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CAULIFLORY IN *FICUS HISPIDA* LINN.[1]

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ABSTRACT

In *Ficus hispida* every leaf has one large primary axillary bud with which are associated 2-7 secondary and tertiary axillary buds. A few primary axillary buds on current shoots quickly develop into lateral branches but most of them become dormant for one or more sesaons. In next season usually many such dormant buds become active and on a node each of them form one cauliflorous shoot which bears syconia. However, the secondary and tertiary buds behave in various ways: (i) a few of them quickly develop into axillary syconia, (ii) most of them remain dormant and later may develop into nodal syconia, (iii) a few may form weak primary cauliflorous shoots in the neighbourhood of an old cuali-florous or a foliar shoot and, (iv) one or two buds, if they are there, on sudden death of a young primary cauliflorous shoot immediately replace it.

As a node becomes old and the primary buds are under constant utilization, there starts *de novo* production of endogenous buds and some of their leaders develop into secondary cauliflorous shoots opening new 'fertile fields' which in course of time form large 'fertile regions'. Thus the cauliflory of *Ficus hispida* is fundamentally similar to that of *Ficus glomerata* (*F. racemosa*) and *F. pomifera*.

Attention has been focussed on some new terms (primary and secondary flowerings and cauliflorous shoots; primary, secondary and tertiary axillary buds; principal and accessory endogenous buds; fertile fields and fertile regions etc.) which have been proposed in reference to cauliflory and used in this text.

INTRODUCTION

The author (see Pundir, 1972a, b, 1975) has already emphasized the need for a detailed investigation of the little known phenomenon of cauliflory. The cauliflory of two species (*Ficus glomerata* and *F. pomifera*) has already been worked out and that of a third species, *F. hispida* is described here.

F. hispida occurs in outer Himalayan Ranges ascending up to 1200 m and also in other parts of the country. The species is fairly common in the forests of Dehra-dun and is perhaps the best represented among all locally available species of the genus. The foliage afford good fodder, therefore, due to regular chopping by natives most of the plants remain subnormal offering a confusing picture of the flowering and only in highly protected places, one may find trees which appear normal. The foregoing account is based on the observations made on such trees.

MATERIAL AND METHODS

The information on flowering was gathered from a number of trees growing in the city and its neighbourhood, however, most of the material used in this investigation was collected from a few trees growing in protected residential area

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of Dehradun, Dehra Dun. The material was killed in F.A.A., dehydrated in T.B.A. series (Johansen, 1940) and was embedded in paraffin wax. 10-20 µ thick sections obtained on a rotary microtome were stained in safranin and fast green and haematoxylin-fastgreen combinations.

OBSERVATIONS

F. hispida is commonly a small tree or a shrub with usually opposite leaves and bears inflorescences (syconia or receptacles) on persistent leafless, stout and branched branches termed here as the 'cauliflorous shoots' which occur almost on all stem parts of the plant extending from the basal part of the trunk to the young branches up to two years old (Figs. 31-36). Although on the latter they are small (Fig. 37) but with the increasing age of the branch they also become long and thick. However, still younger branches may also bear inflorescences (syconia) which instead of developing on a cauliflorous shoot rather develop directly on the branches near the scars of recently fallen leaves or in the axil of an old leaf but this is not of very common occurrence.

All cauliflorous shoots develop in old axillary positions on the nodes which were well marked even on the trunks (Figs. 32, 34). Thus each old node, as it bore in the past opposite leaves, has two flowering regions which remain quite distinct for long and only in basal portion of the trunk of old trees, due to injuries etc., their identity may be lost.

Each 'flowering region' on the trunk and thick branches generally bears more than one cauliflorous shoots and the number may go as high as eight (Figs. 31, 32). With continued production of cauliflorous shoots and the replacement of the old by new ones, the 'fertile regions' became more protruded structures appearing as big tumours. But in very old trees after remaining fertile for long, a 'fertile region' slowly and slowly becomes inactive. At first a few cauliflorous shoots produced from it on withering of the old ones remain small and weak; later on a few syconia directly develop from the tumour and finally the region becomes altogether inactive. It has also been observed that on old trunks and old thick branches the development of the new cauliflorous shoots to some extent is influenced by gravitational force. All nodes on those trunks and the branches which are more or less erect are equally influenced by the gravitational force, therefore, such nodes develop cauliflorous shoots in usual manner. But on those trunks and branches which show steep bending on one side, the nodes which come to lie on the top surface bear hardly any healthy cauliflorous shoots. These shoots first are fewer in number and also remain smaller in size. On the other hand, the nodes which directly face the ground develop most vigorous cauliflorous shoots.

The cauliflorous shoots remain leafless and may or may not bear lateral branches but show usual secondary growth and with time become stout measuring 10cm–1m in length. Their nodes may or may not be separated by long internodes but the former in the axil of their scales always develop syconia. Each cauliflorous shoot persists for several years and the correct age could not be recorded. When it becomes old its capacity of flowering is reduced and finally it dries up, withering soon and the stump is sealed with cork.

Furthermore, it is interesting to note that on the basis of the cauliflorous shoots the plants fall in two major categories. (A). In this type, the cauliflorous shoots are stout and short measuring up to 30 cm in length and in a fertile region their number varies from one to many. The internodes are short and the syconia on nodes are so closely appressed that they form a bunch and a cauliflorous shoot becomes almost invisible due to its coverage from all sides by the syconia. It is worth mentioning that up to early April, the syconia attain their full size. Furthermore, the trees bearing them are comparatively quite tall with thick trunk and the bark is lighter in colour (Figs. 33, 34). (B). Trees are smaller in size with dark coloured bark and show profuse branching. The cauliflorous shoots in a fertile region are many, thin and very long sometimes measuring up to one metre. The syconia on nodes of a cauliflorous shoot attain their full size up to early June and they are separated from one another by long internodes sometimes measuring up to 10 cm (Figs. 31, 32).

