V. ORIGIN AND DEVELOPMENT OF AXILLARY BUD
IN CUMINUM CYMINUM L.

Cuminum cyminum L. is an economically important herbaceous plant belonging to the family Umbelliferae. It may grow to a height of 1-1½ ft. The leaves are spirally arranged with 1/3 phyllotaxy. They are simple with sheathing leaf bases and highly dissected lamina (Fig. 1). Very often the internode between the first emerged leaves is very short. The inflorescence is an axillary umbel.

Shoot apex

The vegetative shoot apex is more or less convex. Two tunica layers enclose a corpus. Anticlinal divisions are predominant in tunica,
while corpus cells divide in various planes. The plastochron is divided into three phases based on stratification in the apical meristem, diameter-height proportions, cytohistological features and leaf initiation. The phases are pre-leaf initiation, leaf initiation and post-leaf initiation.

The pre-leaf initiation phase is mainly marked for the stratified and deep staining peripheral meristem (Fig. 2). The central meristem is not distinct. The rib meristem is well differentiated. The procambial strand towards future leaf site develops precociously (Fig. 2). The maximum diameter varies from 80 to 113 μ and the height, from 53 to 63 μ. The shape, increased volume and stratification of the shoot apex in general indicate the approaching stage of leaf initiation.

In the leaf initiation phase, the periclinal divisions denoting the origin of the leaf in a sector of the peripheral meristem can be observed.
Except for these periclinal divisions the shoot apex is well stratified (Fig. 3). A bulge of leaf buttress is not yet formed. There is no distinct central meristem. The leaf trace procambium is well developed at the site of L1, the first leaf (Fig. 3). The dimensions of the shoot apex are 74 to 108 µ for diameter and 40 to 60 µ for the height.

In the early stages of post-leaf initiation phase the newly borne leaf is visible in the form of a buttress (Fig. 4). During further stages of the plastochron, the leaf buttress differentiates into a leaf primordium. Late in the post-leaf initiation phase the peripheral meristem is comparatively less stratified (Fig. 5). The peripheral meristem cells are denser in contents than those of central meristem and rib meristem. The central meristem is not very conspicuous. The rib meristem shows linearly arranged cubical cells which are comparatively more vacuolated and less stained than other cells of apical meristem. The maximum diameter of the shoot apex varies from 83 to 93 µ. Its height ranges from 40 to 60 µ.
Grgoire (1938) hypothesized that vegetative and floral apices are not homologous, and irreducible differences exist between the two. Recently the French workers (Plantefol, 1947; Buvat, 1955) have given support to this idea. But many (Philipson, 1947, 1949; Boke, 1947; Rauh and Reznik, 1951; Popham and Chan, 1950, 1952; Reeve, 1943; Wetmore, et al., 1959) have opposed this view and given evidences for gradual and progressive changes of the vegetative apex to a flowering apex in a number of cases.

In the course of the present investigation also histological changes of vegetative apex to floral apex were studied in the case of *Trigonella foenum-graecum* and *Cuminum cyminum*. Certain changes are found in the main apex at the time of flowering. In *Cuminum*, during flowering the main shoot apex is conspicuously semispherical in shape (Fig. 6). Except for the rib meristem all cells of the apical meristem stain uniformly. No other cytohistologic zone is distinct in the shoot apex. The stratification is prominent. The inflorescence
primordia of L1 and L2 leaves (Fig. 6) are well protruded when compared to the vegetative bud of L2 leaf (Fig. 5). Similar observations are reported for *Phlox drummondii* (Miller and Wetmore, 1946). The formation of floral or inflorescence buds in the place of vegetative buds indicates gradual changes in the metabolic activities of the constituent cells. Such changes do not support the contention of Grègoire (1958) that the floral and vegetative apices are non-homologous and are with irreducible differences.

