AUXIN APICAL CONTROL OF THE AUXIN POLAR TRANSPORT AND ITS OSCILLATION – A SUGGESTED CELLULAR TRANSDUCTION MECHANISM

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ABSTRACT

The proposed hypothesis concerns the transduction of auxin molecular signals arriving from the apoplast at the plasma membrane or recognized by the proteinaceous receptors of the responding cell, to the concentration gradients oscillating in the supracellular space, associated usually with the specific plant growth and differentiation. Acting as an agonist from outside the target cell auxin stimulates in this cell: (1) the liberation of auxin from the cytosolic pool of its conjugates directly into the basipetal efflux; (2) the synthesis of new auxin which restores the cytosolic reserve of auxin conjugates. The functioning of such a system may be effective in a series of processes initiated by the changing concentration of cytosolic calcium. The hypothesis suggests a molecular mechanism for the development and effective operation of the morphogenetic field in the supracellular space of the plant body, such as the field resulting from auxin waves discovered in cambium.

KEY WORDS: auxin polar transport, morphogenetic field

INTRODUCTION

Evolution of the sessile strategy of life of autotrophic plants, as they became adapted to the arid, highly polarized habitat of the Earth's surface, depended upon the development of an effective control system of polarity expression, contributing to the positional information at the successive levels of ontogenesis (Jacobs 1978). A combination of processes responsible for the plant physiological polarity provides a mechanism integrating environmental signals and genetic programs within a systems of morphogenetic information for coordinated growth and development of the multicellular organism. Excellent reviews of various aspects of plant development associated with polarity expression are available (Went 1932, Bloch 1943, 1965, Bunning 1952, Sinnott 1960, Stebbins 1966, Quatrano 1978, Warren-Wilson 1980). Most studies refer to the mechanism which controls polarity expression in plants with auxin basipetal transport. However, in spite of the extensive experimental work pertaining to the auxin polar transport and availability of several theories explaining its mechanism or its significance in plant morphogenesis (Van der Weij 1932, 1943, Went 1941, Leopold & Hall 1966, Osborne 1968, Goldsmith 1968, 1977, Hertel et al. 1969, Rubery & Sheldrake 1974, Raven 1975, Cande & Ray 1976), little is known about the processes integrating the cellular and supracellular levels of polarity expression within an effective system of controlling plant morphogenesis by auxin (Hertel 1992).

The seemingly dual role of auxin in control of plant body differentiation: (1) its direct effect as an agonist starting the molecular transduction processes which provide a metabolic basis for cell specialization, and (2) its contribution to the formation of morphogenetic field responsible for differentiation of the specific functional pattern at all levels of plant body organization, have usually been studied independently. This paper presents a hypothesis based upon the recent advances in studies on cellular transduction of the hormonal signals, and some older ideas explaining the mechanism of

long distance auxin translocation. The hypothesis may be helpful in future experimental studies on the formation of morphogenetic field closely associated with polarity of cells in respect to auxin transport. The proposed hypothesis focuses on transduction of the auxin molecular signals arriving from the apoplast at the plasma membrane or recognized by the internal proteinaceous receptors of the responding cell, into the concentration gradients oscillating in the supracellular space which have been usually (and in various ways) associated with specific plant growth and differentiation (Shen-Miller 1973a,b, Zajaczkowski & Wodzicki 1978, Zajaczkowski et al. 1984, Wodzicki et al. 1987, Wodzicki & Zajaczkowski 1989).

OUTLINE OF THE HYPOTHESIS

The proposed mechanism of auxin signal transduction, changing the polarity expression in the basipetal auxin efflux from the responding cell is based on the general thesis that auxin acting as an agonist from outside the target cell stimulates in this cell:

1. the liberation of auxin from the cytosolic pool of its conjugates directly into the basipetal efflux;
2. the synthesis of new auxin which restores the cytosolic reserve of the auxin conjugates.

The functioning of such a system may be effective in a series of processes started in conjunction with a changing concentration of cytosolic calcium. These processes are specified below in the complementary hypotheses as follows.

1. Stimulation of the hydrolysis of auxin conjugates occurs as a result of auxin transduction by a cellular control system of calcium concentration in the cytosol of the responding cell.
2. The system controlling cytosolic calcium concentration is also involved in directing the auxin released from the conjugates to its efflux (maybe in the process which involves coupling of the hydrolysis with the action of proteinaceous carrier of auxin efflux) at the cell membrane.
3. The auxin conjugates (or only some of them) constitute an inhibitor of the new auxin synthesis (possibly at the level of transcription of the mRNA encoding the enzymatic proteins of the auxin synthetic pathway).

4. Decrease in the level of auxin conjugates in cytosol, resulting from the induced hydrolysis, abolishes the inhibition, and the synthesis of new auxin proceeds as stimulated by the transduction system of auxin signal.

5. Newly synthesized auxin is conjugated and restores the cellular pool of bound auxin. This contributes to the feedback inhibition of auxin synthesis. The surplus of synthesized auxin is immediately exported.

