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Development of the Helicoid and Scorpioid Cymes in *Myosotis laxa* Lehm. and *Mertensia virginica* L.

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Abstract. The vegetative and inflorescence apices of *Myosotis laxa* and *Mertensia virginica* have been compared and contrasted in order to determine how helicoid and scorpioid cymes differ in development. The apices have been interpreted on the basis of the tunica-corpus theory, since no clear histogenic layers could be determined for these species. The stem apex enlarges and broadens at the onset of flowering, and apical dominance is lost. The number of tunica layers is reduced in both cases, and the enlargement of the apex is found to be due to more, not larger cells. The helicoid cyme of *Myosotis laxa* results from a continuous renewal of meristematic activity on the same side of the apex. The scorpioid cyme of *Mertensia virginica* develops in a stepwise fashion as a result of renewed meristematic activity at ninety degrees from the previous point of growth. Both are sympodial axes.

More than one hundred years ago De Candolle (1827) presented a fairly clear discussion of several types of inflorescences, among them the helicoid and scorpioid types. The majority of recent attempts to categorize inflorescences have been primarily taxonomic in scope and represent only superficial investigations of how these inflorescences originate. Rickett (1944) attempted to explain the origin of the helicoid and scorpioid cymes and gave a rather fragmentary description of their development. He considered the helicoid type a "continuous spiral of flowers" and the "far less common" scorpioid type an "axis that reverses itself" wherever a flower bud is produced.

Because they have been variously described in taxonomic literature and because of their basic similarity in construction, the inflorescences of *Myosotis laxa* Lehm. and *Mertensia virginica* L. provide excellent material for study in their development from vegetative apices to sympodial floral axes. Fernald (1950) described *Myosotis* as bearing "naked racemes," whereas Bailey (1949) called the inflorescence a "terminal raceme." Williams (1937) described the inflorescence of the genus *Mertensia* as a "lax or congested, ebracteate, unilateral, modified scorpioid cyme." Bailey (1949) called them "nodding clusters" and Fernald (1950) referred to them as simply "scorpioid cymes."

Materials and Methods

Vegetative and flowering shoot apices of *Myosotis laxa* were col-

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lected from healthy plants growing in moist soil at the edge of a pond. Apices of *Mertensia virginica* in like condition were collected from plants growing in damp, flood plain soil. The tips were exfoliated, leaving only the youngest leaf primordia, and immediately killed and fixed in formalin-acetic acid-alcohol solution. The material was imbedded in paraffin and sectioned at 12 microns. The apices were stained according to the schedule suggested by Sharman (1943). Only median longisections were used in height and width measurements as well as in determinations of cell size.

Results

Myosotis laxa is a semihydrophytic perennial which produces upright vegetative branches from a procumbent stem. The vegetative apex is a high dome with an average height of 53 microns and a width of 110 microns (Figure 1). During each plastochron both the height and width of the apex increase considerably so that, just before the emergence of a new leaf primordium, the apex is approximately twice the size that it is after the appearance of the leaf. This is due to the fact that the broad leaf base almost completely encircles the stem. Despite the variation, the apex shows an average height to width ratio of 1 to 2 throughout the plastochron. The range of size of the apices studied is given in Table 1.

Table 1
Summary of Apex Dimensions in Microns

	Apex height Av.	Range	Apex width Av.	Range	Height/Width Ratio
Myosotis laxa					
Vegetative	53	33-86	110	81-131	1:2
Inflorescence	60	0-90	125	99-140	1:1.4
Mertensia virginica					
Vegetative	45	35-54	140	128-150	1:3
Inflorescence	53	0-70	141	109-166	1:2

The tunica of the vegetative apex varies from two to three layers; however, there is no clearcut evidence of a relationship between the number of layers in the tunica and the size of the apex. Tunica cells average 7 microns wide and 8 microns in each layer. The corpus is a strongly convex group of heavily staining cells averaging 8 microns in both width and height.

Leaf primordia are initiated by periclinal divisions in the innermost tunica layer followed by rapid cell division in various planes of the outermost corpus cells. Axillary buds are first apparent as heavily staining groups of cells or surface swellings usually at the third node from the tip, never closer.

