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Organ Correlations and Flowering in *Chenopodium rubrum* L.

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Abstract. Correlations within a shoot of *Chenopodium rubrum* L. ecotype 374 grown under continuous light or photoperiodic flower induction were studied using surgical treatments. Removal of a single pair of shoot organs had a variety of effects depending on position: significant changes in the number of leaf pair on the main axis or in axillary buds and in the height of shoot apices; or no effect on the parameters scored. Flowering was not affected by any of the treatments carried out.

Decapitation brought about a significant increase in the number of leaf pairs in axillary buds and flowering was inhibited in 8- and 9-d old plants. Flowering was not affected in 21-d old plants. The role of shoot organ correlations, especially that of apical dominance, in regulation of flowering in *C. rubrum* is discussed.

In plants sensitive to photoperiod, flowering seems to be controlled mainly by environmental signals. However there are some basic internal mechanisms that are still not fully understood, which together with other external factors regulate the "interpretation" of the major environmental signals. These internal and external factors are, to a certain extent, integrated in organ relationships.

Pavlová *et al.* (1990) studied correlations in *C. rubrum* by means of ^{32}P distribution in leaves and axillary buds. They found that axillary buds can be released from an inhibitory influence of the leaves on the main axis, both mature and young ones forming the apical bud, during both flower-inducing and non-inducing photoperiodic regimes. Correlations within the shoot apex in *C. rubrum* were described and their importance with respect to flowering reported by Seidlová and Opatrná (1978), Opatrná *et al.* (1982) and Seidlová (1985). In this study a combination of surgical and photoperiodic treatments was used to gain further knowledge of a possible regulatory role of shoot organ correlations and especially of the role played by apical dominance in the flowering process.

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MATERIAL AND METHODS

Plant Material and its Cultivation.

Chenopodium rubrum L. ecotype 374 was used. The conditions of seed germination and plant cultivation on perlite were as described by Ullmann *et al.* (1985). Experimental plants were kept in continuous light or induced to flower by two or three inductive cycles (12h of darkness + 12h of light). *C. rubrum* is an absolute short-day plant under the conditions of cultivation used. 21-d old plants, described in previous paper (Pavlová *et al.* 1990), were used in most experiments, and these required two inductive cycles for full flowering. Cotyledonary buds were not visible under a stereo-microscope at this stage.

Eight- and nine- d old plants were also used in several experiments as they were the youngest which could be decapitated under a stereo-microscope without damaging axillary structures, i.e. meristems with primordia of the 1st leaf pair just overtopping the apex. In these plants, three pairs of leaves had been developed on the main axis and the primordia of the fourth one were visible at the shoot apex about 0.05 mm long. Three inductive cycles were required for full flowering at this stage.

Surgical Treatments.

One pair of shoot organs (cotyledons, the 1st, 2nd, 3rd leaf pairs, buds of the 1st or 2nd node) was removed, or plants were decapitated above the 1st or 2nd leaf node. Plants were treated at the beginning of the 1st dark period; plants grown in continuous light were treated at the same time.

Morphological Analysis.

Using a stereo-microscope (magnifying ×50) the following criteria were scored: number of leaf pairs on the main axis, number of leaf pairs in axillary buds, height of apex measured from the axils of the youngest leaf pair overtopping the apex and degree of flowering. Plants were analysed after five days of continuous light that followed the end of the last dark period, when flower potency was fully manifested. Flowering was expressed as the percentage of buds with a terminal flower. Plants grown in continuous light were analysed at the same time.

RESULTS

Effects of Photoperiodic Inductive Treatment.

In 21-d old plants the inductive photoperiodic regime resulted in: 1. a significant reduction in the number of leaf pairs on the main axis and in axillary buds of the 2nd or 3rd node; 2. significant elongation of the apex of the main axis and buds of the 1st, 2nd and 3rd leaf node; 3. flower formation in terminal and axillary buds. (Tab. 1, 2).

Effects of Removal of One Organ Pair.

21-d old plants grown in continuous light showed a significant inhibition of the height of the terminal shoot apex following the removal of the 1st or 2nd leaf pair. The number of leaf pairs on the main axis increased significantly when axillary buds in the 1st or 2nd node had been removed. These changes and those caused by the flower inducing treatment are of the opposite character. Removal of cotyledons and of the 3rd pair of leaves elicited no significant effect on the parameters observed, and no significant changes were found in axillary buds (Tab. 1).

Induced plants showed a significantly reduced number of leaf pairs in the buds in the 1st leaf node if the 2nd leaf pair had been removed. In contrast, the number of leaf pairs and the height of the apices increased significantly in buds in the 2nd node if the 3rd leaf pair had been removed. Removal of cotyledons, the 1st leaf pair or axillary buds produced no significant effects. The number of leaf pairs on the main axis and in buds in the 3rd leaf node and the height of their apices were not significantly changed. None of the surgical treatments used had any effect on flowering (Tab. 2).

Effects of Decapitation.

