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Floral Transition as a Sequence of Growth Changes in Different Components of the Shoot Apical Meristem of *Chenopodium rubrum*

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Abstract. The changes in cell division rate were studied in different components of the shoot apex of *Chenopodium rubrum* during short-day photoperiodic induction and after the inductive treatments. Induced and vegetative apices were compared. Accumulation of metaphases by colchicine treatment was used to compare the mean cell cycle duration in different components of the apex. A direct method of evaluating the increase in cell number obtained by anticlinal or periclinal divisions was applied if the corresponding components of induced and non-induced apices had to be compared. The short-day treatment prolonged the cell cycle more in the peripheral zone than in the central zone and still more in the leaf primordia. The importance of changing growth relations for floral transition was shown particularly if the induced plants were compared with the vegetative control with interrupted dark periods. Induced plants transferred to continuous light showed further changes in the rates of cell division. The cell cycle was shortened more in the central zone than in the peripheral zone, *i.e.* there was a further shift in growth relations within the apical dome. The cell cycle in the leaf and bud primordia was also shortened if compared with the vegetative control, the acceleration being stronger in the bud primordia. There was a subsequent retardation in cell division in the leaf primordia formed during and after the inductive treatment if the plants were fully induced. An inhibition of the oldest bud primordia was observed in fully induced apices, as well.

The floral transition brings about a change of the growth pattern. A flowering stem is formed, differing from the vegetative one by many growth parameters, *e.g.* by branching, stem growth, by the shape and position of leaves, *etc.* Most of the growth changes, resulting in the morphology of the flowering stem appear already at the apical meristem as changes in the anatomical structure and organogenesis. In the early papers the structural changes of the apex were interpreted as changing rates and planes of cell division and cell extension in different regions of the apical meristem (PHILIPSON 1947, POPHAM and CHAN 1952, LANCE 1957).

Quantitative methods of growth measurements applied to the shoot apical meristem have supplied more precise information. Most of the studies devoted to floral induction and evocation have concerned the uppermost part

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of the apical meristem (the apical dome). They show an induced acceleration and partial synchronization of cell division and they often demonstrate an enlargement of the apical dome (BERNIER *et al.* 1967, CORSON 1969, BODSON 1975, JACQMARD *et al.* 1976, MILLER and LYNDON 1976, FRANCIS and LYNDON 1978, COCKSHULL and HORRIDGE 1980). Reports on the behaviour of the derived parts of the apical meristem — leaf and bud primordia and newly formed internodes, which are still in the meristematic state — are rather scarce (SUNDERLAND 1961, WILLIAMS 1966, LYNDON 1979).

The sequence of growth changes observed during the floral transition points to the importance of the events in the derived parts of the meristem. There are two more reasons to consider the role of the derived meristematic tissues in floral evocation. First, they respond to the photoperiodic stimulus often in the same way as the apical dome (ARZEE *et al.* 1975, KREKULE and SEIDLOVÁ 1977) and, moreover, they are able to perceive the photoperiodic induction (GRESSEL *et al.* 1980). Second, regulation of flowering by applied growth hormones is to a great extent mediated by their action in the derived meristematic tissue (SACHS *et al.* 1969, SEIDLOVÁ 1980b).

This paper presents a part of the quantitative studies of growth by cell division in the apex of *Chenopodium rubrum*. The vertical direction of growth by cell division in the apical internodes was described in the previous paper (SEIDLOVÁ 1980a). In the present paper an attempt is made to compare the rate of cell division in the apical dome and in the primordia of the vegetative and induced apices during and after the photoperiodic treatments. The aim of these studies was to learn more about the growth changes which take place from the beginning of induction and to gain an insight into how they participate in the transformation of the structure and functioning of the induced shoot apical meristem. The methods had to be adapted to this rather extensive study.

