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REVIEW ARTICLE

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The Interplay of Plant Hormones in Biotic Stress Responses: An Overview

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ABSTRACT

Plant hormones are organic substances found in extremely low concentrations in plants. Plant hormones and growth regulators are chemicals that influence ripening, maturation, root development, organ deformation and loss, stem extension prevention or enhancement, fruit colour enhancement, leafing, splint fall prevention or both, and a variety of other conditions. Extremely low concentrations of these substances cause significant growth changes. Auxin, gibberellin (GA), cytokinin, ethylene, and abscisic acid (ABA) are the five groups of plant growth-regulating compounds, and each group contains both natural and synthetic substances. Plant growth inhibitors, on the other hand, play important roles in the response to wounding as well as biotic and abiotic stresses. Abscisic acid inhibits plant growth, whereas ethylene promotes growth in some ways.
Keywords: Plant, Hormones, Microbes, Growth Regulators and Agriculture.

INTRODUCTION

Plant hormones primarily influence physiological processes in plants, such as development, growth, longevity, differentiation, and reproduction. Plant hormones, also known as phytohormones, are simple compounds that have a wide range of chemical properties. All of the plant's components produce and distribute hormones throughout the plant. Hormones and extrinsic factors both play important roles in processes like vernalization, phototropism, seedling development, and dormancy. The hormone's primary function is to regulate all developmental processes, including cell division, expansion, flowering, seed formation, dormancy, and abscission [Bradford, K.J. and Trewavas, A.J. (1994), Drury, R.E. (1969), Jackson, M.B. (1993)]. Plant hormones are classified as shown in figure 1.

PLANT HORMONES AND PLANT-MICROBE SYMBIOSIS

Plants have a very close relationship with microbes, and microbes have been associated with plants since their evolution. Microbes are present around the plant and also in the plant tissue.

These interactions are general or specific. Based on the effect microbes have on plants, they can be categorized as pathogens, PGPB (plant growth-promoting bacteria), or commensals. Plants depend on their microbial partners for many functions. Soil hosts a wide variety of organisms, and the community of all microbes associated with plants is called the Phyto microbiome. Plant hormones control almost every component of plants' growth and reactions to their surroundings [Ross, J. and O'Neill, D. (2001), Takahashi et al., 1986, Weyers et al., 1995].

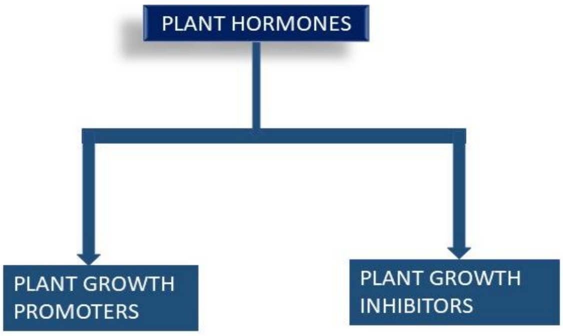

Figure 1. Classification of plant hormones.

Numerous phytohormones play critical roles in interactions between plants and beneficial microbes, participating at extremely low concentrations with tight spatial regulation of synthesis and response. Plant form is determined by a combination of environmental and biological factors, as well as several biological and genetic indicators. Plant hormones are signal molecules that are present in trace amounts throughout the plant body and only elicit responses in cells that have acceptable secretion receptors. In plants, hormones travel massively throughout the body via the plant tissues (xylem and phloem) and cell-to-cell via plasmodesmata.

Hormones derived from each plant and its microbic partner play important roles in communication, symbiosis formation, and performance. This includes intimate endosymbioses with arbuscular mycorrhizal (AM) fungi formed by the majority of land plants and thus a lot of recently evolved modulation, as well as symbioses between a limited set of plants within the fabid biological group and nitrogen-fixing microorganisms [Trewavas, A.J. (1983), Zhao, Y. (2010)].

TYPES OF PLANT HORMONES AND THEIR FUNCTIONS

Auxins, cytokinins, and gibberellins are plant growth promoters, whereas abscisic acid and ethylene are plant growth inhibitors. Ethylene can be thought of as both a growth promoter and an inhibitor of plant growth (Fig. 2). Plant growth hormones (PGRs) or phytohormones are organic substances that are synthesised in minute amounts in one part of the plant body and transported to another part of the plant body where they influence specific physiological processes. PGRs are classified into two categories: plant growth promoters and factory growth inhibitors. Plant growth promoters induce cell proliferation, cell expansion pattern conformation, tropic growth, flowering, regenerating, and seed conformation. There are three of them (Table 1): auxins, gibberellins, and cytokinins.

