FERONIA LIMONIA L.

Feronia limonia is a tree with sharp strong thorns, $\frac{1}{2} - 1\frac{1}{2}$ in. long. It belongs to the family Rutaceae. Leaves are alternate and imparipinnate. The petioles are flat and often narrowly winged. There are three to nine leaflets which are opposite. Flowers are small and numerous in lateral or terminal pubescent panicles, male and female flowers often in the same panicle. The fruit is a berry with many seeds.

Shoot apex

The shoot apex is dome shaped with a biseriate tunica enclosing a massive corpus. The cytohistological
zones are poorly marked out. The distinction of the different regions is based on the comparative size of cells and their nuclei.

The shoot apex undergoes five intergrading phases during a plastochron. They are maximal, minimal, early post-minimal, late post-minimal and pre-maximal phases. They are identified by the histogenic stage of the shoot apex, stratification and the developmental stage of the leaf.

**Maximal phase:** The shoot apex shows maximum height, width and number of stratified layers during this phase. The maximum number of stratified layers varies from 3 - 6 (Figs. 1, 57). The central meristem consists of large cells with large nuclei (Figs. 1, 57, CM). The cells of the peripheral meristem are deep stained. The rib meristem cells are less stained and show high degree of vacuolation (Figs. 1, 57, RB). They do not show the characteristic linear arrangement of cells. Some of the T2 and outer corpus layer cells show periclones indicating leaf initiation. The average height and width are 198 μ and 302 μ respectively.

**Minimal phase:** The shoot apex enters the minimal phase during leaf initiation. In a sector of the
peripheral meristem $T_2$ and outer corpus layer cells undergo various types of divisions along with increased frequency of anticlinal divisions in the $T_1$ (Figs. 2, 58, L). The leaf trace procambium is observed (Figs. 2, 58, PC). The procambium cells are with dense staining contents. The shoot apex is reduced to a height and width of 23 $\mu$ and 78 $\mu$ respectively. The cells of the leaf buttress show deep stainability.

**Early post-minimal phase**: The shoot apex increases in size by the anticlinal divisions in the tunica and various types of divisions in the corpus cells. At this stage the outer corpus layer shows predominant anticlinal divisions. The foliar buttress differentiates into a foliar primordium by the active anticlinal divisions in the outer tunica and various types of divisions in the inner layers (Figs. 3, 59, $L_1$). The leaf trace procambium differentiates acropetally (Figs. 3, 59, LT). The average height and width are 59 $\mu$ and 97 $\mu$ respectively.

**Late post-minimal phase**: The apex shows 3 – 4 stratified layers. The peripheral meristem shows deep
stainability of the contents (Fig. 4, PM). The apex shows an average height of 99 u and width of 138 u.

**Pre-maximal phase:** The shoot apex shows 3-5 stratified layers. It shows cytological heterogeneity (Figs. 5, 60). The average height is 131 u and width is 205 u.

**Primary vascular differentiation of the young shoot**

The primary vascularization of the young shoot is studied in serial transections from the fifth internode up to the tip of the shoot apex. The vasculature at the fifth internode shows a ring of residual meristem and indiscrete procambium groups (Fig. 6, AV). The node is trilacunar (Fig. 7). The median trace consists of more than one procambium strand. The differentiation of the median trace of the fourth leaf is observed at the fourth node (Fig. 8, MLT). The lateral traces differentiate at a higher level of the node (Fig. 9, LLT). The eumeristematic und meristem is observed (Fig. 9, BM). The vasculature of the third internode is a complete ring with indiscrete procambium groups (Fig. 10, AV). It shows the differentiation of the traces of the third leaf at higher levels (Figs. 11, 12).
At the third node one procambium group is prominent in the axial vascular system (Fig. 12, PC). Figure 13 is the transection of the second internode where the axial vasculature is a complete ring with one prominent procambium group, PC. It differentiates as a median trace of the second leaf (Fig. 14, MLT). The lateral traces differentiate later. The axial vasculature shows the presence of a prominent procambium group (Fig. 14, PC). At the level of the first node the axial vasculature is in the form of a ring with one procambium group (Fig. 15).