**Origin of axillary bud**

The earliest bud meristem is visible in connection with the second leaf (Figs. 4, 7). It is a deeply stained zone consisting of T1, T2 and two or three corpus layers. The corpus cells are more stained. The delimiting layer, visible at times, is a zone of long, vacuolated cambium-like cells (Fig. 7). When a few of the peripheral meristem cells adjacent to the bud meristem vacuolate, the bud appears detached. The origin of
the cambium-like cells is from this differentiated meristem. They are more distinct at the region of the bud which is nearer the main apex. The earliest bud meristem is not connected with the vasculature of the axis or of the axillant leaf. In this regard it resembles *Drimys winteri* var. *chilensis* (Gifford, 1951b) and differs from *Syringa* (Garrison, 1949a), *Euptelia* (Garrison, 1949b) and *Solanum tuberosum* (Sussex, 1955).

**Development of the bud before prophyll initiation**

In the beginning the corpus cells of the bud meristem divide in various planes (Fig. 8). The tunica cells undergo anticlinal divisions. The cells of T2 and corpus show greater stainability and frequency of cell divisions. Gradually, the plane of division in corpus becomes predominantly periclinal (Fig. 9). The cells of cambium-like zone elongate more. At this stage the bud meristem is lateral (Figs. 9, 40, 41). The periclinal divisions in the corpus make the bud meristem protrude out (Figs. 10, 42). The cells of tunica
divide anticlinally and keep pace with the bulging bud. The elongation of the cambium-like cells bring about an axillary position for the bud (Figs. 10, 42). More periclinal divisions in the corpus, especially in the third and fourth layers, make the bud meristem prominent (Fig. 11). Anticlinal divisions in the corpus cells also contribute to increase the volume of the bud. Occasionally cells of T2 divide periclinally (Fig. 11). The bud meristem at this stage is eumeristematic.

**Development of the bud during prophyll initiation**

Usually a bud at the fifth or sixth node shows prophyll initiation. Periclinal divisions in a sector of T2 and corpus cells and the procambial differentiation below that sector signify the initiation of prophyll in almost all cases (Figs. 12, 46). Occasionally the precocious development of prophyll trace procambium is also observed (Fig. 16). Only one prophyll is present (Fig. 47) and it is at right angle to the plane of the axillant leaf. The prophyll and the later formed
bud leaves do not differ in structure or morphology. The appearance of cytohistological zonation in the shoot apex of the bud occurs after the emergence of the prophyll (Fig. 13). At this stage, central meristem, peripheral meristem and rib meristem zones are distinct (Fig. 13). Figure 14 and 48 illustrate buds after the formation of prophyll. The bud at this stage is in foliar position. Shah and Rao (1966, unpublished) reported similar disposition of the bud in *Maytenus senegalensis*.

Figure 15 shows an axillary bud that structurally resembles the main shoot apex. The light stained central meristem, the rib meristem and deep stained peripheral meristem are recognized. The initiation of bud leaves, $l_1$ and $l_2$, are due to periclinal divisions in $T_2$. The leaf trace procambial strands are present.

**Primary vascularization of the main apex**

In the main apex all the cells up to 18 $\mu$ from the shoot tip are eumeristematic. At the level
of the first node the procambial strands, LT, of the first leaf, Ll, precocious procambium, PC, for the future leaf, L-l, residual meristem, RE, and cortical ground meristem, GM, are identified. This histogenic development is due to further differentiation of the peripheral meristem of the main apex. The leaf trace procambium appear very distinct because of the vacuolation of surrounding cells (Figs. 23, 24). The differentiation of the procambium is acropetal in the direction of young leaf primordia.

Vascularization of the bud before prophyll initiation

The procambialization of the bud is observed during prophyll initiation. Occasionally a young bud may show precocious presence of prophyll trace procambium (Fig. 16).