The leaves and the axillary buds :

The plants generally bear deccussately arranged opposite leaves which are partly or completely shed off in late February and early March. The quiescent terminal buds of all vegetative shoots, generally in early April, regain activity initially producing a few small leaves on the nodes and the internodes separating them remain very short (Fig. 36). But soon large leaves on nodes separated by long internodes develop and this is continued till August-September, when the terminal buds again become quiescent.

The serial longitudinal sections of various nodes (counting from the first visible leaf node to the old abscised leaf regions) examined so far, from all parts of the plant including (i) young seedlings with only unbranched future trunk, (ii) young plants which have yet to flower and (iii) old trees which are flowering far long, showed that all leaf axils bear at least one large bud which receives vascular connection from the parent stele and a variable number of smaller buds which are directly or indirectly related with this rather than the parent node (Figs. 1-18, 38-41). A large bud in any leaf axil is referred as 'primary axillary bud' and the smaller buds developing in the axil of its cataphylls as 'secondary axillary buds' whereas the remaining buds which are associated with the latter rather than the primary axillary bud as the 'tertiary axillary buds' and in this investigation these terms will be used.

In a longitudinal section the primary axillary bud and the petiole lie in a straight line and two to seven secondary and tertiary axillary buds depending upon their number are arranged according to a definite pattern around the primary axillary bud (Figs. 23-28). In majority of cases each primary axillary bud has two secondary axillary buds which are situated laterally on either side of it when viewed from the petiole side (Figs. 6, 10, 15, 17, 18, 23). But the third and fourth secondary axillary buds are not uncommon and lie in the same straight line which passes through the petiole and the primary axillary bud, the former being on the upper side of the primary axillary bud (Figs. 3, 5, 9, 24) whereas the latter lies in between the petiole and the primary axillary bud (Figs. 16, 25, 40). However, the fifth, sixth and seventh buds are tertiary in nature and are not directly related with the primary axillary bud but they rather lie in close associations of the cataphylls of the first, second and third secondary axillary buds respectively (Figs. 3, 9, 10, 26-28).


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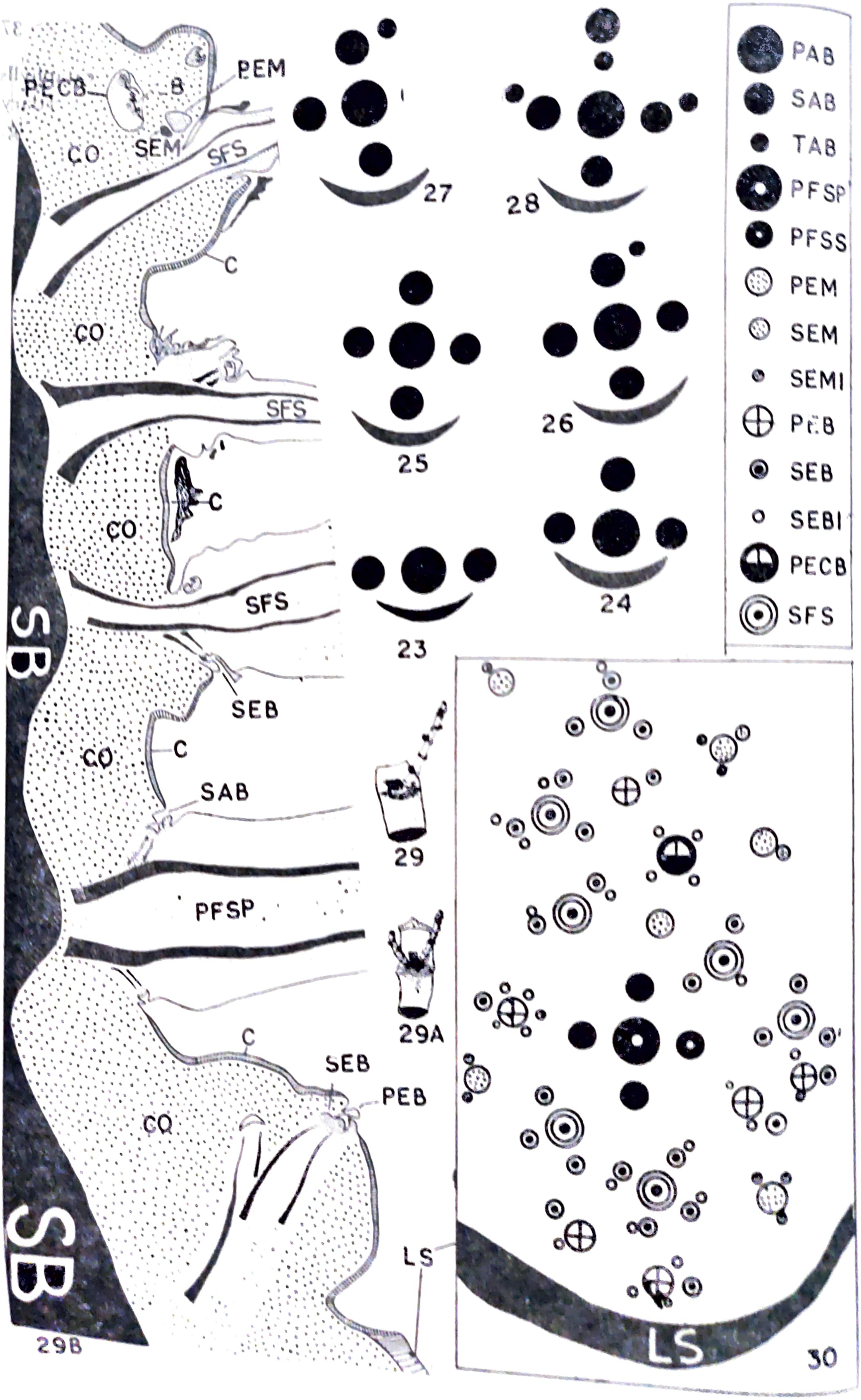
The behaviour of primary, secondary and tertiary axillary buds in young and old plants needs special attention. On young plants of different ages which are yet to flower, the primary axillary buds respond in three ways—(i) on various nodes of young trunks and lateral branches at few places generally before the abscising of the leaves they quickly elongate and develop into foliar shoots (Fig. 9), (ii) a small percentage of them abort leaving their vascular supplies in the bark, later the former also become the important sites of flowering ; (iii) most of them become dormant. In such cases, when nodes from regions where the secondary growth changes have begun, were examined, revealed that the axillary buds did not show any growth in their length nor any increase in the number of foliar structures. At nodes down below, from where the leaves had fallen off and the leaf scars were covered with a few layers of cork, the axillary buds showed some of its outer most cataphylls dying off and secondary and tertiary buds becoming surrounded by cork (Fig. 4). Further down below, the primary axillary buds have lost their some more cataphylls and appeared to be lying in pits surrounded by cork which becomes thickened with time. These buds remain dormant for variable periods depending upon their positions on various nodes of the trunk and branches. Thus the axillary buds on the basal portion of the trunk of an unflowering tree, are those buds which were produced long back when the plant was emerging from a seed and in several years a rapid increase in thickness due to secondary growth in surrounding area makes the buds more deep seated which show the longest dormancy periods extending up to seven or more years than those dormant buds located on the branches (Figs. 5, 6).

