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Rapid Interorgan Communications in Higher Plants with Special Reference to Flowering

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Abstract. Several examples of transmission of rapid signals within plants are described. Most of these signals may be inhibited by pretreating plants with LiCl, with inhibitors of ionic permeability, or with substances interfering with Ca^{2+}. Accordingly, they are dependent on ionic changes. LiCl also prevents or delays the onset of flowering in long-day plants. In addition isolated organs or tissues most often do not react to an external stimulus as do similar organs or tissues within an intact plant. All these facts lead to the conclusion that plants are highly integrated organisms. Any change in the ionic equilibrium occurring in one part of these organisms has rapid consequences in other parts. This hypothesis may be applied to the floral process: after perception of the appropriate environmental conditions, the leaves modify the orientation of meristem differentiation by promoting the redistribution of ions (especially Ca^{2+}, which has a "second messenger" function).

The floral differentiation of an apex in plants sensitive to a photoperiodic stimulus is dependent on a signal produced by the leaves. The hypothesis that this signal simply is a hormone-like substance migrating from the leaves to the meristem was not confirmed by the identification of such a substance. It was also suggested that the flower inducing signal is composed of several substances sequentially reaching the apex (BERNIER 1976).

Alternatively, we have proposed that the displacement of a specific substance is not required to explain flowering (GREPPIN *et al.* 1978). We have hypothesized that the early steps of the floral induction (the first hours) may involve only changes in membrane functions and regulatory mechanisms which promote reproductive development. These changes which are triggered in one part of the organism (*i.e.* the leaves) by the appropriate environmental conditions, may then spread into the whole plant. One of the consequences is the development of floral buds by activation of the cells of the prosporogenous meristem (mitosis). These early steps do not necessitate the synthesis of new proteins (GREPPIN and GAGLIARDI 1980). Our hypothesis is substantiated by the existence of rapidly transmitted signals in plants which in some cases may be translated into a developmental response.

Rapid Interorgan Signals

Peroxidase activity in spinach leaves is quickly modulated by short irradiations with red or far-red light. The shape of this modulation is different

TABLE 1
Plant responses inhibited or modified by LiCl

Plant material	Stimulus	Response	Reference
Internode of *Bryonia dioica*	rubbing	-inhibition of growth -increase of peroxidase and ethylene	BOYER *et al.* 1983
Cotyledons of *Bidens pilosus*	prickings, salt	-development of opposite cotyledonary bud	DESBIEZ and THELLIER 1977
	droplet	-inhibition of hypocotyl growth	DESBIEZ *et al.* 1981
		-increase of peroxidase and ethylene in hypocotyl	DESBIEZ *et al.* 1983
		-changes in Ca^{2+} and Mn^{2+} in hypocotyl	DESBIEZ *et al.* 1984b
Leaves of *Spinacia oleracea*	light	-peroxidase changes in non-irradiated leaves	KAREGE *et al.* 1982b
Plants of *Spinacia oleracea*	photoperiod	-floral induction by continuous light	KAREGE *et al.* 1982a
Leaves of *Sedum album*	ozone	-peroxidase secretion in cut plants	CASTILLO 1984

in vegetative and induced plants (KAREGE *et al.* 1979). It was shown that the peroxidase activity of unirradiated leaves is also modified when other leaves are irradiated. The change in unirradiated leaves practically parallels the change in leaves exposed to R or FR, suggesting either the transmission of a rapid signal between the leaves, or the modification of ionic equilibrium in irradiated leaves which could be transmitted to other leaves (PENEL and GREPPIN 1975). The transmission of this light effect is inhibited by pretreating the plants with LiCl, ouabain, tetrodotoxin, tetraethylammonium, EGTA or the ionophore A23187 (KAREGE *et al.* 1982 b). The inhibition by EGTA and A23187 indicates the involvement of Ca^{2+} in this modulation of the peroxidase activity by light. This peroxidase is mainly associated with the leaf lower epidermis and is activated by Ca^{2+} (PENEL and GREPPIN 1984). A more detailed study showed that LiCl, EGTA and A23187 suppress the delocalised effect of light when they are applied either on irradiated or on unirradiated leaves. Ouabain exerts its inhibitory effect only when it is sprayed on irradiated leaves (KAREGE *et al.* 1982 b). This result indicates that it may be possible to discriminate between the generation, transmission and reception of the signal.

Using *Bidens pilosus* seedlings it was shown that a small number of prickings with a needle in the midrib of one cotyledon results in the preferential development of the axillary bud opposite to the pricked cotyledon after removal of the apical bud (DESBIEZ *et al.* 1984 a). The excision of both cotyledons (pricked and unpricked) immediately after pricking does not suppress the preferential development of the opposite bud. In this experimental system, there is a rapidly transmitted signal generated by the prickings. This signal can be blocked by treatment of seedlings with LiCl or ouabain (DESBIEZ and THELLIER 1977). In addition, pricking in a cotyledon reduces the hypocotyl

growth, and enhances the peroxidase activity (DESBIEZ *et al.* 1981) and the ethylene production (DESBIEZ *et al.* 1983) in the hypocotyl. The enhanced capacity of synthesizing ethylene in hypocotyl is observed immediately after pricking the cotyledon (DESBIEZ, personal communication).

The existence of rapidly transmitted signals was also demonstrated by the experiments of DAVIES and SCHUSTER (1981), who showed that wounding elicited rapid and massive formation of polysomes in pea stems. The kinetics of polysome formation was similar in tissues adjacent to or up to 150 mm distant from the point of injury. This result can only be interpreted by the almost immediate production of a wound signal that travels rapidly both acropetally and basipetally.