**Ontogeny of lateral buds**

Usually one bud is observed corresponding to a leaf. It differentiates into a thorn after the formation of two to six leaves. The prophyll bud is differentiated at a very early stage. The region of the bud axis between its point of insertion and the prophyll does not elongate. As the elongation of the bud axis occurs above the prophyll node, the prophyll and its bud appear very close to the main axis itself. The prophyll bud develops into a vegetative branch. Its differentiation is very slow during early ontogeny.
The earliest bud meristem appears as a group of 3 - 4 layers of cells with large nuclei and less staining contents. It is on the flank of the apex corresponding to the second leaf (Figs. 16, 57, BM). It is connected to the axial vasculature with two strands of residual meristem from its very inception (Fig. 17, RM). The bud meristem shows predominant anticlinal divisions (Fig. 61, BM). A non-median section of the bud shows its residual meristem connection with the axial vasculature (Figs. 18, 62, RM). The residual meristem cells are with comparatively smaller nuclei. The bud protrudes out because of more anticlinal divisions in the tunica and various types of divisions in the corpus layers. The T₂ is stabilised from the early stage of bud differentiation. As the bud protrudes out it attains a structure similar to the shoot apex. A sagittal section shows the presence of two residual meristem strands (Figs. 19, 63, RM). Periclinal and oblique divisions in T₂ and other corpus layers in a sector of the peripheral meristem along with increased anticlinal divisions in the outer corpus layer result in the formation of a prophyll buttress (Figs. 20, 64, P). The prophyll trace procambium is invariably observed (Figs. 20, 64, PC). The prophyll trace procambium
differentiates acropetally (Fig. 21, PT). The bud apex undergoes the same histological changes as those of the main shoot apex during late post-minimal to maximal phases (Fig. 22). At this stage the differentiation of the prophyll bud meristem is observed (Fig. 22, PB).

**Procambialization of the lateral bud**

The bud meristem is connected to the axial vasculature by residual meristem from its very inception. The residual meristem differentiates into procambium simultaneous with prophyll initiation. Serial transections of nodes with lateral buds of different developmental stages are described with respect to their procambialization. The measurements given are from the summit of the bud apex.

**Early procambialization of the lateral bud**: The median trace of the subtending leaf differentiates from the axial vasculature at about 76 μ level (Fig. 23, MLT). The lateral traces differentiate and depart at higher levels (Fig. 24, LLT). Two residual meristematic bud traces are observed at the axial vasculature flanking the median leaf gap (Fig. 25, BT). The bud meristem shows uniform staining (Fig. 26, BM).
Procambialization of a bud with one prophyl

The two bud traces differentiate from the axial vasculature flanking the median leaf gap at 114 µ level (Fig. 27, B₁, B₂). They consist of residual meristem and indiscrete procambium groups. As they depart from the axial vasculature at higher levels they attain an arc-like configuration (Fig. 28). At this stage three procambium groups are observed in each arc. These two arcs represent the provascular system of the bud (Fig. 28, PV). The provascular system attains a horse-shoe shaped structure at higher levels by the differentiation of residual meristem connecting the two arcs (Figs. 29, 30, PV). At 58 µ level one of the procambium strands differentiates as a prophyl trace (Fig. 31, PT). The prophyl is produced at an angle lesser than 90° and it is observed more towards the axis. Figure 32 illustrates the provascular system at a higher level.

Procambialization of a bud with one prophyl and a leaf: The two bud traces differentiate at about 218 µ level (Figs. 33, 69, B₁, B₂). Their free ends "join together" even before their departure from the axial vasculature (Figs. 34, 70, PV). It is the provascular system of the bud. It departs from the axial vasculature at 134 µ level (Fig. 35, PV). At about
113 u one procambium group departs as a prophyll trace (Figs. 36, 71, PT). The prophyll bud is observed at 78 u level (Fig. 37, PB). The provascular system becomes a complete ring at this level (Figs. 37, 72, PV). The median trace, MLT and two lateral traces, LLT, of the first leaf differentiate at the first node (Figs. 38, 73). The provascular system becomes a complete ring with residual meristem and procambium groups at 43 u level (Fig. 39, PV). At slightly higher levels only one procambium group is distinguished (Fig. 40). It is the median trace of the next leaf. Above this level the vascular meristem is not observed.