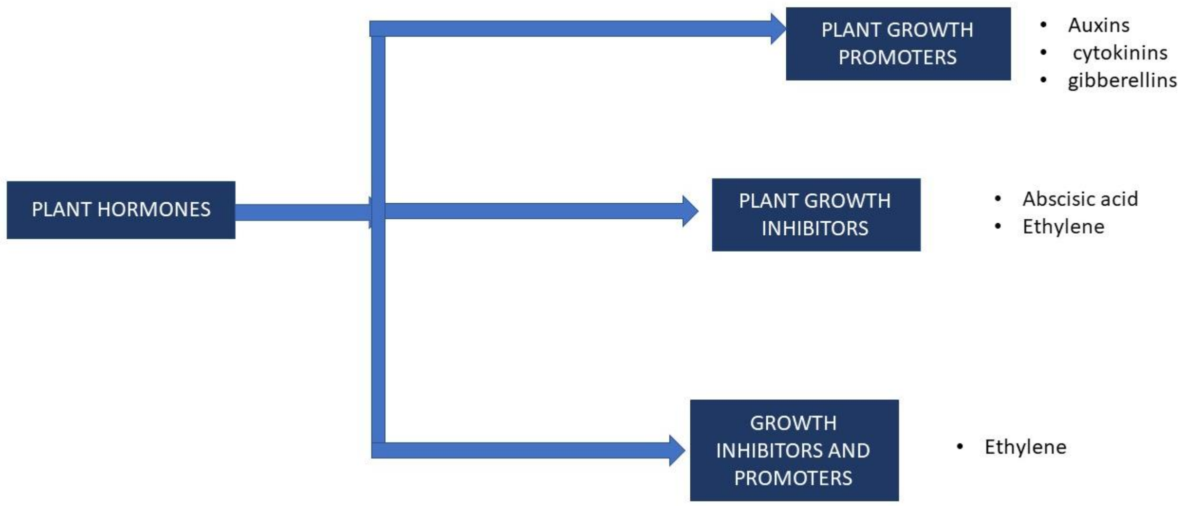

Figure 2. Plant Hormones.

Table 1. Hormones and its major function.

HORMONE	MAJOR FUNCTION
Auxin	Elongation of cells of stems and roots
Gibberellin	Stimulates parthenocarpy
Cytokinins	Promotes lateral and adventitious shoot growth
Abscisic acid	Accelerates seed dormancy, useful for storage purposes
Ethylene	Facilitates rapid elongation of internodes and petioles

Auxin Hormone—Fritz W. Went, a Dutch botanist, discovered auxins in 1928. The scientist conducted a test known as the Avena curvature test. Following the analysis of the Avena sativa grass (oat plants), it was determined that there was a hormone present, which was later called auxin. Auxin means "to be able to grow." The first correlated plant hormone was an auxin, indole-3-acetic acid (IAA). It is mostly found in shoot tips (particularly in lamina primordia and adolescent leaves), embryos, and developing flower and seed regions. It moves from neighbouring cells through the parenchyma surrounding the vascular system, which requires the use of adenosine triphosphate energy (ATP), which is widely used in agricultural and horticultural practices. These growth regulators for plants are produced mainly at the roots and stem tips, from which they are transferred toward other components of the plant. These plant hormones are derived from both natural and chemical sources. Natural plant sources provide indole-3-acetic acid and indole butyric acid, whereas synthetic sources provide naphthalene acetic acid and 2,4-dichlorophenoxyacetic acid [Korasick et al., 2013, Kasahara, H. (2015)].

The activation of vascular differentiation in the shoot apex and calluses; creates meristematic division in the early summer, promoting vascular development in wound healing. It also increases cell wall extensibility, which promotes cellular elongation. Auxin has the ability to move to the plant's darker side, causing the curving known as phototropin. Auxins indirectly maintain apical dominance by stimulating ethylene production, which directly inhibits lateral bud growth.