6. The auxin molecules effective in control of morphogenesis are only these which at the cellular level interact with their proteinaceous receptors. All other molecules of auxin entering the cell from apoplast are metabolically inactivated or exported. The level of free auxin molecules in the cytoplasm is maintained at the minimum.

An outline of the molecular events contributing to the mechanism presented above is summarized in Figure 1.

cell" becomes the „gland" in respect to the next proximal cell. In this concept, polar auxin transport in the stem is effective as a chain of auxin-stimulated auxin effluxes and auxin syntheses taking place in the series of cells arranged along the direction indicated by orientation of their polar axes. The hypothesis presented above proposes the molecular mechanism which conforms to Soding's old idea (1937), explaining in analogous way the long distance polar transport of auxin in cambium of trees.

Apoplast in this hypothesis plays an important role of medium conveying the active free auxin molecules (the hormone) from the apical "gland" to the basal "target" cell. The direct contact of the two cell plasmalemmas with opposite sides of the same thin cell wall, allows sufficiently rapid transfer of auxin by simple diffusion (unlike in animals where the active molecules circulate in the blood or lymphatic system at the expense of metabolic energy). In plants, the apo-

Fig. 1. The proposed mechanism of cellular transduction of the auxin signal received by the responding, structurally polar cell, to a change (or periodic changes) of the amount of auxin basipetal efflux which supports changes of polarity expression in auxin transport throughout multicellular systems. Processes documented or suggested in literature (thin solid or dotted lines), and those specific for operation of the proposed mechanism (thick solid and dashed lines). Processes of stimulation (+), inhibition (-).

EXPERIMENTAL BACKGROUND AND DISCUSSION

The proposed mechanism of regulating by auxin the polarity expression in its own transport, conforms to the main principle of the hormonal theory as it has been originally formulated, but on an extremely reduced space scale. Each of the two vertically neighboring cells acts as the "gland" (producing and secreting the hormone) in respect to its proximal cell. The latter reacts as the "target cell": it is competent in the reception of the hormone and responds by the synthesis of the auxin and by its basipetal efflux, subsequently the "target

plast of the tissues in which cells produce and respond to the auxin, would be a site of free auxin accumulation and transient changes of its concentration. A basipetal gradient and a flow of free auxin molecules across the cell wall separating each pair of axially aligned cells must be expected, if the active auxin efflux occurs only at the basal part of plasmalemma.

Auxin, in its free molecular form, has been proved to be an extremely potent physiological agent. Thus, neither the auxin synthesized by the cell itself, nor that entering the cytoplasm from the apoplast is likely to be accumulated in the cytosol in its free form. Instead, it is probably either: 1) Immediately bound to the receptor proteins as signal molecules, 2) stored

by conjugation with low-molecular substances, as suggested by Bandurski et al. (1992), 3) exported by active efflux, or else 4) irreversibly inactivated. The only other possibility preventing uncontrolled action of free auxin in the cytosol would be the segregation of this phytohormone in the special microsomal fraction. Under such circumstances, the question arises whether various data obtained from measuring of what is called free auxin in the plant tissue extracts should not be referred mainly to its apoplastic or vacuolar pool.

All steps of the hypothesis presented above are supported by published results and suggestions of various authors, although many have only a value of circumstantial evidence and require further investigation. A special role in the origin of the hypothesis is played by the data indicating that auxin stimulates: 1) its own transport (Leopold & Lam 1962, Hertel & Flory 1968, Rayle et al. 1969), 2) the polarity of this transport (Wodzicki et al. 1990, 1992), and 3) the oscillations in the expression of auxin polar transport (Wodzicki et al. 1979, 1988, Wodzicki & Wodzicki 1981). Another inspiration was provided by Soding's (1937, 1940/41) concept of chain-like stimulation by auxin its own production in basipetally successive cells of the cambial zone in trees. Other selected literature pertinent to various parts of the hypothesis is summarized below.

1. The polar transport of auxin in plants is associated mainly with meristematic tissues and zones of growing and differentiating cells (Wangemann 1974, Nix and Wodzicki 1974, Goldsmith 1977). Both of these produce auxin and respond to this phytohormone (Went and Thimann 1937).

2. The auxin-binding proteins (ABP), to which the function of receptors active in transduction of auxin signals is ascribed, are associated with various plant cell membranes and cellular compartments. (Hertel et al. 1972, Hertel 1983, 1987, 1991, Brummel & Hall 1987, Venis 1985, Napier & Venis 1991, Barbier-Brygoo et al. 1989, 1991, Palme et al. 1989, 1991, 1992a,b, Palme 1992a).

3. The polarity of auxin transport is associated with structural differences in the construction of plasmalemma at the apical and basal ends of the cell (Hertel & Leopold 1963, Goldsmith & Ray 1973). The basal portion of the cell membrane enriched in auxin binding protein is assumed to be engaged in the efflux of ionic auxin (Jacobs & Gilbert 1983).

4. All main elements of the Ca²⁺ based signal transduction system are present in plant cells (Morre 1989, Trewavas 1991), including the auxin-mediated phosphoinositide turnover and inositol (1,4,5)triphosphate effect, which may be responsible for the intracellular release of calcium ions (Zbell et al. 1988, 1989, 1990, 1991).

