VI. ORIGIN AND DEVELOPMENT OF AXILLARY BUD IN

TECTONA GRANDIS L.

_Tectona grandis_ L. is a deciduous timber tree of great economic importance belonging to the family Verbenaceae. The branches are quadrangular (Fig. 1), with leaves simple, opposite-decussate, sometimes whorled, petiolate, exstipulate, elliptic or obovate with rough glabrous upper surface and a lower surface covered by stellate grey tomenta. The leaves are 1-2 by ½ - 1 ft. in dimensions. Only one bud is found in connection with a leaf (Fig. 2). Some members of Verbenaceae like Clerodendrum and Duranta have accessory buds besides the axillary bud.

Shoot apex

The shoot apex above the axil of the youngest
pair of leaves, LI, is very slightly convex in certain phases of the plastochron. Mostly it is flat. Three layers of tunica enclose a massive corpus. The outer corpus cells sometimes simulate the tunica layers by more anticlinal divisions in certain phases of the plastochron. The cytohistological zonation is present except in a stage soon after leaf initiation. The central meristem shows large vacuolated cells. The cells of the peripheral meristem are deeply staining and those of the rib meristem are linearly arranged, large and vacuolated.

The plastochronic changes are divided mainly into three phases, the pre-leaf initiation phase, the leaf initiation phase and the post-leaf initiation phase. The early as well as the late pre- and post-leaf initiation phases could also be distinguished. The ratio between the height of the youngest leaf primordium (l₁) and the width of the shoot apex (sa) is one of the criteria used to distinguish the plastochronic phases. The other criteria are, (i) the presence or absence of
cytohistological zonation, (ii) the degree of stratification in the shoot apex and (iii) the divisions denoting leaf initiation.

In the early stages of the pre-leaf initiation phase the shoot apex width is very short (Figs. 3, 4). The shoot apex is very slightly convex or almost flat. The central meristem is conspicuous. The peripheral meristem is deeply stained, dense and small compared to the one in the other phases. The rib meristem is poorly developed below the central meristem. The stratification of the peripheral meristem is only three or four layers deep.

As the pre-leaf initiation phase advances, more anticlinal and periclinal divisions take place in tunica and corpus. These divisions increase the convexity of the shoot apex (Fig. 4). The cytohistological zones are very distinct. The vacuolated cells of the central meristem are irregularly arranged. The stratification of peripheral meristem cells is six or seven layers deep.
A cup-shaped zone of cambial-like cells is observed below the central meristem. It is placed above the rib meristem and extends up to the inner limits of the peripheral meristem (Figs. 4, 42). The wall thickness and alignment of the cells immediately below the cambial-like zone suggest that they are derived from this zone. This zone is instrumental in quickly increasing the radial dimensions of the axis below the shoot apex by giving rise to more rib meristem cells which undergo more vertical divisions than usually happening in the early pre-leaf initiation phase. When the elongation of pith cells formed from rib meristem cells contribute to internodal elongation, the zone of cambial-like cells produce derivatives and merge with the nodal cells. In every plastochron, more or less at the leaf initiation period, the cambial-like zone is differentiated. The zone persists till the shoot apex is in the post-leaf initiation phase.

In *Chrysanthemum morifolium* (Popham and Chan, 1950) a cup-shaped zone of cambial-like cells
is reported. In *Chrysanthemum*, it extends up to tunica layers. The zone is initiated in the early phase of the plastochron and it becomes fully developed by mid-phase. Regarding the function of this zone, Popham and Chan (1950) observe, "Since the zone of cambial-like cells is cup-shaped, growth in diameter at the base of the apex as well as growth in length of the apex results". In *Chrysanthemum* and *Tectona* the zone is a part of the primary meristem. Popham and Chan (1950) show that cambium-like zone is a feature of large apices. But Vaughan (1952) found such a zone in the small apex of *Arabidopsis*.

In the pre-leaf initiation phase of *Tectona* the \( \frac{L_1}{sa} \) ratio ranges from 2 to 2.2. The leaf initiation is identified by periclinal divisions in 3 or 4 cells in the 4th or 5th layer of the peripheral meristem (Figs. 5, 42, 43). The two sectors of leaf initiation are above the two 'free edges' of the cup-shaped cambial-like zone (Fig. 5).
In the early post-leaf initiation phase, the leaf buttresses are formed by anticlinal and periclinal divisions of corpus cells in the respective sectors (Fig. 6). The cytohistological zones are present when the leaf primordia emerge and begin to develop actively in the late post-leaf initiation phase during which the identity of the zonation disappears (Figs. 7, 44). In the late post-leaf initiation phase the stratification is only up to three or four layers (Fig. 7). The maximum width of the shoot apex between the axils of $l_1$ is 75-80 $\mu$ only. The first leaf primordium may grow to a height of 288 $\mu$ in this phase when the shoot apex does not show any zonation. The $l_1$/sa ratio is 31 at this stage.