The primary, secondary and tertiary buds on young branches of old trees also

Figs. 1—22. Fig. 1. Median longitudinal section of a primary axillary bud in the axil of a leaf of an unbranched young trunk before the start of flowering. Fig. 2. M. L. S. of a primary axillary bud in the axil of 14th leaf (just above the scar of first fallen leaf) of the same trunk. Fig. 3. L. S. of secondary and tertiary axillary buds (marked 2, 3 respectively) of the primary axillary bud shown in fig. 2. Fig. 4. M. L. S. of a primary axillary bud situated on the trunk from the region where secondary growth has started. Fig. 5. L. S. passing through a primary axillary bud and its secondary axillary bud (marked as 1, 2 respectively) situated on the basal node of the trunk of an unflowering tree. Note down that the buds lie in deep pits. Fig. 6. L. S. of a laterally situated secondary axillary bud of the primary axillary bud shown in fig. 5. Note down almost coverage of the bud by cork. Fig. 7. L. S. of a primary axillary bud situated in the axil of a leaf of the first visible node of the branch of an old flowering tree. Fig. 8. L. S. of a primary axillary bud of third visible leaf node. Note down many cataphylls surrounding the apex. Fig. 9. L. S. passing through a primary axillary bud of 4th leaf node, developing into a foliar shoot (FOS). Note the positions of secondary and tertiary axillary buds marked 2, 3 respectively. Figs. 10, 11. Secondary and tertiary (marked 2, 3 respectively in fig. 10) of a primary axillary bud (marked 1 in fig. 11) situated on the 9th node from where the leaf has fallen and the buds lie in a depression. Figs. 12, 13. Primary axillary buds of both leaves of 10th leaf fallen node. Note down that the bud in fig. 12 is more deep seated than that in fig. 13. Figs. 14, 15. L. S. of a primary axillary bud (fig. 14) and secondary axillary bud located on 11th node. Here the buds are more deep seated than those on previous nodes. Figs. 16-18. L. S. of primary axillary bud (marked as 1 and one of its secondary bud of petiole side marked 2 in fig. 16) and its both lateral secondary axillary buds (shown in figs. 17, 18) situated just above the flowering node. Figs. 19, 20. L. S. of cauliflorous shoots of both fertile regions on first flowering node of a branch. Note down that one shoot is more than 6 mm long while the other is just coming up from a dormant bud. Figs. 21, 22. L. S. of cauliflorous shoots (left 1.5 cm and right 0.5 mm long) of both fertile regions of the 14th node. Note down unequal size of the shoots.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behave in aforesaid manner, viz. may develop into foliar shoots (Fig. 9) or abort but most of them pass through a dormancy period which in contrast to that for the buds on trunk is highly variable extending from one season to several years (Figs. 7-18, 39-41). A majority of the buds fall under short dormancy periods and the apex of a primary axillary bud with its few innermost cataphylls although lies in a depression but it hardly loses one or two of its outer most cataphylls and some parts of the remaining ones always protrude above the surface of the node (Figs. 14, 16, 39). However, in long dormancy cases which are fewer, a primary axillary bud in course of time certainly loses some of its outer most cataphylls and all such dormant buds are almost as deep seated as those on the trunk and the thick branches.

However, the secondary and tertiary axillary buds regardless of the fate of their primary axillary buds situated on the trunk or branches of the unflowering or old flowering trees, in almost all cases become dormant for at least two years and are quite deep seated being surrounded with cork which thickens with time (Figs. 3, 5, 6, 9, 10, 15, 17, 18, 40, 41). But a small percentage of them on nodes of young or old flowering trees, do not show long dormancy periods and develop in various ways which shall be detailed with flowering.

