Proceedings of the Iowa Academy of Science

Volume 64 | Annual Issue Article 10

1957

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Recommended Citation

Prior, Paul V. (1957) "Alterations In the Shoot Apex of Petunia hybrida Vilm. at Flowering," *Proceedings of the Iowa Academy of Science, 64(1),* 104-109.

Available at: https://scholarworks.uni.edu/pias/vol64/iss1/10

Alterations In the Shoot Apex of *Petunia hybrida* Vilm. at Flowering

By PAUL V. PRIOR

In the past twenty years a number of morphologists and physiologists have studied the organization and behavior of shoot apices during the vegetative and flowering phases of development. Changes in size and shape as well as alterations in stratification have been reported to occur during each plastochron or interval between the production of leaf primordia (Foster 1939). A number of authors have noted differences in size and shape between vegetative and flowering apices in the same species. Although the literature contains numerous references to studies on vegetative and flowering apices, only casual observations have been made on the possible permanent changes that occur in the apex at the onset of flowering.

In most of the literature the terminal meristem is considered to be unchangeable in position and to produce foliar or floral primordia in an opposite or spiral order on the flanks. *Petunia hybrida* Vilm. in the Solanaceae shows unique developmental changes in the shoot apex at flowering. These changes in apical configuration and method of producing floral primordia are constant and of sufficient difference in pattern of development to seem worthy of report.

The present paper contains a detailed description of the size, shape and zonation of the vegetative and inflorescence apices of *Petunia hybrida.* The dynamics of apical behavior during the production of individual flower primordia is contrasted with apical activity during leaf primordia production. Apical criteria that indicate the onset of flowering are discussed.

METHODS AND MATERIALS

Stem apices of *Petunia hybrida* Vilm. were collected periodically during the vegetative and flowering phases. The tops were immediately killed and fixed in formalin-acetic acid-alcohol solution (FAA). All but the youngest leaf or floral primordia were dissected away and apices were imbedded in paraffin and sectioned at 12 microns. Serial sections were stained in tannic acid and iron alum, safranin and orange G according to the schedule recommended by Sharman (1943). Width and height measurements of the apices in median sections were made using the insertion of the distal primordium as a base line. The leaf buttress was not included in the measurements. The number and size of each kind of apex studied is given in Table 1.

Petunia hybrida Vilm. is a perennial vine in its native tropical habitat although it is cultivated as an annual in the temperate zones. Generally a single stem axis is maintained until after flowering has begun. Leaves are borne alternately and are four ranked during the vegetative phase. The broad low domed stem apex has an average width of 135 microns and height of 22 microns, showing a width/height ratio of 6:1 (fig. 7). Table 1 includes the range of apical size. A triseriate tunica is retained throughout the plastochron and cells of this region average 9 microns wide and 10 microns high. The relatively large biconvex corpus is made up of cells averaging 9 microns wide and 8 microns high.

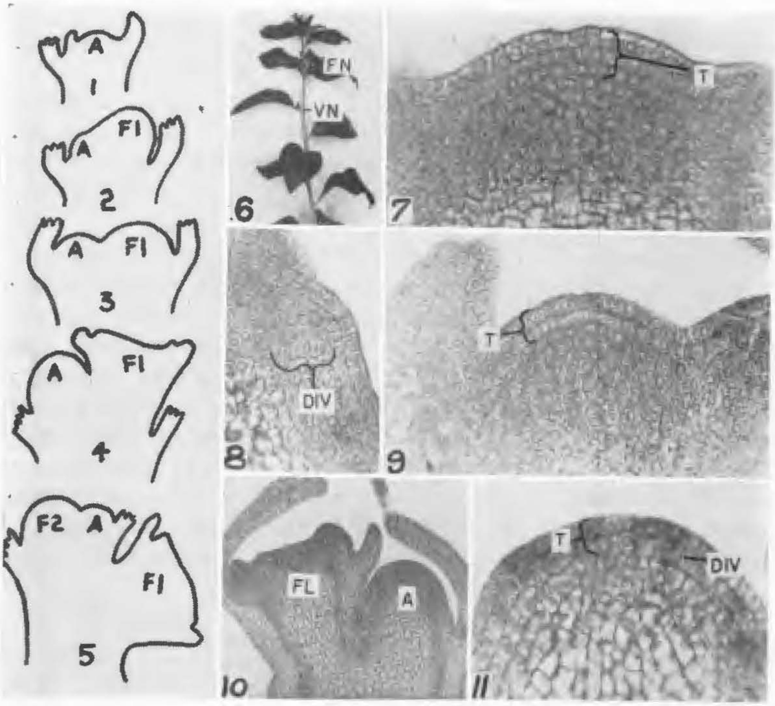
Leaf primordia are initiated by cell divisions in the inner tunica layer followed by meristematic activity to a depth of four or five cells. Eventually even the second tunica layer is involved in leaf production by dividing periclinally. Axillary buds are observable only after two, and in most cases three, leaf primordia have been produced in the vegetative phase. These axillary vegetative buds do not elongate into branches until after flowering has begun. *Petunia hybrida* bears solitary axillary flowers of an indeterminate number; however, flowers are not produced at every node once flowering has started. At the time of floral initiation approximately one-third of the apex shows more vigorous cell division. This region is the new terminal meristem. The remaining two-thirds of the original shoot apex develops rapidly and directly into a flower. Figure 1-5 are a series of camera lucida outlines showing the development of the first flower. All subsequent flowers follow this pattern of development.