**Origin of the bud**

The earliest bud meristem is observed in the peripheral meristem of the main apex adaxial to the second leaf, L2 (Figs. 8, 42). The bud meristem cells are more or less equally stained. The bud meristem is identified by more anticlinal divisions
in the peripheral meristem cells near the axil of the second leaf. The three tunica layers and three or four layers of corpus together constitute the early bud meristem. Non-median section of the early bud meristem shows residual meristematic connections with the axial procambial strands (Fig. 9). The two residual meristem strands become more distinct when the neighbouring ground meristem cells have parenchymatized.

Further development of the bud

The increase in width is due to more anticlinal divisions in tunica and corpus cells (Fig. 10). The basal cells of the corpus divide in various planes and this histologic activity increases the depth of the bud meristem. The cells of the bud meristem adaxial to the shoot apex appear longer and more vaciolated. They form a cambium-like zone almost surrounding the bud. At this stage, the residual meristem connections of the bud differentiate into procambium strands (Fig. 11). Figures 45 and 46 represent the median
and non-median sections of the bud meristem respectively, the latter with bud trace procambium, BT. The vacuolated cells of the peripheral meristem cells of the main apex adaxial to the bud delimit the bud meristem from the nest of the shoot apex (Fig. 43). The sagittal section of the bud shows its tangential growth (Figs. 12, 46). The bud meristem has distinct three layers of tunica and four to five layers corpus (Fig. 12). The two procambial strands are differentiated up to the base of the bud. The bud meristem is eumeristemetic at this stage (Fig. 12).

At the time of the prophyl initiation, the central and peripheral meristems are evident (Figs. 13, 47). The prophyl initiation is identified by periclinal and oblique divisions in the third and fourth layers of the peripheral meristem. The procambial strands differentiate towards the developing prophyls (Fig. 13). The bud meristem emerges due to periclinal divisions in the corpus and anticlinal divisions in the tunica correspond to the increase in the size of the bud.
The distinct zones based on cytohistological features are observed in the well developed bud before the initiation of its first pair of leaves (Figs. 14, 48). The central meristem cells are bigger and more vacuolated than peripheral meristem cells. The rib meristem cells are highly vacuolated and linearly arranged. The cambium-like zone loses its identity by contributing cells towards the pith of the bud and the axis part below the bud.

The initiation of the first pair of bud leaves is by periclinal divisions in the third layer (Fig. 15). The zones are distinct and the bud resembles the main apex.

The well developed buds illustrated in figures 14 and 15 are produced in the month of August in the rainy season. They are developed up to the stage of the first pair of leaves. The bud shown in figure 16 is of the summer season, March. The size of this bud is not as much as that of the rainy season, though both are at the same stage of producing the first pair of leaves. The well
developed prophylls protect the summer bud, and it remains dormant till the favourable season.

**Vascularization of the main apex**

The procambialization of the main vegetative shoot apex is illustrated in figures 17-19. The level at which the transverse section passes through the tip of the main apex is considered to be at 0 µ. 12 µ below, the central meristem, CM, and the peripheral meristem, PM, are evident (Fig. 17). The first pair of leaf primordia, L1, can also be seen at this level. At 24 µ level, the apex shows the rib meristem, RM, in the centre and a deep staining peripheral zone (Fig. 18). The vascular meristem in the peripheral zone shows residual meristem, RE, interrupted by four large procambial groups, PC, at four corners (Fig. 18). The procambium is identified by narrow dimensions and bright staining. The residual meristem cells are bigger than procambial cells. The leaf trace procambium, LT, of L1 is blocked out by vacuolation of cells on the abaxial and adaxial sides of the
leaf primordium (Fig. 18). At 36 μ level, the leaf trace, LT, of L1 becomes associated with the axial vasculature (Fig. 19).

So, the peripheral meristem of the main apex gives rise to residual meristem and procambium in connection with developing leaves. By the time the leaf primordia are formed, some of the residual meristem cells in the respective sectors are already differentiated into procambium. The formation of the leaf trace leaves a single gap in the axial vasculature. The procambialization of the young bud before and soon after prophyll initiation can better be followed after understanding the vascular interrelationship in the plant, and the establishment of the primary vascular system of a well developed bud.

**Vascular interrelationship**

The vascular interrelationship is illustrated in figures 20 and 21. Figure 21 is only modified and magnified part of what is illustrated in figure
20. Figure 20 illustrates the bud traces and the internodal vascular strands.

In every internode a large vascular strand is found at each ridge of the quadrangular stem. These four strands are numbered 1-4 at the base of figure 20. In between these strands there are smaller strands which are collectively named $X_1$, $X_2$, $X_3$ and $X_4$. The node shown in the figure is labelled as N2. The first node, N1, and its leaves L1 are not shown in the figure, but are considered to be immediately above N2. The strand 4 bifurcates into 4' and 4" at the node N2. The branch 4' continues as a leaf trace, LT. It enters the lateral side of the petiole and branches further. The vascular strand, 4" gives rise to a branch, GA which turns horizontally towards the axis and keeps a peripheral course. The vascular strand, GA, meets with the one which is similarly formed from the opposite vascular strand 1", and forms a girdle in the axis. The vascular strand 3 also behaves like 4. In the case of the vascular strands 1 and 2, they show similarity in behaviour.
to 3 and 4. Together with the branches of 3 and 4, the intermediate strands, $X_3$, also enter the petiole at its base. Thus a single leaf gap is formed and the leaf trace consists of many strands. The vascular strands entering the leaf laterally, branch further and form vascular strands traversing the adaxial side of the petiole. The vascular strands in the leaves get interconnected by a girdle, GL, on all the four sides at the proximal end of the petiole. This girdle, GL, and the girdle in the axis, GA, appear more or less continuous.