It is noteworthy that regardless of their position on various parts of young and old trees, the dormant primary axillary buds of both sides on a node are generally seated at unequal depths in the bark i.e. the primary axillary bud of one side lies at a higher level and that of the other occupies lower footing (Figs. 12, 13) and the same is true for their secondary and tertiary axillary buds. Furthermore, this difference is directly related with flowering.

Flowering :

In *F. hispida*, two types in flowering have been recognized. In first, the cauliflorous shoots and direct nodal inflorescences develop from primary, secondary and tertiary axillary buds whereas in second type they all are the product of the newly differentiated endogenous meristems and buds. These types have been referred as 'primary and secondary flowerings' respectively.

Primary flowering :

The flowering is usually first initiated when the tree becomes 4-6 years old, depending mostly on the environmental conditions. In healthy localities which are protected and are little shady with humid and rich humous soil, the plants are broad leaved, rarely show a complete leaf fall and appear more or less evergreen. However, those growing under xeric and poor soil conditions remain stunted with short leaves which are completely shed off in February-March. The plant growing under former climatic conditions flower quite early whereas those of latter localities flower quite late, some of them flowering even after six years.

On young plants the first inflorescences (syconia or receptacles) develop directly

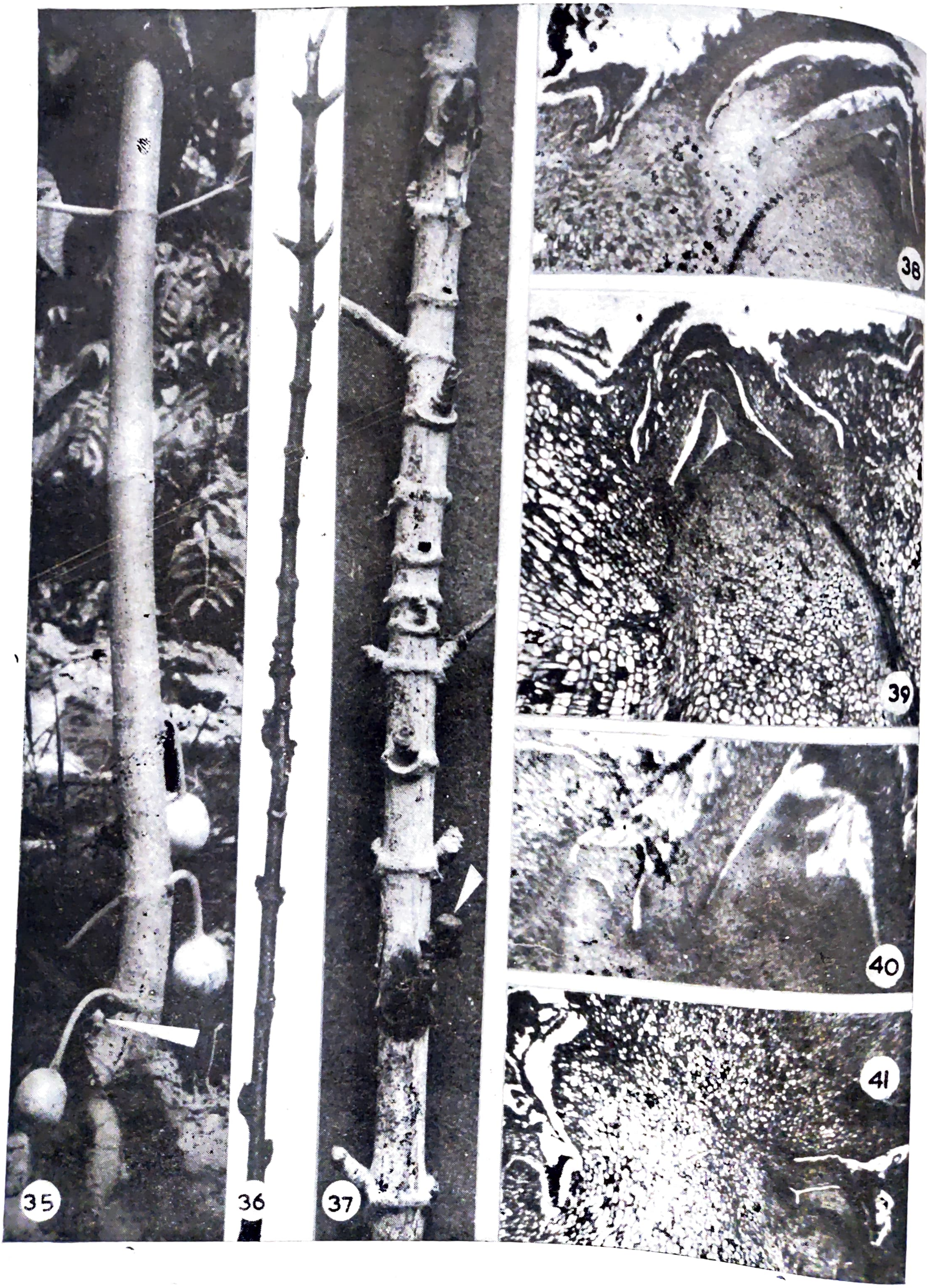
Figs. 23—30. Figs. 23-28. Primary axillary bud and its secondary and tertiary axillary buds on different nodes showing the various arrangements of the latter around the former. Fig. 29. A cauliflorous shoot developed from a secondary axillary bud on a young node immediately after the death of the first which was formed by a primary axillary bud. Fig. 29A. Two cauliflorous shoots developing from two secondary axillary buds on a young node immediately after the death of first formed by a primary axillary bud. Fig. 29B. See explanation of the fig. in the text. Fig. 30. Explanation of the fig. with the text.