Vascularization of the bud during the inception and early growth of the leaf

Interesting features of bud trace development
in dicotyledons have been reported. In *Syringa*, *Betula*, *Bupetelia* (Garrison, 1949a, b) and *Hibiscus cannabinus* (Kundu and Rao, 1955) the bud trace differentiation is acropetal. In *Heracleum* and *Leonurus* (Majumdar and Datta, 1946), it is basipetal. Ramji and Parameswaran (1961) observed the bud trace procambium at the base of the prophylls in *Clerodendron aculeatum* and its further differentiation is acropetal towards the prophyll and basipetal in the direction of axial vasculature. Koch (1893) has recorded similar observations (quoted in Gifford, 1951b). In *Drimys winteri* var. *chilensis* (Gifford, 1951b) the procambium differentiates basipetally from the bud and meets with the acropetally differentiating procambium from the axis.

In *Cuminum* only one bud trace is formed at first. More bud traces are differentiated in the further development. Their number may vary from 4-6 (Figs. 30-35). Each bud trace may branch, and in association with other bud traces and their branches, enter the prophyll or other bud leaves (Figs. 30-35).
There is much variation in the early development of the vascular system of the bud in *Cuminum* (Figs. 30-32). But the histogenetic development of the bud trace connection that is developed between the bud meristem and the axillant leaf trace is similar in all cases. It is described below.

Based on development the vascular connection between the bud and the axillant leaf traces in *Cuminum* is considered to consist of two parts. The first visible part is the one differentiating basipetally from the bud meristem downward. The second part develops acropetally from axillant leaf trace by dedifferentiation and redifferentiation of ground meristem cells below the bud. For convenience of description, the basipetally differentiating procambial strand of bud is termed 'basipetal strand' and the acropetally differentiating one, as the 'acropetal strand'. The second type of procambial strand differentiates as a branch of the axillant leaf trace in acropetal direction toward the bud. The latter meets with the basipetally differentiating procambial strand from the bud and
establishes the bud trace connection. After this histogenic development of the bud trace, its further differentiation is in acropetal order in the developing bud, and in that process it may branch in various manners as illustrated in figures 30-35.

Figures 1/-22, 36-38 and 43-45 illustrate the various developmental aspects of the first vascular connection between the bud and the axillant leaf. In the corpus of the bud meristem the procambial strand differentiates first. Its differentiation below is basipetal (Fig. 17). The part of the procambial strand, pr, is formed by basipetal differentiation (Fig. 17). This is evidenced by the fact that two procambial cells in each of the three rows are found nearer the bud apex and below them the procambial strand tapers to a single-celled row. The basipetal differentiation of the procambial strand continues downward by redifferentiation and dedifferentiation of ground meristem cells below the bud. These cells, dp, are longer and more vacuolated compared to procambial cells, pr, differentiated from the bud
meristem (Figs. 16-18). Figure 18 also shows a procambial strand differentiated basipetally. The procambial cells, pt, related to the first leaf are observed at this stage (Fig. 17). No procambial cells are found below it.

The basipetal strand takes an oblique course in its further differentiation below (Figs. 19, 20, 43, 44). The origin and course of the acropetal strand from the axillant leaf trace, LT, is illustrated in figures 20-22 and 45. It differentiates as a branch of the leaf trace, LT, by dedifferentiation and redifferentiation of ground meristem cells (Fig. 20). Figure 21 is another section of the same bud showing the relation of the acropetal strand, as, with the another procambial strand AV. The basipetal strand, bs, the acropetal strand, as, and a few ground meristem cells, x, which are yet to undergo dedifferentiation and redifferentiation are shown in figure 22.

When a complete histological continuity
between the basipetal and acropetal strands is established the bud trace is considered to be fully developed. Further development of the trace in the bud is acropetal.

Thus, Cuminum is different from many other plants in having one bud trace at first, and having 4-6 bud traces later. They establish direct vascular connections between the axillant leaf and the bud. Each bud trace connection between the axillant leaf and the bud is formed by a twin process of acropetal and basipetal differentiation as described in the previous paragraph. Once the bud traces are completely formed, their further differentiation into the bud and its leaves takes place in an acropetal order.