It also activates a gene involved in the synthesis of dictyosome-produced and secreted wall materials, as well as other genetic mutations involved in the synthesis of dictyosome-produced and secreted wall materials. Auxins promote the formation and growth of adventitious roots in cuttings, as well as the development of a variety of fruits (from the auxin produced by the developing seeds).

Auxin is produced and synthesised via two different biosynthesis pathways (Fig. 3). As tryptophan is a precursor for auxins, the pathways are classified as tryptophan-dependent or tryptophan-independent. The tryptophan-dependent system includes four alternative pathways named the IPA (indole-3-pyruvic acid) pathway, the tryptamine (TAM) pathway, the indole-3-acetaldoxime (IAOX) pathway, and the IAM (indole-3-acetamide) pathway. In plant growth and development, the phytohormone indole-3-acetic acid (IAA) is essential. The Trp-dependent Indole-3-acetic acid biosynthetic pathway uses the precursor tryptophan (Trp) to synthesise IAA. However, has a Trp-independent Indole-3-acetic acid biosynthetic pathway [Korasick et al., 2013, Kasahara, H. (2015)].

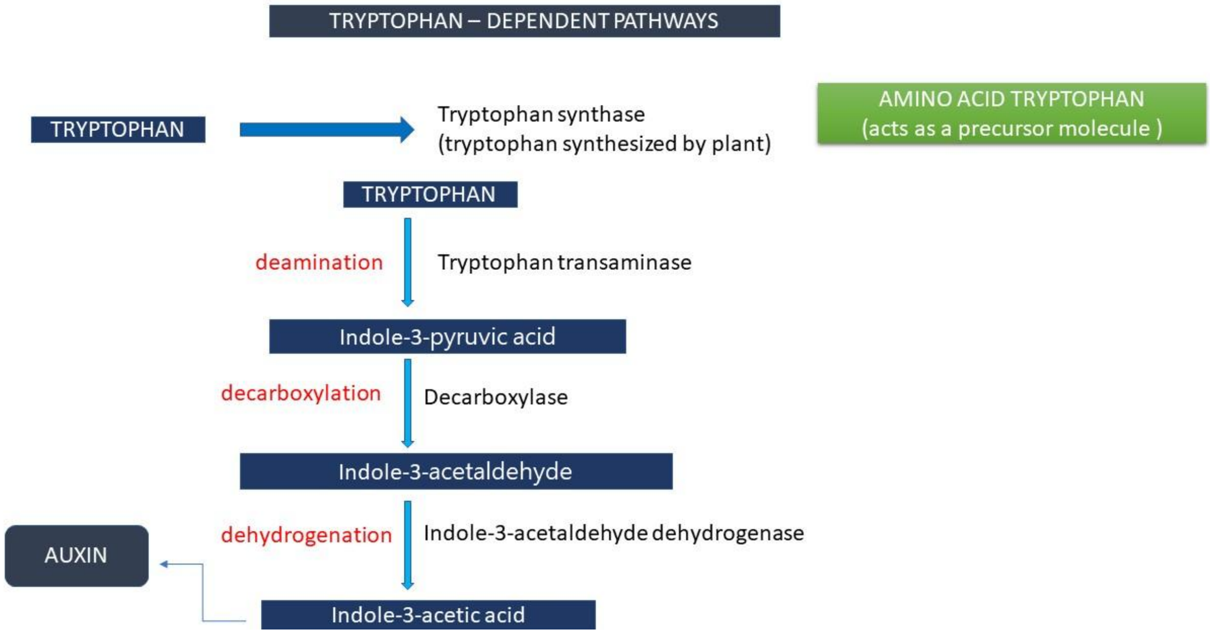

Figure 3.Biosynthesis of auxins (IAA).

The regulated transport of the plant hormone auxin in plants is known as polar auxin transport. Polar transport takes place via vascular parenchyma tissue, specifically the xylem parenchyma in the shoot and the phloem parenchyma in the root. The transport of auxin in the plant is primarily polar and occurs cell-to-cell. The polar transport of auxin in stems is basipetal, that is, it occurs from the apex to the base; similarly, in roots, the auxin transport is polar but primarily acropetal. Polar transport is a gravity-independent and energy-dependent process. Auxin can also be transported non-polarly, but only rarely, and this transport is phloem-based, as demonstrated by Goldsmith et al. in 1974 in Coleus spp. Polar transport is slower than non-polar transport, which is energy-independent and long-distance source-sink transport [Korasick et al., 2013, Kasahara, H. (2015), He et al., 2011].