on one or two nodes of the basal portion of the trunk and each such node hardly bears more than one syconia (Fig. 35). These syconia in contrast to those developing on cauliflorous shoots are with very long stalks each measuring more than 5 cm in length and the body of the syconium is also bigger in size hanging freely downwards (Fig. 35). However, in next season a few and subsequently more and more upper nodes also start producing inflorescences (syconia). All such direct inflorescences develop in old axillary positions from secondary and rarely tertiary axillary buds which became dormant long back and now have started producing inflorescences. But at the same time on lower flowering portions of the trunk, the direct nodal inflorescences (syconia) are replaced by a cauliflorous shoot which develop singly on a node and later bears many syconia (Fig. 35). Such a cauliflorous shoot develops from a dormant primary axillary bud and its secondary and tertiary axillary buds which are not utilized in the formation of direct nodal inflorescences may still be seen in the bark (Fig. 29B). But in the absence of a primary axillary bud which had aborted earlier or died due to injuries etc., the largest secondary bud in the region forms the cauliflorous shoot. The primary cauliflorous shoot regardless of its origin, i.e. whether developed from a primary or secondary axillary bud, dominates the area and when it is well established the second cauliflorous shoot develops in its neighbourhood whose development will be detailed in the foregoing account.

With increasing age of the plant more and more cauliflorous shoots continue to develop vigorously in acropetal progression in old axillary position in aforesaid manner and this proceeds up the branches until, in the mature trees most of the old nodes become fertile with cauliflorous shoots of various ages and many twigs may also start bearing inflorescences (syconia) directly on the nodes of just fallen leaves or even in the axils of a few of their leaves. All such direct nodal inflorescences are again the product of secondary axillary buds.

When mature trees were examined they showed that the primary axillary buds on current shoots at few places quickly elongate and develop into foliar shoots (Figs. 8, 9, 41) or may abort. But remaining buds become dormant mostly for one or more years and are reserved for flowering in next year. A primary axillary bud on previous year shoot, in normal cases after a dormancy of 6-9 months, but individual cases are on record in which the period may be of several years, is activated producing cataphylls on its nodes which are separated by extremely small internodes. Thus a small stout tubercle like structure measuring 1-2.5 cm is formed (Figs. 36, 37) which in majority of cases at first in the axils of its few scales may develop syconia which abort before reaching a diameter of 5 mm. Thus subsequent internodes of this shoot are elongated and the nodes separating them develop fertile syconia thus a small primary cauliflorous shoot is produced (Fig. 37). But in many cases the short tuberculate shoot remains as such for some time and only in next season develops the long internodes which make the nodes distinct and in the axils of the latter's scales the fertile syconia develop. The young primary cauliflorous shoot rapidly elongates producing nodal inflorescences and at places may give rise to the lateral branches which bear the inflorescences like the former and in course of time the cauliflorous shoot becomes a stout and long structure (Figs. 31-34).

Figs. 31—34. Figs. 31, 32. Photographs showing the arrangement of cauliflorous shoots in fertile regions on the trunk (fig. 31) and the branches (fig. 32) in type two. Figs. 33, 34. Cauliflorous shoots in fertile regions on the trunk (fig. 33) and the branches (fig. 34) in type one.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It is worth mentioning here that both the dormant primary axillary buds on a node (as each node has two opposite leaves) in many cases may not be activated in the same season. However, the primary axillary bud which lies at a higher footing first grows vigorously and the other slowly. Thus the cauliflorous shoots formed from these buds also differ in size in the beginning but later this difference is lost and two independent 'fertile regions' are formed (Figs. 19-22, 36, 37). In majority of cases the secondary and tertiary axillary buds on nodes regardless the fate of their primary axillary bud (whether it has developed into a foliar shoot or aborted or became dormant) behave in various ways. At places they quickly develop into direct nodal inflorescences even in the axils of old unabscised leaves or may remain dormant for many years on the branches and come to lie in pits. In cases in which a primary axillary bud has developed into a primary cauliflorous shoot and when the latter is well established in two years, then only a dormant axillary bud may be activated producing a second cauliflorous shoot andt this may be followed by the addition of the others in coming years till the reserve stock of these buds is exhausted. But these cauliflorous shoots under the dominance of the first always remain quite weak and thin producing few inflorescences in a year and rarely show lateral branching and also wither earlier than those cauliflorous shoots which are produced by the primary axillary buds. Furthermore, it also happens in nature that these buds instead of all developing in to cauliflorous shoots, a few of them produce cauliflorous shoots and the other form direct nodal inflorescences or none of them forms a cauliflorous shoot but all of them develop into direct nodal inflorescences at variable long intervals. But cases are not uncommon in which the secondary and tertiary buds do not develop further and remain dormant till the primary shoot produced by the primary axillary bud is there on the branch for many years and only after its withering these buds are activated and develop in any of the aforesaid ways.

Similarly at many places when a foliar shoot developed from a primary axillary bud is generally 3-5 years old, its dormant secondary axillary buds on the parent node supporting the shoot, are activated and in majority of cases in course of time which may be several years develop into weak primary cauliflorous shoots which

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Figs. 35—41. Fig. 35. Basal portion of the trunk of a young plant which has just started flowering ; note the syconia directly developing on nodes and on extreme basal node a very small cauliflorous shoot is coming up (shown by arrow). Fig. 36. Shows first 20 nodes of a young twig ; first 13 nodes are formed in current season and are without tubercles, however, lower nodes, 14th downwards, have become fertile bearing tubercles. Fig. 37. Shows developing cauliflorous shoots on the nodes of the lower portion of the same twig shown in fig. 36. Fig. 38. Explanation is same as for fig. 1. Fig. 39. L. S. of a primary axillary bud situated just above the flowering node. Fig. 40. L. S. of a primary and one of its secondary axillary bud, the latter is lying in between the former and the petiole. Fig. 41. Explanation is same as for fig. 9.

