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Root-Shoot Correlation Linked with Photoperiodic Floral Induction in *Chenopodium rubrum* L.

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Abstract. Inhibition of root growth was observed in *Chenopodium rubrum* under photoperiodic conditions inducing flowering. That this inhibition is mediated by the cotyledons was shown directly by the effect of their excision, which changes the responsiveness of the roots to photoperiodic treatment. On the other hand, decapitation did not lead to such an effect. Some evidence is put forward suggesting that changes in IAA may be involved in these correlations. The existence of two different mechanisms of photoperiodic action in flowering and in root growth is proposed to explain these differences.

Organ correlations are often considered to be part of the control mechanisms for flowering (MIGINIAC 1978, KREKULE 1979, BERNIER *et al.* 1981, MIGINIAC and SOTTA 1985). The apical meristem, due to its largely heterotrophic character, relies in nutritional and hormonal aspects on other organs, and may thus be affected by any changes taking place in the shoot and root. In previous studies we have shown that photoperiodic conditions bringing about flowering of the short day plant *Chenopodium rubrum* considerably affect the growth pattern of shoots and roots (OPATRNÁ *et al.* 1980, ULLMANN *et al.* 1980). The growth of leaves, cotyledons and roots is suppressed whereas stimulation of hypocotyl growth is observed. Most striking of all these growth changes is the inhibition of root growth, which can play a role in the transition of plants to the reproductive stage. Three types of evidence support such an interpretation: 1) The flower enhancing effect of root removal may be cancelled by application of exogenous cytokinins (KREKULE 1976, SOTTA 1978). 2) A drop in the endogenous level of cytokinins was observed in roots due to photoperiodically inductive conditions (PŘÍVRATSKÝ 1974). 3) The exogenous application of cytokinin during induction changes the growth pattern of the shoot apical meristem in a way which partly counteracts the effect of induction (SEIDLOVÁ and KREKULE 1977, SEIDLOVÁ 1985).

The pattern of root growth was thoroughly investigated in a study by OPATRNÁ and JOSEFUSOVÁ (1986). It was found that photoperiodic conditions inducing flowering brought about inhibition of root growth (to 40—50 % of the control values). This effect is not due to the direct action of light and darkness on roots but is mediated by the shoot. An attempt will be described

here to specify which particular organ of the shoot is responsible for such inhibition. Comparing the responsiveness of both reactions (that is photoperiodic floral induction and photoperiodic inhibition of root growth) to different treatments should clarify whether they possess a common control mechanism.

MATERIAL AND METHODS

The qualitative short day plant *Chenopodium rubrum* L. (selection 374) was used. The plants were grown in transparent vessels in water culture on half concentration Knop's solution at 20 $\pm$1 °C and under continuous light from fluorescent tubes (of approximately 30 Wm^{-2}).

Photoperiodic treatment, consisting of three cycles of 16 h darkness and 8 h light, was applied to 8-d old plants. The red light irradiation (2.6 nW $cm^{-2}nm^{-1}$ at 660 nm) was provided by Philips TL 40W (15 fluorescent tubes, with red filter supplied by Röhm and Haas GmBH, Darmstadt). After termination of the photoperiodic treatment all plants were again grown in continuous light.

Surgical treatments such as cotyledon removal and decapitation were done on 7-d old seedlings. Decapitation brought about outgrowth of cotyledonary buds in some plants, and these were excluded from the experiments. Black cloth was used to cover the cotyledons.

The parameters of root system (length of primary root, length of lateral roots and their number) were measured using a slide projector adjusted to give a ten fold magnification.

Estimation of the level of free IAA was done fluorimetrically as described by PAVLOVÁ and KREKULE (1984).

