Ontogeny of palmately compound leaves in angiosperms:  
1. Tabebuia pentaphylla Hense

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Abstract. The palmately compound leaf of Tabebuia pentaphylla is initiated by periclinal division in the hypodermal layer at the flank of the maximal shoot apex, which lacks cytohistological zonation. The growth of the leaf primordium is diffuse until it reaches a height of 50–60 μm after which an adaxial meristem makes it conspicuously thick at the basal region. The first pair of lateral leaflets arise about 50 μm below the tip of the leaf primordium when the latter is about 150 μm high and before the differentiation of a well defined marginal meristem. The second pair of leaflets arises subsequently below the first. The terminal portion becomes the central leaflet. The sites of leaflet initiation are the terminal endings of acropetally differentiating procambial strands. The 6-layered plate meristem of the leaflet lamina arises from a marginal meristem whose submarginal initial is wedge shaped. Leaflet venation is compendromous and the ultimate areoles lack free vein endings.

Keywords. Tabebuia penatphylla; leaf ontogeny; palmately compound leaf; shoot apex; dicot leaf ontogeny.

1. Introduction

The leaf is morphologically prominent and physiologically the most important part of the angiosperms. Several features in which the monocotyledons differ from the dicotyledons, leaf character is an important one, the former exhibiting a parallel venation and the latter a reticulate venation in general. Apart from this, while compound leaves of various types are found in the dicotyledons, most of the monocotyledons are simple leaved and the compound leaf is an exception, occurring only in some members of the Liliaceae, Araceae, Taccaceae and Dioscoreaceae. In Arecaceae the adult leaf is pinnately compound in many species but it has been shown (Eames 1953; Periasamy 1965, 1967) that ontogenetically all palm leaves are simple and the compound nature arises due to disconnections in the plicated lamina during the late stages of ontogeny. The leaves of Cyclanthaceae are ontogenetically similar to those of Arecaceae (Wilder 1976, 1981).

The special attributes that characterise the monocotyledonous leaves have led to morphological interpretations like the phyllode theory (Henslow 1911; Arber 1918), leaf base theory (Knoll 1948; Kaplan 1970a) and the unifacial concept (Knoll 1948; Roth 1949; Thielke 1948), all of which aim at interpreting the monocot leaves in terms of the dicot leaves and to establish morphological difference between them. Difference of opinion also exists with regard to the phylogenetic relation between the simple and the compound leaf (Eames 1961; Sporne 1974). Furthermore, it is not known whether in view of the envisaged morphological differences between the dicot and monocot leaves, there is any difference in the manner in which the formation of the compound lamina is brought about in these two groups. The present paper forms part of a
comparative study (Muruganathan 1982) on the ontogeny of the palmately compound leaves in 3 non-palm monocotyledonous genera and a dicotyledonous plant in order to assess how far the morphological interpretations of the angiosperm leaf are in accord with the little known ontogenetic picture of the palmately compound lamina. An overall discussion of the picture that has emerged from this study will be presented in the final paper of the series.

2. Materials and methods

Shoot apices with leaves at various stages of development were collected from the campuses of St. Joseph's College, Tiruchirapalli and Presidency College, Madras, fixed in FAA, dehydrated in ethanol xylol series and embedded in paraffin wax. Sections were cut 8–10 μm and triple stained with tannic acid-ferric chloride-Heidenhains Iron alum haematoxylin and erythrosin. Leaves and shoot apices were cleared using 5–10% NaOH solution and epidermal peelings were taken using 10% chromic acid.

3. Observations

Tabebuia pentaphylla a member of Bignoniaceae bears trifoliate to pentafoliate palmately compound leaves with reticulate venation. The terminal leaflet has the longest petiole and the petioles of first pair of leaflets are comparatively shorter, while last pair of lateral leaflets are almost sessile. The phyllotaxy is opposite decussate.

3.1 Apical organisation

The maximal apex is convex measuring 300–325 μm in diameter and 50 μm in height (figure 1). The minimal apex is almost flat measuring 140 μm in diameter (figure 2). Even though two anticlinally dividing outer layers are common, occasionally 3 layers are seen. Periclinal divisions occur in the second layer at the time of leaf and bud initiation. The corpus divides in all planes but may become stratified at times and show more than 4 anticlinally dividing layers at the flanks (figure 3). Regular longitudinal files of cells are produced by repeated transverse divisions at the base of the corpus. There is no clear cut cytohistological zonation.

3.2 Leaf initiation

The first sign of leaf initiation is periclinal divisions in the hypodermal layer at the flank of the shoot apical meristem. This is followed by anticlinal divisions in the adjacent portions of the tunica layer and random division of the subjacent corpus layers to result in the formation of a protuberance (figure 2).