**Differentiation of the thorn**

After the formation of two to six leaves the pattern of morphogenetic development and growth in the bud apex changes. Rapid vacuolation of cells starts from the lower region of the bud. The meristematic activity is confined to the tip of the bud (Fig. 41). The cells of the lower region enlarge and the nuclei appear smaller (Fig. 41). The cells of the inner region show divisions at right angles to the longitudinal plane of the bud resulting in the radial arrangement of cells (Fig. 66). The elongation and rapid divisions in the cells, i.e., rapid rib meristem activity enables
the bud to attain more length. The procambium is observed up to the meristematic region of the bud apex (Fig. 41, PC). The epidermis at the lower regions shows deposition of tanniferous contents. Numerous trichomes are observed on the epidermis (Fig. 42, TR). At this stage also one or two leaves are produced at the apex. Figure 42 illustrates the initiation of a leaf from the apex which is gradually transforming into a thorn. The trace procambium is observed very near to the site of leaf initiation (Fig. 66, PC). The reduction in width is observed due to marked cessation of the radial growth. The bud attains more height (Figs. 43, 65, TH). The cells of the bud apex except one or two layers at the tip undergo high degree of vacuolation and elongation (Fig. 44). The outer tangential wall of the protoderm cells shows small projections. The inner cell layers show high vacuolation and very small nuclei (Fig. 44). At a later stage deposition of tanniferous contents appears in the epidermal cells first at the basal region, later towards the apex. The inner region shows less avidity for stain. The procambium is observed up to 97 μ below the apex (Fig. 67, PC). The meristematic activity ceases and the apex finally differentiates into a pointed structure.
Ontogeny of the prophyll bud

The initiation of the prophyll bud occurs when the lateral bud initiates the first leaf (Fig. 22, PB). It appears as a group of light stained cells, 3–4 layers deep. Its developmental stages are similar to those of the lateral bud (Figs. 45, 46).

Procambialization of the prophyll bud

Serial transections of the node from 309 μ below the apical summit up to the tip of the prophyll bud are described. A transection at 309 μ shows the horse-shoe shaped provascular system of the lateral bud (Figs. 47, 74, PV). At a higher level some of the procambium groups show an oblique course resulting in the formation of a bulging on one side of the horse-shoe shaped provascular system (Figs. 48, 49, 75, arrows). At the node one procambium strand differentiates and departs as a prophyll trace (Figs. 50, 76, 77, PT). The traces of the prophyll bud originate from the portion of the provascular system of the lateral bud which flanks the prophyll gap (Fig. 78, PBT). The differentiation of the horse-shoe shaped provascular
system is observed at 98 $\mu$ level (Figs. 51, 79, PVB). It becomes a complete ring at 63 $\mu$ level (Fig. 52). The prophyll traces depart at a higher level (Figs. 53, 80). The prophyll node of the lateral bud is unilacunar but that of the prophyll bud is trilacunar *(Fig. 54).*

**Vascular interrelationship:** The axial vasculature is a continuous cylinder. Figure 55 is a three dimensional diagram illustrating the primary vascular relationship between the axis, leaf and lateral bud. The node is trilacunar. The two bud traces $B_1$ and $B_2$ differentiate from the axial vasculature flanking the median leaf gap.

Figure 56 is a schematic three dimensional diagram showing the relationship between the main axis, leaf, lateral bud and the prophyll bud. The prophyll trace, PT, departs from the horse-shoe shaped provascular system, PV. The two traces of the prophyll bud differentiate from the portion of the provascular system flanking the prophyll gap.
PLATE 66

FIGS. 1 - 4. *FERONIA LIMONIA*

Figs. 1 - 4. L. s. shoot apex, maximal, minimal, early post-minimal and late post-minimal phases respectively, X 480.

(BM - bud meristem; CM - central meristem; L - leaf buttress; L₁ - first leaf; LT - leaf trace; PC - procambium; PM - peripheral meristem; RB - rib meristem.)
PLATE 67

FIGS. 5 - 15. **FERONIA LIMONIA**

Fig. 5. L. s. shoot apex, pre-maximal phase, X 480.

Figs. 6 - 15. T. s. young shoot, X 120. Fig. 6, fifth internode; Fig. 7, fifth node; Figs. 8 and 9, fourth node; Fig. 10, third internode; Figs. 11 and 12, third node; Fig. 13, second internode; Fig. 14, second node; Fig. 15, first node.

(AV - axial vasculature; BM - bud meristem; CM - central meristem; L₃, L₄, L₅ - third, fourth and fifth leaves; LLT - lateral leaf trace; MLT - median leaf trace; PC - procambium; PM - peripheral meristem.)
PLATE 68

FIGS. 16 - 21.  **FERONIA LIMONIA**

Figs. 16 - 21.  L. s. bud, developmental stages, X 480. Figs. 16 - 18, early stage. Note residual meristem connection in Figs. 17 and 18; Fig. 19, sagittal section showing two residual meristem strands; Fig. 20, prophyll initiation; Fig. 21, prophyll with prophyll trace procambium.

(A - axis; BM - bud meristem; L - leaf; P - prophyll; fPC - procambium; PT - prophyll trace; RM - residual meristem.)
PLATE 69

FIGS. 22 - 32. *PERONIA LIMONIA*

Fig. 22. L. s. bud, leaf initiation, X 480.

