Chemistry Research Journal, 2017, 2(2):139-145

Available online www.chemrj.org

Review Article

ISSN: 2455-8990
CODEN(USA): CRJHA5

The effect of auxin and cytokinesis hormones on some characteristics of crop plants

Saeedeh Ghorbani

Department of Biology, Payame Noor University, Tehran, Iran

Abstract Introduction Among the most important functions of plant hormones is controlling and coordinating cell division, growth and differentiation. Plant hormones can affect different plant activities including seed dormancy and germination. Plant hormones including abscisic acid (ABA), ethylene, gibberellins, auxin (IAA), cytokinins, and brassinosteroids are biochemical substances controlling many physiological and bio-chemical processes in the plant. These interesting products are produced by plants and also by soil microbes. Auxin is a plant hormone, which plays a key role in regulating the following functions: cell cycling, growth and development, formation of vascular tissues and pollen and development of other plant parts. Cytokinins are plant hormones, regulating a range of plant activities including seed germination. They are active in all stages of germination.

Keywords Auxin uptake, Crop plants, Plant growth regulators

Introduction

Plant Growth Regulators

Some chemicals occurring naturally within plant tissues (i.e. endogenously), have a regulatory, rather than a nutritional role in growth and development. These compounds, which are generally active at very low concentrations, are known as plant hormones (or plant growth substances). Synthetic chemicals with similar physiological activities to plant growth substances, or compounds having an ability to modify plant growth by some other means, for example polyamines, are usually termed plant growth regulators. Some of the natural growth substances are prepared synthetically or through fermentation processes and can be purchased from chemical suppliers. When these chemicals have been added to plant tissue culture media, they are termed plant growth regulators in this book, to indicate the fact that they have been applied from outside the tissues [1]. This article is review and the aims are the effect of auxin and cytokinesis hormones on some characteristics of crop plants.

Auxins

Auxins are very widely used in plant tissue culture and usually form an integral part of nutrient media. Auxins promote, mainly in combination with cytokinins, the growth of calli, cell suspensions and organs, and also regulate the direction of morphogenesis. The word auxin has a Greek origin: *auxein* means to enlarge or to grow. At the cellular level, auxins control basic processes such as cell division and cell elongation. Since they are capable of initiating cell division they are involved in the formation of meristems giving rise to either unorganised tissue, or defined organs. In organized tissues, auxins are involved in the establishment and maintenance of polarity and in whole plants their most marked effect is the maintenance of apical dominance and mediation of tropisms [2]. Auxins are a group of tryptophan-derived signals that are involved in most aspects of plant development [1]. 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 [3]. 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 [4]. Auxin has a central role in shoot/root relation, correlating the presence and development of leaves with root initiation. In addition, auxin induces the dierentiation of vascular tissues, it inhibits or induces the dierentiation of branches and prevents the abscission of leaves [5-6]. 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 [5]. Multiple across the plant result from its control of cell division, cell elongation, and certain stages of dierentiation. 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 [6-7]. 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). e inductive phase is the auxin sensitive, when the plants are responsive to exogenous auxin application. During the root expressive phase, IAA is again needed to promote the growth of root's initials [8]. 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 [9-11]. 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 [12]. Triiodobenzoic acid (TIBA), an auxin polar transport inhibitor, applied to the top of the hypocotyls, lowered the rate of root formation [13].

Synthetic Auxins

The most commonly detected natural auxin is IAA (indole-3-acetic acid) (1); but endogenous occurrence of 4-chloro-IAA (2) [14] and of indole-3-butyric acid (IBA) (3) [15] have also been demonstrated. Furthermore, the weak auxin phenylacetic acid (PAA) (4) occurs naturally in plants [16] and there are precursors and metabolites of IAA present in plant tissues, like indole-3-pyruvic acid, tryptamine [17] or tryptophol [18-19]. In addition, the intermediate of agrobacterial IAA biosynthesis, indole-3-acetamide (5), has been detected in plant tissues. Most of the IAA produced within plants is conjugated to other compounds to form esters, amides or glycosyl esters. The most commonly occurring IAA-conjugates are indole- 3- acetylaspartic acid (IAAsp) (6) and a range of IAA glucose esters (IAAGlu) (7). Conjugation seems to be a mechanism for storing IAA in cells, stabilising the level of free auxin in the plant, and metabolising its excess [20].

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 an 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 [21-26]. 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 [27]. 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 [28].

Proton pumps

Plant hormone such as auxin is able to regulate the activity of the proton pumps eliciting key physiological responses [29]. 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 [30-31]. 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 [32-33] and mRNA levels [34-35] of plasma membrane proton ATPase (PM H+-ATPase), in a similar way of those effects of auxin on PM H+-ATPase reported in maize [36]. This enzyme plays a crucial role on nutrient uptake and root growth, as confirmed by its abundance in root tissues [37]. 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 [38], and has also been strongly related to plant capacity to cope with low amounts of PO4 and NO3 in phosphorous- and nitrogen- deprived environments [31, 39-40] a very common problem in tropical soils.

Root Formation

Some observations on natural levels of auxin protectors might suggest that their low levels are coupled with root initiation, but high levels with root growth. For example, shoots of apple grown in vitro were found to have low phenol contents at the root induction phase, but high contents as roots were growing [41]. In Sequoia Dendron giganteum, phenolic compounds were found to decrease in concentration when shoots were moved to a root induction medium. The activity of peroxidases in the induction medium increased during 7-11 days and then decreased, roots appearing as phenols were decreasing. In each of these plants, peroxidase activity was inversely correlated with phenol content. In chestnut, rhizogenesis occurred during an increase in the level of auxin protectors, whose basipetal transport was inhibited by applied IBA. The best time to explant shoot tips from adult chestnut material to a root inducing medium, was during one of the first two peaks of growth of shoots, which coincided with the occurrence of maximum quantities of natural phenolics. 4-chlororesorcinol (21), a polyphenol oxidase inhibitor (i.e.inhibiting the conversion of monophenols and dihydric phenols to polyphenols) has been found to improve the rooting and subsequent growth of cuttings [42].

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 [43], nutrient mobilization [44], apical dominance, the formation and activity of shoot apical meristem [45], floral development [46], the breaking of bud dormancy [47] and seed germination. Cks also appear to mediate many aspects of light–regulated development, including chloroplast differentiation [48] the development of autotrophic metabolism [49] and leaf and cotyledon expansion [50].

Cytokinin signaling and other plant hormones

Ck are important regulators of development and environmental responses of plants that execute their action via the molecular machinery of signal perception and transduction. The characterization of the molecular mechanisms regulating hormone synthesis, signaling, and action are facilitating the modification of Ck biosynthetic pathways for the generation of transgenic crop plants with enhanced abiotic stress tolerance [51]. Since plant hormones generally are assumed to interact with specific receptors that reside either on the cell surface or within the cytoplasm. Two candidates for a cytokinin receptor have recently been identified. One of which tends to fit the steroid hormone receptor model while the other fits the membrane receptor model. It is possible, although unlikely, that both of these are cytokinin receptors. Until recently, our knowledge of how cytokinin works at the cellular and molecular levels is still quite fragmentary, significant progress has been achieved in regard to biosynthesis, metabolism, perception, and signal transduction.

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). 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 function

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) [52] 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 [53]. 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 [54]. 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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