MATERIAL AND METHODS

Cultivation of Plants and Photoperiodic Treatments

Seeds of *Chenopodium rubrum* were germinated in alternating temperatures (SEIDLOVÁ 1980b). The plants were grown on half-strength Knop's solution at the temperature of 20 °C in non-inductive conditions of continuous light of 8000 lx. At the age of five or six days after sowing, when two leaf pairs were present, the photoperiodic treatments started, with all the other conditions of cultivation being maintained. The photoperiodic induction consisted of one to three 24 h photoperiodic cycles with 16 h or 8 h dark periods. The non-induced control plants were either maintained in continuous light or, if the 8 h dark periods were used, a 15 min light break was applied in the middle of each dark period. After the photoperiodic treatments the plants were transferred back to continuous light. Collection of selected uniform plants started simultaneously with the beginning of the photoperiodic treatments. The day at which the photoperiodic treatment was begun was designated day 0. The formation of flower buds was evaluated under the dissection microscope. Each experiment was repeated at least two times.

Evaluation of Cell Cycle Duration from the Accumulation of Metaphases after a Colchicine Treatment

Colchicine was applied either immediately after the last dark period or later on at 24 h intervals as indicated in Table 1. A 0.5 per cent aqueous solution of colchicine in 0.1 per cent of Tween was applied to a small piece of cotton wool placed on the plumule between the cotyledons. The piece of cotton wool was changed after four hours. The upper part of the hypocotyl together with the plumule and the petioles of the cotyledons were collected after the colchicine treatment, fixed in a mixture of ethanol-formol-acetic

TABLE 1

Per cent of blocked metaphases (in parentheses) and the mean cell cycle duration [h] in different components of the shoot apical meristem of *Chenopodium rubrum* evaluated after colchicine treatment; a) non-induced control in continuous light, b) two days of 16 h of darkness and 8 h of light, c) three days of 16 h darkness and 8 h of light (flowering: a — 0%, b — 80%, c — 100%)

Part of meristem	at termination of inductive treatments	
	a) vegetative	b) induced
Central zone	(5.4) 64	(4.9) 70
Peripheral zone	(9.6) 36	(1.8) 190
Bud primordium B2	(5.7) 60	(0.2)
Leaf primordium L2	(24.7) 14	(0)
	24 h after termination of inductive treatments	
	a) vegetative	b) induced
Central zone	(3.1) 110	(24.7) 14
Peripheral zone	(12.4) 28	(20.4) 17
Bud primordium B2	(11.1) 31	(17.3) 20
Leaf primordium L2	(23.1) 15	(17.1) 20
	48 h after termination of inductive treatments	
	a) vegetative	b) induced
Central zone	(2.3) 150	(26.7) 13
Peripheral zone	(8.1) 43	(23.1) 15
Bud primordium B4	absent	(16.5) 19
Leaf primordium L4	(10.2) 25	(17.3) 20
Bud primordium B2	(20.4) 34	(18.2) 21
Leaf primordium L2	(13.9) 17	(17.2) 20
	24 h after termination of inductive treatments	
	a) vegetative	c) induced
Central zone	(2.3) 150	(43.3) 8
Peripheral zone	(8.1) 43	(28.5) 12
Bud primordium B4	absent	(23.2) 15
Leaf primordium L4	(10.2) 25	(17.4) 20
Bud primordium B2	(20.4) 34	(20.6) 17
Leaf primordium L2	(13.9) 17	(20.5) 17

acid, dehydrated in a tertiary butanol series and embedded in paraffin wax. Longitudinal sections of the shoot apex were cut at 5 μm thickness in the plane of the insertion of the cotyledons. The slides were stained by the Feulgen technique after a 30 min cold hydrolysis by 5 μ HCl (FRANCIS and LYNDON 1978), counterstained with Heidenhain's haematoxylin, as the Feulgen staining of the interphase nuclei was very poor. Three median sections of the apex with the even pairs of primordia were evaluated. The nucleoli (one per cell) were counted and the percentage of the metaphases blocked by colchicine was evaluated in ten apices per sample selected out of fifteen apices sectioned. Thus, the apices which showed no colchicine metaphases or those showing wrong orientation were left out. Analysis of variance was applied after transformation of per cent values to 2 arc sin $\sqrt{x}$. The results are presented in Table 2. The regions of the apical dome — the central and the peripheral zone as well as the leaf and bud primordia — were delineated and evaluated separately (Fig. 1).