The chemiosmotic model was developed to explain the mechanism underlying the plant's unique ability to transport auxin through living cells. According to this model, the proton motive force (PMF) drives auxin influx, while the difference in membrane potential and specific auxin efflux proteins present at the base of conducting cells drive efflux. There are two types of auxin influx: IAAH is a protonated form that is lipophilic and can enter via simple diffusion. IAA, on the other hand, can enter via secondary active transport via the 2H+-IAA-symporter. Aux1 is one example. The auxin efflux is mediated by: PIN1-PIN8, or Arabidopsis eight-pin proteins, are integral membrane proteins found at the cell's base (polar distribution). The other protein is known as PGP (P-glycoproteins), which is also known as ABCB (ATP binding cassettes subfamily B), and it is found on all sides of the cell [Korasick et al., 2013, Kasahara, H. (2015), He et al., 2011].

Gibberellin hormone—In 1926, Japanese scientist Eiichi Kurosawa discovered that foolish seedling disease was caused by a fungus disease of rice. The name is derived from *Gibberella fujikuroi*, a phylum Ascomycota hormone-producing fungus that causes excessive growth and poor yield in rice plants. Teijiro Yabuta and Sumuki isolated it in 1935 from fungal strains (*Gibberella fujikori*) provided by Kurosawa, the isolate was later given the name gibberellin. The gibberellin hormone controls a variety of developmental processes. Gibberellic acid (GA) is a tetracyclic di-terpenoid compound that stimulates plant growth and development. Tetracyclic and diterpenoid acids characterise all gibberellic acids. GAs promote seed germination, trigger transitions from meristem to shoot growth, juvenile to adult leaf stage, and vegetative to flowering, and determine sex expression and grain development in conjunction with the interaction of various environmental factors such as light, temperature, and water. Gibberellins have a variety of effects on plant growth, the most noticeable of which is stem elongation. When a low concentration of it is applied to a bush, the stem begins to grow. Internodes become so long that the plants can no longer be distinguished from each other. Gibberellins overcome genetic limitations in various dwarf varieties. The terpenoid pathway in the plastid synthesises the hormone, which is then modified in the endoplasmic reticulum and cytosol until it is active [Hedden, P. and Sponsel, V. (2015), Yamaguchi, S. (2008), Rademacher, W. (2000)].

Plants, fungi, and bacteria all contain gibberellic acid. Gibberellic acids help to regulate stem elongation, germination, dormancy breaking, flowering, flower development, and leaf and fruit senescence. In general, gibberellin has two active forms known as C19 and C20. carbon 19 (C19) and carbon 20 (C20). The inactive form is C20, whereas the active form is C19, and the enzyme G20 oxidase aids in the conversion of the inactive form to the active form. After conversion, the C19 performs all of the functions assigned to the plant hormone gibberellin. GA1, GA3, GA4, and GA7 are the only bioactive gibberellin plant hormones produced; all of these bioactive gibberellins are C19 in nature (i.e., active form). Synthesis occurs in apical tissue, young leaves, the root region, and at the highest level in immature and developing fruits. Gibberellin hormones are synthesised in the plastid, cytosol, and endoplasmic reticulum. The biosynthesis begins in the plastid, then moves to the cytosol, and finally to the endoplasmic reticulum. The maturation process occurs in the cytosol after reaching the endoplasmic reticulum, which is the final destination of biosynthesis. The biosynthesis is affected by temperature and photoperiod, which can affect it both positively and negatively, and the bioactive form is produced in the cytosol.

