International Journal of Research in Agronomy 2024; SP-7(4): 315-325

International Journal
of
Research in Agronomy

E-ISSN: 2618-0618
P-ISSN: 2618-060X
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www.agronomyjournals.com
2024; SP-7(4): 315-325
Received: 07-01-2024
Accepted: 15-03-2024

Exploring plant growth regulators (PGRS): Classification, structural features, and functional significance

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DOI: https://doi.org/10.33545/2618060X.2024.v7.i4Sd.645

Abstract

The discovery of plant growth regulators, or phytohormones, has revolutionized horticulture by offering means to control virtually all aspects of plant growth and development, thereby enhancing production, quality, and the post-harvest life of crops. This impact is particularly evident in the production of tree fruits, where even minor enhancements can significantly improve productivity, product quality, and consumer appeal, thus increasing the value of these high-value crops. Phytohormones despite being produced in minute quantities by plants, exhibit potent physiological activity. Among these, auxins and cytokinin are primary categories, with auxins produced in apical meristems, young leaves, seeds, and fruits to promote shoot elongation and root initiation, and cytokinin generated in root tips, seeds, and unripe fruits to encourage lateral shoot growth and cell division. The study delves into the role of the plant hormone auxin as a key signaling molecule throughout all stages of plant growth, highlighting its involvement in a myriad of developmental processes. Recent research has shed light on the molecular details of auxin responses, elucidating the roles and control mechanisms of the canonical transcriptional auxin response and categorizing the molecular processes underlying various auxin-mediated effects on plant development.

Keywords: Biosynthesis, growth regulation, hormonal signaling, plant development, plant growth regulators

Introduction

PGRs are organic substances that are found in small amounts and regulate several facets related to plant growth and development. Based on their physiological effects and structural similarities, they may be divided into many types. Auxins, gibberellins (GAs), cytokines, abscisic acid (ABA), and ethylene are few of the main PGR classes. Furthermore, several additional substances have also been shown to have PGR-like properties, including fatty acids, steroid hormones, salicylic acid (SA), jasmonates, polyamines, nitric oxide (NO), Strigolactones, Karrikins, as well as others. Phytohormones or plant growth regulators are organic compounds that are naturally produced by plants and affect their growth or other physiological functions at low concentrations and at distant sites from where they are synthesized. The hormones mentioned above are unique to plants and come in several forms, including ethylene, auxins, gibberellins, cytokinins, and growth inhibitors1. Over the past fifty years, PGRs have been the subject of much research in the nation to increase the quantity and quality of fruits produced, taking into account variables like cultivating, harvesting, irrigation, training, and variety. PGRs may increase fruit crops' productivity and quality by adding them to their foliage, but many of the fruits are still of low quality. PGRs can boost fruit output to a higher standard, which makes them a crucial component of contemporary crop management. PGRs are organic compounds that, in modest doses, can alter or control a plant's physiological processes (Jain *et al.*, 2023) [21]. They can be applied to the different parts of the plant, and they are rapidly absorbed and translocated. In small amounts, they can affect any physiological function of the plant and have distinct ways of action.

PGRs have improved growth, productivity, and quality of a variety of fruit crops with some quite impressive outcomes. PGRs currently influence or regulate several physiological effects, including the enhancement of fruit shape, the avoidance of before harvesting drop, induction of fruit/flower abscission to thin the plant, the development of branching, and the controlling of vegetative growth. Given that fruit trees are high-value commodities, small adjustments to production procedures, product quality, or visual appeal can have a significant impact (Jain *et al*., 2023) [21]. Genetically modified organisms (PGRs) represent a new frontier in biotechnology, offering a fresh approach to modifying plant biology to improve nutritional value, growth, production, and quality while mitigating both abiotic and biotic stress. Plant growth regulators (PGRs), which include the chemical's methyl jasmonate (MJ), and jasmonic acid, as well as other derivatives referred to as jasmonates (JAs), are widely distributed signalling molecules that facilitate plant reactions to environmental stressors like damage, pest, and virus assault. Even while PGRs are frequently utilized to enhance plant development, growth, resistance to pathogens, and productivity, it is still unclear what molecular pathways underlie these advantages. Auxins are (IAA, NAA, IBA, 2-4D, 4-CPA), Gibberellins (GA3), Cytokines (Kinetin, or, Zeatin), Ethylene (Ethereal), Abscissic acids (Dormins, Phaseic Acids), Phenolic compounds (Coumarin), Flowering hormones (Florigin, Anthesin, Vernalin), Growth inhibitors (AMO-1618, Phosphon-D, Cycosel, B-999) are a few classes of plant growth regulators.

Principal five hormones

The "classical" phytohormones fall into five well-established groups, sometimes known as the "big five," namely:

1. Auxins
2. Gibberellic acid
3. Cytokinin
4. Abscisic acid
5. Ethylene

The PGRs are classified into different groups according to their structure and function in plant physiology. Each group has both stimulating and inhibiting effects and often interacts with other groups to regulate plant growth (Hajam *et al*., 2017) [17].

