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Growth Regulators in Changing Apical Growth at Transition to Flowering

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Abstract. Reorganization of growth in the shoot apex of *Chenopodium rubrum* during transition to flowering is described. Growth and morphogenic changes — a rise in cell division rate, changes in leaf and bud formation and changes in directions of cellular growth — are viewed from the aspect of a possible role of growth hormones in controlling these changes. Growth and morphogenic effects of exogenous growth regulators in the shoot apex of *Chenopodium* are summarized and their floral effects explained in terms of changing apical growth correlations. New evidence concerning the timing of increased cell division rate and showing the limited requirement of axillary cell division and a shift to more vertical direction of growth in the apex in the floral developmental pathway was obtained in experiments with kinetin application and by surgical treatments.

As soon as the events in the shoot apical meristem became a part of the studies of flowering, "flower formation" could be understood as a sequence of changes by which the shoot apex is transformed. Studies of the apical growth pattern provide information about what happens before the flower is formed and, moreover, provide some ideas of the internal changes which have to be evoked before a given change occurs. An absolute photoperiodic requirement makes it possible to investigate floral evocation and differentiation from the very beginning.

Reorganization of the apical growth resulting from photoperiodic induction suggests the involvement of hormonal factors. Looking at the growth changes of the whole reacting system of the shoot apical meristem, including young meristematic leaves and internodes, one may assume that plant growth regulators play an important role in flowering, in spite of the fact that exogenous plant growth regulators — except for gibberellin — are ineffective in flower formation if there is an absolute developmental block. A list of growth changes in the shoot apices of *Chenopodium rubrum* induced to flower is given in Table 1.

Acceleration of cell division in the apical dome of induced plants is the first growth change mentioned in Table 1 as it has been found in all plants and in some of them it occurs before other changes. The quantitative data show that the cell doubling time at the apex may decrease several times in long-day plants (BODSON 1975, MILLER and LYNDON 1976) as well as in short-

TABLE 1

The growth changes in the shoot apex of *Chenopodium rubrum* induced to flower by three short days at the age of six days (SEIDLOVÁ and SÁDLÍKOVÁ 1983) or by one short day at the age of four days (in preparation)

1. Acceleration of cell division in the apical dome (non-equal in different zones)
2. Shortening of the plastochron
3. Acceleration of cell division in leaf primordia (less than in other apical components)
4. Bud formation close to the apical dome (lowering of apical dominance in the apical region of the stem)
5. A rise in the proportion of cell divisions contributing to longitudinal growth
6. A change in the shape of the apex and the direction of primordial growth
7. A decrease in cell division rate in leaf primordia initiated during and after photoperiodic induction (a late growth effect)

day plants (JACQMARD *et al.* 1976, SEIDLOVÁ and SÁDLÍKOVÁ 1983). Due to the similarity of the increase in cell division rates produced by a long day or by applied cytokinin in *Sinapis* a possible role of cytokinin as a mitotic component of the floral stimulus has been assumed in this plant (BERNIER *et al.* 1977). Gibberellin stimulates cell division in different components depending on its capability to induce flowering (JACQMARD 1970, MILYAEVA and CHAÏLAKHYAN 1974, BESNARD-WIBAUT *et al.* 1983).

The increased rate of cell division is not necessary for all the sequential changes in the apical dome. Photoperiodic induction and, presumably, a part of floral evocation may proceed without an increase of the growth rate at the apex in some plants (MILLER and LYNDON 1976, SEIDLOVÁ and SÁDLÍKOVÁ 1983), and even with inhibited cell division (ULLMANN *et al.* 1971). The growth rate was shown to decline again during formation of the floral members in *Silene* (LYNDON 1979). Local differences in shortening of the cell cycle duration are important for the changes in organogenesis. The reason for such a differential response between different regions of the apex is unknown but it may be assumed that a mechanism involved in changing growth correlations is involved in changing the zonal pattern of the apical dome. Changes in distribution of growth in the central and the peripheral zones of the apex were observed in *Chenopodium* before the rise of the cell division rate (SEIDLOVÁ and SÁDLÍKOVÁ 1983).

