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Initiation and Early Development of Axillary Buds in *Cyclamen*

MARSHALL D. SUNDBERG*

ABSTRACT — The development of axillary buds along the primary shoot axis of *Cyclamen persicum* Mill. F-1 Rosemunde was examined. Vegetative buds usually formed in the axils of the cotyledon and first 5 leaves. Flowers were produced from the majority of the buds which developed in the axils of later-formed leaves. The first indication of vegetative bud development was the appearance of a shell zone. Proliferation of the cells set off by this zone soon led to the establishment of a branch shoot apex producing leaf primordia. Formation of a shell zone was not associated with the initiation of floral buds. These arose as a detached meristem and the proliferation of the axillary cells soon led to the establishment of an apical organization. Vigorous activity of the rib meristem and its derivatives initiated rapid peduncle growth. The differentiation of initials into vegetative vs reproductive buds may be due to different environmental conditions influenced by the subtending and adjacent leaves, as well as to cytological differences between the cells of the respective shoot apices.

The presence of a shell zone during formation of axillary buds was first described by Schmidt (1924). This zone may act to isolate cells from the shoot apical meristem (Shah and Patel, 1972). Wardlaw (1943) described another means, the detached meristem, by which the axillary meristem may be isolated from the shoot apical meristem. Subsequent workers have found evidence for both mechanisms during the formation of axillary buds in various plants. The purpose of the present report is to describe and compare the initiation and early development of both the vegetative and reproductive buds along the primary shoot axis of *Cyclamen persicum* Mill. F-1 Rosemunde (Primulaceae).

Sampling of seedlings and plants

One thousand seeds of *Cyclamen* were sown in August of 1975 and again in April of 1976. The plants were grown according to the schedule of Widmer et al. (1974). A total of 700 plants were sampled from the two populations during the course of the study. Sampling was at random and without replacement. The presence of vegetative or reproductive axillary structures was recorded for each node. Shoot apices, along with the youngest leaf primordia, of all plants were fixed in acrolein, dehydrated, and stored in n-butanol (0 C) after scoring (Feder and O'Brien, 1968). More than 100 of these apices were transferred to t-butanol, embedded in "Tissuemat", serially longitudinally sectioned at 8 microns and stained according to the procedure of Sharman (1943). An additional 50 apices were sectioned at 5 microns and stained with 2 percent Pyronin Y (Trepper and Gifford, 1962).

Two development trends

Axillary buds may develop into either branch shoots or flowers depending on their vertical position along the primary shoot axis. Table 1 presents the percentage of buds developing into flowers at nodes cotyledon (cot) through 15. Vegetative buds differentiated in the axils of the cotyledon

and leaves 1-4. The axillary structure at node 5 was usually vegetative while over half the buds at node 6 developed into flowers. The percentage of flowers formed at successively distal nodes increased gradually until by node 13 virtually all buds differentiated into flowers. It should be pointed out that not every vegetative bud developed into an axillary branch during the first year. In most plants only 3 or 4 branches formed. Those in the axils of the most basal nodes, cot - 3, became displaced laterally as the lower internodes expanded along with the subjacent hypocotyl. On rare occasions one of these branches actually overtopped the primary axis and became the dominant shoot axis.

The first bud began to differentiate in the axil of the cotyledon by week 7. The origin of this bud followed the pattern described by Garrison (1949a, b). A shell zone formed in the axil of a leaf 5-6 plastochrons from the shoot apex (Figure 1). Anticlinal divisions in a series of cells formed a somewhat crescent-shaped file of columnar cells. This zone set off the group of axillary meristematic cells from the surrounding cortical cells. The subdermal cells of the meristematic region then began to divide actively, apparently in a random fashion, to produce a cluster of highly meristematic cells. As the mass of dividing cells became larger, an apical meristem was organized which began to produce its own leaf primordia (Figure 2). This meristem was broadest in the plane tangential to the shoot axis. A well developed branch shoot apex is shown in Figure 3. This branch, at node 5, had already produced 3 leaves. The first 2 were in front of and behind the plane of section. Leaf 3 occurred on the abaxial side of the bud. Although it is not evident in this section, the arrows on the left indicate periclinal divisions in tunica layer 2 which are associated with the lateral portion of leaf base 2. The site of inception of the fourth leaf is marked by the densely staining organogenic zone beneath the right hand arrow. A zone of dense staining includes cells of both the tunica and corpus beneath the site of the incipient leaf primordium. As

