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The role of auxin and cytokinesis in plants

Maryam Shahriari, Elham Rastine, Foruzan Mir, Parvane Mir

M.Sc. student, Department of Agronomy, Islamic Azad University, Zahedan Branch, Zahedan, Iran

Abstract

Auxin is mainly formed in young leaves and stem-tips, and is then transported to the roots, both in the phloem and by a special polar mechanism. Auxins play a major role in controlling the growth and development of plants, the early stages of embryogenesis, the organization of apical meristem and the branching of the plant's aerial parts (apical dominance), formation of the main root, and lateral and adventitious root initiation. Cytokinesis are defined as compounds that have biological activities similar to those of trans-zeatin, while Kinetin is not a naturally occurring PGR, and it does not occur as a base in the DNA of any species. It is a by-product of the heat-induced degradation of the DNA, in which the deoxyribose sugar of adenosine is converted to a furfuryl ring and shifted from the 9 position of the adenosine ring. On the cellular level, the response to auxin includes a rapid initial cell-growth response that may involve auxin-induced changes in pH, calcium and gene expression.

Keywords: uptake, metabolism, Proton pumps

Introduction

Auxin biosynthesis during adventitious root formation

Auxins are a group of tryptophan-derived signals that are involved in most aspects of plant development (Woodward and Bartel 2005) [42]. Auxin is mainly formed in young leaves and stem-tips, and is then transported to the roots, both in the phloem and by a special polar mechanism. Auxins play a major role in controlling the growth and development of plants, the early stages of embryogenesis, the organization of apical meristem (phyllotaxy) and the branching of the plant's aerial parts (apical dominance), formation of the main root, and lateral and adventitious root initiation (Went and imann 1937) [40].

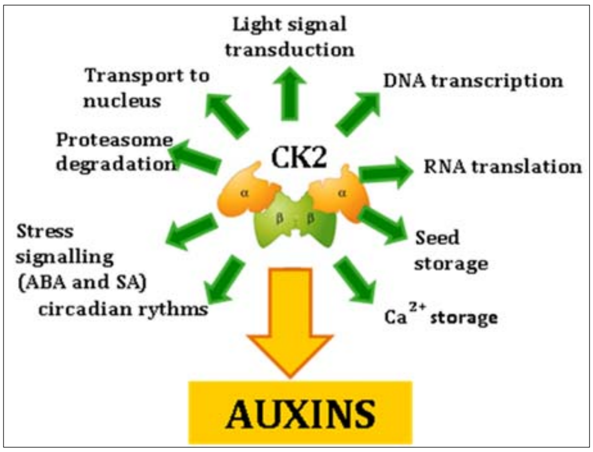

Fig 1: Role of protein kinase CK2 in auxin-signaling functions.

Furthermore, it elicits those responses throughout the plant required for the function of developing leaves and roots. Auxins are also involved in gravitropism and phototropism (Kepinski and Leyser 2005) [21]. Auxin has a central role in shoot/root relation, correlating the presence and development of leaves with root initiation. In addition, auxin induces the differentiation of vascular tissues, it inhibits or induces the differentiation of branches and prevents the abscission of leaves (Sachs 2005, Pop *et al.* 2011) [35, 29]. High photosynthesis could be coupled with auxin synthesis, thus enhancing root formation. High ion and water absorptions could be coupled with high auxin catabolism, thus enhancing leaf development (Sachs 2005) [35]. Multiple across the plant result from its control of cell division, cell elongation, and certain stages of differentiation. On the cellular level, the response to auxin includes a rapid initial cell-growth response that may involve auxin-induced changes in pH, calcium and gene expression (Davies 2004, Pop *et al.* 2011) [5, 29].