The increase in the rate of primordial initiation and the decrease in plastochrone duration as well as the early stimulation of primordial growth (2 and 3 in Table 1) are related to growth activation in the apical dome. Microsurgical treatments of vegetative apices have yielded some information about the relations between the apical dome, the leaf primordia already formed and the leaf primordia to be formed. The results show that the older leaf primordia exert some inhibitory influence on the newly forming primordia which may be diminished by isolating the leaf primordia from the rest of the apex (SNOW and SNOW 1947). Phyllotaxis has been assumed to be the result of inhibitory fields around the leaf primordia, auxin being the most probable candidate for the morphogen (SCHWABE 1971). A certain displacement of leaf primordia was obtained by auxin applied directly on the exposed meristem of *Lupinus* (VARNELL and VASIL 1978). Effects on growth distribution in the apex and on phyllotaxis were reported in *Chrysanthemum* after a treatment with TIBA, modifying the auxin transport. Increased vertical

TABLE 2
Effects of exogenous growth regulators on apical growth and morphogenesis in *Chenopodium rubrum*

Growth regulator	Growth effects	Morphogenic effects
IAA 10^{-4}M	inhibition of cell division in the axillary meristem	delayed initiation of buds, inhibition of initiated buds
Kinetin 10^{-4}M	stimulation of cell division in the whole meristem	enhanced leaf initiation and leaf growth, stimulation of initiated buds
ABA 10^{-4}M to 5.10^{-4}M	higher proportion of cell division and extension contributing to growth in width	stimulated initiation of all laterals
GA_3 10^{-5}M to 10^{-4}M	higher proportion of cell division and extension contributing to growth in height	elongation of the apex and all primordia

spacing of leaf primordia was observed in connection with a lower order of phyllotaxis (SCHWABE 1971). In *Xanthium* a changed apical growth and a higher order of phyllotaxis resulted from applications of gibberellin; identical changes were obtained by a short-day induction (MAKSYMOWYCH *et al.* 1976).

A close relationship between apex growth, the rates of initiation of primordia, their size and position has been shown in transition to flowering in different plants (LYNDON 1978, HORRIDGE and COCKSHULL 1979, MEICENHEIMER 1979). Hormonal interactions in which all the known growth regulators participate seem to be causally related to the changes in leaf organogenesis at transition to flowering.

Initiation of bud primordia in the axils of leaf primordia is usually delayed in vegetative apices. The delay is one to two plastochrones in *Chenopodium*. Lateral bud initiation begins with formation of a characteristic structure, the shell zone (SHAH and PATEL 1972). The inhibitory effect of the vegetative apical dome was demonstrated in some experiments in which enhanced bud development was obtained after the isolation of the leaf with axillary tissue from the apex (SNOW and SNOW 1942). At transition to flowering the shell zone appears close to the apical dome, in the axils of newly formed leaf primordia. This precocious apical branching at floral transition resembles release from apical dominance and it is usually accompanied by a release of buds along the shoot. We may assume that both phenomena have some regulatory mechanisms in common. Growth activation in axillary buds on the differentiated stem is related to formation of the vascular connections with the main stem (LARSON and PIZZOLATO 1977). Growth activation in the basal part of the axillary bud was reported as a very early event of release from apical dominance in *Cicer* (USCIATI *et al.* 1972). Similarly, in the branch-

TABLE 3
Floral effects of exogenous growth regulators in *Chenopodium rubrum*

Growth regulator	Conditions inhibiting flowering	Conditions stimulating flowering
IAA	application about or at induction	application at meristem branching (after induction)
Kinetin	application about or at induction	application during advanced branching (after induction)
ABA	apices with poor branching	vigorous apex growth and prolonged branching
GA_3	?	numerous laterals formed?

ing meristem of *Chenopodium* stimulation occurs at the base of the buds and the buds become more closely connected with the rest of the meristem in induced apices.