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Figures 1-6: Development of Axillary buds

BAR = 100 MICRONS

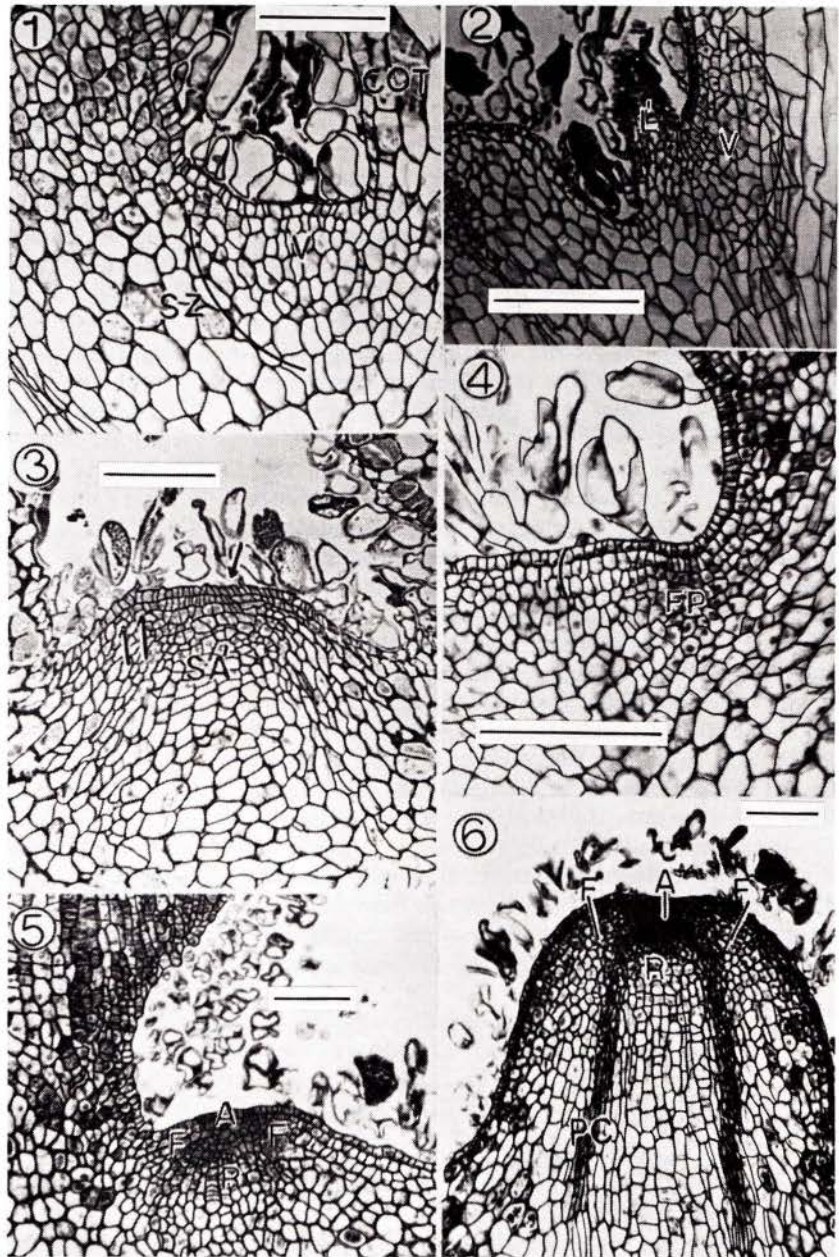


Fig. 1 - 3 vegetative, Fig. 4 - 6 floral. Fig. 1 Shell zone (SZ) isolating meristematic cells (V) in the axil of the cotyledon (COT). Fig. 2, First leaf primordium (L') produced by the cotyledonary bud (V). Fig. 3, Branch shoot apex (SA') showing periclinal divisions in tunica-2 (HALF ARROWS) associated with a leaf primordium. Arrow indicates site of incipient leaf primordium. Fig. 4. Floral primordium (FP) in axil of third youngest leaf (L) indicating stratified layers (T) contiguous with tunica of shoot apex. Fig. 5, Floral meristem developing apical zonation pattern, central zone (A), peripheral zone (F), and rib meristem (R). Fig. 6, Elongating floral bud with procambial strands (PC) differentiating in peduncle, flattened floral apex with central zone (A), peripheral zone (F), and rib meristem (R).