PGR is used in tree fruit production

Since they improve yield and quality, plant growth regulators, or PGRs, are more crucial to the production of tree fruits than other crops. To illustrate the history of PGR use and the state of our knowledge regarding its effects on plant physiology, a few commercial uses are selected. The production of tree fruits frequently involves the utilisation of the PGRs ethylene, gibberellins, cytokinins, auxins, and abscisic acid.

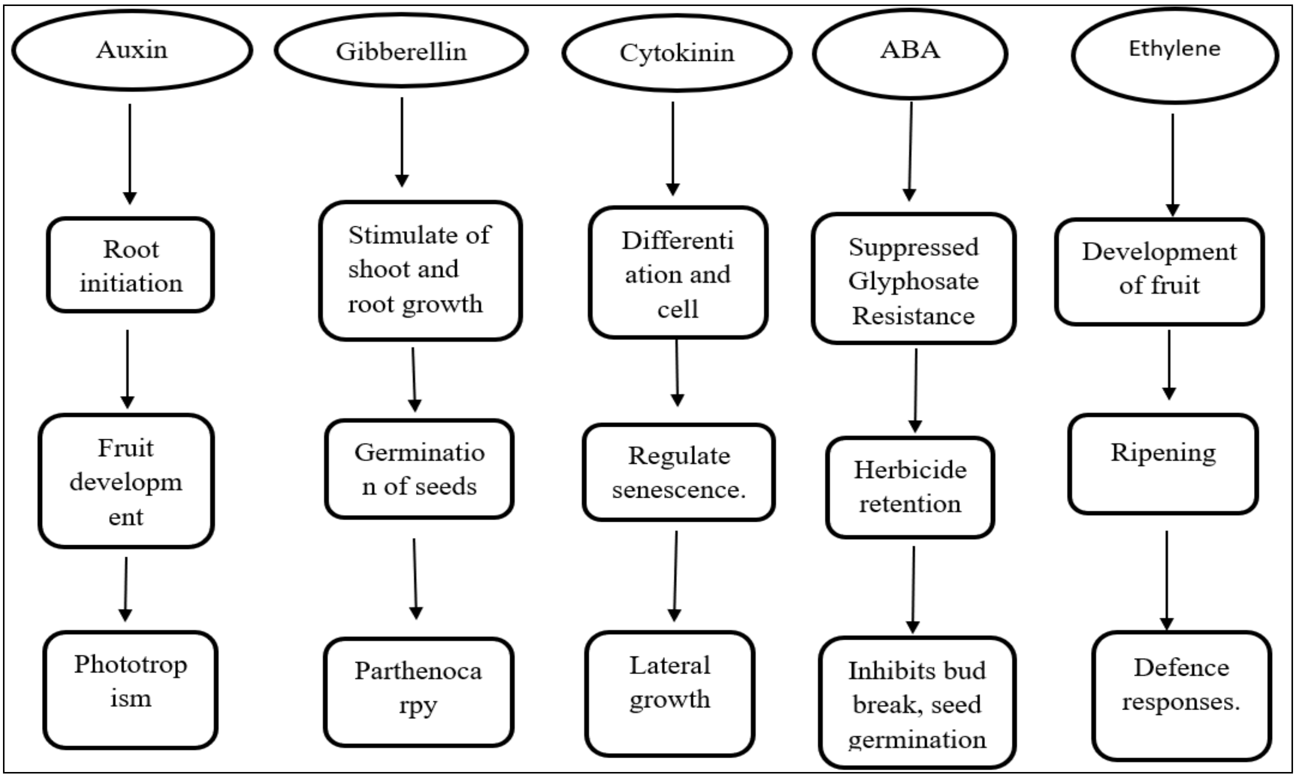

Fig 1: Different types of Plant Growth Regulators

Fruit abscission: the role of PGRs in preharvest drop

Fruits separate from plants through a physiological process called fruit abscission. There are two distinct stages at which it might happen: the first is in the early stages of fruit development, sometimes referred to as the flower abscission or chemical thinning stage. In the second phase, fruit drops prematurely or drops just as they are approaching the harvesting period. Bisht *et al*. (2018) [3] reported that Gardner *et al*. (1940) [15] discovered in the late 1930s that naphthalene acetic acid (NAA) and naphthalene acetamide (NAAm) could lower the preharvest drop of fruits, and that auxins might delay the abscission of leaf petioles. After testing, other auxins such 2,4-D (2,4-dichlorophenoxyacetic acid) were shown to be ineffective. Auxin-active substances such as 2, 4-D (2, 4-dichlorophenoxyactic acid), Fen prop (2- [2, 4, 5-trichlorophenoxy]), and Daminozide (2, 2-dimethylhydrazide) are important in preventing pre-harvest fruit drop. By using 2, 4-dichlorophenoxyactic acid and 2, 4-D + GA3, fruit ripening was postponed, ethylene production was minimal, fruit size was raised, and fruit drop was minimized (Sobia Chishti *et al*., 2022)