**Vascular relationship of a well developed bud**

The bud with a prophyll and one or more leaves is considered as well developed. Figures 25-29 are transections of a bud with a prophyll and a leaf. They represent sections from the base of
the bud upward. There are four bud traces, one each from each lateral leaf trace, LT, and two from the median leaf trace, MT (Figs. 25-27, 49, bt₁, bt₂, bt₃, bt₄). The origin of the bud trace, bt₁, from the lateral leaf trace is not shown in the figures 25 and 49, but it is similar to the origin of bt₂. But the trace bt₁ is related to the prophyll and is associated with the next leaf of the bud. At the base of the bud, the bifurcated bud traces, bt₁ and bt₂, the median traces, bt₃ and bt₄ and the residual meristem formed by the bud constitute a ring-shaped configuration of vascular meristem (Figs. 25-27, 49-54). At higher levels of the bud, the procambial continuity of the bud trace is maintained by differentiation of residual meristem and peripheral meristem of the bud, thus forming an anastomosing vascular system. At this level, the transverse section shows procambial strands related to the prophyll (mp, median prophyll trace; lp, lateral prophyll trace), and the procambial strands of the first leaf (mt, median leaf trace; lt, lateral leaf trace) (Figs. 28, 29, 55, 56).
Pattern of bud vascularization

During the vegetative period of growth trilacunar nodes are observed, but the nodes produced at the time of flowering are tetra- or pentalacunar in one and the same plant. Very occasionally only four leaf traces are found with one of the laterals giving rise to a branch after entering the leaf (Figs. 36, 38, 39). The above mentioned variations of leaf trace patterns contribute to different types of vascular relationship of the bud.

Figure 30 illustrates the vascular relationship of a bud in a trilacunar node. The median leaf trace, MT, and the two lateral traces, LT, are associated with the bud. The vascular strands A and B travel horizontally at the base of the bud after their origin from the respective lateral leaf traces. 'A' develops into two strands 'A_1' and 'A_2', and 'B' into 'B_1' and 'B_2'. The strand 'A_2' takes an upward course as the median trace of the prophyll, PL. The strand 'B_2' likewise
becomes the median trace of the first leaf, \( l_1 \). The strands 'A\(_1\)' and 'B\(_1\)' traverse horizontally and meet in the middle of the bud to form a single strand, 'X'. The strand 'X' after taking an upward course in the bud, bifurcates into A3 and B3. The strand A3 becomes one of the lateral prophyll traces and B3 forms the lateral trace of the first leaf, \( l_1 \). The strands C and D derived from the median leaf trace, MT, become the lateral prophyll trace and the lateral leaf trace respectively. The vascular strands A2, A3 and C join together at the base of the three lobes of the prophyll. Similar is the behaviour of the strands B2, B3 and D in the case of the first leaf, \( l_1 \).

Figure 31 is the second pattern of bud vascularization. One of the lateral leaf traces, LT, gives rise to two vascular strands, A and B for the bud. Only one strand, C, develops from the other lateral leaf trace, LT. The strand A develops into A1 and A2 near the apex of the bud. A1 and A2 become lateral traces of prophyll, PL, and the first leaf, \( l_1 \), respectively. The strand B develops
into Bl and B2, Bl forming the median trace of the prophyll and B2 becoming its lateral trace. For the 1\textsubscript{1} leaf of the bud, the strand C forms the median trace, A2 and D the lateral traces. The strand D is derived from the median leaf trace, MT, of the axillant leaf. Further course of the vascular trace is as described earlier.

