissected in *Schefflera*.

The number of leaflets produced from a terminal bud increases with the age of the bud. Allsopp (1967) relates such heteroblastic development to the nutritional status of the terminal bud and change in the nutritional status as the terminal bud ages. One more reason is that the increase in the number of leaflets is the increased dimension of the terminal bud with the age.The shoot apical meristem of *Schefflera* does not deviate from the structure of the other angiosperms. A cytohistological zonation with a single layer of tunica and a subjacent corpus without pith rib meristem is evident here. The absence of pith rib meristem probably is related too much crowding of leaves without intermodal region.

The initiation of the leaf primordium by periclinal division in the hypodermal layer of shoot apical meristem is wide spread among the angiosperms. Such initiation of leaf primordium from the hypodermal layer is reported by earlier workers like Avery (1933) and Foster (1936). A perusal of literature on leaf ontogeny reveals that the early apical growth of the primordium is either by a single apical cell or by a group of sub apical initials (Boke, 1940; Ramji, 1968). But in contrast, in *Schefflera,* the early growth is rather diffuse.

Hazman (1970) considers that the unifaciality of the petiole peltate leaves is brought about postgenitally by the increased meristematic activity of primordial margins which equates the adaxial meristem. The histogenesis of leaf venation begins with acropetal progression of the procambial strand that becomes the precursor of the midrib (Avery 1933;Foster,1933; Slade,1957) with commencement of the development of the lamina, the procambial strands of the large lateral vein begin to form gradually (Avery 1933). Some researchers have suggested that the precursor secondary veins are also procambial strands that arise directly from the midrib in the middle layer of the lamina (Avery,1933; Foster,1936). Few others consider that the secondary veins arise as independent strands (Isebrands and Lerson,1980).In most of the monocots the mid vein and the lateral are independent and are successively developed (Kaplan,1970a; Sharman and Ann Hitch,1967 Pray,1955a). In almost all monocotyledons, the first procambial strand to develop is the median vein (Stevenson,1973; Pray,1955b;Periasamy,1966) However, In Acorus Kaplan (1970), has reported the development of lateral procambial strands prior to median strand. When the primordium is 200µ periclinal divisions are seen in the sub-epidermal layer in the upper region of the basal half of the primordium. As the behaviour and location of this meristem is similar to that of the adaxial meristem it would be appropriate to call this as adaxial meristem. However, the earlier literature on peltate leaves refer this zone as querzone (fig.13) This meristem is involved in solidification of the tissue of the upper region of sheath and below the leaflets. It would be worthwhile to note the initiation and the maximum activity of this zone is quite late in the early morphogenesis of the leaf primordium. This adaxial meristem cannot be compared to that present in Acacia and Acorus described by Kaplan (1970) where it forms the lamina. Late in the ontogeny, the upper region of this zone gets completely integrated with the rachis which is produced purely by intercalary growth.The initiation of leaflet primordia takes place when the leaf primordium reaches the height of 500µ. The first pair of leaflets gets initiated at the adaxial margin about 200µ below the distal end of the leaf primordium.

A similar type of leaflet initiation has been reported in Carya (Foster, 1935) and in Tabebuia (Periasamy and Muruganathan, 1985). However when more than five leaflets are initiated, the ontogeny differs from that of palmately compound leaves.In a leaf having more than five leaflets, the leaflet primordium is initiated 220 µ below the distal tip which is radially symmetrical. The first pair of leaflet is intiated from the adaxial hypodermal cells on either side of the tip.

The leaf architecture of Arisaema and Schefflera are identical but their ontogeny is quite different. In Arisaema (Periasamy and Muruganathan, 1986) the lamina is initiated first and the leaflets are initiated as folding of the lamina prior to development of veins. But in *Schefflera* each leaflet is independently initiated and the lamina develops at a later stage. The reason for the development of independent leaflet primordial is probably the precocious development of veins. This is an evidence for presence of different ontogenesis for a similar mature morphological structure.