There is a question of why the induced apex with very high growth activity exerts a lower apical dominance over the axillary buds and thus behaves as if it had been removed. We may assume that in apical dominance the growing leaves of the apical bud play the major role. At transition to flowering not only do the buds appear sooner and grow faster but also there is often a tendency for the rate of cell division to decrease in the leaf primordia. This is a well known event in many plants, *e.g.* in the *Gramineae*. It was shown that in *Chenopodium* the leaf primordia initiated at or just after induction have

TABLE 4
Response of the apex to kinetin applied to plants induced by two short days at the age of six and seven days (2×3 µl per plant)

Treatment on 6th and 7th day		Kinetin 10^{-4}M	Control
Mean cell doubling time [h] for anticlinal division in T2 (from top to axil L2)	during the period of		
	6th–8 th day	37	120
	8th–10th day	65	62
Cell number in T2			
in the apical dome	10th day	19	18
in leaf L4		8	0
in bud B2		9	5
Per cent of flowering	12th day	10	60

TABLE 5

Response of the apex to kinetin or root removal applied to plants induced by one short day at the age of four days

Treatments on 5th day		Kinetin 10^{-4}M *via* roots	Root removal+	Control
Mean cell doubling time [h] for anticlinal divisions in T2	during the period of 5th—6th day			
from the top to the axil L2		14	22	15
from the top to the axil L1		14	24	18
in leaf L2		11	30	14
Cell number in T2	6th day			
in the apical dome		11	10	9
in leaf L3		8	0	0
in leaf L2		19	7	13
in bud B2		6	1.3	6
in bud B1		8	4	6
Size of primordia (projection area — $mm^2 . 10^{-3}$)	7th day			
in leaf L3		4.5	0.7	1.4
in leaf L2		14.3	5.6	10.4
in bud B3		4.2	0.8	2.1
in bud B2		6.3	1.9	3.2
Width of the apical dome [mm]	7th day	0.16	0.09	0.11
Height of the apex from axil of L2 [mm]		0.24	0.18	0.18
Per cent of flowering	9th day	10	90	40

+ Root regeneration starts on the 8th day.

a lower rate of cell division than the corresponding leaves in vegetative apices (SEIDLOVÁ and SÁDLÍKOVÁ 1983). This is a relatively late result of induction, listed at the bottom of Table 1. Hormonal regulation plays an important role in leaf-bud correlations of the plant. On transition to flowering there is a gradual shift in these correlations in the apical region. It may be presumed that evocational events of axillary bud formation and leaf formation are closely related and are both subject to the hormonal control of growth.

A change in the longitudinal component of apical growth and a corresponding change in the direction of lateral outgrowth of primordia are the other important changes at transition to flowering in *Chenopodium* (5 and 6 in Table 1). The prevailing direction of cell division contributing to the longitudinal growth of the axis was studied in connection with the flowering

response to gibberellin (LANG 1966). An increase in cell division contributing to the longitudinal growth was found within the induced *Chenopodium* apex (SEIDLOVÁ and SÁDLÍKOVÁ 1983).

Initiation of lateral primordia is linked with local changes in the plane of cell division. Information about the contribution of hormonal factors to those shifts are scarce and indirect. The plane of cell division was changed by exogenous cytokinin in intercalary meristems (JONES and KAUFMAN 1971). Microtubule reorientation was observed after hormone treatment in non-dividing tissue (VOLFOVÁ *et al.* 1977). The site of pre-prophase band and the arrangement of cortical microtubules was shown in *Azolla* roots to be connected with the position of the future cell plate and with the prevailing direction of cell extension, resp. (GUNNING *et al.* 1978). We may assume that similar mechanisms may be working in the shoot apical meristem and may also contribute to the reorganization of growth in the induced apex.