Figure 32 is the third pattern of vascular relation of a bud connected to a trilacunar node. The vascular strands A and B originate from the two lateral leaf traces. The vascular strands C and D develop from the median leaf trace, MT, of the axillant leaf. The strand A gives rise to A\textsubscript{1} and A\textsubscript{2} which become the median and lateral prophyll traces respectively. Similarly B differentiates into Bl and B2, Bl becoming the median trace of the leaf, l\textsubscript{2}, and B2, its lateral trace. The vascular strand C originating from the median leaf trace, MT, develops into C\textsubscript{1} and C\textsubscript{2}, C\textsubscript{1} forms the lateral leaf trace of the leaf of the bud l and C\textsubscript{2}, a lateral prophyll trace. The course of the vascular strands D\textsubscript{1} and D\textsubscript{2} derived from D is
related to $l_1$ and $l_2$ leaves of the bud. The strand $D_1$ becomes the median trace of $l_1$ while $D_2$ develops into $D_3$ and $D_4$ strands, $D_3$ is a lateral leaf trace of $l_2$ and $D_4$ is a lateral leaf trace of $l_1$.

Figure 33 illustrates the vascular relationship between the bud and the axillant leaf in a pentalacunar node. The vascular strands $A$, $B$, $C$ and $D$ arise, respectively, from the axillant leaf traces, $LT_1$, $LT_2$, $LT_3$ and $LT_4$. The median leaf trace, $MT$, gives rise to two vascular strands $E$ and $F$ for the bud. The strands $A$ and $C$ are lateral traces for the prophyll, $PL$, and the first leaf $l_1$ respectively. The vascular strand $B$ forms $B_1$ and $B_2$, $B_1$ is the median prophyll trace and $B_2$ associates with the strand $E$ derived from the median leaf trace, $MT$. The strand $X_1$ thus formed, becomes a lateral prophyll trace. The developmental pattern of $D_2$ and $F$ in forming $X_2$ is similar to that of $B_2$ and $E$.

Figure 34 illustrates a variation of the vascular relations of bud vasculature found in
connection with pentalacunar condition. The median leaf trace, MT, and the lateral leaf traces, LT1, LT2, LT3 and LT4 have vascular connections with the bud. 'A', 'E' and 'D' arise from lateral leaf traces LT1, LT3 and LT4 respectively for the bud. The median leaf trace, MT, gives rise to a single bud trace strand, 'F'. The strands 'A' and 'B' join to form the median prophyll trace, X. 'C' differentiates into 'Cl' and 'C2', 'Cl' is the lateral prophyll trace. 'C2' and the strand 'D' form 'X2'. The vascular strand 'X2' forms 'X3' and 'X4'; 'X3' is a lateral prophyll trace and 'X4', the lateral trace of leaf, l1. The strand 'E' forms 'El' and 'E2'; 'El' is a median trace of leaf, l1, and 'E2' with 'F' derived from the median trace, MT, form a lateral leaf trace, 'X5', for l1.

Figure 35 illustrates the bud vascular relationship in a tetralacunar node. The bud traces arise from median axillant leaf trace, MT, and the three lateral leaf traces, LT1, LT2 and LT3. The lateral leaf trace, LT3, later branches into LT3', thus giving an appearance of a
penta-trace condition. The vascular strand 'A' travels horizontally, then takes an upward course in the bud and develops into 'A1' and 'A2'. 'A1' forms the lateral prophyll trace and 'A2', the lateral leaf trace for the leaf of the bud, l₁. 'B1' and 'B2' arise from 'B'. 'B2' is a median prophyll trace and 'B1' with 'D' from the median leaf trace forms 'X₁', a lateral trace for the prophyll. The vascular strands 'C1' and 'C2' arise from 'C'. 'C2' is the median leaf trace of l₁. 'C1' with 'E' from the median leaf trace MT, forms 'X₂', a lateral trace of l₁ leaf.