Till the protuberance reaches a height of 50–60 μm, its growth is diffuse by cell division throughout its tissue (figure 4). After this, the primordium begins to thicken dorsiventrally and a conspicuous adaxial meristem arises at the basal region. The adaxial meristem divides by periclinal divisions of the hypodermal layers to produce radial files of cells (figure 5). When the primordium reaches a height of 100 μm, a procambial strand differentiates acropetally in continuation with the procambial strand of the axis. Simultaneously, the wave of tissue maturation commences on the abaxial side at the base and progresses both adaxially and acropetally.
Figures 1–6. *Tabebuia pentaphylla*. 1–2. L.S. of shoot apex at the maximal and minimal phases respectively. × 100 × 215. 3. L.S. of shoot apex with stratified corpus × 585. 4. T.L.S. of leaf primordium exhibiting diffuse initial growth × 285. 5. T.S. of basal portion of leaf primordium showing adaxial meristem with radial files of cells × 215. 6. T.L.S. of leaf primordium at the time of initiation of first lateral pair of leaflets; section has passed through one leaflet primordium on the right side only × 325.
3.3 Leaflet initiation

The primordia of the first pair of lateral leaflets arise in the leaf primordium when it reaches a height of about 150 µm and before the differentiation of a well-defined marginal or laminal plate meristem (figure 6). At about 50 µm below the tip of the primordium, periclinal divisions in the hypodermal layer initiate the primordia (figure 6). The primordia of the second pair of leaflets arise below those of the first when the latter reaches a length of 80–100 µm. The location in which the leaflets are initiated corresponds to the place where the marginal meristem is usually formed in the simple leaf of dicots (figure 7). The terminal portion of the leaf axis becomes the terminal leaflet. Thus, leaflet development is basipetal.

The procambial strands of the midveins of the respective leaflets are initiated prior to their visible outward inception and in fact the inception takes place at the terminal end of a progressing procambial differentiation.

3.4 Lamina initiation

Usually the lamina is first initiated in the terminal leaflet at the fourth plastochron when the leaf primordium reaches a height of 250 µm. This is followed by lamina initiation in the first pair of leaflets and lastly in the second pair of leaflets. The marginal meristem that gives rise to the lamina comprises the marginal and submarginal initials and their immediate derivatives. The marginal initials give raise to protodermal initials by anticlinal divisions. The mesophyll of the leaves is produced by the activity of submarginal initials. In the marginal as well as submarginal meristem, it has not been possible to establish a definite demarcation between the initials and their immediate derivatives because of the absence of any morphological or cytological distinction between the two.

The submarginal initial is more or less wedge shaped with two cutting faces (figure 8) and produces an abaxial and an adaxial layer by anticlinal divisions (figure 8). However, the submarginal initial itself may divide anticlinally also (figure 9) and the derivative divide to form the adaxial and abaxial layers. The abaxial layer produces a middle layer by a periclinal division at varying distance from the leaf margin (figure 9). The middle of these 3-layers again undergoes one more periclinal division to organise very early in the ontogeny of the lamina, a 6-layered plate meristem (figure 10). The marginal meristem is active only for a short period until the lamina reaches a length of 25 mm and a width of 2 mm.

Further growth of the lamina takes place by the activity of the 6-layered plate meristem (figure 10) which extends from the midrib to the margin of the leaflet primordium. The cells of the abaxial hypodermis adjacent to the middle layer divide periclinally to form 4-layers of spongy parenchyma. The number of cell layers in a lamina of 3 mm length, still enfolded within the bud is the same as in mature leaf. A mature leaf has a single layer of palisade parenchyma and 4–5 layers of spongy parenchyma (figure 11). The lamina increases in thickness by cell enlargement and by development of intercellular space.

3.5 Vein ontogeny—Major veins

The leaflet is reticulately veined. The venation is comptodromous and characterised by the termination of secondary veins within the margins. The secondary veins are
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upturned and connected to super-adjacent secondaries by cross veins, which do not form a prominent marginal loop. 7–9 pairs of secondaries are arranged in a pinnate manner on either side of the midrib and the tertiary veins are irregularly distributed.

The midrib region of each leaflet is a composite structure comprising several independent vascular strands, each of which eventually diverges into the lamina as a secondary vein. The course of the vascular strands is very distinct in cleared preparations of the lamina.