[34]. According to Bisht *et al.* (2018) [3], in 1978, aminoethoxyvinylglycine (AVG), an inhibitor of ethylene production, was identified as a drop control PBR and is still the most often used PBR for drop control. Naphthaleneacetic acid combined with aminoethoxyvinylglycine (AVG) or 1-methylcyclopropene (1-MCP) can reduce fruit drop more than NAA, AVG or 1-MCP alone. These combinations can also inhibit the expression of genes involved in ethylene production and cell wall breakdown in the fruit abscission zone (Yuan & Li, 2008) [41].

Table 1: Terms used commonly and chemically to refer to substances that lower preharvest drop Source: (Raja *et al*., 2017) [31]

Common name	Chemical name
NAA	naphthaleneacetic acid (Raja *et al*., 2017) [31]
NAAm	naphthalene acetamide ((Raja *et al*., 2017) [31]
Fenoprop, 2,4,5-TP	2-(2,4,5-trichlorophenoxy) propionic acid (Raja *et al*., 2017) [31]
Daminozide, SADH	butanedioic acid mono(2,2-dimethylhydrazide) (Raja *et al*., 2017) [31]
Dicamba	3,6-dichloro-2-methoxybenzoic acid (Raja *et al*., 2017) [31]
Dichlorprop, 2,4-DP	2-(2,4-dichlorophenoxy) propanoic acid (Raja *et al*., 2017) [31]
AVG	Aminoethoxyvinylglycine hydrochloride N-(phenylmethyl)-1H-purine-6-amine (Raja *et al*., 2017) [31]
2,4-D	(2,4-dichloro phenoxy) acetic acid (Raja *et al*., 2017) [31]
lactidichlor ethyl	benzoic acid 3,6-dichloro-2 methoxy, 2-ethoxy,1-methyl, 2-oxoethyl ester (Raja *et al*., 2017) [31]
triclopyr	[(3,5,6-trichloro-2-pyridinyl) oxy] acetic acid (Raja *et al*., 2017) [31]
fenclopyr, CPPU	[(3,5,6-trichloro-2-pyridinyl) oxy] acetic acid (Raja *et al*., 2017) [31]
No common name	triethanolamine salt of 2-(2,4,5-trichloro phenoxy) propionic acid (Raja *et al*., 2017) [31]
No common name	2-methyl, 4-chlorophenoxyacetic acid (Raja *et al*., 2017) [31]
No common name, 2,4,5-TA	triethanolamine salt of 2,4,5-trichloro phenoxy acetic acid (Raja *et al*., 2017) [31]
No common name, 2,4,5-TAA	2,4,5-trichlorophenoxyacetamide (Raja *et al*., 2017) [31]
MCPB	4-(2-methyl-4-chlorophenoxy) butyric acid (Raja *et al*., 2017) [31]

PGRs' function in floral abscission: The chemical thinning phase

Abscission is the process of detaching plant parts, such as leaves, flowers, and fruits. It is regulated by hormones and enzymes that affect the expression of genes involved in this process (Costa *et al*., 2005) [7]. Applying plant growth regulators (PGRs) or other chemicals to a plant to limit its fruit yield while enhancing the size and quality of the fruits that remain is known as chemical thinning (Fallahi and Greene, 2009) [13]. PGRs can influence flower abscission by affecting the hormonal balance between auxins and ethylene, which are the main regulators of this process. Auxins can delay flower abscission, while ethylene can induce it. Several PGRs have been used to manipulate flower abscission in various fruit crops, such as naphthalene acetic acid (NAA), naphthalene acetamide (NAAm), gibberellins (GA), cytokinins (CK), and aminoethoxyvinylglycine (AVG). Among them, NAA and NAAm are the most widely used PGRs for chemical thinning, as they can reduce flower and fruit sets by enhancing ethylene production and sensitivity. GA and CK can also be used to thin flowers and fruits by inhibiting pollen germination and fertilization. AVG, on the other hand, can inhibit ethylene biosynthesis and delay flower abscission, which can increase fruit set and yield (Bisht *et al*. 2018) [3].