RESULTS

The shoots of experimental plants consisted only of cotyledons, hypocotyl and terminal bud, which on day 7—8 is composed of a terminal meristem with four leaves, at most 2 mm long. An experiment was designed to find out which part is responsible for the root growth inhibition. For that purpose

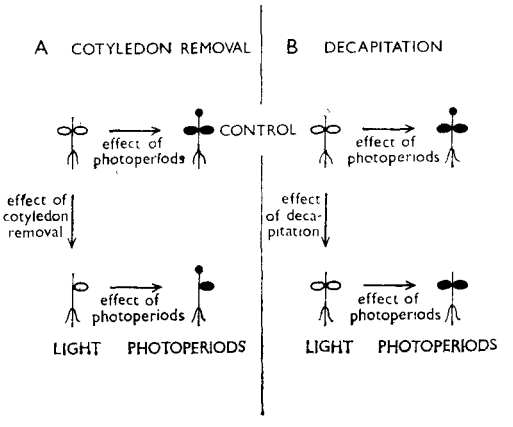

Fig. 1. Scheme of experiment.

the progress of root growth was followed in intact plants subjected to photoperiodic treatment and compared with the root growth of plants induced after removal of a cotyledon or after decapitation (Fig. 1). We assumed that removal of the organ responsible for root growth inhibition might change the response of roots to the conditions of photoperiodic induction.

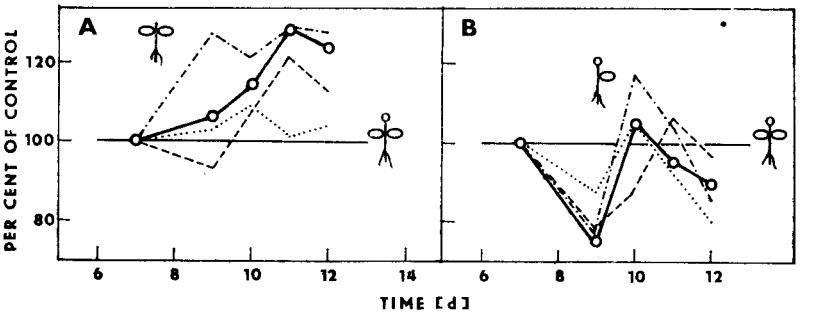

Fig. 2. Effect of A) terminal bud removal and B) cotyledon removal on root growth of *Chenopodium rubrum* in continuous illumination; — full line: total length of root system; dashed line: length of primary root; dot-and-dashed line: total length of lateral roots; dotted line: number of lateral roots.

The effect of cotyledon removal or decapitation in themselves was tested in plants grown under continuous illumination (Fig. 2). Decapitation resulted in stimulation of root growth which was demonstrated by the third day after surgical treatment in all the parameters of root growth. Cotyledon removal resulted in a temporary inhibition of root growth.

The next experimental step was to compare the root growth response to photoperiodic treatment in intact plants and in plants deprived of an organ (Fig. 3). The results clearly show that cotyledon removal alters the root growth response to photoperiodic induction as compared with that of intact plants. On the other hand decapitation did not lead to such a change. It follows that cotyledons represent the organ mediating root growth inhibition due to photoperiodic flower induction.