The intermediate strands, $X_4$ and $X_2$ travel up to the node, N2. They take a course beneath the girdle while traversing the internode above. They do not fuse with the girdle in the young shoot, but in the matured condition connections are observed. These intermediate strands, $X_4$, behave in the first node, N1, as $X_3$ strands in the second node, N2. The strands 1" and 4" also travel up to N1. The vascular strands, 1", $X_4$ and 4" can be compared to the strands 3, $X_3$ and 4.
At the level of the bud, the vascular strand 4" gives rise to a branch, CT, which takes a short horizontal course and then bifurcates. The common trace, CT, again forkes into a bud trace, BT, and a common vascular strand for the internode above, IV. The bud trace, BT, takes a horizontal but outward diversion towards the base of the bud. The common vascular strand for the internode, IV, meanwhile takes a horizontal but inward diversion. From this the intermediate strands, $X_i$, arise in the internode above. Each bud trace, BT, divides into two. The plane of bifurcation of the bud trace, BT, is at right angles to the plane of bifurcation of the common trace, CT.

The two branches of each bud trace from opposite side meet and form an oval ring at the base of the bud (Figs. 21, 22). The prophyll traces and traces for bud leaves are associated with this vascular tissue (Fig. 22).
Primary vascular system of the bud

Schematic representation of the bud with its primary vascular system is illustrated in figure 22. A part of the common trace, CT (see figures 20, 21), is shown in figure 22. The vascular trace, BT, and the common vascular strand for the internode above, IV are branches of the common trace, CT. The prophyllary and the other leaf traces of the bud differentiate partly from the residual meristem formed by the bud apical meristem and partly from procambium directly formed by peripheral meristem of the bud. Each bud trace bifurcates at the base of the bud. The plane of bifurcation of the bud traces, BT, is at right angles to the plane of bifurcation of the common strand, CT. The branches from the opposite bud traces fuse and form an oval provascular ring at the base of the bud. During the formation of the provascular ring, the two trace complexes, TC, arise from which the prophyll trace, pt, and the other leaf traces, It, of the bud are differentiated. Each of the complex traces, TC, gives rise to two branches, A and B, or C and D.
These vascular strands, A-D, develop into four large vascular strands of the bud axis as described in figures 20 and 21. The intermediate smaller strands arise from the vascular ring. The arrangement of the primary vascular system of the young bud is represented below the summit of the bud apex.

Figures 23-29 give the transverse view of the vascular system of the bud as observed from the base of the node. The common traces, CT, bifurcate and form an oval ring in the plane of the lamina of the axillant leaf (Fig. 23). The part of the oval ring, IV, gives rise to vascular strands for the internode above (Fig. 24). At a higher level, the three basal intermediate strands, X, of the bud are observed (Figs. 24, 25). When the section passes through the middle of the bud, the trace complexes, TC, and the prophyll traces are observed (Fig. 26). At still higher level, the intermediate strands, X, are observed again (Fig. 27). Figures 28 and 29 show the internodal regions above the level of the bud. The part of the vascular strand, IV, shown in
figure 24 has given rise to the internodal slender strands shown in figure 29.
strand, IV, for the internode above, are observed (Fig. 34). The branches of the bud traces travel horizontally and fuse to form an oval ring at the base of the bud (Figs. 34, 35). This ring is visible as the bud at this stage is not in cauline position. 84 μ above, the bud tissue is eumeristematic (Fig. 36).

Procambialization of the bud after prophyll initiation

The departure of the leaf trace for L5 leaf, from the axial vasculature is considered at 0 μ level (Fig. 37). The common procambial strands, CT, from which the vascular connections of the bud and the internode above originate, arise from the edge of the axial vasculature. At 48 μ level, the procambial strands, BT, traverse horizontally (Fig. 38). The fusion of branches of bud trace, BT, forms an oval ring of provascular tissue (Fig. 38).

Two big groups of procambial strands, i.e.,
trace complexes, TC, and two smaller procambial strands, X, are observed in this ring (Fig. 38). Each of the former divides into three forming a median strand, pt, and two laterals, lt (Figs. 39, 40).

The procambial strand, pt, is the prophyll trace. The strands, lt, will develop as prominent groups of vascular strands in each corner of the quadrangular internode of the branch. X is one of the intermediate strands.

At 108 μ level, the bud shows the provascular ring consisting of eight procambial strands and the intervening residual meristem (Figs. 39, 40).