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VERSATILE ROLE OF AUXIN AND ITS CROSSTALK WITH OTHER PLANT HORMONES TO REGULATE PLANT GROWTH AND DEVELOPMENT

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ABSTRACT

Plant growth regulators are significant chemical compounds which are synthesized inside the plant cells and play vital role in plant growth and development. Such compounds are usually active at very low concentrations. These plant growth regulators act as a signalling molecule, which influences the growth of plants. Throughout the previous year's remarkable investigation have been done for understanding the synthesis of auxin and its effect on various physiological progressions. Auxin is a plant hormone that is involved in various physiological activities, including basic cellular processes such as cell enlargement, regulation of the cell cycle and distinction progress. Plants and several other microorganisms together produce auxin in order to carry out their cell cycle. The chemically synthesized auxins like NAA (naphthalene acetic acid) and IBA (Indole- butyric acid), also take part in various cellular processes. Against various types of biotic and abiotic stress conditions, these plant hormones significantly contribute in promoting acclimatization and adaptation in combination with other phytohormones. The present review highlights some of the important features of auxin role in regulation of plant growth either alone or in crosstalk with other plant hormones.

Keywords: Auxin, phytohormones, physiological, cell cycle, regulation, growth.

INTRODUCTION

Plant growth regulators play an important part in various functional processes related to plant growth and development. These are biological constituents generally synthesized in advanced group of flora, regulating various evolutionary and biological purposes, distant from manufacturing sites and vigorous in tiny quantities. Generally, hormones are synthesized in a particular place and then these are distributed in different parts of plants. Plant hormones are functional message-carriers that must be used to alter the entire plant natural life, including propagation, radicalisation, fruit maturing, flowering, leaves and fall. Five groups of hormones are typically registered, the most common being auxins, gibberellins, abscisic acid and ethylene. Among, this Auxin is considered as the chief hormone for plants.

The word 'auxin' derived from the Grecian expression "Auxein" that involves increase in growth (Salehin *et al*., 2015; Sauer *et al*., 2013). Auxin acts as a plant growth regulator which is synthesized inside the plant body chemically as well as biologically. Synthesis of Indole acetic acid occurs biologically, as it is a natural plant growth regulator; whereas Naphthalene acetic acid and Indole-butyric acid are synthesized chemically. Auxin was acknowledged as the plant growth regulator due to its potential to promote variation progress in response to light inducements. In laboratory immunoassay, where auxin- carrying agar blocks stimulated the growth of oat coleoptile which identify Indole-3- acetic acid as an occurring auxin in plants. Reflective improvements in plant growth and production have been initiated by the application of IAA or synthetic auxins on plants. In plants, auxin biosynthesis is incredibly complex phenomenon. Several pathways may have engaged in the development of new auxins via hydrolytic breakdown of IAA methyl ester, IAA sugar.

All cellular activities in advanced plants are regulated by phytohormones and play an important role in coordinating several signal transduction pathways in plants (Pieterse *et al*., 2009). Abscisic acid, salicylic acid, jasmonate and ethylene are known to provide resistance against different types of stress conditions (Pieterse *et al*., 2012).

Role of Auxin in plant Growth and Development

In plants, development is seen as an irreversible increase in the scale attained through expansion of discrete cells, a process occurring due to absorption of water. Auxin belongs to such class of phytohormones which is related to the optimal quantifiable growing changes throughout the plant life cycle. The effect of auxin was first realized when The Power of the Movement in plants was published by Charles and Francis Darwin. They discovered that an "effect is transferred" from one side of the grass coleoptile exposed to sun to another part as shown by the latter bending towards light. In 1926, auxin was extracted from plant tissue, and its ability for stimulation of growth was found. These days, the term auxin describes the group of vital molecules in plants that may be there in microorganisms and humans. One of the most important auxins, IAA is well known for its ability to regulate various attributes of plant growth. Artificial auxin, for example, 2, 4- dichloro-phenoxyacetic acid is a vital herbicide. The amount and concentration of auxin used determines its influence on the plant development. Endogenous IAA is involved in embryonic and post-embryonic development, and tropisms for e.g. movement with respect to light and gravity.