A survey of the effects of applied growth regulators on apical growth and on flowering is given in Tables 2 and 3. The basic growth effects were independent of the developmental stage and occurred in induced, partially induced and non-induced plants (SEIDLOVÁ and KHATOON 1976, SEIDLOVÁ and KREKULE 1977, SEIDLOVÁ *et al.* 1981). Similar responses — a stimulation of leaf growth by cytokinin, inhibition of bud formation by IAA, elongation by gibberellin and growth in width by ABA — were shown in excised *Dianthus* shoot apices (SHABDE and MURASHIGE 1977). In *Opuntia* dormant shoot apices could be activated to produce leaves if treated with a cytokinin, or spines if treated, instead, with gibberellin (MAUSETH 1976).

In contrast to the growth effects showing a similar tendency in different apices, the floral response to each of the growth regulators varied greatly according to the developmental state of the apex (SEIDLOVÁ and KHATOON 1976, SEIDLOVÁ and KREKULE 1977, SEIDLOVÁ *et al.* 1981). In non-induced *Chenopodium* the growth effects have never resulted in flowering. In induced apices inhibition or stimulation of flowering occurred if the growth and morphogenic effect were in concert with the vegetative or with the floral programme of apical development (Table 3). The dependence of the floral effects of applied regulatory substances on the physiological tate is well documented in other plants, too, (BESNARD-WIBAUT 1981) and particularly in explants (TANIMOTO and HARADA 1981, TRINH T. HAHN *et al.* 1981).

MATERIAL AND METHODS

Experiments were performed with *Chenopodium rubrum* induced by one short day at the age of four days or by two short days from the age of six days (ULLMANN *et al.* 1985). The other treatments were 1) kinetin application to the plumule or *via* roots, 2) removal of all roots and further cultivation of derooted plants in perlite, 3) careful removal of the first leaf pair under the dissection microscope, and further cultivation of the plants in perlite.

The mean cell cycle duration was calculated for the anticlinal divisions (in the second tunica — T2) in the median sections. This single direction of surface growth was taken as a measure for the cell division rate (SEIDLOVÁ and SÁDLÍKOVÁ 1983). In more advanced stages drawings from the projection microscope were used for area measurements. All measurements were made on selected three to six average apices per sample.

RESULTS AND DISCUSSION

An enhancement of cell division in the apical dome is a transient event occurring immediately after kinetin application (Table 4). As a result new leaf primordia are initiated earlier and the growth of bud primordia is stimulated (Figs. 1—4). Similar results were obtained in younger plants (Table 5).

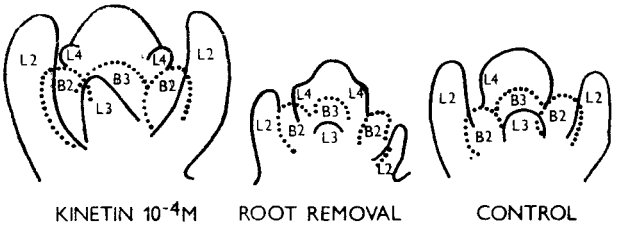

Fig. 7. The shoot apex of *Chenopodium rubrum* two days after kinetin application or root removal. L — leaf; B — bud.

We may speculate that the enhanced leaf formation (and reduced flowering) is a consequence of changing interactions within the apex as suggested by SCHWABE (1971) and, that the conditions for the action of another hormone, *e.g.* auxin, may be changed by cytokinin-induced growth.

Stimulation of flowering by root removal was reported in *Scrophularia* and was explained by removal of the source of endogenous cytokinin (MIGINIAC 1971). A similar response was obtained in derooted plants of *Chenopodium* (Table 5). The floral response is preceded by a decrease in the growth rate at the apex. The cell number in the apical dome itself is not changed very much but leaf and bud formation is suppressed. The initial decrease of apical dominance and the precocious formation of axillary buds is represented by very few cell divisions only (Figs. 5, 6) and further steps of floral