Role of PGRs in vegetative growth

Proper vegetative growth management is crucial for fruit production due to the inverse link between growth and flowering. Excessive vegetative growth can harm fruit quality, postharvest life, and the establishment of an efficient tree structure. Different types of PGRs have been used for this purpose, such as auxins, gibberellins, cytokinins, ethylene, and their inhibitors or antagonists. Some of the PGRs that have been used for controlling the vegetative growth of fruits are daminozide, ethephon, paclobutrazol, and prohexadione-calcium. Ethephon was identified as a very effective growth retardant, but it also thinned the fruits. It was also reported that daminozide and paclobutrazol were used in combination with ethephon or alone for growth control and increased flowering (Currey and Lopez, 2009) [9]. Paclobutrazol was originally employed as a growth suppressant in several nations, but its use was restricted because of worries about its protracted persistence in trees, possible contamination of groundwater, and detrimental effects on the size of pome fruit. The biosynthesis inhibitor of gibberellins, prohexadione-calcium (Pro-Ca), was subsequently discovered and approved for use under the trade names Regalis in Europe and the US and Apogee in Canada. Unlike paclobutrazol, Pro-Ca degrades relatively rapidly in the (Far *et al*., 2019) [14]. According to Far *et al*. (2019) [14], paclobutrazol suppressed vegetative growth and improved yield as well as fruit quality.

PGRs' function in promoting flower bud formation

Research has shown that various PGRs can promote flower bud formation, leading to increased flowering. For instance, NAA (naphthaleneacetic acid) has been found to promote flower bud formation distinct from effects related to thinning, while daminozide and ethephon have also been identified as effective promoters of flower bud formation (Atucha, 2022) [2]. Moreover, PGRs have been shown to affect bud formation and flower opening, among other stages of plant growth. They can be used to induce specific crop responses, such as promoting flowering, without substituting proper crop culture and environmental control (Bisht *et al*. 2018) [3].

AUXIN

Production site: Shoot tips one class of phytohormones called auxins regulates many aspects of plant growth and development. Auxins can cause root initiation, vascular differentiation, cell division, and elongation. The Greek word "auxin," which meaning "to grow/increase," is whence the term "auxin" originates. (Zhang *et al*., 2022) [42].

Kogl and Haagen-Smit used the term "auxin" in 1931 to describe a class of hormones that might stimulate cell proliferation or shoot growth. Using an Avena coleoptile or curvature test, Went discovered auxin in the tips of Oat coleoptiles in 1926 and 1928 and came to the conclusion that auxin is necessary for all growth. (Bisht *et al*. 2018) [3]. Tryptophan or the breakdown of carbohydrates produce ß-indoleacetic acid (IAA), the most significant naturally occurring auxin.

Auxin, a critical plant hormone, regulates most of the plant's growth and developmental responses. It modulates diverse processes such as tropical responses to light and gravity, root and shoot architecture, and organ formation (Weijers, D. and Wagner, D. 2016) [38]. Additionally, auxin transport and response are often involved in interactions with other plant hormones, adding further complexity to its role in plant development (Liu *et al*., 2017; Zhang *et al*., 2022) [26, 42]. Although auxin was once thought of as a "growth hormone," it actually controls the molecular process of cell division and expansion. It promotes cell growth and elongation, alters plant wall plasticity, and influences various developmental processes such as phototropism, geotropism, apical dominance, flower formation, fruit set, and the formation of adventitious roots (Perrot-Rechenmann, 2010) [30].

Discovery of Auxin

Auxin was discovered through a series of experiments and observations. The existence of a mobile signal that promotes the elongation of grass coleoptiles was hypothesized by Charles and Francis Darwin. Subsequently, scientists including Boyen-Jensen, Paal, and Went independently conducted experiments showing that the bending of coleoptiles was promoted by a hydrophilic, mobile signal, which was later identified as indole-3-acetic acid (IAA), a type of auxin (Paque & Weijers, 2016) [29]. Following this discovery, the field of auxin study took off, resulting in the identification of several auxinic chemicals and the growth of a vibrant and active research community. The discovery of auxin has since spurred the development of a better understanding of its role in plant development and its context-dependent functions (Perrot-Rechenmann, 2010) [30].

Naturally and synthetic occurring auxins

Indole-3-acetic acid (IAA) is the natural auxin that is most frequently seen (1). Nonetheless, it has also been shown that indole-3-butyric acid (IBA) (3) and 4-chloro-IAA (2) occur naturally. Furthermore, plants naturally produce the weak auxin phenylacetic acid (PAA) (4), and plant tissues contain IAA precursors and metabolites such as indole-3-pyruvic acid, tryptamine, and tryptophol.

In plant tissues, the intermediate of agrobacterial IAA production has been identified as indole-3-acetamide (IAM) (5). The majority of the IAA that is made by plants is conjugated to create amides, glycosyl esters, or esters. Indole-3-acetyl aspartic acid (IAAsp) (6) and various IAA glucose esters (IAAGlu) (7) are the most frequently occurring IAA-conjugates. Conjugation is a mechanism that helps plants metabolise excess auxin, stabilise the amount of free auxin in the plant, and store IAA in their cells.

It is thought that auxin conjugates, including indole-3-acetic acid (IAA), act as storage forms for the active plant hormone. Enzymes can then liberate these conjugates after protecting them from oxidative degradation. IAA is quickly metabolised in plant tissues and is susceptible to oxidation in the media, despite the fact that it can be utilised as an auxin in plant tissue culture media. This feature can be beneficial because in certain plants, the oxidation of IAA causes its effective concentration to decrease, which might result in the development of shoots or embryos from the callus. Furthermore, IAA has been employed in conjunction with other regulators to cause direct morphogenesis in a variety of plant species, including the roots of micro-cuttings and meristem and shoot cultures.