In 21-d old plants, decapitation above the 1st node caused a significant increase in the number of leaf pairs in axillary buds of both induced and non-induced plants; induced plants also exhibited a significant elongation of axillary apices. Removal of subtending leaves reduced these changes, but the difference between the intact and decapitated plants remained significant. The number of flowering buds was not significantly affected by any treatment, although it was appreciably lower in the decapitated and defoliated plants.

Decapitation above the 2nd node brought about a significant increase in the number of the leaf pairs in the axillary buds at that node in plants grown in continuous light as well as in the induced ones. Removal of the 2nd pair of leaves reduced these effects. No significant effects were found in buds at the 1st node. Decapitation above the 2nd node did not significantly affect flowering in these 21-d old plants.

In 8- and 9-d old plants decapitation above the 1st node brought about a significant increase in the number of leaf pairs in axillary buds and flowering was significantly inhibited (Tab. 3).

DISCUSSION

Surgical treatment has been generally adopted in studies of correlations. However, removal of an organ affects a complex network of correlative relationships. Thus it is difficult to atribute the observed effect solely to the loss of the manipulated organ. Moreover, wounding effect itself may also contribute to the observed changes.

Table 1

Effects of removal of selected organs on the mean number of leaf pairs and apex height in 21-d old *Chenopodium rubrum* plants grown in continuous light (non-induced plants and no flower was found). Intact and surgically treated plants are compared. s.d. – standard deviation . * stimulation $t > P$ 0.05 ; **, $^{--}$ stimulation, inhibition resp. $t > P$ 0.01.

	node 1 axillaries		node 2 axillaries		node 3 axillaries		leaf pairs on main axis	apical bud
	leaf pairs	apex [mm]	leaf pairs	apex [mm]	leaf pairs	apex [mm]		apex [mm]
intact plants	2.50	0.050	2.51	0.070	2.51	0.081	7.70	0.393
± s.d.	0.12	0.020	0.11	0.004	0.15	0.006	0.22	0.033
removed organs								
cotyledons	2.60	0.050	0.31	0.050	2.61	0.050	6.80	0.321
± s.d.	0.28	0.002	0.03	0.003	0.15	0.003	0.31	0.054
1st leaf pair	2.21	0.050	2.62	0.050	2.42	0.050	7.81	0.171^{--}
± s.d.	0.27	0.003	0.16	0.003	0.33	0.003	0.33	0.022
2nd leaf pair	1.92	0.050	2.31	0.050	3.12	0.051	8.21	0.152^{--}
± s.d.	0.22	0.005	0.15	0.015	0.17	0.015	0.37	0.031
3rd leaf pair	2.60	0.450	2.70	0.050	2.82	0.075	7.42	0.371
± s.d.	0.18	0.005	0.16	0.007	0.25	0.016	0.57	0.070
node 1 axillaries			2.90	0.055	3.12	0.092	8.62*	0.440
± s.d.	–	–	0.09	0.005	0.10	0.014	0.24	0.067
node 2 axillaries	2.82	0.055			2.62	0.085	8.81**	0.322
± s.d.	0.19	0.005	–	–	0.16	0.013	0.19	0.030

Table 2

Effects of removal of selected organs on the mean number of leaf pairs, apex height and flowering in 21-d old *Chenopodium rubrum* plants induced to flowering by two cycles (12h of darkness + 12h of light). Intact and surgically treated plants are compared. s.d. – standard deviation. $^{-}$ inhibition, * stimulation $t > P$ 0.05; $^{--}$, ** inhibition, stimulation resp. $t > P$ 0.01.

	node 1 axillaries			node 2 axillaries			node 3 axillaries			leaf pairs on main axis	apical bud	
	leaf pairs	apex [mm]	flowering [%]	leaf pairs	apex [mm]	flowering [%]	leaf pairs	apex [mm]	flowering [%]		apex [mm]	flowering [%]
intact plants	2.41	0.130	10.0	1.60	0.411	90.0	1.80	0.64	100.0	6.61	1.220	100.0
± s.d.	0.05	0.020	9.2	0.11	0.054	8.3	0.20	0.02	0	0.21	0.018	0
removed organs												
cotyledons	2.10	0.220	28.0	1.10	0.500	100.0	1.31	0.720	100.0	6.80	1.160	100.0
± s.d.	0.22	0.411	6.8	0.22	0.015	0	0.15	0.019	0	0.17	0.021	0
1st leaf pair	2.21	0.191	23.0	2.01	0.470	100.0	1.70	0.540	100.0	7.81	1.060	100.0
± s.d.	0.23	0.018	8.8	0.15	0.012	0	0.19	0.047	0	0.17	0.054	0
2nd leaf pair	1.70^{-}	0.081		1.61	0.322	90.2	1.20	0.531	100.0	7.41	1.281	100.0
± s.d.	0.28	0.019		0.15	0.041	5.8	0.23	0.041	0	0.58	0.260	0
3rd leaf pair	2.42	0.160	30.1	3.12**	0.621**	90.0	1.81	0.541	100.0	7.20	1.101	100.0
± s.d.	0.15	0.041	8.2	0.26	0.056	6.2	0.23	0.044	0	0.33	0.491	0
node 1 axillaries				0.900	0.420	100.0	1.12	0.611	100.0	7.22	1.080	100.0
± s.d.	–	–	–	0.315	0.020	0	0.25	0.041	0	0.17	0.067	0
node 2 axillaries	2.31	0.131	5.1				0.90	0.542	100.0	7.22	1.281	100.0
± s.d.	0.14	0.027	2.2	–	–	–	0.22	0.041	0	0.33	0.085	0