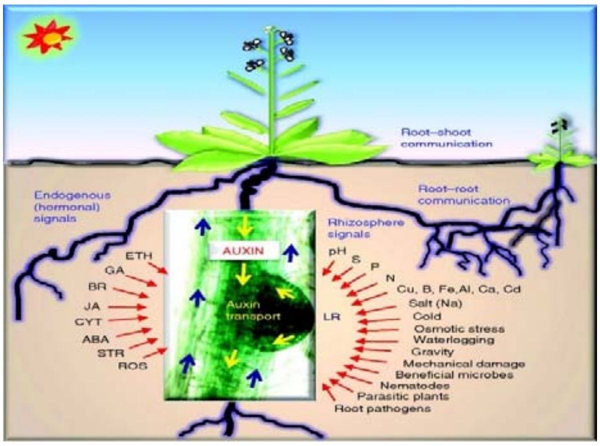

Fig 2: Auxin plays an essential role in the integration of diverse biotic and abiotic environmental signals to plant root development. Auxin signalling interacts with the signalling pathways of all other known plant hormones. Auxin is also proposed to have roles in regulating the communication both within the same plant (root–shoot communication) and between different plants (root–root communication). The central image is a β-glucuronidase (GUS)-stained section of a primary root with emerging lateral root from a DR5-GUS-expressing arabidopsis seedling (Ulmasov *et al*., 1997) and the intensity of GUS staining correlates with increased auxin activity. The arrows indicate an effect but do not necessarily suggest a positive interaction. ABA, abscisic acid; LR, lateral root; ETH, ethylene; GA, gibberellin; BR, brassinosteroid; STR, strictogalactones; JA, jasmonate; CYT, cytokinins; ROS, reactive oxygen species. See the text for additional details.

Rooting-phases have different auxin requirements. auxin is always a temporary increase in the endogenous level of free indol-3-acetic acid (IAA) during the inductive phase (corresponding to a minimal level of peroxidase/oxidase activity). The inductive phase is the auxin sensitive, when the plants are responsive to exogenous auxin application.

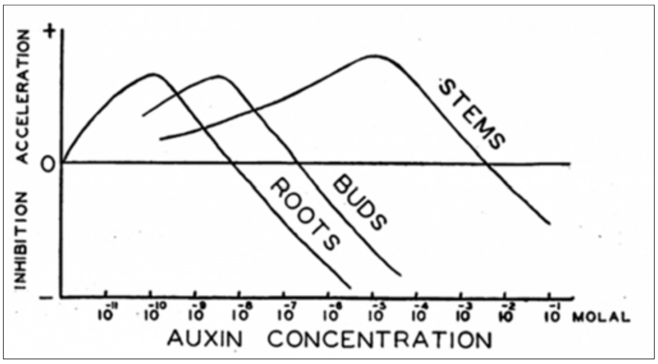

Fig 3: Auxin inhibits root growth but accelerates stem growth, auxin has an opposite effect on growth of stems and roots, Root growth is more sensitive to auxin than stems, Buds are insensitive to auxin, auxin concentrations that promote elongation in stems can be inhibitory in roots.

It is followed by the auxin insensitive phase (initiation phase) characterized by a decrease in IAA levels to a minimum and high peroxidase and oxidase activity (Nag *et al*. 2001, Faivre-Rampant *et al*. 2002) [26, 12]. The IAA oxidation at this stage of rooting (initiation phase) seems to be related to the auxin response. Oxidation products of IAA may promote root formation, especially when linked to the phenolic compounds present (Günes 2000) [19].

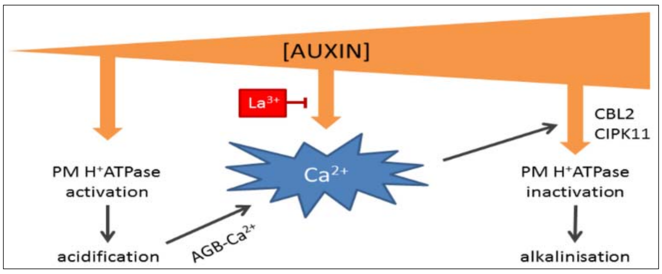

Fig 4: Hypothetical model of auxin concentration-dependent control over apoplastic pH. At low concentrations, auxin activates plasma membrane (PM) H+ ATPases, thereby lowering apoplastic pH and increasing apoplastic Ca2+ concentrations via arabinogalactan glycoproteins (AGBs). At high auxin concentrations, auxin induces a Ca2+ signal that inactivates H+ ATPases. The auxin-induced Ca2+ signal can be inhibited by La3+.

During the root expressive phase, IAA is again needed to promote the growth of root's initials (Štefancic *et al*. 2007) [37]. Importance of auxin during the production of lateral or adventitious roots was demonstrated with several 'gainof-function' as well as 'loss-of-function' iaa mutations (Fukaki *et al*. 2002, Rogg *et al*. 2001, Tatematsu *et al*. 2004) [14, 32, 39]. In Arabidopsis, the super root mutants, accumulate IAA, developing numerous adventitious roots on the hypocotyl and cuttings of different organs in the case of sur1 (Delarue *et al*. 1998) [6]. Triiodobenzoic acid (TIBA), an auxin polar transport inhibitor, applied to the top of the hypocotyls, lowered the rate of root formation (Fabijan *et al*. 1981) [9]. Rice mutants affected in the expression of the PIN -FORMED (OsPIN1) gene, potentially involved in auxin polar transport, are affected in adventitious root emergence and tillering confirming that the auxin concentrations and distributions within the different tissues are essential (Xu *et al*. 2005).