In the preliminary experiments the collections were made 2, 4, 6, 8 and 10 h following the addition of colchicine. In all the regions of the apical meristem a lag phase of two hours was found and an approximately linear accumulation of metaphases was observed betwen the fourth and the eighth hour of the colchicine treatment in the induced apices and between the second and the eighth hour in the non-induced ones (Fig. 2). The mean cell cycle duration (T)

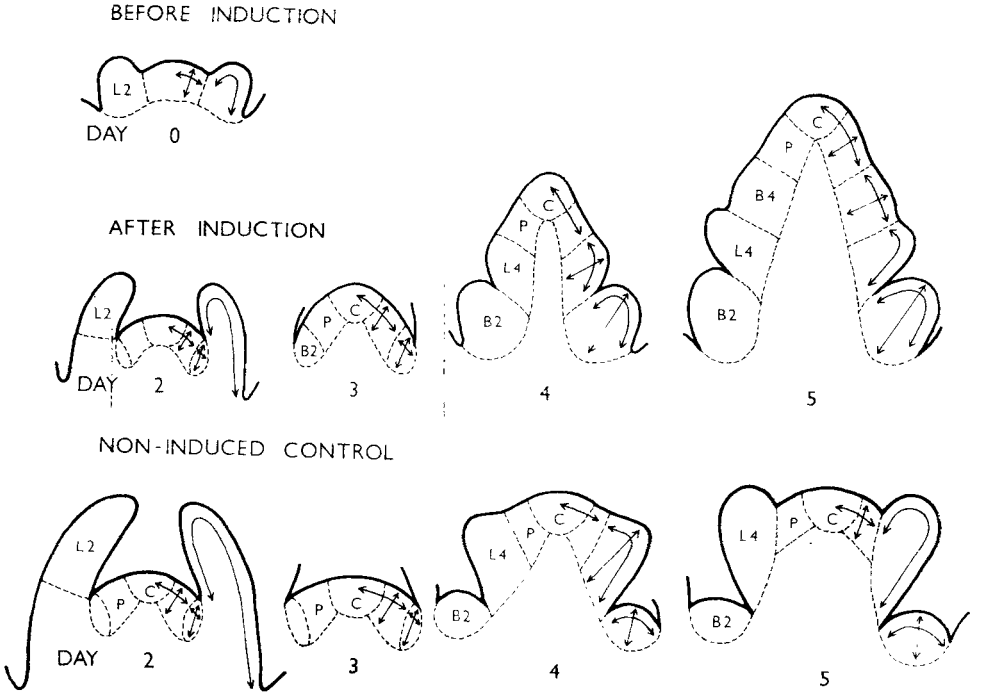

Fig. 1. Delineation of components in the apical meristem of *Chenopodium rubrum* for evaluation of metaphases blocked by colchicine (dotted lines) and for counting cells produced by anticlinal and periclinal divisions (indicated by arrows); C — central zone, P — peripheral zone, L2 and L4 — leaf primordia, B2 and B4 — bud primordia.

TABLE 2
Statistical treatment (analysis of variance) of per cent metaphases blocked by colchicine

Short-day inhibition of cell division	
The affect of induction	$F = 115.9$ ($F_{0.01} = 7.19$)
Apical components	$F = 5.8$ ($F_{0.01} = 4.22$)
Interaction between the effect of induction in different components	$F = 14.5$ ($F_{0.01} = 4.22$)
Induced enhancement of cell division	
The effect of induction	$F = 35.3$ ($F_{0.01} = 7.01$)
Apical components	$F = 6.4$ ($F_{0.01} = 4.08$)
Interaction between the effect of induction in different components	$F = 13.8$ ($F_{0.01} = 4.08$)

was then calculated from the accumulation of metaphases between the fourth and the eighth hour of the colchicine treatment. The procedure of EVANS *et al.* (1957) simplified for a cell population where all cells are meristematic was used (LYNDON 1970):

$$T = \ln 2 \times 100/D ,$$

where D is the rate of cell division (per cent per hour). A still more simplified method was used consisting of a single sampling seven hours after colchicine application and the mean cell cycle duration was calculated for the presumed five hour action of colchicine, assuming a two—hour lag phase.