TABLE 1
Percentage of Plants Flowering at Various Nodes

NODE	COT	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Percent Flowering	0	0	0	0	0	12	53	62	75	85	94	96	99	100	100	100

in the primary axis, there was little or no internodal elongation.

Axillary primordia which would develop into flowers arose from a detached meristem 3 plastochrons below the shoot apex. The outer 3 tunica layers (T) of the shoot apex maintained their integrity in the developing axillary floral meristem of leaf 12 (Figure 4). It was only after the differentiation of intercalary cells that the axillary meristem could be distinguished from the shoot apex proper. This differentiation included the production of large, multicellular hairs from some of the cells of T1 and the increase in size and

vacuolization of the cells of T2 and T3. A shell zone was not produced. Shortly thereafter, the cells of the axillary meristem began to proliferate. The earliest divisions, producing predominantly periclinal walls, occurred in the sub-tunica core. Further divisions produced a lenticular mound of meristematic tissue in the axil of the leaf (Figure 5). The flower primordium at this stage resembled a floral induced shoot apical meristem. A 2-layered tunica covered the entire primordium and a large, central, densely stained zone included cells of both the tunica and corpus. Below the central zone was a conspicuous rib meristem, a peripheral

meristem occurred in the tunica surrounding the central zone. Growth of the peduncle, due to the activity of the rib meristem, soon commensed (Figure 6). The distal portion of the floral apex became flattened due to the meristematic activity of the peripheral zone while strands of procambium began to differentiate internally.

Explanation of the Observed Trends

Axillary buds are theoretically derived from the shoot apical meristem at the time of leaf initiation. The subsequent differentiation of the axillary meristem, however, is repressed for some time. It is generally agreed that this delayed development is due to correlative inhibition of the axillary bud by the shoot apex (Galston and Davies, 1970). It appears that growth resumes only after the inhibition of the bud is removed. This model fits the anatomical data presented for *Cyclamen*. Axillary buds, both vegetative and reproductive, were first seen to be differentiating 3 or more leaves distal from the shoot apex. The formation of the shell zone between the apex and vegetative axillary bud may act as a physical or physiological block to the inhibitory stimulus. In many plants, the elongation of internodes may help to isolate the axillary buds from the influence of the shoot apex. However, this was not the case in *Cyclamen* because there was little internodal elongation.

As the axillary bud became further removed from the shoot apex, additional differentiation of the meristem occurred. Prior to the initiation of the first leaf, the apex was a low, lenticular dome with the elongate axis tangential to the main shoot axis. This shape was the result of physical crowding and affected the position of leaf initials. The first leaf of the axillary bud arose either to the right or left of the median line and a spiral phyllotactic pattern ensued.

Floral buds arose as detached meristems; no shell zone was formed. Separation of the axillary meristem from the apical dome was due to the differentiation of the intermediate tunica derivatives. The very young floral meristem appeared

similar to the apical meristem of the vegetative bud. In surface view it appeared to be a low, lenticular dome with the long axis extending laterally. This apical asymmetry was maintained until the rib-meristem produced enough cells to raise the floral apex above the level of the shoot apical meristem.

In addition to the manner of separation from the shoot apical meristem, there were other early differences between the vegetative and reproductive buds. The former were initiated prior to floral induction and subsequent evocation of the shoot apical meristem. It is therefore likely that the initials of the vegetative and reproductive buds were different cytologically, from the time of their inception.

In addition to probable cytological differences between the initials of vegetative and reproductive buds, there were also physical differences between the environments of the respective organogenic tissues - the number of leaf primordia on the shoot apex and the size of the subtending leaf at the time of initiation. Sundberg (1981) showed that both the early rates of leaf initiation and leaf emergence followed similar exponential patterns. Because of the delay between initiation and emergence, the number of leaf primordia on the shoot apex gradually increased. At the time of initiation of the vegetative bud in the axil of the cotyledon there were only 2 leaf primordia less than 10mm long. By the time the vegetative bud in the axil of leaf 5 was initiated, there were at least 5 leaf primordia on the shoot apex. At least 7 leaf primordia were on the apex by the time buds were produced at nodes 9 or beyond. Likewise, as the number of leaf primordia on the apex increased, the size of the subtending leaf, at the time of bud initiation, decreased. The cotyledon through leaf 5 were all at least 10mm long at the time of initiation of their axillary buds. However, buds were initiated in the axils of later leaves while the subtending leaf was less than 10mm long.

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