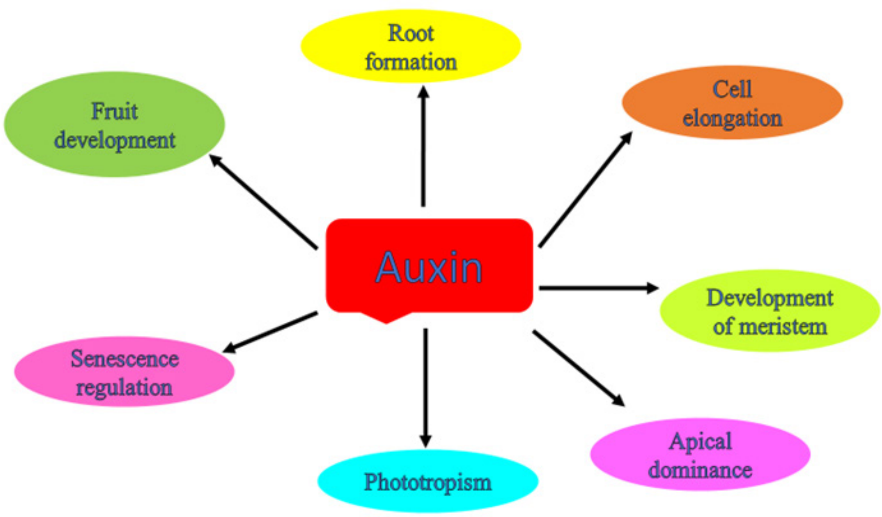

Figure 1: Role of auxin in regulating plant growth and development.

Although auxin plays an important role in phototropism and apical dominance, its main function remains the elongation of coleoptile and rooting (Went, 1934) (Fig 1). Auxin acts as a pivotal phytohormone for plant growth and regulation of different plant functions such as, pathogens stress (Fu and Wang, 2011), abiotic stress (Wang *et al.*, 2010), senescence regulation (Elis *et al.*, 2005), fruit forming (De Jong *et al.*, 2009) and leaf abscission (Rubinstein and Leopold, 1963). Auxin also regulates the development of meristems, the division of the cells, and enhances the development of adventitious roots. Indole-3-acetic acid is the naturally occurring auxin, that triggers the synthesis coleoptile parts of oat (Bonner and Bandurski, 1952). Auxin is present in large amounts in early leaves, floral organs and developing fruits and seeds (Law and Davies, 1990). The growth and development of the plants is mainly regulated by phytohormone auxin. Auxin supports polarity development and preservation, apical superiority and tropical light and or gravity reaction (Woodward and Bartel, 2005). It regulates cell division at the cellular level, e.g. the organisations of meristem development results in new structures like lateral and adventitious roots and elongation of cell through changes in cell wall plasticity. In addition, auxin also crosses talks with other plant hormones through various biochemical pathways (Vanstraelen and Benkova, 2102).

Physiological role of auxin in plants

Stimulatory effect of auxin on cell elongation could be identified in parts of coleoptiles or stems with physiologically significant IAA absorptions. Auxin shows its maximal effect in the concentration ranging from 0.1-10μm in most of the cases (Funada *et al.*, 2001). Initiation, development and regulation of the cell division in buds monitored by auxin. Similarly, auxin takes part in mitosis and DNA replication (Jouanneau, 1971), is involved in the dissimilarity between buds and roots and stimulates separation of vascular bundles (Aloni, 2010). Development of adventitious roots is promoted by auxin. In the normal growth of the plants, auxin promotes cell elongation and can promote the effect of light and gravity on the plant growth (Bernier and Kinet, 1986). Phototropism may be considered as the cause of the lateral reorganisation of auxin. The apical dominance is conveyed downhill through the stem to the neighbouring buds and hampers development under the influence of the auxin synthesized at the terminal bud. (Badescu and Naper, 2006). Higher auxin concentration hinders elongation of root, but the number of lateral roots is highly increased, i.e. (Benjamins and Scheres, 2008). Respiration rate in plants is increased obliquely by rapid usage of ATP in growing cells that brings an increase in the amount of ADP. Auxin plays an important role in development of callus. Several synthetic auxins, in particular 2,4-D and 2,4,5-T, are effective at higher concentrations in marijuana abolition (Zhao,2010). Auxin however inhibits flowering, but it enables unchanging flowering in Lettuce and pineapple (Petrasek and Friml, 2009).