GA12 is the precursor of all the gibberellic acids. Phosphon D, AMO-1618, Cycocel (CCC), Ancymidol, and Paclobuterzol are five important gibberellin inhibitors. Paclobuterzol is a second-stage inhibitor that inhibits the functioning or biosynthesis pathway at the secondary stage of pathways. When GA20 is converted to GA1, GA3 oxidase is used to aid in the process, and a lack of GA3 oxidase can cause dwarfism in plants. The translocation of produced gibberellin is bidirectional; if the gibberellic acid is synthesised in the root, it is translocated via the xylem, and if it is synthesised in the shoot, it is translocated via the phloem. The gibberellin acid signalling pathway includes subcomponents such as Della (nuclear protein), which contains the Della motif, which is a combination of amino acid sequences (aspartate-glutamate-leucine-leucine-alanine) [Hedden, P. and Sponsel, V. (2015), Yamaguchi, S. (2008), Rademacher, W. (2000), Nakayama et al., 1990].
Della functions as a repressor, inhibiting gibberellic acid signalling. It is divided into two domains: the Della domain and the Gras domain (where the receptor binds). The Della protein's target is to bind to PIF or prefoldins (PFDS), preventing subcomponents from functioning properly. The entire signalling pathway is completed with the help of 26S protease degradation, in which two cases occur: one in which gibberellic acid is absent and Della protein binds to the receptor GID1, and because it does not allow the receptor to function properly, there is no transcription and thus no response. In the second case, gibberellic acid is present, and because it is present, the Della protein cannot bind to the receptor, which is GID1. As a result, the SCF protein binds to the entire complex, leading to the degradation of the Della repressor protein, and transcription and the process are completed [Hedden, P. and Sponsel, V. (2015), Yamaguchi, S. (2008), Rademacher, W. (2000), Nakayama et al., 1990].

Cytokinin Hormone: Cytokinins were discovered in the late 1950s while searching for the molecule responsible for autoclaved herring sperm DNA's growth-promoting activity. F. Skoog, C. Miller, and colleagues discovered cytokinins in 1955. It is an autoclaved adenine derivative isolated from herring sperm DNA. As a result of this, cytokinin-like zeatin was isolated from coconut milk and corn kernels. Kinetin is a cytokinesis-promoting protein. Currently, the kinetin-auxin interaction regulates the morphogenetic differentiation of shoot and root meristems. Skoog (1956–57) demonstrated that tobacco pith callus tissue is grown in high auxin environments. Cytokinins are essential components of plant morphogenesis [Sakakibara, H. (2006), Werner, T. and Schmülling, T. (2009), Koshimizu et al., 1967].
High kinetin and low auxin produced only roots, whereas high kinetin and low auxin promoted the formation of shoot buds. Cytokinins also stimulate the formation of buds in leaf segments of plants such as Bryophyllum, Begonia, and others. Other morphogenetic responses induced by cytokinins include protoplast maturation into plastids, tracheid differentiation, parthenocarpy induction, and flowering induction. Cytokinins are produced in areas where cell division is rapid, and they stimulate the growth of new leaves and chloroplasts in leaves. Cytokinin is a basic protein that uses a two-component histidine system for signalling. If it is produced in the roots, which is a major source, it is transported to the upper part of the plant via the xylem, and if it is produced in the shoot, which is a minor source, it is transported to the lower area via the phloem. Cytokinin is also involved in cell division areas such as the endocarp region of seeds, growing embryos, developing seeds, young fruits, and developing shoot buds, among many other places.

Cytokinin also mediates responses to external conditions such as light conditions in the shoot and nutrient and water availability in the root, and it is involved in both abiotic and biotic stress. These activities, taken together, contribute to the fine-tuning of quantitative growth regulation in plants. Other roles or effects of cytokinins include differentiation of interfascicular parenchyma and nodulation, solute accumulation, stimulation of several enzymes, particularly those involved in photosynthesis, and so on [Werner, T. and Schmülling, T. (2009), Koshimizu et al., 1967].

Abscisic Acid Hormone: Abscisic acid (ABA) is a plant hormone that influences plant growth, development, and stress response. It exists in two enantiomorphic forms due to the antisymmetric carbon atom (carbon-1): R-abscisic acid and S-abscisic acid. It is synthesised in almost all cells that contain chloroplasts and other plastids, but it is primarily synthesised by leaf vascular tissue. Since it was found in such high concentrations in newly abscised or freshly fallen leaves, it was given the name "abscisic acid." It is also known as the stress hormone because it is stimulated by drought, waterlogging, and other negative environmental conditions. Abscisic acid is referred to as dormin because it causes dormancy in buds, subsurface stems, and seeds. It is also known as Abscission II and Inhibitor-B. It is required for many physiological functions in plants, including stomatal closure, cuticular wax accumulation, defoliation, bud-stunted growth, germination, osmolarity regulation, and growth inhibition. There are two pathways for the biosynthesis of the abscisic acid hormone: direct synthesis from mevalonic acid and indirect synthesis from carotenoid oxidation. Water stress increases abscisic acid formation occurs in the direct synthesis of abscisic acid from mevalonic acid via farnesyl pyrophosphate. The initial reactions of abscisic acid synthesis are identical to those of gibberellins, sterols, carotenoids, and other isoprenoid compounds [Ohkuma et al., 1963, Finkelstein, R. (2013), Meguro, A. and Sato, Y. (2014)].