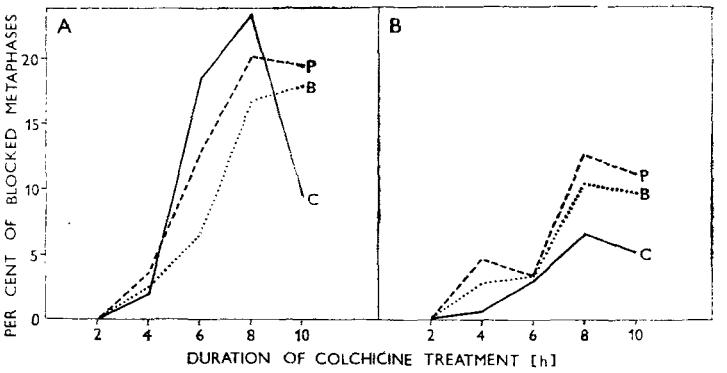

Fig. 2. Accumulation of metaphases by colchicine in induced (A) and vegetative (B) shoot apices of *Chenopodium rubrum*; C — in central zone, P — in peripheral zone, B — in bud primordia.

Considering the results obtained by the colchicine method it must be taken into account that the precision of the absolute values of the cell cycle duration is limited due to the difficulties in colchicine penetration into the shoot apices and due to its overall effects. We must also take into consideration the partial synchronization of cell division after photoperiodic treat-

ment (FRANCIS and LYNDON 1978, MILYAEVA and CHAILAKHYAN 1981). However, using the colchicine method one can obtain reliable relative values for comparing the growth rates within the meristem. This is of great importance if the growth relations have to be examined.

Evaluation of Cell Cycle Duration from the Increase in Cell Number

Collections were made at 24 h intervals during and after the inductive and non-inductive treatments. Fixation, dehydration, embedding and sectioning were described above. Median longitudinal sections either in the plane of the cotyledons and all the even pairs of primordia, or in the plane of the first leaf pair and all the subsequent odd pairs of primordia were prepared. The slides were stained with alcian blue, a selective stain for the cell walls in the meristematic tissue, and were counterstained with pyronine or fast red. Four shoot apices per sample were selected out of ten apices sectioned for cell counting. Thus, only the apices with perfect orientation and those showing the average developmental stage were used for the calculations, not taking into account the real variability of the plants.

The outline of the median sections was divided at the inflection points into the apical dome, leaf primordia and bud primordia (Fig. 1). The cells of the second tunica layer of each component of the apex were counted in two most median sections per apex. It might be supposed that the displacement of cells through the boundaries, *i.e.* through the axils of primordia, is negligible and that the increase in cell number within the components is the result of the anticlinal cell division in the plane of the median section. The central zone could not be delineated from the peripheral zone by this method. Therefore, they were studied together with the assumption that the tunica cells of the peripheral zone are derived from the tunica of the central zone. The second tunica layer of the apical dome was divided for cell counting into two halves at the highest point of the outline of the apex. The evaluations of the cell cycle duration in the apical dome were terminated by the formation of the next pair of leaf primordia in the same plane. The cells of the second tunica layer in the plane of the median section were considered to be a population of cells dividing in this particular one-dimentional direction with a mean duration of cell cycle:

$$T = \frac{\ln 2 \times t}{\ln x_2 - \ln x_1},$$

where x_1 and x_2 are the initial and the final cell numbers, respectively, in the second tunica layer and t is the time interval between the two countings. Periclinal cell divisions were calculated in the same way, the cells being counted from the surface to the start of the visible cell extension (Fig. 1). This boundary is not very stable. However, the bud primordia have cell walls of considerable thickness on their bases, which points to a great deal of independence of the cell populations on each side of the boundary.

The rate of leaf growth varies in the course of leaf development (WILLIAMS 1966). This may cause some errors, if the cell cycle in leaf primordia of the induced and non-induced plants is to be compared. The rate of leaf initiation is delayed during a short-day treatment and it is enhanced following inductive

treatment (Fig. 3). An attempt was made to get the initiation of the fourth leaf pair at the same time in the experimental sets compared.