Patterns of bud vasculature and homology between vegetative and inflorescence buds

In Cuminum, during the vegetative period of growth trilacunar nodes are observed, but the nodes differentiated at the time of flowering are tetra- or pentalacunar in one and the same plant. Figures 30-35 illustrate variations in the vascular relationship of vegetative and inflorescence buds, which are related respectively to trilacunar and
tetra- or pentalacunar nodes. The following points emerge from this aspect of the investigation:

i. If we take the number of bud traces related to each leaf trace as the criterion, the varying vasculatures of the bud can be typified into certain categories.

ii. Thus, the buds related to the trilacunar condition as illustrated in figures 30 and 32 belong to one category. In both each lateral leaf trace gives rise to one bud trace only, the median leaf trace forms two bud traces (Figs. 30, 32; A, B, C, D).

iii. The bud represented in figure 31 is also of a trilacunar node but belongs to another category, for here it is one of the lateral leaf traces that produces two bud traces, whereas the median as well as the second lateral leaf trace gives rise to one bud trace only in each case.

iv. In the case of tetra- or pentalacunar nodes, the buds represented in figures 33 and 35 are of one type, because both have one bud
trace from a lateral leaf trace and two bud traces from the median leaf trace.

v. The vascular interrelationship between the five leaf traces and the bud as in figure 34 is of a different category from the above. Here it is one of the lateral leaf traces which is associated with two main bud traces. The median leaf trace and the other lateral leaf trace have only one bud trace each.

vi. In *Cuminum* we can expect the same plant to show the vascular interrelationship shown in figures 30 and 32 at vegetative period, and the vascular interrelationship illustrated in figures 33 and 35 in the buds produced during flowering time. Or, the plant having vasculature of figure 31 type during vegetative period may have buds having vasculature of figure 34 type at the flowering time.

vii. These observations show that there is basic similarity between vegetative and inflorescence buds. It lends support to the fact that the vegetative and floral (in this
case inflorescence) apices are not having 'irreducible differences', nor they are nonhomologous.

Vascular interrelationship in young shoot

Nine to sixteen primary vascular strands are found in the axis of *Cuminum cyminum*. In the internode usually larger bundles of outer ring alternate with smaller ones of the inner ring. An internode with ten primary vascular strands is illustrated in figures 36 and 37. Figure 37 represents the schematic pattern of the primary vascular system on one plane. Of the larger outer strands 1, 3 and 5 are the leaf traces or complexes for the leaf at the fourth node, N4. The strand 1 gives rise to a branch 1A before entering the leaf. The smaller strands 2 and 4 alternating the leaf traces 1, 3 and 5, bifurcate at the nodal level forming 2A, 2B and 4A, 4B. The other traces 6, 7, 8, 9 and 10 along with 1A, 2A, 2B, 4A and 4B restore the original number of the vascular bundles in the next internode. The strand 1A
travels up to the second node, N2, and divides into 1B and 1C; 1B becoming the lateral leaf trace at the first node, N1, and 1C dividing into two at the same level. The strand 2A is one of the lateral leaf traces in the second node, N2. The strand 2B enters the leaf of the first node as its lateral leaf trace. The course of the strand 4A in the first node, N1, is similar to that of 4 in the fourth node, N4. 4B becomes a lateral leaf trace in the third node, N3. It gives rise to 4C before entering the leaf; 4C on its turn enters the leaf of the first node, N1, as its lateral trace. The vascular strand 6 bifurcates into 6A and 6B in the third node, N3; similar is the branching of the strand 8 into 8A and 8B. But 8A becomes the lateral leaf trace in the second node, N2. 8E arises from 8A before it enters the leaf. The strand 8B bifurcates at the second node, N2, into 8C and 8D. The vascular strands 7 and 9 form the median and lateral leaf traces in the third node, N3. The strand 10 becomes the median trace of the leaf at the second node.
Figure 38 illustrates a five leaf trace condition. The alternating smaller strands are not shown in the diagram. In some cases only four traces enter the leaf, but one of the laterals branches later (Fig. 39).