In apple micro cuttings, the IAA concentration matters because, whereas high IAA at the start of culture promotes the production of roots, lower IAA concentrations later on encourage root growth. In tissue cultures, synthetic auxins-which share biological characteristics with IAA-are frequently employed. The most used synthetic auxins in culture media include 2,4-dichlorophenoxyacetic acid (2,4-D) and naphthalene acetic acid (NAA). These synthetic auxins are more stable than natural auxins and are used to supplement the media with auxin. Other synthetic plant growth regulators are also widely used in the tissue culture industry.

Types and functions of auxin

An artificial auxin like NAA is commonly used in stems and cuttings to reproduce plants vegetatively. The application of nitrogen oxide (NAA) significantly impacts plant development, increasing cellulose Fiber synthesis and preventing fruit drop when sprayed after fertilizing the blooms. *In vitro* propagation of bananas, for higher root induction we have to apply a mixture of IBA and NAA. Auxin, also known as indole-3-acetic acid (IAA), delays fruit ripening and is transformed into amino acids by the GH3 gene. Its effects are mediated by hormone signalling pathways, including ethylene biosynthesis and ABA biosynthesis. Auxin stimulates root initiation, primordium growth, and shoot multiplication, while cytokinins promote root development. (Hajam *et al*., 2017) [17].

The importance of Auxins in plant growth and development processes

Auxins represent a crucial class of phytohormones, playing a pivotal role in the regulation of plant growth and development, akin to cytokinins in their ability to promote stem cell elongation. The genesis of auxin research traces back to the eighteenth century, marking significant milestones in the understanding of plant biology. Early experiments revealed the coleoptile of Elymus canadensis exhibited phototropism, bending towards the light source, a phenomenon attributed to the movement of a growth-promoting substance from the plant's apex to the bending site. Subsequent studies using oat coleoptile tips placed on an agar medium further corroborated these findings, demonstrating the agar's acquisition of growth-stimulating properties (Zhang *et al*., 2022) [42].

Indole-3-butyric acid (IBA) is a potent auxin that promotes lateral root formation and stem elongation in leguminous plants. Its unique 4-chloroindole-3-acetic acid introduces a chlorine atom, while compounds like phenylacetic acid and p-hydroxyphenylacetic acid have auxin-like activities (Hajam *et al*., 2017) [17].

Derived from the Greek word meaning "to grow," auxin aptly reflects the hormone's function in promoting plant growth. Indole-3-acetic acid (IAA) is the quintessential auxin, spearheading the family of compounds characterized by an indole ring structure. The discovery of additional endogenous auxins such as 4-CL-IAA and IBA underscores the diversity and complexity of this hormone class.

The complex mechanisms of auxins, a crucial element of plant physiology, are being researched. They are primarily produced in young, growing plant tissues like shoot tips, leaves, and seeds. Although they oxidize and degrade quickly, their degradation can induce shoot formation and enhance morphogenesis. IAA has been effectively employed alongside other growth regulators to facilitate direct morphogenesis, enhancing the germination of micro cuttings, as well as meristem and shoot culture facilitating various plant species' growth practices.

Physiological effects of auxins

Previously, it was believed that auxins only served to encourage cell growth. However, research conducted in more recent years has shown that they are closely related to several functions. They can operate as a stimulant, an inhibitor, or a required participant in the growth activity of other phytohormones like gibberellins and cytokinins under specific situations.

1.	Cell elongation and division	The elongation and division of cells in shoots are the primary physiological effects induced by auxin. It is essential for the differentiation of the xylem, phloem, and stem tissues throughout their secondary development.
2.	Apical dominance	In many plants, if the terminal bud is still alive and growing, the number of lateral buds that sprout immediately below it is decreased. The lateral buds will sprout swiftly upon removal of the apical bud. Apical dominance is the situation wherein the apical bud grows before the lateral buds and prevents the lateral buds from growing. (Thimmann and Skoog, 1933).
3.	Root initiation	A higher auxin concentration prevents roots from elongating, but it greatly increases the number of lateral roots; in other words, a higher auxin concentration causes more lateral branch roots. If we placed IAA in lanolin paste—a soft fat made from wool that works well as a solvent for auxin—to the young stem's cut end, it caused significant roots. This finding has been widely used to encourage root growth in economically useful plants that are propagated by cuttings and is of tremendous practical relevance.
4.	Prevention of abscission	Natural auxins stop the formation of the abscission layer, which causes leaves, flowers, and fruits to fall off tree plants.
5.	Parthenocarpy	Auxin has the ability to stimulate the creation of parthenocarpic fruits, which are fruits that do not require pollination or fertilisation. The ovaries of these fruit kinds have a larger concentration of auxin than the ovaries of plants that only bear fruit after fertilisation. In the latter scenarios, the concentration of auxin in the ovaries will rise following fertilisation and pollination.
6.	Respiration	Auxin improves respiration, and there is a connection between respiration and auxin-induced growth. Auxin can indirectly increase the rate of respiration by boosting the availability of ADP by rapidly depleting ATP in the developing cells.
7.	Callus formation	Both cell elongation and division may be influenced by auxin. In tissue culture, the callus grows relatively normally; optimal callus growth requires the inclusion of auxin.
8.	Eradication of weeds	Certain synthetic auxins, such as 2, 4-D and 2, 4, 5-T, are administered at higher quantities in order to eradicate weeds.
9.	Flowering and sex expression	Auxin stimulates flowering in pineapple and lettuce but inhibits it in other fruit crops.