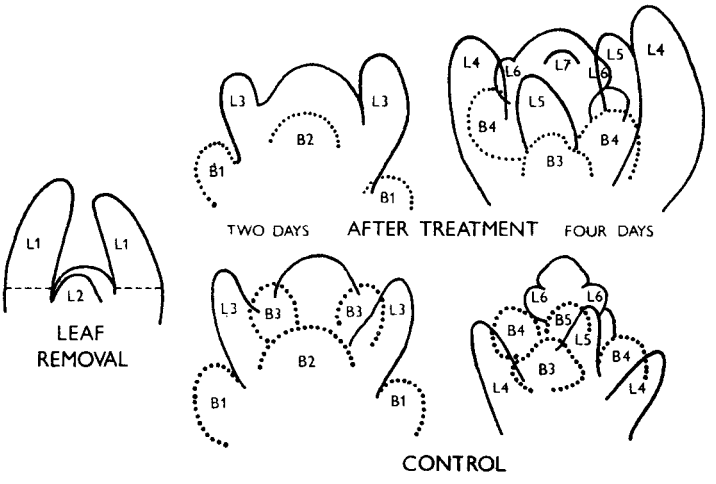

Fig. 8. The shoot apex of *Chenopodium rubrum* at and after the leaf removal. L — leaf; B — bud.

TABLE 6

Response of the apex to the removal of the first pair of leaves in plants induced by one short day at the age of four days

	Treatment on 5th day	Leaf removal	Control
Size of primordia (projection area — $mm^2 . 10^{-3}$)			
in leaf L3	7th day	8.4	10.9
in bud B3		0	4.7
in leaf L7	9th day	0.7	0
in leaf L6		0.9	1.9
in leaf L5		8.7	4.0
in leaf L4		23.9	5.8
in bud B4		7.4	4.0
Width of the apical dome [mm]	9th day	0.15	0.08
Height of the apex from axil of L3 [mm]		0.23	0.26
Per cent of flowering	11th day	10	60
Number of leaf pairs	11th day	6.4	4.8

differentiation proceed with rather limited sizes of all primordia (Table 5, Fig. 7).

The surgical treatments on the first pair of leaves in a seedling which has formed two leaf pairs altogether makes it possible to easily manipulate leaf growth on the apex. Direct microsurgical treatments performed by SNOW and SNOW (1947) on very young leaf primordia demonstrate the inhibitory influences of existing primordia on the nearest subsequent primordia. In *Chenopodium*, after leaf removal there is an increase in number and size of newly formed leaf primordia concomitantly with a delay in bud formation. There is an inhibition of flowering resulting from this shift of growth correlations (Table 6, Fig. 8).

The stimulatory effects of cytokinins on cell division in the shoot apical meristem have been shown in the apical bud (BERNIER *et al.* 1977, SEIDLOVÁ and KREKULE 1977, BESNARD-WIBAUT 1981) as well as in axillary buds (USCIATI *et al.* 1972). Stimulation of leaf growth after cytokinin application has also been demonstrated (MIGINIAC 1971, SEIDLOVÁ and KREKULE 1977, SHABDE and MURASHIGE 1977, BESNARD-WIBAUT 1981). Congruence of leaf growth stimulation and flowering inhibition was confirmed in the present experiments which show that the stimulated cell division, taking place before meristem branching, did not result in floral development.

The leaf-bud relations within the apex have to be stressed again due to the results obtained by excision of the leaves. However, both surgical treatments and kinetin applications show that only the early inhibition of the axillary buds — not their further growth — is linked with ready flowering.

There is a shift in the direction of growth, suggesting some changes in planes of cellular growth in induced apices. In a vegetative plant of *Chenopodium*, a wide and flat apex is present. At transition to flowering there is a higher ratio of divisions contributing to growth in height (SEIDLOVÁ and SÁDLÍKOVÁ 1983). The results of root removal show that the vertical direction of growth is the least suppressed component of growth. It was shown that this important shift in the direction of apical growth may be manipulated by abscisic acid and by gibberellin (SEIDLOVÁ *et al.* 1981). Thus, the data obtained in *Chenopodium* provide some examples of possible participation of growth regulators in changing the vegetative apex into the floral one.