At the beginning of floral initiation there is a complete cessation of leaf or bract formation. The inflorescence that develops on this

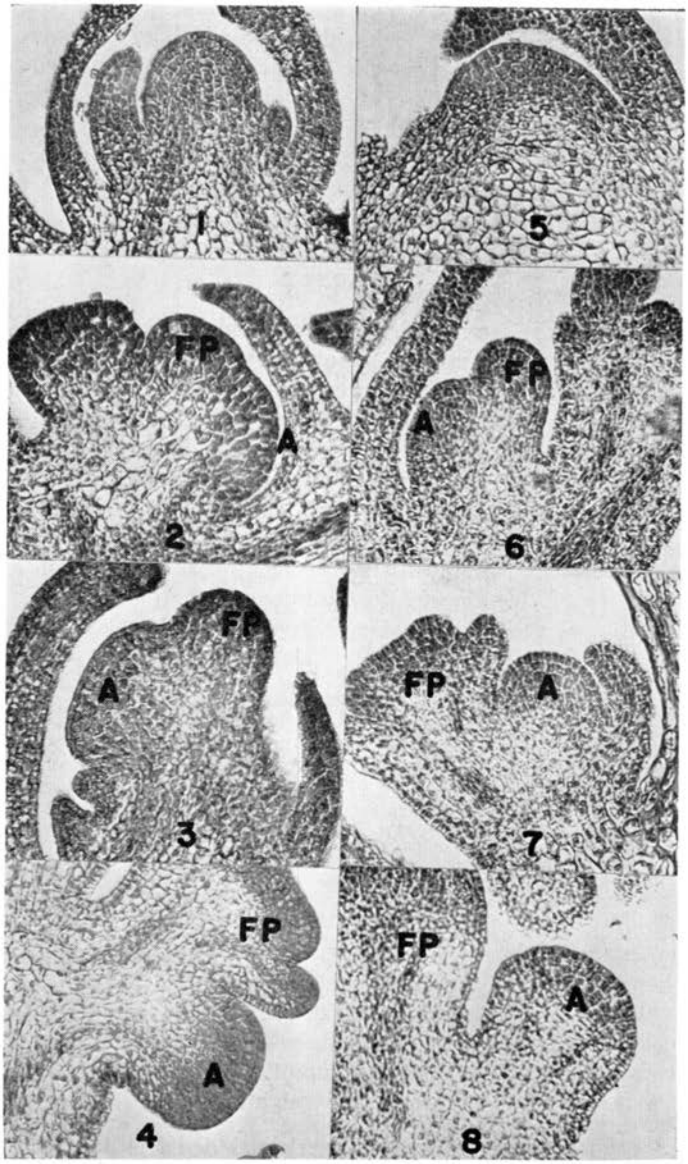

Figure 1. Vegetative apex of *Myosotis laxa*.
Figures 2, 3 and 4. Successive stages in the production of a flower bud in *M. laxa*. (A—inflorescence apex; FP—floral primordium.)
Figure 5. Vegetative apex of *Mertensia virginica*.
Figures 6, 7 and 8. Successive stages in the production of a flower bud in *M. virginica*. (A—inflorescence apex; FP—floral primordium.)

plant is the result of a shift from the production of alternate, five-ranked leaf primordia and axillary buds to the development of strictly single-ranked floral primordia. The first clear indication of the onset of flowering is a rapid increase in the height of the terminal meristem to approximately twice that of the vegetative apex. A concomitant increase in width is only half as great, even in the largest apices studied. Immediately following the rapid upthrust of the apex a notch develops, centrally located, that seems to bisect the whole tip. The notch is the result of the devlopment of two rapidly growing meristematic regions. The one which is terminal develops directly into a flower. The other, which is lateral, continues elongation of the main axis in a sympodial fashion. Each flower in the inflorescence arises in the same way. Figures 2, 3, and 4 show the stages in production of a single flower in the inflorescence. Inasmuch as the increased meristematic activity leading to the extension of the main axis is always directly opposite the previously formed flower bud, a one-sided inflorescence results.

