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Auxin biosynthesis, its role in plant growth, development and physiological process

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Abstract

Unbelievable research has been made in understanding Auxin biosynthesis and its effect on physiological process and developments in plants over the last few years. Auxin is a phytohormones that's involved in many physiological and biological functions of the plants i.e. basic cellular processes and cell cycle control over localized responses such as cell elongation and differential growth. Both plants and some plant pathogens produce Auxin for completing normal life cycle. But, however, how Auxin produces in plant this process is difficult to be proven. Number of research studies had discovered biochemical reactions and several genes in tryptophan-dependent Auxin biosynthesis pathway. Even though the history of auxin research reaches back more than a hundred years, we are still far from a comprehensive understanding of how auxin controls plant growth and physiological process. Some answers to this question may lie in the auxin molecule itself. Naturally occurring auxin-like substances have been found and they may play roles in specific developmental and cellular functions. The molecular mode of auxin action can be further explored by the utilization of synthetic auxin-like molecules i.e NAA (naphthalene acetic acid) and IBA (indole-butynic acid). Auxin is actively modified, metabolized, and intra-cellular compartmentalized, that's have a great impact on its availability and activity. In this review, we will give an overview of these recent and emerging areas of auxin and its effect on plant physiological process and developments and try to formulate some of the open questions. Without doubt, the manifold facets of auxin biology will not cease to amaze us for a long time to come.

Keywords: auxin biosynthesis, plant growth, physiological process

Introduction

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 concentration, are known as phytohormones. These phytohormones have no nutritional benefits but they are directly involved in plant physiological process and act as signaling molecules that promote and influence plant development (Darwin & Darwin, 1888) ^[9]. Plant growth regulators have key role in different physiological processes related to growth and development of plant. It is obvious that changes in the level of endogenous hormones due to biotic and abiotic stress alter the crop growth and any sort of manipulation including exogenous application of growth substances would help for yield improvement. Plant growth hormones are organic substances produced naturally in the higher plants, controlling growth or other physiological functions at a site remote from its place of production, and active in minute amounts. Hormones usually move within plant from a site of production to site of action. Phytohormones are physiological intercellular messengers that are needed to control the complete plant life cycle, including germination, rooting, growth, flowering, fruit ripening, foliage and death. Traditionally five major classes of plant hormones are listed: auxins, cytokinins, gibberellins, abscisic acid and ethylene, But auxin has prime importance among all. However as research progresses, more active molecules are being found and new families of regulators are emerging; one example being polyamines such as putrescine or spermidine.

The term 'auxin' derived from the Greek word 'auxein', which means to enlarge/grow (Salehin, Bagchi, & Estelle, 2015; Sauer, Robert, & Kleine-Vehn, 2013) ^[35, 36]. Auxin is a plant growth hormone that can be produce chemically or produced biologically by the plant.

In biological synthesis, the natural hormone is IAA (indole-3-acetic acid), while chemically produce auxin are NAA (1-naphthalene acetic acid) and IBA (indole-3-butyric acid). NAA and IBA are available in markets (Vanneste & Friml, 2012)^[44].

1) The Role of Auxin in Plant growth and development

Auxin is play important role in apical dominance and phototropism, but its main function is cell elongation in coleoptile and rooting (Went, 1934)^[47]. Auxin is most essential for plant development and managing diverse function in plant i.e. controlling of senescence (Ellis *et al.*, 2005)^[12], resist to pathogens attack (Fu & Wang, 2011)^[14], abiotic stress (Wang *et al.*, 2010)^[46], fruit formation (De Jong, Mariani, & Vriezen, 2009)^[11] and leaf abscission (Rubinstein & Leopold, 1963)^[34]. Auxin stimulates apical dominance and tropic movements to light or gravity (Woodward & Bartel, 2005)^[49]. Besides this, auxin controls cell division, meristem formation and enhance the production of adventitious roots. Further auxin is not only act directly on plant life but it control many functions indirectly (Swarup, Parry, Graham, Allen, & Bennett, 2002; Vanstraelen & Benková, 2012)^[40, 45]. Indole-3-acetic acid (IAA) is the naturally occurring auxin, that stimulated the growth of oat coleoptile segments (Bonner & Bandurski, 1952)^[6]. Auxin is abundant in young leaves, floral organs and developing fruits and seeds (Law & Davies, 1990)^[22]. IAA concentrations are high in young, fast growing organs and decline with age and are affected by external factors, e.g. by light, drought, saline soil and other environmental abiotic stresses (Naser & Shani, 2016)^[31]. The plant hormone auxin is a key regulator of plant growth and development. Auxin has been shown to be essential for plant development mediating diverse responses, such as the control of senescence (Ellis *et al.*, 2005)^[12], response to pathogens and abiotic stress (Fu & Wang, 2011)^[14]. It also regulates fruit formation and leaf abscission (De Jong *et al.*, 2009)^[11]. Auxin promotes the establishment and maintenance of polarity, apical dominance, and tropic response to light or gravity (Woodward & Bartel, 2005)^[49]. At the cellular level, it controls cell division, e.g. regulation of meristem formation giving rise to new organs such as lateral and adventitious roots and cell elongation by altering cell wall plasticity. In addition, auxin is not only acting through linear pathways, but is also involved in many cross-talk responses with other phytohormones (Vanstraelen & Benková, 2012)^[45].