Table 1
Summary of Apex Dimensions in Microns

Species	Apex height Avg.	Min.	Max.	Apex width Avg.	Min.	Max.	Width/height ratio	No. of Apices
Petunia hybrida								
Vegetative.....	22	6	28	135	65	155	6:1	28
Inflorescence...	60	32	102	180	118	217	3:1	35

The apex at flowering increases in size to an average width of 180 microns and a height of 60 microns or a width/height ratio of 3:1 (fig. 11). The tunica becomes reduced from three to two layers at transition and is composed of cells averaging 8 microns in width and height (fig. 9). The corpus is a massive region, the cells of which average 9 microns wide and 8 microns high.

Cells in the second tunica layer begin dividing periclinally at the initiation of each flower bud (fig. 11 DIV). Greater meristematic activity of the corpus to a depth of 8-10 cells ultimately produces the new terminal meristem. Every flower on the stem develops directly from the apex and the terminal meristem is renewed by cell division on the flank of the enlarging floral primordium. Figure 10 is a median longisection of the enlarged stem apex and a developing floral primordium.



Figures 1-5. Camera lucida outlines of the shoot apex at transition to flowering.
Figure 6. Photograph of a branch showing the alternate arrangement of leaves at the vegetative nodes (VN), and the opposite leaf arrangement at the flowering node (FN).
Figure 7. The vegetative apex at maximum size. (X450)
Figure 8. An early stage in the production of a leaf. Diverse divisions are initiated in the third tunica layer. (X450)
Figure 9. The shoot apex midway in its development to maximum size. The floral primordium, not shown, is at the right. (X450)
Figure 10. Median longisection of the apex which has regained maximum size and the most recently formed floral primordium being shifted to a lateral position. Note the opposite leaf primordia at this point. (X100)
Figure 11. Enlarged flowering shoot apex. Periclinal divisions in the second tunica layer indicate the beginning of another floral primordium. (X600)
(A—Apex; F1, F2—successive flowers; T—Tunica; VN-Vegetative Node; FN-Flowering Node; DIV—Periclinal divisions.)

A very unusual gross morphological change occurs at each flowering node in that two opposite leaves are produced (fig. 6). Wherever a flower does not occur only one leaf is produced. It would seem that the stem does not elongate during the plastochron in which a floral primordium is produced. The location of an axillary vegetative bud between the flower peduncle and the base of the leaf in the axil of which the flower is borne contrasts with the absence of a like bud in the axil of the leaf on the opposite side at every flowering node. This seems to bear out the interpretation of the renewal of an axis apex at the production of each flower.

DISCUSSION

As a result of many investigations of the shoot apex, particularly in the past thirty years, certain generalizations have been made recently that clearly indicate the plastic nature of this region. Histogenic layers have not been clearly demonstrated and the Tunica-Corpus concept of Schmidt (1924) still remains the most widely used despite the objections of some workers as indicated by Gifford (1954) in his excellent review of work on angiosperm apices. Since, as this study shows, the inflorescence axis elongates through activity of the terminal meristem or its derivatives and the planes of cell division remain essentially the same, there is little need for assigning new names to the zones in an inflorescence apex.