The tunica of the inflorescence apex varies from one layer at minimum size to two layers at maximum size. The average cell size is the same as in vegetative apices; however, the corpus cells are about one micron higher.

The sympodial nature of the inflorescence apex, that is the termination of the growth of the axis by a flower bud and the production of a new meristem in a lateral position, is readily apparent in this species.

Mertensia virginica is an herbaceous perennial which bears alternate leaves on a shortened stem during the vegetative phase. The high domed vegetative apex has an average height of 45 microns and a width of 140 microns, roughly a height to width ratio of 1 to 3. The range of apical size is given in Table 1. A biseriate tunica is present throughout the plastochron. Cells of the tunica average 7 microns in height by 8 microns in width (Figure 5). Corpus cells are 6 by 7.

Leaf primordia are initiated by divisions in the second tunica layer. Meristematic activity involved in producing the leaf primordium extends to a depth of four or five cells. Axillary vegetative buds begin development at approximately the third node from the tip but ordinarily remain dormant until the first flowers are produced. It is only when the plant has attained the flowering condition that the main axis elongates and the axillary buds develop further.

The numerous inflorescences of *Mertensia virginica* are borne in the leaf axils as well as terminally. The inflorescence is bractless;

the floral primordium develops at the apex from the previous terminal meristem whereas the continued extension of the main axis is made possible by the development of a new growth center in a lateral position. Thus, there is small chance of mistaking the new inflorescence apex. The onset of flowering is characterized by an increase in the height of the apex. Inflorescence apices average 70 microns in height and 141 microns in width, a height to width ratio of 1 to 2.

At the initiation of the first flower bud and of each succeeding one, cells of the second tunica begin numerous divisions in both periclinal and anticlinal fashion. The scope of the divisions broadens and deepens until almost one-third of the original apex is involved in extending the new axis. The remaining two-thirds of the original apex is immediately involved in production of the flower. Every floral primordium is produced in the same way; however, the continuation of apical growth is always revolved about 90 degrees, resulting in a sharply angled, stepwise development of the inflorescence.

The tunica of the inflorescence is composed of cells averaging 9 microns high by 8 microns wide arranged in two layers at maximum apex size and reducing to one layer at minimum size. The corpus cells are 8 microns in both dimensions. Figures 6, 7, and 8 are representative steps in the development of a flower bud.

Discussion

The fact that clearcut changes occur in the shoot apex when flowering begins has been noted by numerous authors. An attempt has been made to define these changes and to show which are reversible (Prior, 1954). A comparison of shoot apices of *Myosotis laxa* and *Mertensia virginica* shows that the apex increases in size at flowering as a result of an increase in cell number rather than cell size. The apices of both these species show a 50 percent greater increase in height than in width. The loss of apical dominance is probably one of the most commonly noted phenomena that attend flowering in many species. This is particularly significant in species where a sympodial axis develops. In addition, it should be noted in this connection that lateral meristems are not cytohistologically apparent any closer than three nodes from the tip at the vegetative stage. The two species used in this study were found to display a clear state of apical dominance that was terminated by flowering. After flowering starts, the floral primordium and its allied laterally-produced inflorescence apex develop with no cessation of meristematic activity whatsoever.

Although both foliar and floral appendages are initiated at the same cell depth, the second tunica layer, subsequent meristematic activity can be traced to a greater depth in an apex producing flowers than one producing leaves. The apices of both *Myosotis laxa* and *Mertensia* virginica show a reduction from two or three tunica layers during the vegetative phase to one or two layers during the flowering phase.

The lateral continuation of the inflorescence of *Myosotis laxa* is always on the same side relative to the position of the latest formed flower bud, producing a coil or spiral. This development fits the description of the helicoid cyme given to Rickett (1944). The renewal of the inflorescence apex of *Mertensia virginica* always takes place at right angles to the previous direction of apical extension and does not "reverse itself," as stated by Rickett (1944), if he meant a complete 180 degree revolution. According to Lawrence (1951) the scorpioid cyme is a very rare type and without doubt *Mertensia* produces such an inflorescence, but it appears that some variation in development of the apex is possible.

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