The disadvantage of this method is the impossibility of comparing the results with total values for three-dimensional cell division. However, using this method one can easily get a sufficient amount of representative data for comparing the growth rates within the induced and non-induced apices. Using the method of direct cell counting one can avoid the undesirable effects of experimental techniques of isotope or colchicine application.

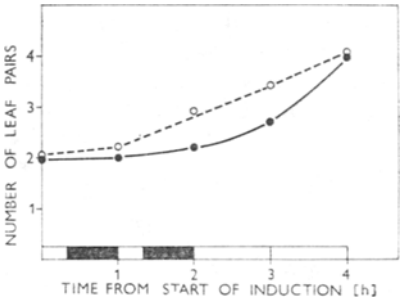

Fig 3. Initiation of leaf pairs in plants induced by two short days (solid circles and continuous line) and in non-induced plants kept in continuous light (open circles and dashed line).

RESULTS

Photoperiodically Induced Changes in the Cell Cycle Duration in Different Components of the Apices of *Chenopodium* found by the Colchicine Method

The cell cycle is prolonged during the photoperiodic short day treatment, the inhibition not being equal in all the components. It is more pronounced in the derived parts of the meristem. Inhibition in the central zone is surprisingly low (Table 1). The significance of interaction between different apical components and inductive treatment is still higher than that of different components of the same shoot apex (Table 2).

Activation of cell division in the whole meristem as well as a further shift in the rate of cell division ratio between the components occurs one day after the inductive photoperiodic treatment. The cell cycle in the induced shoot apices is the shortest on the summit and, a day later, it gets still shorter. The cell cycle after induction in bud and leaf primordia is of almost equal duration in contrast to the heterogeneous vegetative apex. Three short days result in a stronger shortening of the cell cycle. Simultaneously, the leaves initiated after the induction show a longer cell cycle than the other components of the shoot apex.

There are some differences in cell cycle duration within the vegetative apices of the plants kept in continuous light (Table 1). The mean duration of the cell cycle in the central zone is two times, later more than three times longer as compared with the peripheral zone. In the bud primordia, if they are present in the vegetative apex, the cell cycle is four times, later two times longer than in the subtending leaf primordia.

The Rate of Anticlinal and Periclinal Cell Division in Different Components of the Induced and Non-Induced Shoot Apices of *Chenopodium*

Cell division is inhibited during the short day treatment (Tables 3 and 4). The mean duration of the cell cycle gets longer, comparing with the continuous light control, by approximately 100 per cent in the leaf primordia and by 50 per cent in the bud primordia. After the photoperiodic induction, in continuous light, the cell cycle becomes 50 per cent shorter as compared with the control. In the leaf primordia L3 and L4 which are formed after the transfer from the inductive short days to continuous light the cycle becomes longer than in the control apex. At that time the shoot apex has undergone some developmental changes.

The mean duration of the cell cycle in the bud primordia of the vegetative plants is variable. At induction the cell cycle is long, then it gets temporarily shorter and soon it is prolonged again. Delayed and small lateral buds are found in control apices. The induced shortening of the cell cycle for periclinal divisions is stronger than for anticlinal divisions. However, the differences in the shape of the buds in the vegetative and floral shoot apex depend also

TABLE 3

The mean cell cycle duration [h] for anticlinal division in the second tunica layer in different components of the shoot apical meristem of *Chenopodium rubrum*; a) plants induced by two days of 16 h of darkness and 8 h of light (100% flowering), b) vegetative control in continuous light

Part of meristem	Photoperiodic treatment	Periods [d]			
		during treatment	after treatment		
		0–2	2–3	3–4	4–5
B1	a-inductive	–	33	64	
	b-vegetative	–	110	40	
B2	a	42	30	22	31
	b	27	62	170	320
B3	a	–	–	20	16
	b	–	–	forming	60
B4	a	–	–	–	22
	b	–	–	–	absent
L2	a	48			
	b	24			
L3	a	–	21	26	72
	b	–	53	30·	28
L4	a	–	–	forming	100
	b	–	–	forming	45
Apical dome above L2	a	72	45		
	b	36	60		
Apical dome above L3	a	–	35	35	31
	b	–	72	90	