2) The role of auxin in plant physiological functions

The stimulatory effect of auxin on cell elongation can be demonstrated in segments of coleoptiles or stems at physiologically significant IAA concentrations. Auxin is in most cases active in the concentration range 0.1–10 μM (Funada, Kubo, Tabuchi, Sugiyama, & Fushitani, 2001)^[15]. Auxin is involved in bud initiation, growth and regulates cell division which appears during cell cycle. Auxin is also involved in mitosis and DNA replication (Jouanneau, 1971)^[18], stimulate differentiation of vascular bundles and take part in differentiation of buds and roots (Aloni, 2010)^[2]. Auxin is known for their ability to promote adventitious root formation. This action is linked with stimulation of cell division (Hemerly *et al.*, 1993)^[17]. IBA is by far the most commonly used auxin to obtain root initiation and is readily convertible to IAA, but it probably also has an effect on its

own (Krieken, Breteler, & Visser, 1992)^[21]. Auxin promote cell elongation in the normal plant development, and may mediate the effects of light and gravity on plant growth (Bernier & Kinet, 1986)^[5]. Phototropism may be due to lateral redistribution of auxin. An unequal lateral distribution of auxin and calcium at the tip results in gravitropism in roots (Taiz & Zeiger, 2006)^[41]. The apical dominance is under the control of auxin produced at the terminal bud, which is transported downward through the stem to the lateral buds and hinders the growth (Badescu & Napier, 2006)^[3]. Higher concentration of auxin inhibits the elongation of roots but the number of lateral roots is considerably increased i.e., higher concentration of auxin induces more lateral branch roots (Benjamins & Scheres, 2008)^[4]. Natural auxin prevent the formation of abscission layer which may otherwise result in the fall of leaves, flowers and fruits (Leyser, 2009)^[24] and can induce the formation of parthenocarpic fruits (Napier, David, & Perrot-Rechenmann, 2002)^[30]. Auxin increases the rate of respiration indirectly by increasing supply of ADP by rapidly utilizing ATP in the expanding cells. In many tissue cultures, the normal growth of callus is due to addition of auxin. Some synthetic auxin especially 2, 4- D and 2, 4, 5-T are useful in eradication of weeds at higher concentrations (Y. Zhao, 2010)^[50]. Auxin generally inhibit flowering but in pineapple and lettuce it promotes uniform flowering (Petrášek & Friml, 2009)^[32].

3) Biosynthesis of auxin

Tryptophan-dependent (TD) and tryptophan-independent (TI) are the two known pathways for indole-3 acetic acid (IAA) production in the plants (Y. Zhao, 2010)^[50]. However TD is found to be the most unambiguous and essential pathway for distinct developmental processes and growth of the plant (Yunde Zhao, 2012)^[51]. Tryptophan-dependent pathways are named on the basis of intermediate compounds formed during IAA production as stated below;

5.1) Indole-3-pyruvate (IPA) pathway

The Weak Ethylene Insensitive8, *WEI8/TAA1* represents tryptophan aminotransferase of Arabidopsis and YUCs encoding flavin monooxygenase like proteins are the two main participating protein families involved in the two step biosynthesis of auxin in Arabidopsis and Maize (Phillips *et al.*, 2011; Sauer *et al.*, 2013; Won *et al.*, 2011)^[33, 36, 48]. Mutant studies of *TAA1* under shade revealed the importance of *TAA1* protein in the IPA-dependent auxin biosynthesis. However, overexpression of *TAA1* suggesting it to be a rate limiting enzyme in the auxin biosynthesis as no significant increase was observed in IAA level and also no elongation in hypocotyl (Mano & Nemoto, 2012; Stepanova *et al.*, 2008; Tao *et al.*, 2008)^[26, 38, 42]. The YUCs family proteins have also been reported as a rate limiting step in IPA-dependent pathway of auxin biosynthesis (Mashiguchi *et al.*, 2011)^[27]. Recent biochemical study confirmed the catalytic oxidative decarboxylation of IPA to IAA via YUC6 of YUCs protein family in Arabidopsis (Dai *et al.*, 2013; Sauer *et al.*, 2013)^[8, 36]. So the simple two step auxin biosynthesis through IPA pathway can be summarized as; The aminotransferase (*TAA1*) of TAAs first catalyze the conversion of tryptophan into indole-3-pyruvic acid by transferring amino group from tryptophan and then the conversion of IPA to IAA is catalyzed by the YUC Flavin monooxygenase through oxidation (Mashiguchi *et al.*, 2011; Yunde Zhao, 2012)^[27, 51].