Figs. 23 - 26. T. s. node, showing residual meristematic bud traces, X 120.

Figs. 27 - 32. T. s. node, procambialization of the bud with prophyll; X 120. Fig. 27, differentiation of the bud traces; Fig. 28, arc-like provascular system; Figs. 29 and 30, horse-shoe shaped provascular system; Fig. 31, differentiation of the prophyll trace; Fig. 32, ring like provascular system.

(AV - axial vasculature; BM - bud meristem; BT - bud trace; L1 - first leaf; LLT - lateral leaf trace; LT - leaf trace; MLT - median leaf trace; P - prophyll; PB - prophyll bud; PT - prophyll trace; PV - provascular system of the bud.)
PLATE 70

FIGS. 33 - 43. *PERONIA LIMONIA*

**Figs. 33 - 40.** T. s. node, stages of procambialization of a bud with a prophyll and a leaf, X 120. Fig. 33, differentiation of the bud traces; Figs. 34 and 35, differentiation of the horse-shoe shaped provascular system; Fig. 36, prophyll trace; Fig. 37, prophyll bud; Figs. 38 - 40, differentiation of the traces of the first leaf.

**Figs. 41 - 43.** L. s. developmental stages of thorn. Figs. 41 and 42, X 480; Fig. 43, X 50.

(AV - axial vasculature; B₁, B₂ - bud traces; BM - bud meristem; L - leaf; LLT - lateral leaf trace; MLT - median leaf trace; P - prophyll; PB - prophyll bud; PC - procambium; TH - thorn; TR - trichome.)
PLATE 71

FIGS. 44 - 51. PERONIA LIMONIA

Fig. 44. L.s. thorn apex, X 480.

Figs. 45 and 46. L.s. prophyll bud, developmental stages, X 480.

Figs. 47 - 51. T.s. node, procambialization of prophyll bud, X 120. Fig. 47, horse-shoe shaped provascular system of the lateral bud; Figs. 48 - 50, differentiation of the prophyll trace; Fig. 51, horse-shoe shaped provascular system of the prophyll bud.

(PB - prophyll bud; PT - prophyll traces; PV - provascular system of the lateral bud; PVB - provascular system of the prophyll bud.)
PLATE 72

FIGS. 52 - 56. **PEROMIA LIMONIA**

Figs. 52 - 54. T. s. prophyll bud, differentiation of the provascular system, X 120.

Fig. 55. Three dimensional diagrammatic representation of the vascular interrelationship of a young node.

Fig. 56. Three dimensional diagram showing vascular interrelationship of axis, leaf, lateral bud, prophyll and prophyll bud.

(AV - axial vasculature; LLT - lateral leaf trace; MLT - median leaf trace; P - prophyll; PC - procambium; PF - prophyll of the prophyll bud; PT - prophyll trace; PV - provascular system of the lateral bud; PVB - provascular system of the prophyll bud.)
PLATE 73

FIGS.  57 - 64.  FERONIA LIMONIA

Figs.  57 - 60.  L. s. shoot apex, maximal, minimal, post-minimal and pre-maximal phases respectively, X 300.

Figs.  61 - 64.  L. s. bud meristem, developmental stages, X 300.

(BM - bud meristem; CM - central meristem; L - leaf buttress; L₁ - first leaf; LT leaf trace; PC - procambium; PM - peripheral meristem; RB - rib meristem; RM - residual meristem.)
PLATE 74

FIGS. 65 - 72. **PERONIA LIMONIA**

Fig. 65. L. s. thorn, X 150.

Fig. 66. L. s. tip of a young thorn, X 150.

Fig. 67. L. s. tip mature thorn, X 150.

Fig. 68. L. s. prophyll bud, X 150.

Figs. 69 - 72. T. s. node, stages of procambialization of the lateral bud, X 150.

(A - axis; B₁, B₂ - bud traces; L - leaf; LLT - lateral leaf trace; MLT - median leaf trace; P - prophyll; PB - prophyll bud; PV - provascular system of the lateral bud; TH - thorn; TR - trichome.)
PLATE 75

FIGS. 73 - 80. *PERONIA LIMONIA*

Fig. 73. T. s. lateral bud, X 150.

Figs. 74 - 80. T. s. lateral bud showing procambialization of the prophyll bud, X 150.

(A - axis; L - leaf; L₁ - first leaf; P - prophyll; PBT - traces of the prophyll bud; PT - prophyll trace; PV - provascular system of the lateral bud; PVB - provascular system of the prophyll bud.)