Auxin biosynthesis

The predominantly studied bioactive formofauxinisindole-3-aceticacid (IAA). Multiple inputs into the pool of free IAA govern auxin homeostasis (Rozov *et al*., 2013) [32]. The primary source of free IAA appears to be the indole-3-pyruvic acid (IPyA) route. The first stage is the conversion of tryptophan to IPyA by the Tryptophan Aminotransferase of the Arabidopsis family of tryptophan aminotransferases. Flavin monooxygenases then convert IPyA to IAA. The Yucca is the family of flavin monooxygenases. The major pathway to auxin through IPyA, IAA can also be generated from indole-3-acetonitrile, indoleacetamide, C10H9N0, the chain-lengthened precursor indole-3-butyric acid (IBA), sugar combines, and amino acid combines. (Gomes & Scortecci, 2021) [16]. Through regulation of one or more of these pathways, distinct developmental events and stimuli may differentially impact IAA levels (Wang *et al*., 2022) [37]. For instance, it has been demonstrated that high temperatures cause free Indole-3-Acetic acid levels to rise, which causes hypocotyl elongation (Gray *et al*., 1998). In a similar vein, it has been demonstrated that the IPyA biosynthetic pathway is especially necessary for the shadow avoidance response (Wang *et al*., 2022) [37].

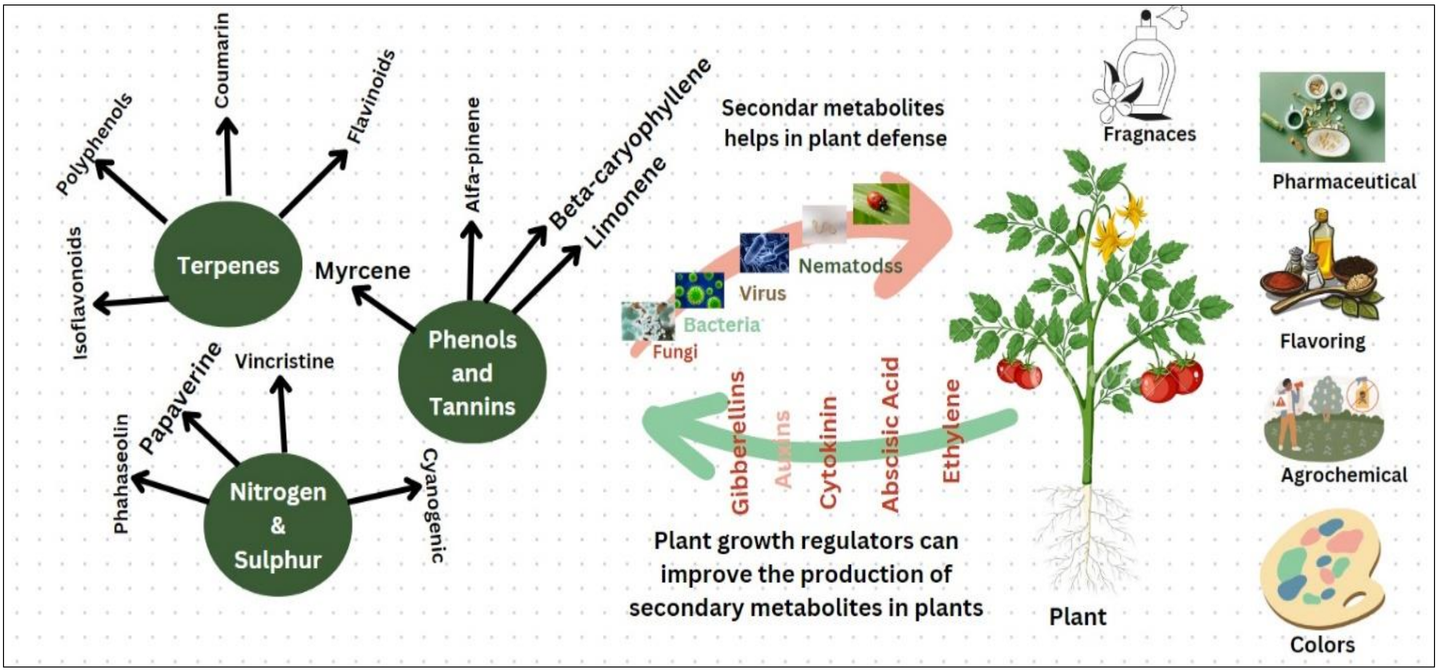

Fig 2: Exploring the Dynamics of Plant Growth: From Functions to Deficiencies, Challenges, and Toxicities