The two step pathway is supported by the genetic study of the interaction between *yuc* and *taa* mutants and also by the analysis of IPA levels in them, which reduced in *taa* mutants and accumulate in *yuc* mutants (Gallavotti, 2013; Mashiguchi *et al.*, 2011) [16, 27].

5.2) Indole-3-acetaldoxime (IAOx) pathway

The tryptophan is converted to IAOx by enzyme CYP79B2/CYP79B3 which is then converted to either indole-3-acetonitrile (IAN) or indole-3-acetaldehyde. The IAN and indole-3-acetaldehyde are then converted to IAA by enzymes nitrilases and aldehyde oxidases respectively (Y. Zhao, 2010) [50]. The phylogenetic assays indicated that the IAOx pathway is not common for all plants because of the restriction of the CYP79B2 gene family to certain species (Arabidopsis, Brassicaceae) (Mano & Nemoto, 2012) [26].

5.3) Tryptamine pathway

In this pathway the tryptophan is converted to tryptamine (TAM) catalyzed by cytosolic enzyme tryptophan decarboxylase (TDC). Phylogenetic analysis shows that TDC is found in several dicots and monocots species (Mano & Nemoto, 2012) [26]. Accumulation of TAM in overexpressing TDC transgenic tobacco confirmed the importance of TAM-pathway in auxin biosynthesis, however, no increase was observed in IAA level (Mano & Nemoto, 2012; Songstad, De Luca, Brisson, Kurz, & Nessler, 1990) [26, 37]. YUC encodes flavin monooxygenase like protein family essential for auxin biosynthesis, mediating IAA production through catalyzing tryptamine (TAM) conversion to N-hydroxy-TAM (Kim *et al.*, 2007; Y. Zhao *et al.*, 2001) [19, 52]. However present studies indicated that YUC family mediates rate limiting step in IPA pathway by catalyzing the conversion reaction of IPA to IAA (Mashiguchi *et al.*, 2011; Yunde Zhao, 2012) [27, 51].

5.4) Indole 3-acetamide (IAM) pathway

In this pathway the IAA synthesis reaction is catalyzed by the enzymes encoded by *aux1/iaaM/tms1* and *aux2/iaaH/tms2* genes. First the conversion of tryptophan to IAM is catalyzed by the *aux1* encoded tryptophan 2-monooxygenase enzyme and then IAM to IAA conversion is catalyzed by *aux2* encoded indole-3-acetamide hydrolase enzyme (Mano & Nemoto, 2012) [26]. For long time it was believed that the IAM pathway is restricted to bacteria only, as no evidence was found in plants. But currently novel techniques and equipment made it possible and unveil the pathway in many plants (Lehmann, Hoffmann, Hentrich, & Pollmann, 2010) [23]. The presence of IAM has been detected in seedlings of squash, maize, rice, tobacco, Arabidopsis and in fruits of citrus unshiu and Japanese cherry. Also the activity of indole-3-acetamide hydrolase has been detected in fruits of poncirus trifoliolate and in cells of rice (Mano & Nemoto, 2012) [26].

4) Factors regulating auxin biosynthesis

Both environmental and developmental signals may affect the biosynthesis of auxin, such as light or shade and tissue/organ development. To know whether the factors upregulate or downregulate the auxin level in the plant, it is reliable to analyze the changes in gene expression with changes in environmental signals and also by generating mutants. For example, transferring a plant from light to shady environment enhances the biosynthetic level of auxin (Tao *et al.*, 2008; Y. Zhao, 2010) [42, 50]. Many gene families have been identified