5. Auxin may increase the cytosolic level of calcium ions (Morris & Northcote 1977, Kubowicz et al. 1982, Brummer & Parish 1983, Hertel 1983) or initiate oscillations of this concentration as well as of cytosolic pH (Brummer et al. 1984, Felle 1988).

6. The increase of cytosolic concentration of calcium ions stimulates the enzymatic activity of some hydrolases (Hepler & Wayne 1956, Poovaiah & Reddy 1987), although there is no evidence of such an effect upon the hydrolytic system involved in the breakdown of auxin conjugates, e.g. the auxin binding protein 60 kDa with β -glucosidase activity which has been suggested for this type of hydrolytic action (Campos et al. 1992, Palme 1992b).

7. The cytosolic concentration of calcium ions is suggested to cooperate in regulation of the activity of auxin efflux carrier (Dela Fuente 1984, Dela Fuente et al. 1985).

8. Auxin-binding protein 23 kDa associated with auxin efflux (Zettl et al. 1992) is under control of the changing concentration of cytosolic calcium (Hertel 1992, Palme 1992a,b).

9. Auxin stimulates protein synthesis (Meyer et al. 1984a,b) and transcription of selected nuclear genes (Walker et al. 1985, Guiofoyle 1986, Theologis 1986, Kuhlemeier et al. 1987, Kikuchi et al. 1989, Guilfoyle et al. 1992, Palme 1992b). Nevertheless there is no evidence of auxin effect upon synthesis of enzymatic proteins involved in a system responsible for the cellular production of auxin.

10. Auxin conjugates constitute the cytosolic reserve of active auxin and the conjugate metabolism is most important for regulation of the free IAA concentration level (Cohen & Bandurski 1982).

11. The synthetic auxin supplied to the plant tissue is readily converted to its conjugated form (Riov & Gotlieb 1980). The conjugation may prevent peroxidase attack upon IAA (Cohen & Bandurski 1978, Epstein et al. 1980).

12. The exogenous auxin applied apically to the stem cambial region quickly modifies the amplitude and the pattern of oscillations of the stem polarity expression at the long distance from its application site. This excludes the direct action of supplied phytohormone (Wodzicki et al. 1979). The inhibitors of auxin polar transport prevent the effect (Wodzicki & Wodzicki 1981).

13. The auxin synthesized in transgenic cells is immediately exported or metabolized to its inactive forms undetectable by the specific bioassays (Malepszy et al. 1993).

The hypothesis presented in this paper conforms to the important generalizations of Cohen (1983) that: 1) metabolic degradation, or some other mechanism for removal of IAA, is necessary for the auxin responsive system to recover, 2) degradation and biosynthesis must be under rigorous metabolic control in order to establish an appropriate auxin level in a given tissue, and 3) all plants and all plant tissues that have been studied contain most of their IAA as one or more conjugates which in some tissues may account for over 98% of the IAA. The hypothesis suggests a molecular mechanism for the development and effective operation of the morphogenetic field in the supracellular space of the plant body, resulting from the auxin waves discovered in cambium.

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MECHANIZM TRANSDUKCJI KOMÓRKOWEJ EFEKTU AUKSYNY NA JEJ POLARNY TRANSPORT I OSCYLACJE EKSPRESJI POLARNOŚCI TRANSPORTU

STRESZCZENIE

Auksyna spełnia dwoistą rolę w regulacji różnicowania ciała rośliny. Po pierwsze, działa bezpośrednio jako czynnik wzbudzający serię procesów transdukcji, które stanowią metaboliczną bazę dla specjalizacji komórkowej. Po drugie, przyczynia się do tworzenia pola morfogenetycznego, które określa specyfikację wzoru funkcjonalnego struktury na wszystkich poziomach organizacji. Zaproponowana hipoteza opiera się na współczesnej wiedzy, dotyczącej komórkowej transdukcji sygnałów hormonalnych i niektórych elementach starszych koncepcji, objaśniających mechanizm polarnego transportu auksyny. W szczególności, hipoteza ta dotyczy przetwarzania sygnałowego działania molekuł auksyny z apoplastu, odbieranego przez błonę komórkową lub receptory białkowe komórki, na gradienty koncentracji z ich okresowymi zmianami w przestrzeni ponadkomórkowej. Dyskutowana koncepcja sugeruje molekularny mechanizm odpowiedzialny za oscylację przejawów polarności w procesie bazypetalnego wydzielania auksyny z reagujących komórek. Podstawę tych reakcji stanowić może stymulacja uwalniania auksyny przez hydrolizę komórkowego zapasu jej form związanych. Postuluje się też sprzężenie mechanizmu regulującego proces uwalniania auksyny z czynnością białek receptorowych układu wydzielania auksyny, skoncentrowanych w bazalnej części plazmalemy reagujących komórek, a także z indukcją syntezy auksyny *de novo*. Dyskutowana jest możliwość funkcjonowania takiego systemu w powiązaniu ze zmianami koncentracji wapnia w cytozolu.

SŁOWA KLUCZOWE: polarny transport auksyny, pole morfogenetyczne