Gibberellin

Site of production = Formed in the plastids by the terpenoid pathway and then transformed in the ER

Gibberellins (GAs) are a group of diterpenoid phytohormones that regulate various aspects of plant growth and development, such as stem elongation, seed germination, flowering, and fruit development. From the fungus Gibberella fujikuroi (now Fusarium fujikuroi) the first gibberellins were isolated, which caused the foolish seedling disease in rice. This disease results in excessive growth, lodging, sterility, and empty panicles in infected plants. The fungal metabolites responsible for this effect were identified as growth-promoting substances in the 1920s by a Japanese plant pathologist, Eiichi Kurosawa (Jain *et al*., 2023) [21]. However, his work was not widely known outside Japan until after World War II. In the late 1930s, Teijiro Yabuta and his colleagues at Tokyo Imperial University purified and crystallized several active components from the fungus, which they named gibberellins A1, A2, and A3. The structure of gibberellic acid (gibberellin A3) was introduced in 1954 by John W. Mitchell and his co-workers at the University of California, Berkeley, and the first chemical synthesis of this compound was achieved in 1955 by Percy W. Brian and Harry G. Hemming at the Imperial Chemical Industries in England. Since then, more than 130 gibberellins have been isolated and characterized from various plant and fungal sources, and many more have been synthesized in the laboratory. Gibberellins are classified into two main groups based on their carbon skeleton: the C20-GAs, which have 20 carbon atoms, and the C19-GAs, which have 19 carbon atoms and a lactone ring. The C19-GAs are the only bioactive gibberellins in plants, and the most important ones are GA 1, GA 3, GA 4, and GA 7. The polarity and activity of gibberellins depend on the number and position of hydroxyl and carboxyl groups, the degree of saturation, and the presence of methylene or sugar moieties. The C19-GAs have an acidic character, with a pKa of about 4.8 (Iqbal *et al*., 2011) [19-20], (Salazar-Cerezo *et al*., 2018) [33].

Discovery of Gibberellin

The discovery of gibberellins dates to a Japanese pathologist who was researching the silly rice disease in the 1920s. This disease caused rice plants to develop so quickly that the stems were too fragile and lodged (Jain *et al*., 2023) [21]. It was discovered that the creation of a growth-stimulating chemical by the fungus Gibberellia fujikuroi was the root of this accelerated growth. In the late 1930s, impure crystals were extracted that included several active components. Because the material was published in Japanese publications and there was a dearth of information flow with the Western world due to World War II, this knowledge and the significance of the discovery did not become public until the 1950s. The 1950s saw the discovery, crystallisation, and synthesis of gibberellic acid (Iqbal *et al*., 2011) [19-20].

Types and function of Gibberellin

Fruit development is a complex and regulated process that involves different stages, from pre-pollination to senescence. Plant hormones, such as gibberellins (GAs), modulate this process by affecting the metabolism and sink strength of the developing fruits. GAs are a group of diterpenoid phytohormones that influence various aspects of plant growth and development, including cell division and expansion, which are essential for fruit growth after fertilization. GAs also have practical applications in fruit production, such as breaking seed dormancy, enhancing fruit sets, and improving fruit quality (Cronjé *et al*., 2019) [8]. However, the effects of GAs on fruit development are not uniform and depend on the type, concentration, timing, and interaction of GAs with other factors, such as environmental cues and other phytohormones. For example, GAs can promote or inhibit flowering and fruiting in citrus, depending on the season and the GA mixture applied. Moreover, the responses to GAs may vary among different species and cultivars, especially between trees and crops, due to differences in GA-related developmental processes, such as adventitious rooting or flowering (Fahad *et al*., 2015). Therefore, careful planning and optimization are required for the effective use of GAs in fruit production. Recent advances in the identification of key genes involved in GA biosynthesis and signalling have opened new avenues for research and breeding programs that aim to manipulate GA levels and responses in fruits (Castro-Camba *et al*., 2022). However, there are still many challenges and questions to be addressed, such as the transferability of knowledge between species, the integration of GA cues with other signals, and the coordination of GA actions with other phytohormones in specific responses, such as stress and flower development (Jain *et al*., 2023) [21].