that transcribed the YUC gene family which subsequently regulate the auxin synthesis and affect the developmental processes in the plant. Short Intenotes (SHI), Ngatha (NGA) gene families and Leafy Cotyledon 2 (LEC2) gene positively regulate the production of auxin in plant. Stylish1 (STY1) is one of the family members of SHI genes whose inactivation cause abnormalities in the development of style and vascular tissues patterning. Further studies unveil that STY1 regulate the YUC4 gene which affect the concentration of auxin in the plant and hence fail to develop tissues and organs well. NGA gene families were found to act redundantly in regulating the activity of YUC2 and YUC4 auxin biosynthetic genes and their quadruple mutant loss to develop gynoecium (style and stigma tissues) in Arabidopsis (Trigueros *et al.*, 2009) [43]. LEC2 was also found in positively regulating the auxin biosynthesis by activating the YUC2 and YUC4 genes in embryo development (Stone *et al.*, 2008) [39]. Another gene Sporocytes (SPL) was found to negatively regulate the activity of YUC2 and YUC6 auxin biosynthetic genes (Li *et al.*, 2008; Y. Zhao, 2010) [25, 50].

5) Auxin transport in plant

By definition phytohormone is the chemical/signal molecules produced in the one part of the plant, especially in meristematic tissues of shoots, young leaves and roots in extremely low concentration and transported to the local targeted cells/ faraway location for functions in other parts of the plant ("Plant hormone", n.d.). As clear from the definition that not only biosynthesis but transportation of hormone throughout the plant is very critical for the physiological functions and hence survival of plants. The transportation of auxin is carried out by two ways in plants; non-polar auxin transport through phloem and cell to cell regulated polar auxin transport reviewed in (Adamowski & Friml, 2015; Michniewicz, Brewer, & Friml, 2007) [1, 28]. The existence of non-regulated phloem pathway was detected first by foliar application of radioactively labeled tryptophan which were loaded rapidly in phloem and transported with comparatively fast speed of 5-20 cm/h (Morris & Thomas, 1978) [29]. The mass flow auxin along with photosynthates in phloem is then redistributed in the sinks (organs and tissues) through connected polar auxin transport pathway. The connection between phloem pathway and cell to cell polar auxin flow was found by detecting the labeled auxin later in polar auxin transport system (Cambridge & Morris, 1996) [7]. Though the directional polar auxin transport is considered more important for the plant development however the non-directional flow of auxin via phloem cannot be underestimated in long distance distribution and also because of its higher velocity and capacity (Michniewicz *et al.*, 2007) [28]. The polar auxin transport, as the name indicates its strictness to directional flow of auxin was established in bryophytes and also found in higher plants species. It is cell to cell movement of auxin with a relatively slow speed of 5-20 mm/h throughout the whole plant or to the short distance targeted tissues. However the mechanism of cell to cell transport is same as explained in chemiosmotic hypothesis (Adamowski & Friml, 2015; Michniewicz *et al.*, 2007) [1, 28] which mainly depends on the chemical nature of indole-3-acetic acid (IAA). In acidic protoplast the ionic form of Indole-3-acetic acid (IAA⁻) can easily pass through the cell membrane, however the protonated form of IAA (IAAH) cannot exit the cell at relatively higher pH of cytosol. The exit of IAAH out of the

cell is carried out by specialized transmembrane efflux carrier proteins whose polarity determines the direction of auxin flow. The polar localization of the transporters are found to be regulated by Pinoid kinase enzyme (Friml *et al.*, 2004; Křeček *et al.*, 2009) [13, 20].

Conclusion

Phytohormones are physiological intercellular messengers that are needed to control the complete plant life cycle, including germination, rooting, growth, flowering, fruit ripening, foliage and death. Traditionally five major classes of plant hormones are listed: auxins, cytokinins, gibberellins, abscisic acid and ethylene, But auxin has prime importance among all. Auxin is a plant growth hormone that can be produced chemically or produced biologically by the plant. In biological synthesis, the natural hormone is IAA (indole-3-acetic acid), while chemically produced Auxin are NAA (naphthalene acetic acid) and IBA (indole-butynic acid). Auxin plays an important role in apical dominance, controlling of senescence, resist to pathogens, abiotic stress and phototropism, But its main function is cell elongation in coleoptile and rooting. Tryptophan-dependent (TD) and tryptophan-independent (TI) are the two known pathways for indole-3 acetic acid (IAA) production in the plants. However, TD is found to be the most unambiguous and essential pathway for distinct developmental processes and growth of the plant. The auxin is synthesized in meristematic tissues of the plant especially in shoot meristems and root tips and then distributed for various physiological functioning throughout the plant via transporter proteins. Both environmental and developmental signals may affect the biosynthesis of auxin, such as light or shade and tissue/organ development. To know whether the factors upregulate or downregulate the auxin level in the plant, it is reliable to analyze the changes in gene expression with changes in environmental signals and also by generating mutants.

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