Mevalonic acid→ Isopentenyl pyrophosphate→ Farnesyl pyrophosphate→ Abscisic acid

The oxidation of carotenoids or oxidised carotenoids (xanthophylls such as violaxanthin or neoxanthin) results in the indirect synthesis of abscisic acid. The xanthophyll, violaxanthin has been identified as an ABA precursor. Violaxanthin is produced by a reaction catalysed by the enzyme zeaxanthin epoxidase from zeaxanthin (also a 40-C xanthophyll) (ZEP). In the presence of the enzyme 9'-cis-epoxycarotenoid dioxygenase, violaxanthin is converted into 9'-cis-neoxanthin, which is then cleaved into the 15-C compound Xanthoxal (previously known as Xanthoxin) and a 25-C epoxy aldehyde. Xanthoxal (xanthoxin) is finally converted into ABA in the cytosol via two oxidation steps catalysed by the enzyme aldehyde oxidases, with abscisic aldehyde as an intermediate. The enzyme aldehyde oxidases require Mo as a cofactor. The first steps of ABA biosynthesis occur in chloroplasts or other plastids, while the final steps take place in the cytosol. Abscisic Acid's physiological role is to neutralise the stimulatory and inhibitory activity of other hormones [Ohkuma et al., 1963, Finkelstein, R. (2013), Meguro, A. and Sato, Y. (2014), Xiong, L. (2003)]. i) ABA inhibits IAA-induced cell growth, ii) ABA inhibits amylase produced by gibberellin-treated seeds, and iii) ABA promotes chlorosis, which is suppressed by cytokinin. This could be because ABA is a Ca++ antagonist, and its inhibition of the stimulatory effects of IAA and cytokinin could be due to Ca++ metabolism interference.

Other effects include: inhibiting the division of cells and cell elongation, inducing parthenocarpic development in roses, and increasing plant resistance to cold. inhibits gibberellin-mediated amylase synthesis during cereal grain germination, inhibits fruit ripening, and so on.

Ethylene Hormone: Dimitry Neljubov discovered ethylene as the "active" component in illuminating gas in 1901 and published his findings. Plants were shown to produce ethylene in the 1930s, establishing ethylene as an exogenous controller of plant growth and development. Ethylene is the simplest of the olefin gases and was the first gaseous biological signalling molecule discovered. It is synthesised by plants at different stages of development and in response to abiotic and biotic stressors. Ethylene has the general formula C_2H_4. It is highly flammable and volatile, and it is the only plant hormone that exists in nature as a gas at normal temperature and pressure. $KMnO_4$ can absorb ethylene. It is a colourless gas with a sweet and musky odour. Gas chromatographic techniques, a flame ionisation detector, and a laser-driven photoacoustic detector can all detect ethylene. It is formed by the breakdown of methionine and is produced by almost all organs, with the highest concentration in ripe fruits. It prevents leaf expansion during the early stages of growth or germination. Ethylene is thought to be a functionalized phytohormone that controls both growth and senescence. Ethylene acts as both a plant inhibitor and a plant promoter, but it primarily inhibits plant growth. Depending on the concentration, duration of application, and types of plants, it helps promote or inhibit growth and senescence [Larsen, P.B. (2015), Yang, S.F. and Hoffman, N.E. (1984), Sun, et al., 2017].

Ethylene is obtained from the amino acid methionine, which is converted to S-adenosylmethionine (AdoMet) in the first step by AdoMet synthetase. AdoMet is a precursor in several biosynthetic pathways, including the synthesis of polyamines. AdoMet is converted to 1-aminocyclopropane-1-carboxylic acid (ACC) by ACC synthase (ACS), which is the first committed and, in most cases, the rate-limiting step in ethylene biosynthesis.