Auxin and its crosstalk with other Phytohormones

The plant hormones function together by stimulating various biological processes, either during the release of chemicals when prone to external stimulus or during the addition of phosphate to ADP molecule. These chemical signals control DNA, produce functional proteins, which then influences the production or activity of various hormones and growth of plant in synchronization with various stimuli generating external factors. Plant hormonal signalling procedures manage the developmental aspects and vigour of plants, either alone or crosstalk between them. The content of hormones, released by plants such as auxin, ethylene, cytokinin, abscisic acid, gibberellin, and brassinosteroids vary at the cellular level and exhibit their functions either individually or in crosstalk with each other.

Auxin and gibberellic acid

Gibberellins, agroup of plant hormones influence the several aspects to influence the development of plant and inhibition in their biosynthesis results in dwarf plants (Fleetand Sun, 2005; Ninnemann *et al*., 1964). Moubayidin *et al.,* (2010) showed that in the early stages of meristem development, the high concentrations of gibberellic acid block the regulation of transcription factor *ARR1*. The *ARR1*stimulates the *SHY2* gene, that shows antagonistic control over the auxin carrying PIN genes. So gibberellic acid forms a route to control the stability occurring during auxin signalling. During the tuber development, both GAs and auxin participate together. During the stolen developmental phase of plant life cycle, the concentration of GA is fairly elevated which result in the increase of stolen length whereas, the auxin concentration is less and has the role to maintain the apical dominance of plant stolen (Roumeliotis *et al*., 2012). Supplementation of GA together with auxin caused fruit developments in which cell expansion and quantity of pericarp cells were alike asthat in seeded fruits, signifying that GA and auxin are needed for standard fruit formation (Serrani *et al*., 2007). Whereas, auxin triggered fruit formation was considerably declined by the instantaneous supplementationof GA biosynthetic inhibitors, which showing that influence of auxin on fruit development is mediated by GA (Serrani *et al*., 2008) . GAs network with auxin to stimulate lateral root formation where firstly, auxin amount significantly increased in the roots of the GA-deficient and GA-insensitive lines and then functioning of the gene expressing *PIN9*, was greatly escalated in both transgenic plants primarily in the roots (Farquharson, 2010).

Auxin and Cytokinin

The balance between auxin and cytokinin signaling is critical at initial growth stages: for example, auxin promotes cell division in *Arabidopsis* root meristems (DelloLoio *et al*., 2008) whereas cytokinin activates cell differentiation in shoot (Perilli *et al*., 2010). Cytokinin and auxin association significantly helpful in stimulating the root development (Dello *et al*., 2008; Bielach *et al*., 2012). In *Arabidopsis thaliana*, the cytokinin endorses the cell differentiation, suppressing transport of auxin and signalling across the cell. At the molecular level, the auxin and cytokinin do show interdependent relations to control the direction of the root towards the gravity experienced by it (Buer *et al*., 2006), the development of the root (Rahman *et al*., 2001), the growth of lateral root (Ivanchenko *et al*., 2008; Negi *et al*., 2008, 2010) and the variation shown by the relative humidity (Pitts *et al*., 1998). These two hormones interact to mediate the meristem size of the root and also mediate the root growth. Crosstalk between auxin and cytokinin responsible for maintaining stability between cell differentiation and cell division, required for regulating root meristem dimensions and root development; which happens via a direct controlling network uniting on the SHY2 (SHORT HYPOCOTYL 2) gene, a member of the Aux/IAA gene group (Moubayidin *et al*., 2009).