TABLE 4

The mean cell cycle duration [h] for periclinal divisions in the section plane in different components of the shoot apical meristem of *Chenopodium rubrum*; treatments indicated in Table 2

Part of meristem	Photoperiodic treatment	Periods [d]			
		during treatment	after treatment		
		0–2	2–3	3–4	4–5
B1	a-inductive	52	38		
	b-vegetative	33	165		
B2	a	500	44	75	
	b	∞	230	133	
B3	a	—	—	27	
	b	—	—	∞	
L3	a	—	34	42	51
	b	—	55	42	28

TABLE 5

The effect of different number of short days on the mean cell cycle duration [h] for anticlinal divisions in the second tunica layer in different components of the shoot apical meristem of *Chenopodium rubrum*; A, B, C: one, two and three short days of 16 h of darkness and 8 h of light with 0%, 60% and 100% flowering, respectively

Part of meristem	Periods [d]			
	0–1	1–2	2–3	3–4
A	During inductive treatment	After inductive treatment		
B2	—	30	22	125
B3	—	—	forming	72
B4	—	—	—	absent
L2	36	36	21	
L3	—	—	17	28
L4	—	—	forming	37
B	During inductive treatment		After inductive treatment	
B2	—	71	26	31
B3	—	—	—	23
B4	—	—	—	forming
L2	36	115	24	
L3	—	—	23	30
L4	—	—	forming	55
C	During inductive treatment			After inductive treatment
B2	—	71	52	44
B3	—	—	—	19
B4	—	—	—	forming
L2	36	115	78	
L3	—	—	36	47
L4	—	—	—	82

on the cell extension which has a prevailing horizontal direction in the vegetative apices (SEIDLOVÁ 1980b). After some time, the cell cycle in the lower bud primordia of the induced apices is prolonged, too. This corresponds to the induced shift of activity of cell division from the lower to the higher apical segments (SEIDLOVÁ 1980a).

The inhibition is cumulative if more inductive photoperiods are added (Table 5). The leaf growth during the second inductive photoperiod slows down compared with the situation after one-day induction and the bud primordia are inhibited by the second and third photoperiods. In the bud primordia of the uppermost segments, after return to continuous light the cell cycle is shortened, if compared with two-day induction, and it is three times shorter than in the apices which received one-day induction only. On the contrary, the more complete the floral induction, the longer the duration of the cell cycle in the leaf primordia. Thus a different response of leaf and bud primordia is demonstrated.

A photoperiodic treatment of 8 h of darkness and 16 h of light was used in the next experiment. The length of the dark period is threshold for flowering and could be annulled by a 15 min light break. The plants have different parameters of apical growth and organogenesis than the plants which received optimal induction. Floral differentiation is delayed and the shoot apex branched abundantly. In the vegetative control growth is slowed down by the treatment with interrupted dark periods if compared to the continuous light (Tables 6 and 7). There is a particularly strong inhibition

TABLE 6

The mean cell cycle duration [h] for anticlinal divisions in the second tunica layer in different components of the shoot apical meristem of *Chenopodium rubrum*; a) plants induced by three threshold photoperiods (8 h darkness and 16 h of light) with 100% flowering, b) vegetative control plants with 15 min light break in the middle of each dark period

Part of meristem	Photoperiodic treatment	Periods [d]			
		during treatment	after treatment		
		0–3	3–4	4–5	5–6
B2	a-inductive	33	30	72	70
	b-vegetative	50	∞	∞	∞
B4	a	—	—	25	34
	b	—	—	—	absent
B6	a	—	—	—	24
	b	—	—	—	absent
L2	a	27			
	b	23			
L4	a	—	—	24	46
	b	—	—	—	48
Apical dome above L2	a	38	38		
	b	51	44		

TABLE 7

The mean cell cycle durations [h] for periclinal divisions in the section plane in different components of the shoot apical meristem of *Chenopodium rubrum*; treatments indicated in Table 5