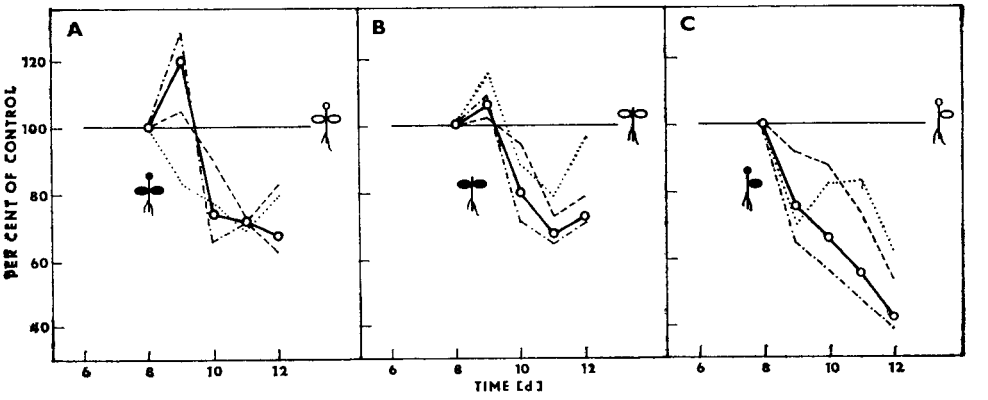

Fig. 3. Effect of photoperiodic induction on root growth of A) intact plants, B) decapitated plants and C) plants deprived of one cotyledon. See Figs. 1 and 2 for other details.

The cotyledons represent the main receptors of the photoperiodic signal in these plants. The next question is: Does the root growth inhibition rely on the same control mechanism as flower induction? Two sets of experiments were designed to investigate this problem. In the first case cotyledons only were darkened during the inductive cycles (Fig. 4). In the second case red light breaks were used to cancel the inductive effect of the dark period on

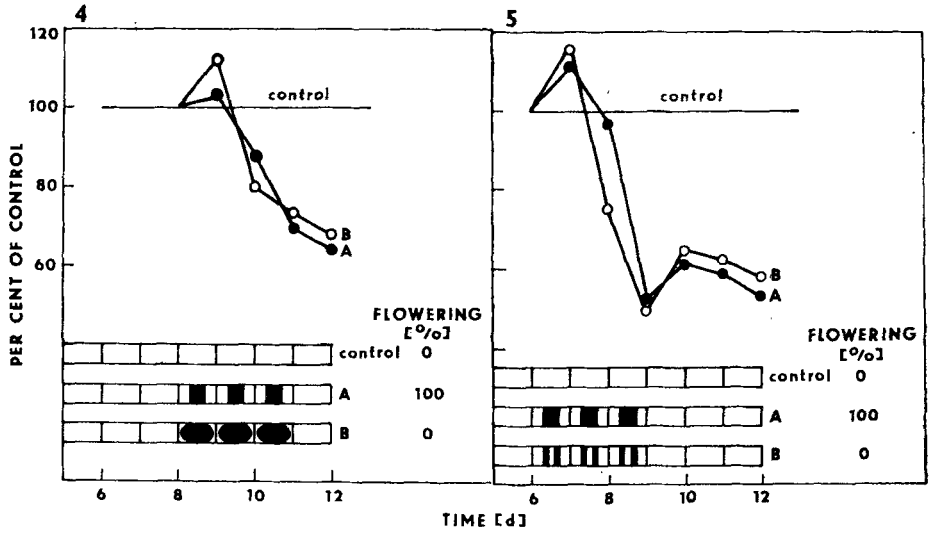

Fig. 4. Effect of A) photoperiodic induction and B) cotyledon darkening on root growth.
Fig. 5. The changes of root growth due to A) photoperiodic regime with continuous dark period and B) with dark period interrupted by red light breaks.

flower induction (Fig. 5). In both cases inhibition of root growth was observed comparable with that caused by normal photoperiodic treatment. However, flowering did not occur. Hence, we may conclude that the control mechanism involved in flowering and root growth seems to be different.

Auxin supplied by the shoot is usually considered to be the most important regulatory system of root growth. We estimated the changes in the endogenous level of free IAA in shoots and in roots during photoperiodic induction. Results are presented in Fig. 6, which shows a striking similarity between the auxin fluctuation in shoots and roots that is caused by the second dark period. In both cases the auxin level increased immediately following the onset of darkness and decreased later on.