(C, cork ; CO, cortex ; FOS, foliar shoot ; LS, leaf scar ; P, petiole ; PAB, primary axillary bud ; PEB, principal endogenous bud ; PECB, principal endogenous compound bud ; PEM, principal endogenous meristem ; PFSP, primary flowering shoot formed by a primary axillary bud ; PFSS, primary flowering shoot formed by a secondary axillary bud ; SAB, secondary axillary bud ; SB, stele of the branch ; SEB, subordinate endogenous bud ; SEBI, subordinate endogenous bud of second order ; SEM, subordinate endogenous meristem ; SEMI, subordinate meristem of second order ; SFS, secondary flowering shoot ; SYB, syconial bud ; TAB, tertiary axillary bud) hang freely downwards and appear as directly developing from the base of the foliar shoot or may develop into nodal inflorescences or both.

On flowering twigs, when the sites of those primary axillary buds which have aborted earlier leaving their vascular supplies and commonly a few secondary and tertiary axillary buds on the nodes ; were examined showed that they were still flowerless and only when the node became 3-4 years old these buds were activated producing primary cauliflorous shoots and the direct nodal inflorescences (syconia).

However, it is worth mentioning here that in cases when a cauliflorous shoot produced from the primary axillary bud died, even when it is hardly a few cm. long, due to external injuries or other physiological conditions not known at present or is chopped off, one or two secondary axillary buds without the consideration of age of the supporting node quickly produced another cauliflorous shoot/s to replace the former (Figs. 29, 29A). On the other hand, it is striking that when a primary axillary bud developing into a foliar shoot or a well established tender foliar shoot, one year or a little more old, was removed from the base (as such shoots are usually chopped off for fodder) immediately a secondary axillary bud became active and rather developing into a cauliflorous shoot produced a second foliar shoot. If this shoot is also removed then another bud produces the third. But up to this time the supporting node becomes more than three years old and if the old conditions again prevail then the buds rather developing into foliar shoots also produce cauliflorous shoots mixed with the former. However, the nature of the participating buds may vary, i.e. if the secondary axillary buds have exhausted then such shoots are the product of new endogenous buds, described in detail with secondary flowering.

Secondary Flowering :

With the utilization of the axillary buds, a fertile region does not become inactive but before the exhaustion of the reserve stock of these buds there starts *de novo* production of endogenous buds which develop in the proximity of the primary cauliflorous shoots and primary dormant buds or a little away from their vicinity. However, in some cases they develop far away from the recognized centres of activity thus establishing their own 'fertile fields'. Furthermore, it is worth mentioning here that at this time the sites of old ephemiral buds on old nodes also become the important regions of active endogenous activity.

The so called bark in *F. hispida* at the time of initiation of the endogenous buds has a few layered cork and phellogen covering the underlying secondary and primary cortex in which the latter constitutes the major bulk and its cells contain large amount of tannins. The phloem is in the form of patches and is traversed by medullary rays. Large number of crystals and laticifers are frequently distributed in all parts of the bark.

Differentiation of new meristems and endogenous buds :

The development of new meristems and endogenous buds is almost similar to that of *Ficus glomerata* and *F. pomifera*, therefore, here only important salient features will be recalled. The meristems of variable sizes that form new buds differentiate at various depths in the parenchymatous cells of the primary cortex and sometimes in the secondary cortex too. Occasionally meristematic patches appear in groups of 2-5 or more, one of them being the largest and the others surround it. The former forms the largest bud and the others produce the smaller buds. The buds here have been referred as 'leader or the principal endogenous bud' and 'subordinate endogenous buds' respectively.

The meristematic mass which is destined to form a principal endogenous bud, first shows a gradual organization of its outermost cells into a continuous layer enclosing the other cells of the group. Thus an apex is formed and on this, a few prophylls in long time are gradually out lined. With this the bud proceeds towards the periphery and the associated smaller meristems, if they are there, also start developing into subordinate buds which in course of time join the principal endogenous bud. However, in some cases smaller meristems associated in extreme proximity of the leader, rather developing into independent subordinate buds, develop as the lateral buds of the leader but falsely appear as the axillary buds of the leader. Such a complex association of buds is referred here as a 'leader or principal endogenous compound bud'.

As more and more prophylls are outlined with the bud, the peripheral cells of the cortex, phellogen and cork are subjected to a pressure resulting in stretching of the cell walls which later separate producing a narrow passage which continues broadening till the underlying buds are fully exposed.

Vascular connections and new fertile fields :

In most cases meristematic activity was found maximum in an area of approximately 6-9 sq. cm. around the vascular cylinder of an old primary dormant bud, primary cauliflorous shoots and their stumps and ephemiral buds. All the endogenous buds developing from these meristems receive their vascular connections directly or indirectly from these stumps rather than the main stele. As soon as a leader bud is differentiated, it becomes connected with the stele of the stump by procambial strands and many buds developing near to it as its subordinate buds also establish their vascular connections with the supply of the leader bud.

However, besides these, there are many new buds which are more near to the parent stele or are developing far away from the old vascular traces, seem to have little connections with these so far recognized centres of activity. Rather they have their vascular connections, established directly with the parent stele in close neighbourhood of the previous vascular cylinders. Therefore, in course of time this leader bud establishes a new independent 'fertile field' which broadens as more and more new leader and their subordinate buds developing in its proximity establish their vascular connections with its stele rather than the parent stele or the old ones.