Auxin uptake and metabolism in tissue cultures

It is not quite correct to talk about uptake, because what we can measure, is in fact accumulation, i.e., the amount of a regulator in a tissue, which was taken up from the medium and not yet metabolized. IAA a synthetic auxins such as NAA and 2, 4-D are rapidly taken up into cultured tissues from media with a pH less than 5-6. The compounds are subsequently absorbed into cells as whole molecules (via uptake carrier or diffusion, see above), but dissociation then causes them to be retained within the cell, because the plasmalemma is impermeable to auxin anions (Norris and Bukovak, 1972; Raven, 1979; Edwards andvGoldsmith, 1980; Minocha and Nissen, 1985; Minocha, 1987) [7, 24, 25]. IAA and NAA anions can be exported only by the efflux carrier (see above). Besides uptake through the tissue surface, in cultures using segments, diffusion through the cut surfacemust be taken into account. In apple microcuttings, applied auxin is taken up predominantly via the cut surface and not via the epidermis (Guan and De Klerk, 2000) [18]. The rate of uptake of NAA into tobacco pedicel explants was proportional to the concentration in the medium and its presence is necessary for 4 d only (Smulders *et al*., 1988).

Proton pumps

Plant hormone such as auxin is able to regulate the activity of the proton pumps eliciting key physiological responses (Marré and Ballarin-Denti 1985). Plants regulate the interaction of their proton pumps in order to respond to the constant environmental changes. At the same time, they preserve optimal metabolic conditions for growth and development (Serrano 1989, Gaxiola *et al*. 2007) [36, 16].

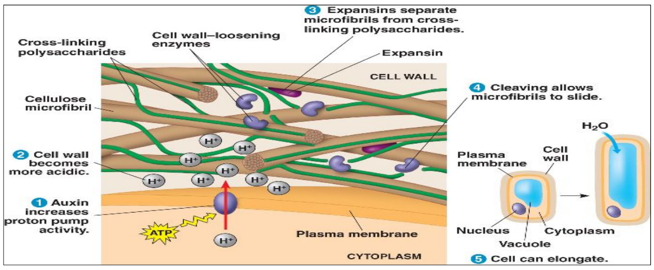

Fig 5. Effect of auxin in Proton pump activity

Therefore, it is not surprising that likely other signals, several organic matter fractions can affect the electrochemical gradient of protons across the cell membranes via modulation of the proton pumps. In this regard, HS affect this enzyme activity, protein expression, proton extrusion (Canellas *et al*. 2002, Façanha *et al*. 2002) [2, 10]. And mRNA levels (Quaggiotti *et al*. 2004, Elena *et al*. 2009) [31, 8] of plasma membrane proton ATPase (PM H+-ATPase), in a similar way of those effects of auxin on PM H+-ATPase reported in maize (Frías *et al*. 1996) [13]. This enzyme plays a crucial role on nutrient uptake and root growth, as confirmed by its abundance in root tissues (Palmgren 2001) [28]. In addition, the vacuolar H+-PPase (type 1 H+-PPase, AVP1) has been reported as important to the regulation of apoplastic pH and to auxin transport (Li *et al.* 2005) [22], and has also been strongly related to plant capacity to cope with low amounts of PO4 and NO3 in phosphorous- and nitrogen-deprived environments (Yang *et al.* 2007, Gaxiola *et al.* 2012, Paez Valencia *et al.* 2013) [43, 17, 27] a very common problem in tropical soils.

Cytokinesis

The Cks were discovered in the course of studies aimed at identifying factors that stimulate plant cells to divide (i.e. undergo cytokinesis). Since their discovery, Cks have been shown to have effects on many other physiological and developmental processes as well, including leaf senescence (Gan and Amasino, 1996) [15], nutrient mobilization (Roitsch and Ehness, 2000) [33], apical dominance, the formation and activity of shoot apical meristem (Synkova *et al.* 1997) [38], floral development (Faiss *et al*., 1997) [11], the breaking of bud dormancy (Pospilova *et al*., 2000) [30]. And seed germination. Cks also appear to mediate many aspects of light–regulated development, including chloroplast differentiation (Wingler *et al*., 1998) [41]. the development of autotrophic metabolism (Chernyadev, 1993) [3]. and leaf and cotyledon expansion (Ma *et al*., 1998).