DISCUSSION

It has been demonstrated that the inhibition of root growth due to photoperiodic conditions that induce flowering is mediated by the cotyledons. The correlations between cotyledon area and root growth is rather weak under conditions of continuous illumination. The removal of one cotyledon is thus reflected only by temporary drop in root growth rate. However, under conditions of photoperiodic induction the absence of one cotyledon

distinctly changes the response of roots to photoperiodic induction. Photoperiodic treatment possibly brings about changes in production of compounds regulating root growth. HENSON and WAREING (1977) also established the existence of shoot to root signals in *Xanthium* which control the decrease of cytokinin production in roots due to short day. BEEVER and WOOLHOUSE

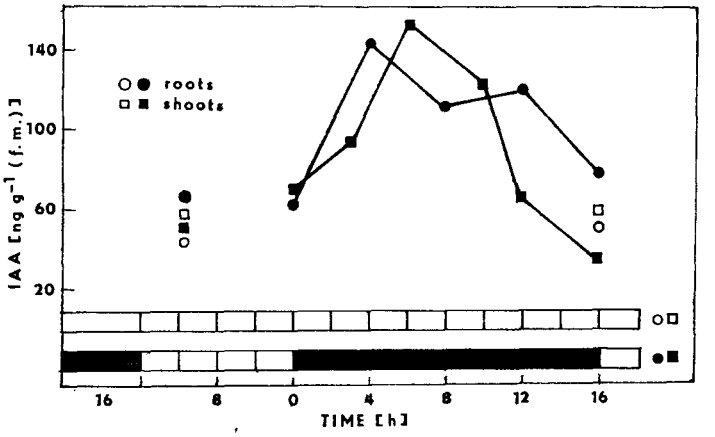

Fig. 6. Fluctuation of free IAA level in roots (○);and in shoots (□) during the 2nd dark cycle of photoperiodic induction, compared with controls in continuous light.

(1975) interpret the decreasing in diameter of roots after photoperiodic induction in *Perilla* as a result of an insufficient supply of growth substances from the shoot to maintain normal root growth.

In order to investigate the physiological mechanism of root-shoot correlation related to photoperiodic induction of flowering, the levels of free IAA have also been studied. PAVLOVÁ and KREKULE (1984) found characteristic patterns of free IAA fluctuation in shoots during photoperiodic induction. The absolute amount of IAA was higher in plants induced by dark treatment than in those grown under continuous illumination. A practically identical situation, *i.e.* similarity in the level and fluctuation pattern of free IAA was found in the roots.

The rise in root growth rate after decapitation suggests that supra-optimal levels of free IAA may be involved in its control. The shoot apex represents an important source of IAA and its absence possibly leads to a decrease of IAA in the roots, where optimal levels for growth may thus be reached. Similarly, the root growth inhibition due to inductive short days may involve shifts in endogenous IAA concentration. Some reports suggest marked effects of inductive photoperiods on the auxin status of cotyledons of a short day plant (PODOLNYÏ and CHAÏLAKHYAN 1970).

In general, root growth inhibition and floral induction possess some common features. The magnitude of the effect is related to the number of short days, and the critical photoperiod is of the same length (OPATRNÁ and JOSEFUSOVÁ 1986). On the other hand red light breaks which cancel flowering do not disturb the growth reaction of roots. Moreover, darkening of cotyledons will bring about root growth inhibition but not the induction of flowering. (However, it is not clear whether the darkening treatment as performed was

light-proof, nor whether cotyledons were overheated.) The existence of two different control mechanisms responding to the same ecological signal may be inferred from this indirect evidence. These two mechanisms do not seem to be causally related as the flowering induction always leads to root growth inhibition but not *vice versa*.

The inhibition of root growth due to cultivation conditions (SHINOZAKI and TAKIMOTO 1982), and/or root removal (MIGINIAC 1978, SOTTA 1978) is not usually associated with induction of flowering under strictly non-inductive conditions. However, such treatments may be accompanied by distinctly enhanced flowering when acting together with other factors affecting growth rate, such as low temperature (WELLENSIEK 1968, CHAMONT *et al.* 1982) or treatment with plant growth regulators (SHINOZAKI 1985).

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