In 1970, KANDELER reported that under long days LiCl inhibited flowering in the long-day plant *Lemna gibba* but stimulated flowering in the short-day plant *Lemna perpusilla*. Since that report, LiCl was often shown to suppress or modify rapid responses of plants to external stimuli, as well as the transmission of interorgan signals within the plants (Table 1). Pretreatment of spinach, a long-day plant, with LiCl delays the appearance of floral buds after a transfer of plants from short days to continuous light (KAREGE *et al.* 1982 a). A plant may be induced by exposing a single leaf to continuous light, the other remaining under short days. If the leaf is treated with LiCl, the floral differentiation of the shoot apex occurs later and the acquisition of the floral state by the leaves kept under short days is also delayed. Therefore, the floral process, like the rapid intercellular signals, is sensitive to Li^+.

Several explanations of the effect of Li^+ were proposed. It could take the place of K^+ in the cells and thereby lower the faculty of these cells to respond to external stimuli (DESBIEZ and THELLIER 1977). In helix neurons it was shown that Li^+ causes an elevation of intracellular Ca^{2+} concentration, thus maintaining the cells in a chronic stimulated state (ALDENHOFF and LUX 1982). It must be pointed out that the plant responses inhibited by Li^+ are related to Ca^{2+} redistribution (KAREGE *et al.* 1982b, DESBIEZ *et al.* 1984 a,b).

The Floral Induction

The flowering process, in photoperiodic plants at least, depends on interorgan communications. Something happens in the leaves which is transmitted to the apex. But the flowering process does not only correspond to the differentiation of floral buds. It affects the whole plant organism. This is demonstrated by grafting experiments in which leaves of non-induced plants become competent to transmit the floral stimulus when an induced leaf has been grafted to the plant. It is also shown by using the photomodulation of peroxidase as a test to detect the appearance of the induced state in spinach leaves kept under short days, when a single leaf is subjected to the inductive continuous light (KAREGE *et al.* 1982 a).

A better explanation is that the floral induction corresponds to a "cellular state" that may be present in each part of the plant. This "cellular state", which is not yet defined, would concern membrane properties (membrane potentials, permeability), ion distribution or other discrete parameters.

There are many examples of responses which can be observed in whole plants but not in isolated organs. This is the case of the rapid suppression of cucumber stem growth by blue light (COSGROVE 1981), of the effect of gibberellic acid on elongation of spinach leaf petiole (data unpublished), or of the

ozone-induced secretion of peroxidases in *Sedum album* leaves (CASTILLO 1984). Put together with the data concerning the transmission of rapid signals in plants, these experimental facts allow the conclusion that the diverse parts of a plant are strongly interdependent. This dependence is not only based on the migration of chemical regulators, but also on ionic equilibria. Experiments with *Bidens* seedlings have shown that pricking one cotyledon results within one hour in great changes in the distribution of ions: there is a decrease of K^+ in the roots, a decrease of Ca^{2+} and an increase of Mn^{2+} in the hypocotyl (DESBIEZ *et al.* 1984 b).

All these experimental facts offer new clues to study the floral process and give the opportunity to leave the old track of the hormonal explanation. In particular, the redistribution of ions, among which Ca^{2+}, a "second messenger", following an exposure of plants to flower promoting conditions, is an attractive hypothesis to explain the floral differentiation of meristems.

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BOOK REVIEW

KOZLOWSKI, T. T. (ed.): FLOODING AND PLANT GROWTH. Physiological Ecology. A Series of Monographs, Texts, and Treatises. — Academic Press, Orlando — San Diego — San Francisco — New York — London — Toronto — Montreal — Sydney — Tokyo — São Paulo 1984. Pp. 356.

The name of the editor — professor of forestry and director of the Biotron at the University of Wisconsin T. T. Kozlowski — is certainly well-known to every reader for a large amount of his scientific papers as well as his previous books (*e.g.* Water Deficits and Plant Growth, Vol. I—VII, Growth and Development of Trees, Vol. I—II, Seed Biology, Vol. I—III, The Growth and Environmental Stresses, Responses of Plants to Air Pollution). Similarly, the other contributors (K. J. Bradford, M. C. Drew, D. D. Hook, M. B. Jackson, S. G. Pallardy, F. N. Ponnamperuma, D. M. Reid, R. E. Sojka, L. H. Stolzy, S. J. Wainwright) are famous specialists. In this book they turn to a very interesting topic — the effect of flooding on metabolism and growth of herbaceous and woody plants. Even if temporary or continuous flooding with fresh or salt water is very common throughout the world, responses of plants to flooding have received less attention than their responses to drought. That is the reason why the appearance of this book is so valuable.

The opening chapter discusses the causes and extent of flooding throughout the world. The second chapter deals with the effects of flooding on physical, chemical and biological processes that determine the quality of the soil as a medium for plant growth. The subsequent two chapters treat in detail the effect of flooding on growth and development of herbaceous and woody plants (from the anatomical and morphological changes of their roots and shoots to the changes in the composition of communities). As the effects of environmental stresses on growth of plants are mediated through the changes in physiological processes, chapters 5 and 6 present an overview of the effects of flooding on some important aspects of water, carbohydrate and mineral relations and on synthesis, metabolism and transport of hormones. The flooding in relation to plant diseases is summarized in the seventh chapter. The final two chapters give examples of the physiological and morphological adaptations of individual plant species to flooding with fresh or salt water.

The book — as all volumes of this Series — is well printed and arranged. The text is supplied with numerous instructive figures and summarizing tables which enable easy orientation and understanding. Extensive bibliography is added to every chapter.

The book will be very attractive to all those interested in the pertinent research field as a remarkable source of up-to-date informati on.

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