One of the very important points about ethylene hormone is the "ethylene triple response." Ethylene shows three responses in plants, and seed growing in the dark because of the ethylene present in the plant leads to three very crucial features such as i) a short or reduced hypocotyl, ii) an increase in the width or thickness of the stem, and iii) the curling of the apical hook. In the ethylene signalling pathway, the main ligand will be ethylene, and the receptor is ETR1 (ethylene response 1). It is a copper-based ion-based receptor, present on the ER membrane with the receiver in the lumen. RAN1 is the transporter of copper ions, other receptors in Arabidopsis are ETR2, ERS1 (Ethylene Response Sensor 1), ERS2, and EIN4 (Ethylene Insensitive 4). The pathway's regulators are ETR1, ERF1, CTR1 (constitutive triple response) 1, EIN2, EIN3, and ETP. The receptors are homologous to bacterial two-component receptors, binding of ethylene inactivates receptors due to negative regulators [Larsen, P.B. (2015), Yang, S.F. and Hoffman, N.E. (1984), Sun, et al., 2017].

APPLICATIONS OF PLANT GROWTH REGULATORS IN AGRICULTURE

Plant growth regulators are chemicals that are naturally synthesised in plants and that affect physiological processes. Their synthetic analogues trigger many biochemical and physiological processes involved in plant growth and development.

The importance of plant growth regulators in agriculture [Larsen, P.B. (2015), Yang, S.F. and Hoffman, N.E. (1984), Sun, et al., 2017, Li et al., 2016] includes the following:

- Plant growth regulators are used to modify crops, increasing secondary growth, suppressing stem elongation, increasing return bloom, excreting fruit, or modifying fruit maturity are all examples of methods.
- They are used in fruit production as growth regulators. They are organic chemical substances that, in small amounts, regulate plant growth in addition to nutrients and vitamins.
- Auxins, gibberellins, cytokinins, ethylene, inhibitors, and growth retardants are examples of growth regulators.
- Plant hormones stimulate the production of other hormones and, in collaboration with cytokinins, stimulate the number of stems, roots, and fruits, as well as the conversion of stems to flowers. The first class of growth regulators to be discovered were auxins. They influence cell elongation by changing the plasticity of the cell wall. Because some of these (NAA, 2-4, and D) is mainly artificial and synthetic, we should technically refer to them as 'plant growth regulators," or PGRs, instead of hormones. In vegetative propagation, auxins such as indolebutyric acid (IBA) are used to induce cutting rooting.
- Auxin aids in the rooting of cuttings and the prevention of abscission. It promotes root growth at low concentrations and shoots growth at higher concentrations.
- Auxin application results in seedless or parthenocarpic fruit such as grapes, papaya, banana, orange, and tomato.
- Gibberellin aids in the emergence of seeds, buds, and tubers from dormancy. It also aids in the germination of seeds, such as lettuce and cereals.
- Nepthalin in cold storage Acetic acid is sprayed on potato tubers to prevent buds from sprouting.
- to produce low-temperature resistance, to grow more crops, to ripen more fruits, to test sterility, and to store seed. Plant hormones are employed.
- Growth retardants slow cell division and cell elongation, suppress the growth of plants.
- Synthetic inhibitors accelerate the loss of chlorophyll.
- Abscisic acid controls organ size and facilitates seed dormancy.
- In the field of horticulture, plant hormones are used to promote growth in the form of rooting powder, for example.

CONCLUSION

The goal of researching plant growth hormones is to promote all aspects of plant development and plant responses to their surroundings. Plant growth hormones improve plant quality by providing other nutrients required for the development of a plant's shoots and roots, as well as reducing stress. There are various types of plant growth regulators available, and each one serves a specific purpose. Auxins, gibberellins, and cytokinins promote growth, whereas abscisic acid and ethylene inhibit it. Plant hormones also allow plants to withstand environmental stresses. Plant hormones regulate all growth-related activities, including organ size regulation and pathogen defence.

Researchers have also discovered a link between plant hormone consumption and a variety of human illnesses, including diabetes, depression, and cancer. Plant hormones such as Indole-3-acetic acid have anti-tumor and anti-cancer properties; gibberellins aid in apoptosis; abscisic acid has anti-depressant properties and regulates glucose homeostasis; and cytokinin has anti-aging properties.

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