The previous workers on the ontogeny of compound leaves (Foster, 1936; Denne, 1966; Hageman, 1970; Kaplan, 1970 b; Coleman and Greyson, 1976; Merril, 1979) have reported that in both pinnately and palmately compound leaves, the leaflets are formed by fractionation of an initial marginal meristem that would produce a continuous simple lamina. The initiation of the leaflets in *Schefflera stellata* before the differentiation of a well defined marginal meristem in the leaf primordium however, does not support this view. Furthermore the leaflet

meristem has other fundamental differences from the lamina initiating marginal meristem. The lamina initiating marginal meristem is a characteristically 5-layered plate that undergoes only surface extension whereas the leaflet meristem is more than 5-layered and grows longitudinally as does the leaf primordium. The marginal meristem directly gives rise to the lamina where veins develop subsequently from the middle layer whereas the leaflet meristem first forms the future midrib portion of the leaflet on which the lamina is initiated subsequently by a marginal meristem along with its lateral face.

It is more probable that the formation of compound or simple leaf is correlated with the development of the provascular starnds of the leaf. In compound leaves, the procambia of the future midribs of the leaflets appear to be formed precociously so that the leaflet primordial arise at the terminal end of a differentiated procambium of the future midrib of the leaflet. Such mechanism of compound leaf formation has been described in Tabebuia (Periasamy and Muruganathan, 1985).

As the marginal and submarginal initials do not display any cytomorphological difference from their immediate derivations their presence and activity is to be presumed by observing occasional divisions in them. It cannot also be determined with certainity whether these initials are permanent or are replaced periodically. The relation between the submarginal initial and cell layers of plate meristem is variable and does not warrant a categoric cell lineage diagram of leaf histogenesis. Histogenesis of the lamina commences when it expands by the 5 or 6-layered plate meristem in Schefflera and this appears to be a feature that is general for all the angiosperms the histogenesis and maturation, the number of layers does not usually increase due to the strictly anticlinal divisions of the plate meristem except at the region of the veins as has been reported in Xanthium (Maksymowych and Wochock, 1969).

In Troll's (1932) monographic work on peltate leaves, the radiality, of petioles of peltate leaves arose by the suppression of adaxial side and the accentuation of expansion of abaxial side of the leaf primordium. However Troll's work is criticised as his interpretation was not based on actual observations of the leaf development but was as theoretical detection derived from the study of mature leaves. Moreover, Troll (1932) asserted that suppression of adaxial leaf surface is a congenital developmental process. Roth (1949, 1952) has shown that the radial sector arose from a bifacial primordium thereby disproving the congential origin of radial sector. Hagemann (1970) proposed that the meristem incorporation and its fusion around the adaxial face of the petiole is responsible for the formation of adaxial extension of peltate lamina. Arisaema, a plant belonging to Araceae has similar radiating leaflets from a central point like that of Schefflera stellata where according to Periasamy and Muruganathan, (1986), the lamina originates as a simple and gets subsequently folded. The foldings get separated late in the ontogeny and there is no evidence for differential development of adaxial leaflets from that of abaxial leaflets.

Venation

The median veins of all the leaflets have independent origin from the stem. The presence of such independent midveins is reported in *Populus* (Isebrands and Larson, 1980), Arisaema (Periasamy and Muruganathan, 1986) and Acorus (Kaplan 1970). The Lateral veins for a particular leaflet is also formed by the splitting of the first formed midvein. The later split strands occupy more and more adaxial position. In the sheath and petiole, bundles are arranged in radial rows. In the sheath and petiole, bundles are arranged in radial rows. In this respect it resembles the venation pattern of palms. The bundles in each radial row have common origin. In Tobacco (Avery, 1933) the lateral veins are produced as branches of the midvein but in Schefflera the lateral veins enter independently into the petiole and sheath.

CONCLUSION

The observation on Schefflera stellata provide a clarity on the ontogeny of leaf origin, a peculiar phenomenon, which has not been reported before by any botanist. The mechanism of ontogeny of leaf in Schefflera species is an essential characteristic to be included in plant taxonomy. This study could involve experimental enthusiasm of ecologists who are dealing with diversity in plant anatomy and organisations concern with conservation of forest environment.

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