Table 3

Mean number of leaf pair, height of apices and flowering in *Chenopodium rubrum* plants induced to flower. Intact plants and ones decapitated above the 1st node are compared. ± s.d. – standard deviation, * stimulation $t > P$ 0.05,**, $^{--}$ stimulation, inhibition resp. $t > P$ 0.01.

Plant age [d]	number of inductive cycles		node 1 axillaries			leaf pairs on main axis	apical bud	
			leaf pairs	apex [mm]	flowering [%]		apex [mm]	flowering [%]
8	2	intact	1.09	0.28	19.0	5.31	0.531	71.0
		± s.d.	0.09	0.01	5.2	0.10	0.020	9.3
		decapitated	3.23**	0.23	2.0^{--}	–	–	–
		± s.d.	0.10	0.01	2.4			
	3	intact	1.16	0.360	100	5.61	0.581	100
		± s.d.	0.12	0.014	0	0.14	0.052	0
		decapitated	2.81**	0.351	33.0^{--}	–	–	–
		± s.d.	0.11	0.011	5.6			
9	3	intact	2.00	0.422	93.7	5.00	0.743	100
		± s.d.	0.09	0.017	7.9	0.04	0.031	0
		decapitated	2.60*	0.440	37.5^{--}	–	–	–
		± s.d.	0.26	0.015	12.9			

Correlations are usually explained in terms of hormonal and/or nutritional relationships. In the present experiments no phytohormones or sugars were applied to substitute for the removed organs and any explanation of described correlations would be mere speculation. These aspects will be dealt with in another paper.

Depending upon position, removal of one pair of shoot organs brought about significant changes in the number of leaf pairs, in height of apices or it had no effect. In plants grown in continuous light significant changes were observed in terminal bud. In induced plants, axillary buds, mainly those in the 2nd node were significantly affected.

The same surgical treatment generally resulted in different effects in plants grown under continuous light and in induced plants. For example, removal of the 2nd leaf pair brought about a significant shortening of the terminal shoot apex in plants grown in continuous light while in induced plants a reduction in the leaf pair number in axillary buds of the 1st node was found. Studying correlations by means of ^{32}P distribution, different shoot organ relationships were again found in plants grown in continuous light and in dark treated plants (Pavlová *et al.* 1990). Axillary bud activation was observed already during the first four hours of darkness. These results are further evidence that "... a modification in the environment (change of photoperiod, for instance) disturbs the correlative context previously realized." (Miginiac 1978).

Decapitation also markedly changed the expression of mutual organ relationships. In non-decapitated plants, whether grown in continuous light or induced, there were no significant relationships between axillary buds and their subtending leaves. In induced plants positive or negative correlations were found between leaves on the main axis and axillary buds of the next node below. This may perhaps reflect the architecture of the vascular system, for a main stem leaf trace and the trace of its axillary bud do not necessarily connect with vascular bundles of a central cylinder in the same node. A leaf trace may traverse one or more internodes before it diverges towards the leaf, whereas a developing bud establishes a direct vascular connection with the nearest vascular strand (Esau 1977).

However, in decapitated plants there was a clear positive correlation between mature leaves and their axillary buds regardless of the light regime.

Flowering was not significantly affected by removal of one pair of leaves, indicating that the remaining leaves took over their photoreceptive function.

Flower inducing regimes bring about precocious formation of axillary buds and growth of previously existing ones in many plant species (Bernier *et al.* 1981). This phenomenon is interpreted as a decrease of apical dominance (Thomas 1961, 1962). Moreover, axillary buds of *C. rubrum* show a lower flower potency then the terminal bud (Opatrná *et al.* 1980). Thus it was suspected that apical dominance would play an important role in regulating the flowering process.

However, decapitation causing a complete release of buds from apical dominance resulted only in the activation of young leaf formation in axillary buds, whereas flowering was not affected in 21-d old plants and was even significantly inhibited in the 8- and 9-d old ones.

It seems, that in flowering control we should distinguish between the lowering of apical dominance by decapitation which enhances the vegetative growth of axillary buds and that which is accompanied by leaf growth inhibition due to flower inducing photoperiod. It is not clear so far, whether the physiological regulation of apical dominance is identical in both cases.

The inhibitory influence of roots, described previously in *C. rubrum* by Krekule and Seidlová (1973), Josefusová and Opatrná (1985) and Josefusová *et al.* (1985) should also be considered in connection with regulation of flowering in axillary buds. Moreover, no difference between the flowering of terminal and axillary buds was observed if the axillary buds with their subtending leaves were cultivated in vitro without roots (Vondráková and Opatrná 1989).

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