Auxin and ethylene

The auxin in association with ethylene conjointly controls a diversity of biological progressions that lead to growth in plants. Auxin which is a crucial regulator of plant development, induce ethylene synthesis, cellular signal transduction and regulates the response of growth to ethylene. The crosstalk between auxin and ethylene is much significant to regulate several aspects of plant morphogenesis, cell division within the root cells, emergence of root hairs, the development of lateral root and seed germination. The 1-aminocyclopropane- 1-carboxylate synthase (ACS) gene is under the control of auxin, that encrypts the main enzyme during the synthesis of ethylene (Muday *et al*., 2012).Ethylene mediated1^{o} root growth need auxin production, passage, and signalling (Qin and Huang, 2018).In *Arabidopsis*, treatment with ethylene improve the functioning of IAA production genes and IAA concentration and also enhanced the whole auxin action at the root tip (Růžička *et al*., 2007).TFs which involve in the ethylene signalling, like EIN3, ERF1 and PIF4, acts as crosstalk branches amongst ethylene and auxin in root development (Liu *et al*., 2016; Mao *et al*., 2016).Auxin and ethylene show contrary roles in lateral root growth for instance, ethylenedecline DR5erv:GFPfunctioning in those areas where lateral roots arise, showing decrease dauxin reaction in the vicinity of cell (Lewis *et al*., 2011).OsERF3, which encodes an AP2/ERF protein, affect ethylene production and functions as a WOX11-association moiety in rice crown root growth. Furthermore, auxin and ethylene application stimulate the functioning of OsERF3, exhibiting synergistic association between ethylene and auxin during crown root growth (Qin and Huang, 2018).

Auxin and other plant hormones

ABA is an isoprenoid hormone, concerned with controlling dormancy of seeds as well as plant response to various environmental stresses (Frankelstein and Rock, 2002). The gene VIVIPAROUS 1 (VP1) in maize and its *Arabidopsis* ortholog AB13, which encrypts a transcription factor tangled in ABA signalling, has been experimentally discovered to be auxin-inducible (Suzuki *et al*., 2001; Brady *et al*., 2003). ABA thus interrelates with the framework of crosstalk via auxin action.*WRKY46*recognized to regulate the stimulation of lateral root development by triggering auxin stability and ABA perception in response to osmotic stress (Ding *et al*., 2015).Auxin associated with ABA triggered tolerance to limited water supply, hence, improve the functioning of ABA mediated gene expression of RAB18, RD22, RD29A, RD29B, Dehydration responsive element binding factor 2A,and 2B) (Shi *et al*., 2014).Brassinosteroids (BRs) interrelate with auxin, for example, the appearance of multiple auxin- responsive genes is coordinated by both BRs and auxin pathways in combination (Mouchel *et al*., 2006).ARF2 considerably influence auxin biosynthetic genes, which signifies that BRs might regulate auxin production (Vert *et al*., 2008). BRs trigger the development of dark grown hypocotyls and cause phenotypic alterations, thar are triggered by *IAA19* and *ARF7*, 2 crucial constituents of auxin signalling, via precise modulation of BZR1 (Zhou *et al*., 2013). *OsMYB-R1* TFsregulate the cross-talk between auxin &salicylic acid perception as well as additional stress related genes by amending genetic perception, endogenous tissue stability and root apparatus (Tiwari *et al*., 2020).