Several workers have observed an increase in size of terminal meristems at the time of flowering, although specific measurements have not been given in many cases (Cooper, 1932; Hubbell, 1934; Laurie and Bobula, 1938; Miller and Wetmore, 1946; Mustard and Lynch, 1946; Chan, 1950; Mills, 1951; Rotor and MacDaniels, 1951; Kasapligil, 1951; Bonnett, 1953; Tepfer, 1953, and Hacskaylo, 1953). Abbe and Phinney (1951) reported an increase in size of the apex of *Zea Mays* by a certain constant progressive amount from plastochron to plastochron. Kasapligil (1951) could find no relationship between growth increment and plastochron stage in two plants with which he worked, *Umbrellularia californica* and *Laurus nobilis.* Further investigation is necessary to clarify this point. The present study does show that there is an average increase in both width and height at the onset of flowering as summarized in Table 1. Even more noteworthy perhaps, is the relatively greater increase in apical height at flowering. The width/height ratio in Table 1 shows the average increase to be twice as great in height as width in *Petunia hybrida.* Since the cells of the tunica and corpus do not change appreciably in size at transition to flowering there must be more cells in those regions resulting from a greater meristematic activity attending transition. That the cell size does not change when the apex increases in size has already been observed in Zea by Abbe, Phinney and Baer (1951), and Millington and Fish (1956).

Miller and Wetmore (1946) reported that the loss of a decussate phyllotaxis was the first indication of a change from vegetative to flowering condition in *Phlox Drummondii.* In the present study the change of phyllotaxis was found to be simultaneous with the change in apical configuration. The alteration is quite striking in *Petunia hybrida* which bears alternate leaves during the vegetative phase and immediately produces opposite leaves when flowering starts (fig. 6). It suggests a further investigation of the physiological or morphogenetic factors involved.

During the vegetative phase of growth, vegetative bud primordia were never found higher than the third leaf axil from the stem tip. Development of the lateral vegetative meristems was generally found to be inhibited until after the first floral primordium was produced.

Whatever physiological inhibition is exercised over lateral meristems during the vegetative phase is lost at the time of flowering. The loss of apical dominance is not only reflected in the development of the lateral buds at transition but in the inflorescence itself. That is, once the floral primordium is initiated there is no cessation of meristematic activity until the flower is formed completely. In *Chrysanthemum morifolium* the loss of apical dominance at flowering was noted and found to proceed in a basipetal direction (Popham and Chan, 1952). This also is true of the species used in this study.

Floral buds are initiated at the same depth in cell layers as strictly foliar appendages, usually the second tunica layer. However, subsequent meristematic activity in the production of a flower can be traced to a depth of seven to ten cells beneath the surface (fig. 9), while in the production of a leaf it reaches a depth of only four to five cells (fig. 8).

There has been some differences of opinion among anatomists with respect to variation in tunica layers during ontogeny. Schuepp (1926) and Priestly (1928) maintained that the number of tunica layers vary rhythmically with the height of the apical dome. More recently Popham and Chan (1950) and Rouffa and Gunkel (1951) could find no correlation between the number of tunica or mantle layers and apical height. The number of layers may vary, however, without invalidating the tunica concept. A consistent variation in number of tunica layers has been observed in *Petunia hybrida* which changes from three tunica layers in the vegetative apex to two layers when flowering begins.

Probably the most striking characteristic of the transition to flowering stage in *Petunia* is the manner in which the stem apex is renewed. That the apex is not merely cutting off floral primordia on its flanks is quite evident. Actually the shoot apex is transformed from a region of indeterminate growth to one of determinate growth, that is the floral primordium. Coincident with this transformation the new shoot apex is initiated by cell divisions on one side which increase in scope and frequency during the subsequent plastochron. As a result the former apical region, now a floral primordium, is pushed into a lateral position.

SUMMARY

The structure and development of vegetative and flowering apices of *Petunia hybrida* have been compared and contrasted in an effort to determine what apical changes take place when this plant initiates flowers. It has been found that an increase in width and height of the apical meristem occurs at transition, that there is an increase in the depth to which cells are involved in the production of the primordium. Phyllotaxis is strikingly modified during transition; and an immediate loss of apical dominance occurs. The characteristic

Proceedings of the Iowa Academy of Science, Vol. 64 [1957], No. 1, Art. 10

change in the number of tunica layers during a plastochron, as well as the permanent change in the number of layers at transition to flowering, is described. Special note is made of the development of a new shoot apex which carries on extension of the main axis during each succeeding plastochron. This new apex replaces that meristem which has gone into a strictly floral condition.

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