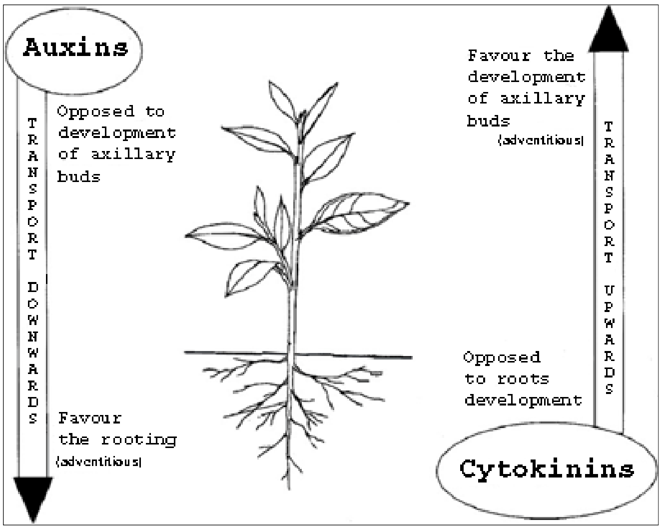

Fig 6: Transport of auxin and cytokinins

Define and classification of cytokinesis

Cks are defined as compounds that have biological activities similar to those of trans-zeatin, while Kinetin is not a naturally occurring PGR, and it does not occur as a base in the DNA of any species. It is a by-product of the heat-induced degradation of the DNA, in which the deoxyribose sugar of adenosine is converted to a furfuryl ring and shifted from the 9 position of the adenosine ring. Some molecules act as cytokinin antagonists are able to block the action of Cks, and their effects may be overcome by adding more cytokinin. Even the most frequent used synthetic Cks, Benzyladenine (benzylaminopurine) (BAP), tetrahydro-pyranylbenzyladenine (THPBA) and NN1-diphenlyurea (non-amino purine with weak activity) do not completely share their mechanism of action with native cytokinin. Unlike native cytokinin (eg., zeatin) these are not the good substrates for the cytokinin-binding protein-CREi/WOL/AHK4, AHK2 and AHK3 which initiate intracellular phosphotransfer and is poorly transported by cytokinin efflux carriers (Beveridge *et al*., 1997a) [1]. Only dihydrozeatin, isopentyladenine, zeatinribosides, zeatinribotides and 2-methylthiocis- ribosylzeatin, cis-or transzeatin and their riboside and ribotides are naturally found in plants and bacteria, respectively, and therefore, qualify as endogenous Cks, but their roles and mechanisms of action have not been satisfactory described.

Cytokinin as plant growth regulators

Cks are plant growth promoting hormones involved in the specification of embryonic cells, maintenance of meristemtic cells, shoot formation and development of vasculature. Cks have also emerged as a major factor in plant-microbe interactions during nodule organogenesis and pathogenesis. Microbe-originated Cks confer abnormal hypersensitivity of Cks to plants, augmenting the sink activity of infected regions. However, recent findings of Choi *et al.* (2011) [4]. have shed light on a distinct role of Cks in plant immune responses. They suggest that plant-borne Cks systemically induce resistance against pathogen infection which is orchestrated by endogenous Ck and salicylic acid (SA) signaling. Numerous reports ascribe a stimulatory or inhibitory function to Ck in different developmental processes such as root growth and branching, control of apical dominance in the shoot, chloroplast development, and leaf senescence. Conclusions about the biological functions of Ck have mainly been derived from studies on the consequences of exogenous Ck application or endogenously enhanced Ck levels, up to now, it has not been possible to address the reverse question: what are the consequences for plant growth and development if the endogenous Ck concentration is decreased. Ck function as a regulatory factor in leaf cell formation is supported by the fact that transgenic Arabidopsis plants with an enhanced Ck content produced more leaf cells than control plants (Rupp *et al*., 1999) [34]. Further, Ck appear to restrict leaf cell size as the cells of transgenic leaves are larger than in control plants. Alternatively, a compensatory mechanism may be activated in transgenic plants to reach a genetically determined organ size, as has been reported for plants expressing dominantnegative forms of cdc2 (Hemerly *et al*., 1995) [20]. This suggests that the role of Ck in the regulation of development of reproductive organs might be less important than it is during the vegetative phase. It may be that once the plant has entered the reproductive cycle, a more stringent mechanism operates in the meristem to ensure the proper course of the developmental programme.

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