Role of Auxin under abiotic stress conditions

Plants are often exposed to several abiotic stresses during their life cycle. The commonly occurring abiotic stresses that a plant experience, includes limited water supply, salinity, high or low temperature, heavy metal stress(Ahmad and Prasad, 2011; Iqbal *et al*., 2018). To cope with these unfavorable environmental conditions, plants develop advanced mechanisms to maintain equilibrium between their development, reproduction and survival (Fig 2). Reactive oxygen species (ROS), reactive nitrogen species (RNS), as well as phytohormones, are the essential signaling assets in plant tolerance responses to ever changing ecosystem (Kazan, 2013; Baxter *et al*., 2014; Kolbert, 2016). These signaling assets crosstalk with each other to improve plant tolerance to stress circumstances through various defense mechanisms (Mittler *et al*., 2011; Corpas and Barossa, 2013; Xia *et al*., 2015; Tognetti *et al*., 2017; Choudhary *et al*., 2017; Raja *et al*., 2017). Review of genome- wide induction suggested thatunder abiotic stresses such as drought, action of auxin sensitive genes stimulated (Jain and Khurana, 2009; Van Ha *et al*., 2013). ABA mediated inhibition of lateral root growth is opposed by the auxin positive regulation. However, it was also shown that ABA can regulate the auxin transport to manage the root development under water stress by stimulating proton gradient at root tips (Yamaguchi and Sharp, 2010; Xu *et al*., 2013).

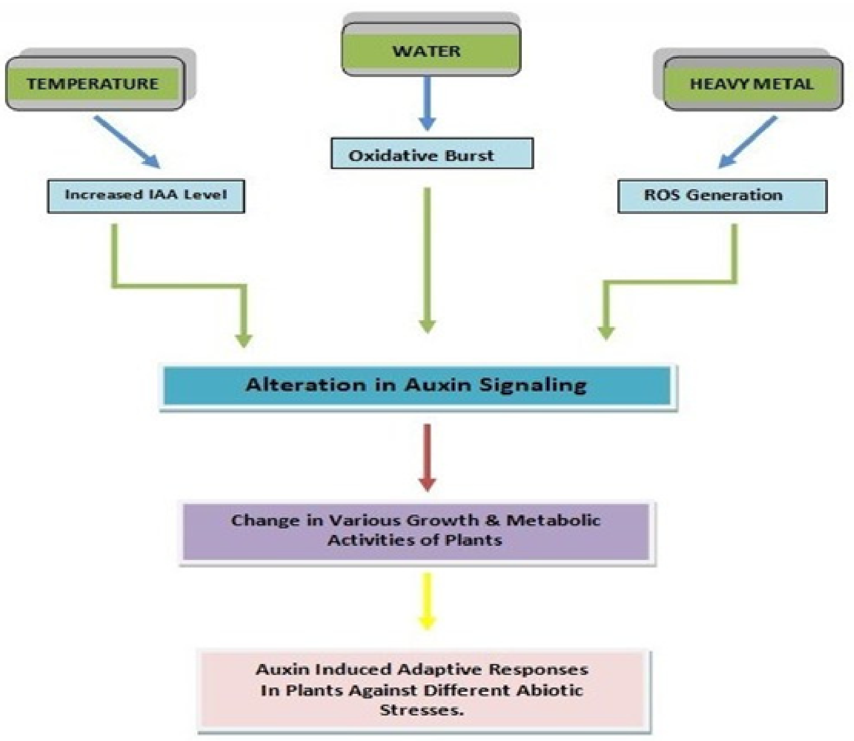

Figure 2: Auxin induced plant responses to various abiotic stresses.

Drought stress

Increased amount of IAA resulted in inhibition of plant growth, which is due to the altered hormonal balance in response to stress environments (Fahad *et al*., 2015). IAA supplementation controlled the apo plastic H_2O transport flow in non- arbuscular and arbuscular mycorrhizal maize plants under limited water supply conditions (Quiroga *et al*., 2020). Application of auxin significantly provided tolerance to drought stress in *Arabidopsis* by improving the root architecture, particularly lateral root number, functioning of ABA-mediated genes, and also regulated the level of metabolites like amino acids, organic acids, aromatic amines, carbohydrates, sugar alcohols; ultimately diminished the ROS level by decreasing amount of H_2O_2 and $O_2^{\cdot-}$,and increased the antioxidative activities of SOD, CAT, POD, and GR enzymes(Shi *et al*., 2014).Auxin supplementation considerably elevated the relative water content, chlorophyll amount, the amount of endogenous ABA & JA phytohormones, the functioning of auxin responsive genes, and also altered the expression of genes associated with leaf senescence to confer drought tolerance to white clover plant genotypes (Zhang *et al*., 2020).