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Figs. 1—6 are at the end of the issue.

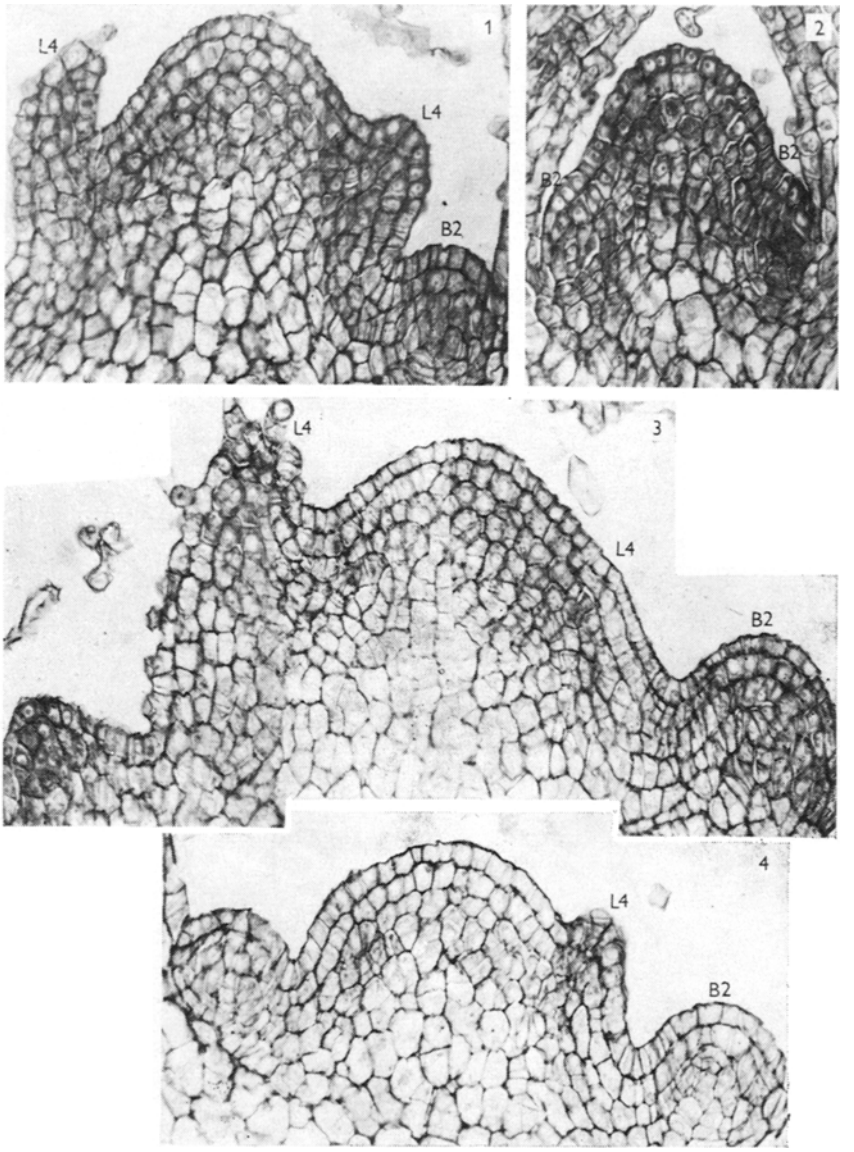
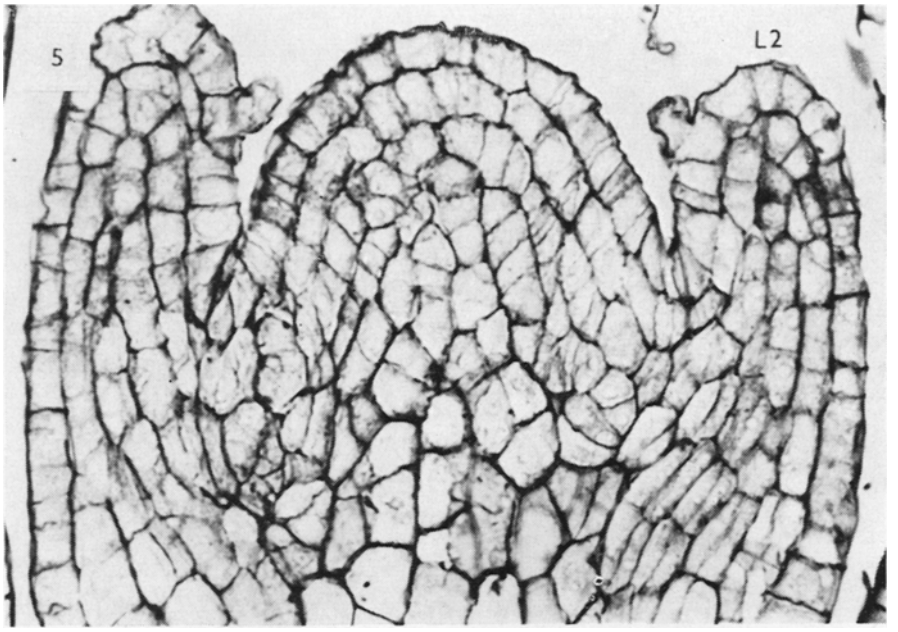