The vascularisation of the leaf starts when a procambial strand from the stem deviates from the vascular cylinder and progresses acropetally into the leaf primordium. The first procambial strand develops at the abaxial side of the leaf primordium and progresses acropetally till it reaches the terminal portion. This becomes the precursor of the midvein of the terminal leaflet. Two lateral strands develop on either side of first formed one and enter the first two lateral leaflets as their midveins. Lastly two more strands develop acropetally and lateral to those of the first pair of leaflets and these form the precursor of the midveins of the last pair of leaflets. Thus at a very early stage of ontogeny, 5 independent midvein strands extend into the leaf from the stem. The node is of unilacunar multitrace type.

3.6 Secondary veins

Within a leaflet, the primordia of different strands originate basipetally on either half. However, the procambium of secondary strands first originate at the place where the leaflet joins the rachis and develops both basipetally and acropetally. Nevertheless, the differentiation of the vascular elements in the secondary strand is always acropetal at various levels at the base of the rachis. The secondary strands either unite among themselves or with primary strands to form the leaf trace components.

In a developing leaf, the vascular elements of the secondary strands seem to be discontinuous because of the rapid growth produced by the intercalary meristem just below the region where the leaflets join the rachis. However, this discontinuity is eliminated by the subsequent differentiation of vascular elements in the gaps.

The procambial secondaries of the lamina differentiate in an uninterrupted progression from the midvein towards the margin in continuation with the already differentiated secondary strands running parallel to the midvein (figure 12).

3.7 Veins of higher order

The tertiary veins divide the intersecondary panel into many bigger areoles. The panel formed by the tertiary veins is further divided by the procambium of quaternary veins into smaller areoles. The procambium of the fifth order veins divide the areoles formed by the quaternary veins into ultimate areoles. The ultimate areoles are not provided with free vein endings.

4. Discussion

As per the tunica corpus concept, all the outer layers that divide anticlinally in the shoot apex, have been designated as tunica. However, Periasamy and Swamy (1964) and Periasamy (1983) have shown that the outermost layer, from which the protoderm and ultimately the epidermis differentiate, cannot be morphologically equivalent to the
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inner layers which are part of the corpus irrespective of their division plane. *Tabebuia* shows two or occasionally three anticlinally dividing outer layers which may further increase at times of stratification. Such variability which is due to the behaviour of the corpus alone does not support labelling the layers other than the outermost as tunica in the shoot apex. According to the terminology suggested by Periasamy (1983) the shoot apex of *Tabebuia* is differentiated into a dermogen, hypogen and axiogen.

As in most angiosperms, leaf initiation in *Tabebuia* begins with periclinal division in the hypodermal layer of the shoot apical meristem. The early growth of primordium is rather diffuse, contrary to the apical growth with a single apical cell reported in tobacco (Avery 1933), or by a group of sub apical initials in *Acacia* and *Polyalthia* (Boke 1940; Ramji 1961).

A significant feature of *Tabebuia* is the development of an adaxial meristem at the basal region when the primordium reaches a height of 50–60 μm. The presence and activity of such an adaxial meristem has also been reported in *Acacia* and *Acorus* (Boke 1940; Kaplan 1970a). The adaxial meristem has been variously interpreted. Knoll (1948) and Thielke (1948) interpret the adaxial meristem of the unifacial leaves as the arrested primary apex of the primordium. However, Kaplan (1970a) has shown that in *Acorus* the adaxial meristem is responsible for lamina formation in the unifacial leaves and it is not the arrested primary apex. In *Tabebuia* the adaxial meristem is not so conspicuous as in *Acorus* and contributes to the radial thickening of the primordium.

The previous workers on the ontogeny of the compound leaf (Foster 1936; Denne 1966; Hagemann 1970; Kaplan 1970b; Coleman and Greyson 1976; Merrill 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 *Tabebuia* 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 its lateral face.

It is more probable that the formation of compound or simple leaf is correlated with the development of the provascular strands of the leaf. In compound leaves, the procambia of the future midribs of the leaflets appear to be formed precociously so that the leaflet primordia arise at the terminal end of a differentiated procambium of the future midrib of the leaflet. In simple leaves, the procambia of the lateral veins are formed from the middle layer of the plate meristem that is derived from the marginal meristem.

As in all plants with imparipinate leaves, in *Tabebuia* also, the terminal portion of the leaf primordium forms the terminal leaflet. The basipetal leaf initiation in *Tabebuia* seems to be common to all palmately compound leaves.

As the marginal and submarginal initials do not display any cytomorphological difference from their immediate derivatives, their presence and activity is to be presumed by observing occasional divisions in them. It cannot also be determined with certainty whether these initials are permanent or are replaced periodically. The relation
between the submarginal initials 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 *Tabebuia* and this appears to be a feature that is general for all the angiosperms irrespective of whether the lamina is compound or simple. During 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* (Maksymowycz and Wochok 1969).

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