Salinity stress

Auxin (IAA) treatment improved the level of photosynthetic pigments and functioning of antioxidative enzyme i.e. GPX, CAT, SOD in okra plants under salinity stress, therefore it was found that application with IAA in okra seeds could be a promising strategy for cultivar upgrading under high salt concentrations (Esan *et al*., 2017). IAA supplementation improved the salt tolerance in rice cultivars through increasing grain yield, filled grain %age, which are related with elevation in the amounts of carbohydrates moieties such as starch, sucrose, glucose and fructose in rice grains via IAA treatment (Javid *et al*., 2011).Exogenous supplementation of IAA significantly increased the plant growth by increasing the level of photosynthetic pigments, decreased the Na^+ amount and increased the amount of K^+, Ca^{2+}, and however, increased the leaf Na^+/K^+ ratio. It also declined the membrane permeability, and changed the functioning of antioxidative enzymes such as SOD, CAT under salinity stress in*Zea mays*plants (Kaya *et al*., 2013).

Heavy metal stress

Abiotic stress circumstances result in stress-triggered morphological changes, for instance, suppression of 1° root length, improved lateral root development and escalated root hairs formation. In this context, auxin play crucial role in regulating these morphological alterations, and modify plant reaction to heavy metal stress by altering auxin homeostasis involving auxin relocation, passage and steadiness (Yuan *et al*., 2013). Treatment with IAA at small amounts alleviated Cd toxicity, through considerable decrease in Cd uptake, as well as by escalating the plant growth by improving the functioning of photosynthetic apparatus and antioxidative enzymes activities in *Trigonella foenum-graecum*s eedlings grown under Cd stress (Bashri and Prasad, 2015). Application of IAA improved the root and shoots growth and elevated the rate of Cd, Pb and Zn phytoextraction in sunflower and maize (Fässler *et al*., 2010; Hadi *et al*., 2010). Exogenous application of IAA, GA_3, and citric acid increased plant shoot dry weight *Panicum virgatum* in lead contaminated soil (Aderholt *et al*., 2017). Treatment with IAA considerably enhanced stem length, amount of photosynthetic pigments, and antioxidative enzymes activities, and also decreased the proline level in leaves, obstructed the Cd passage from roots to shoot in *Triticum aestivum* under Cd toxicity (Agami and Mohamed, 2013).

IAA application obstructed the Cd accumulation in roots& its transport from roots to shoot, improved plant growth, functioning of photosynthetic apparatus, proline content, strengthens the plant antioxidant defense system by improving the activity of antioxidative enzymes, regulated the C and N metabolism to alleviate adverse effects of Cd in tea plants (Zhang *et al*., 2020b).IAA treatment improved the plant growth, biomass, amount of photosynthetic pigments & net photosynthetic rate, soluble sugars content, decreased the endogenous amount of Cd and escalated the activities of POX, SOD enzymes while reduced the protein amount in *Cyphomandrabetacea* seedlings to alleviate Cd toxicity (Li *et al*., 2020). Auxin alleviated the Cd stress by significantly enhancing the plant growth, amount of photosynthetic pigments, relative water content, diminished the ROS induced oxidative stress through improving functioning of antioxidative enzymes i.e. SOD, CAT and POX to mitigate Cd toxicity in wheat (Agami and Mohamed, 2013).

CONCLUSION

Phytohormones are essential internal messengers that involve germination, rooting, development, flowering and fruit ripening etc. to control the entire plant life cycle. Among various plant hormones like auxins, gibberellins, cytokinin's, abscisic acid and ethylene, auxin is of critical importance. Auxin plays a vital role in controlling cell elongation, cell division, proliferation, root initiation, apical dominance and tropical responses, and is crucial regulator for plant growth and development. It is also quite important that auxin plays a vital role in generating & sustaining primary meristems, and in the development of axillary meristems. Therefore, it is proved that auxin is an essential phytohormone which play vital role in numerous cellular processes along with providing resistance against different biotic as well as abiotic stress conditions.

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