Fig. 1. Effect of kinetin (10^{-4}M) in the shoot apex of *Chenopodium rubrum* two days after application to plants during photoperiodic floral induction; — L — leaf; B — bud.
Fig. 2 Induced control apex.
Fig. 3. Effect of kinetin in a vegetative apex of *Chenopodium rubrum*. (Kinetin application and sampling as in Fig. 1).
Fig. 4. Non-induced control apex.



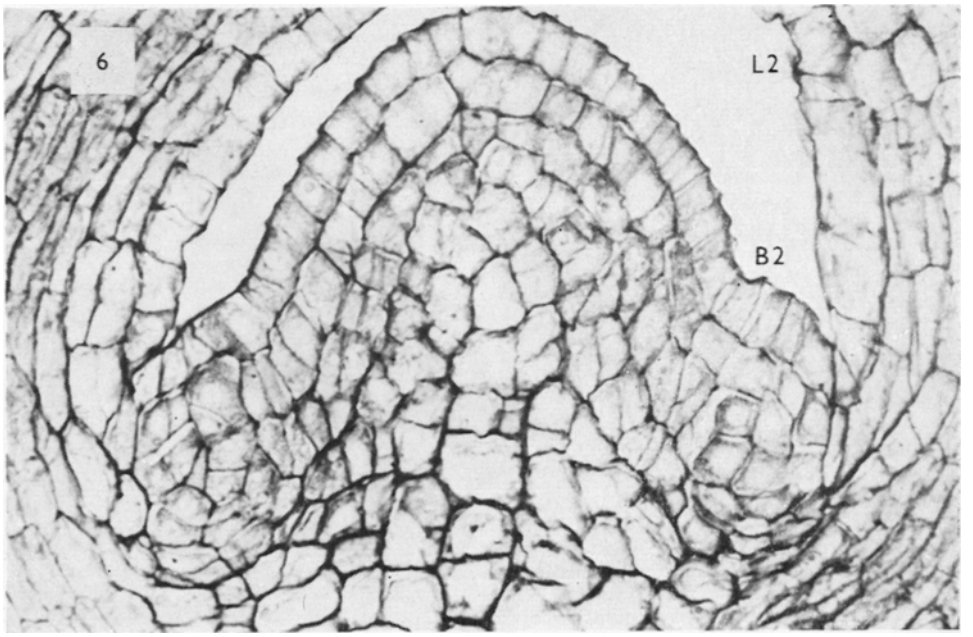


Fig. 5. Inhibition of growth in the bud (B) and leaf (L) primordia two days after root removal.
Fig. 6. Induced control apex. (Plants induced at the age of four days).