The addition of new fertile fields goes on indefinitely, till a 'fertile region' remains active, however, with the advancing age of the fertile region, the fertile fields which have become old and inactive are replaced time to time by new ones. Thus in old regions (Fig. 30) I have counted as many as 20 independent active and inactive fertile fields of various ages, moreover, this fertile region was medium sized, therefore, it appears if still older fertile regions are examined, will certainly show more fertile fields than those recorded here. It is striking that some fertile fields do not develop their independent vascular connections but receive their vascular supplies from the stele of a neighbouring old fertile field which may be active or inactive at this time. Therefore, the number of fertile fields in a fertile region is generally higher than those of the independent vascular connections joining the parent stele. Although in an old fertile region several lateral vascular cylinders join the parent stele in close neighbourhood of one another and a knot like structure to which different cylinders appear to join is formed but in very old fertile regions on the trunk and thick branches the basal portions of the vascular cylinders with continued growth broaden and enlarge and the whole underlying stelar region appears in form of a shallow dome which is covered with bark. At this stage all the new vascular cylinders of the new buds join at various places to this raised structure and the whole fertile region appears like a big tumour.

Initiation of secondary endogenous cauliflorous shoots and direct nodal inflorescences :

It will be recalled here that due to the pressure exerted by the principal endogenous and its subordinate buds, the overlying cortical cells rupture and the buds are exposed to outside appearing as lying in pits. The efurther development and the behaviour of these buds are almost similar to those of the primary and secondary axillary buds dealt in detail in previous pages and suggest that the principal endogenous bud and its subordinate buds are comparable with the primary and secondary axillary buds respectively.

The further development of the endogenous buds is influenced by the existing primary and in old fertile regions by the secondary cauliflorous shoots. Thus a leader bud developing in the proximity of a cauliflorous shoot has to wait for long and only after the withering of the latter it quickly elongates and protrudes above the surface and in course of time forms a 'secondary endogenous cauliflorous shoot'. However, many such buds do not wait and emerge out but under the influence of the cauliflorous shoot fail to develop further and fall off in varying stages of development. It is important to note here that after falling off of the dried buds their scars are covered with fresh cork but their vascular cylinders which are left in the bark become important regions and from these other buds developing in their neighbourhood receive their vascular connections and in course of time, out of these, one leader bud after the withering of the dominating shoot may replace it. On the other hand an old principal endogenous bud which is developing far away from the vicinity of a cauliflorous shoot and has established its own fertile field also, does not wait and protrudes above the bark but it quickly forms a fertile secondary cauliflorous shoot which produces inflorescences. in usual manner. It is noteworthy that this shoot does not inhibit the formation of new endogenous buds in its neighbourhood but usually does not allow them to form cauliflorous shoots. This continued activity of meristems and buds formation in the neighbouring areas of such shoots is helpful in replacing them immediately after their withering. This process of replacement of withering cauliflorous shoots by new ones continues indefinitely till a fertile region remains active.

Fertile regions :

Each fertile region before the commencement of endogenous activity generally measures 4-5 sq cm in area and has only one primary cauliflorous shoot and axillary buds. Later on, as more and more secondary cauliflorous shoots, endogenous buds and meristems are developing in new fertile fields; the region becomes broad and instances are not rare in which some of them occupy an area of approximately 50 sq cm each. Furthermore, in many cases both the fertile regions of a node on old branches continue broadening until a condition prevails in which they touch each other and the whole node appears more or less fertile.

With advancing age a region becomes complex and in serial longitudinal sections passing through old regions of different ages one can find that they are occupied by variable number of cauliflorous shoots and large number of meristems and buds of different ages (Figs. 29B, 30).

Fig. 29B is a reconstruction from serial longitudinal sections of a five years old fertile region. It is worthy to mention that this fertile region was selected at the time when it was young occupying an area of less than 1.0 sq cm and was without any cauliflorous shoot in May, 1970. Later it remained under constant watch up to 10th April, 1975 and on this day, when the bark was removed for sectioning it occupied an area of approximately 9.0 sq cm and bore one primary cauliflorous shoot and three secondary endogenous cauliflorous shoots. But the region in all showed five fertile fields of bud formation and the field numbered as one was of primary cauliflorous shoot and was the oldest one and the field numbered as five was the youngest whose leader bud was approaching the surface. However, orientation of the leader compound bud shown on extreme top of the figure also suggested the possibility of independent fertile field of its own.

However, figure 30 shows a more older fertile region than that shown in figure 29B, its age could not be determined at the time of removing bark. This fertile region was measured 23.5 sq cm in area and with the help of small pieces of bark which were sectioned tangentially, I could count more than 80 in all, the leader meristems (LEM), subordinate meristems (SM), leader endogenous buds (PEB), subordinate endogenous buds (SEB), and 8 primary (PFS) and secondary flowering cauliflorous shoots. However, if still bigger active fertile regions on some protected trunks and thick branches are examined will certainly show more buds and the fertile fields than those reported here.

A fertile region after flowering for long becomes old and slowly and slowly its capacity of flowering is lost. The first sign of this, is evident with very slow growth of the new developing secondary cauliflorous shoots which remain short and bear a few syconia. Later, on their withering other endogenous buds may not produce cauliflorous shoots but generally develop directly into syconia. Although this continues for several years but the number of protruding buds goes on decreasing and in last the region becomes almost inactive. However, time to time one or two abortive buds may be seen in such inactive regions.