Part of meristem	Photoperiodic treatment	Periods [d]			
		during treatment	after treatment		
		0–3	3–4	4–5	5–6
B2	a-inductive	∞	∞	33	57
	b-vegetative	∞	∞	150	400
B4	a	—	—	28	80
	b	—	—	—	absent

of bud growth after this treatment. The first growth changes caused by the threshold floral induction if compared with the light break vegetative control appear as a selective shortening of the cell cycle in the apical dome and in the bud meristem, the length of the cell cycle in the leaf primordia being almost unchanged. The results of the two different inductive photoperiodic treatments (16 h dark and 8 h dark) are in accordance as far as the growth stimulation of the apical dome and the change of the growth ratio between the leaf and bud components of the meristems is concerned.

DISCUSSION

The photoperiodic induction brings about a series of growth changes within the shoot apical meristem of *Chenopodium rubrum*. The changes which occur as an immediate effect of changing light conditions and those which appear as a results of floral induction after the transfer to continuous light (conditions identical with the vegetative control) should be discussed separately.

The prolonged darkness during the inductive treatment causes inhibition of growth. The shorter the dark periods the weaker the inhibitory effects (OPATRNÁ *et al.* 1980). The present results show that it is not the short-day suppression of growth in the apex itself but, particularly, the simultaneous shift in the growth ratio between the components which is important for the floral transition in *Chenopodium*. The different effects of the floral induction in the central and peripheral zone and in the derived meristematic tissue, leaf and bud primordia, are apparent already during the inductive treatment. It was shown that the cell cycle in the apex is affected by the phytochrome-mediated reversible reaction of the leaves (FRANCIS 1981) and that the response may be different in the apical components (ROLINSON and VINCE-PRUE 1976).

The postinductive growth changes in the apex start with an enhancement of cell division in *Chenopodium rubrum* as well as in other plants (CORSON 1969, BODSON 1975, JACQMARD *et al.* 1976, MILLER and LYNDON 1976). However, in *Chenopodium* the cell cycle is shortened much more in the central zone than in the peripheral zone. There is a similar shift in the ratio of RNA accumulation in the two zones (SEIDLOVÁ 1976). The enhanced cell division results in a shortening of the plastochrons and in an initial stimulation of

cell division in the newly formed leaf primordia. Nevertheless, the cell cycle of leaf primordia which are initiated already after the inductive treatment is slowed down. A reduction of leaf growth at the onset of floral differentiation was described in *Triticum* and *Brassica* (WILLIAMS 1966, KOHLI and SEIDLOVÁ 1981). The importance of the change in the growth ratio between the apical dome and the leaf primordia was stressed by LYNDON (1979). The occurrence of growth inhibition in leaf primordia in *Chenopodium* may be correlated with the amount of photoperiodic floral induction.

The acceleration of cell division in the axils of the leaf primordia is one of the first and most striking phenomena of the floral transition in *Chenopodium rubrum*. The postinductive change of growth correlations between the leaf and bud primordia results from a stronger stimulation of cell division in the bud. This is in line with the findings of a changing ratio of RNA accumulation in the leaf and bud primordia (SEIDLOVÁ 1976). As the branching of the shoot apex proceeds the cell division in the lower buds is slowed down as compared with the control. This retardation may be also correlated with the amount of photoperiodic induction. It has been shown in a previous paper that the upper segments of the induced apex are stimulated in cell division, while in the maturer regions cell division is suppressed (SEIDLOVÁ 1980a).

The sequence of changes in the rate of cell division in different components results in the organogenic changes by which the vegetative apex is transformed to the floral one. In *Chenopodium rubrum*, shortening of the cell cycle duration in the apical dome, the acceleration of the leaf initiation and of axillary growth as well as the first changes in the growth ratio between the components are the very early events of floral transition but they may be not sufficient for full flower formation. Further growth changes in the growth ratio including also some decrease in cell division rate in newly formed leaf primordia are required for a ready transition to the floral stage. The sequence of growth changes occurring during the transition to flowering may be manipulated by growth hormones (SEIDLOVÁ 1980b).

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