On old trunks and also on some lower old thick branches where the chances of injury are more, in a fertile region some buds often develop into weak foliar shoots each with long internodes and smaller leaves which in contrast to those occurring on axillary foliar shoots usually bear syconia in their axils. These shoots sooner or later wither but in many cases one or two of them have been observed changing into cauliflorous shoots and foliar branches which persist for several years on the trunks.

DISCUSSION

In *Ficus hispida*, first flowering is initiated on the trunk and the receptacles directly develop on nodes from dormant secondary and tertiary buds of a primary axillary bud. Later on, there is a gradual shift in flowering until young twigs also start flowering. However, with upward shift in flowering, on lower portions the direct nodal inflorescences on a node are replaced by a cauliflorous shoot developing from a dormant primary axillary bud or in its absence the largest subordinate bud forms it. With the production of the cauliflorous shoots, there starts *de novo* production of endogenous buds which go on producing cauliflorous shoots for indefinite periods establishing many new 'fertile fields' in a 'fertile region'. The old cauliflorous shoots are constantly replaced by new ones.

Thus the cauliflorous state of *F. hispida* is fundamentally similar to that of *Ficus glomerata* and *F. pomifera* (Pundir, 1972a, 75). In all the three species, in young trees which are to flower and in old trees on their young branches, without the consideration of age, which are flowering for the first time, the flowering is initiated by exogenous buds. Thus the first cauliflorous shoot, termed as 'primary cauliflorous shoot', in normal cases is the result of dormant primary axillary bud and the direct nodal inflorescences are the product of secondary and tertiary axillary buds. But in the absence of a primary axillary bud, the largest existing secondary bud forms the primary cauliflorous shoot. The dormancy period for primary and its secondary and tertiary axillary buds, however, is variable in different species. In old trees of *F. glomerata* and *F. pomifera* it is several years whereas in *F. hispida* it is hardly one year. Further, flowering after the utilization of axillary buds, is continued by the endogenous cauliflorous shoots, called here as 'secondary cauliflorous shoots', which develop from newly differentiated endogenous buds.

However, there are some noteworthy differences which deserve some attention. In contrast to the two previously described species (*F. glomerata* and *F. pomifera*) the secondary and tertiary buds in *F. hispida* exhibit more characteristic arrangement pattern and their number is frequently variable on different nodes. Furthermore, *F. hispida* shows an acropetal progression in flowering from base upward until in mature trees young twigs at least one year old also start flowering and this continues in the life time of the plant. However, in *F. glomerata* there is a basipetal shift in flowering from young twigs to the thick branches and the trunk. Shortly after the appearance of the inflorescences on the thick limbs, the former lose the capacity of flower production and the mature trees flower only on more than 3 cm thick portions of the stem.

In *F. hispida* two distinct types have been recognized which are based on morphological variations exhibited by cauliflorous shoots. First type has short and stout cauliflorous shoots with no visible nodes and on them the syconia are closely appressed forming a bunch so that most part of the cauliflorous shoot becomes invisible closely resembling to those of *F. glomerata*. However, in second type the cauliflorous shoots markedly differ from those of the type one and those of *F. glomerata*. They are thin, weak and very long with their nodes separated by distinct long internodes. The receptacles developing on these nodes are far away from one another and the arrangement appears more near to that of *F. cunia*.

Lent (1966) has focussed some attention on the terms which have been used to describe the multiple buds at leaf axils. According to him such terms as 'serial buds' (Troll, 1937), 'accessory buds' (Thompson, 1951) and 'secondary buds' (Garrison, 1955 ; Majumdar and Arshad, 1956) are inappropriate and writes that the accessory bud "denotes the contribution of aid or assistance to some primary object. The term secondary bud has been used variously......but its use should be restricted to the sense in which it was used by Garrison". Therefore, in *Theobroma cacao* he refers the largest bud in the axil as principal axillary bud and other buds which under typical conditions differ in point of origin and in their ultimate development from the former, as subordinate buds. But it appears that the terms accessory and subordinate buds are common language words, which according to Webster's (1971) dictionary, denote almost the same sense, therefore, they may be safely used without entering into any controversy, for any bud which is assisting a large bud differing in origin from the latter.

In the present investigation, the term primary and secondary buds (Garrison, 1955) have been retained with a slight modification. This has been done to avoid confusion as a young fertile region at one stage may contain both exogenous and endogenous buds. Therefore, the largest first formed mature axillary bud and young buds of different ages in the axils of its foliar organs (leaves or cataphylls) have been referred to as 'primary axillary buds' and 'secondary axillary buds' rather than primary and secondary buds, respectively. Whereas, other young buds axillary to a second generation bud as 'tertiary axillary buds' and so on.

On the other hand, usually the largest and first initiated endogenous buds in an area and any other smaller buds developing from different endogenous meristems in its proximity have been termed as 'leader or principal endogenous bud' and 'subordinate endogenous buds' respectively. However, the smaller meristems in close association of the largest meristem, instead of developing into subordinate buds, join the latter and they all may form a large bud which has been called as 'compound bud' by Thompson (1952) in *Couroupita guianensis* and the same has been referred here too with a modification being called as 'leader or principal endogenous compound bud'.

In this investigation, for those cauliflorous plants which first flower from exogenous axillary buds and later by newly differentiated endogenous buds ; new terms 'primary and secondary flowerings' respectively have been proposed. And if the inflorescences or flowers are produced on shoots developing from such buds have been termed as 'primary and secondary cauliflorous shoots' respectively. These terms will be helpful in a clear understanding of the complex heterogenous mode of flowering among many cauliflorous plants.

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