Physiological effects of gibberellin

1.	Seed germination	Lettuce and tobacco are examples of certain light-sensitive seeds that show poor germination in the dark. These seeds will germinate rapidly if they are exposed to light, especially red light. This light requirement is met if gibberellic acid is administered to the seeds when they are in the dark.
2.	Dormancy of buds	Potatoes go through a latent phase after harvesting, but when they are treated with gibberellin, the roots actively sprout. The autumn buds in temperate climates also stay dormant until the following spring. Using gibberellin treatments, we can break the bud dormancy.
3.	Root growth	Gibberellins have little to no effect on root growth. At greater doses, root growth can be slightly suppressed. In solitary cuttings, gibberellins strongly prevent the beginning of roots.
4.	Elongation of internodes	The elongation of the internodes is gibberellins' most noticeable influence on plant growth. Gibberellins may thus be able to compensate for genetic dwarfism in a variety of plants, including dwarf peas, dwarf maize, etc.
5.	Flowering and bolting	Small leaves and short stems characterise the rosette habit of herbal plants. This habit is maintained on short days; bolting, elongation, and flowering occur on long days. In Hyoscyamus niger, gibberellin administration causes bolting and flowering, which causes long-day plants to flower earlier. Nevertheless, gibberellin either has no effect on short-day plants or can even cause them to blossom.

Biosynthetic pathway

The gibberellin biosynthetic pathway has been widely investigated in plants, and research on fungal strains has also added to our understanding of this process. The route in bacteria is beginning to become clearer thanks to more recent investigations. Further mentioned are specific characteristics of the various creatures. Isopentenyl diphosphate (IPP), the 5-carbon building block of all terpenoid/isoprenoid compounds, initiates the metabolic process that yields GAs. The mevalonic acid (MVA) pathway in the cytoplasm and the methyl erythritol phosphate (MEP) pathway in plastids are the two pathways that generate the basic isoprenoid unit IPP in the green tissue of most plants (Hedden and Thomas, 2012). The entire pathway can be divided into three stages based on their subcellular compartmentalization and the enzymes involved. In the cell's cytosol, 2-oxoglutarate-dependent di-oxygenases catalyse the pathway's third and last step. The MVA pathway, which produces IPP for the synthesis of all terpenoids, including gas, in fungi, is the biosynthetic route (Salazar-Cerezo *et al.*, 2018) [33].

There are 3 steps

- Plastids
- Endoplasmic reduction
- Cytosol

Pathway

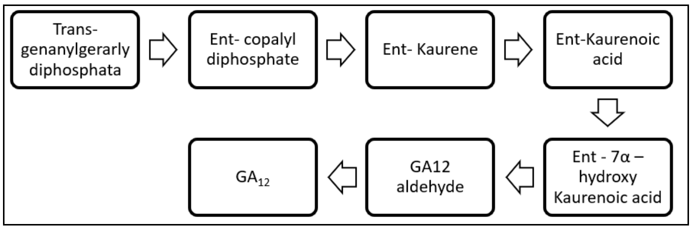

Fig 3: Biosynthesis of Gibberellins

Cytokinin

Site of production= Root tips

All naturally occurring chemicals known to encourage cell division are collectively referred to as cytokinins. Letham (1963) first proposed the word "cytokinin." They have a reputation for delaying senescence. Zeatin, the first naturally occurring cytokinin, was discovered in maize. Numerous different species have been revealed to contain specific cytokinins as part of their transfer RNA molecules. Additionally, they have a role in the stimulation of organ development, such as the development of leaves, fruit, buds, and branches. They often break dormancy and contract or overpower apical dominance. They also improve consistent blooming and seed germination. Cytokinins control how metabolites are transported via the phloem. Additionally, cytokinins help keep flowers, fruits, and green vegetables fresh (Sosnowski *et al*., 2023) [35].

Discovery of cytokinin

Cytokinin was first identified by Skoog and Miller, who were studying the factors that influence cell division in tobacco pith callus cultures in the late 1940s at the University of Wisconsin. They found that a purine-like substance from the chromatograms was responsible for the cell division activity (Kieber & Schäller, 2010) [24]. They also detected similar activity in yeast extracts and coconut milk. They later isolated and purified the active compound from autoclaved herring sperm DNA and named it kinetin, but they realized that it was not a natural product but a degradation product of DNA (Li *et al*., 2020) [25]. The first natural cytokinin, zeatin, was isolated and characterized by Letham from immature maize kernels in 1963, using a bioassay method (Moore, 1989)

Types and functions of cytokinin

Through the preservation of S-adenosyl-methionine (SAM), an immediate metabolite for the manufacture of ethylene, cytokinin may play a significant role in leaf start. Throughout a plant's life cycle, cytokinins control a variety of growth and developmental activities, such as seed germination, leaf expansion, blooming induction, and seed and flower development. It can prevent leaf senescence, which increases chlorophyll retention. The impact of cytokinins on leaf senescence was demonstrated by the autoregulation of cytokinin production during leaf senescence using an isopentenyl transferase (IPT) gene under the control of the senescence-associated gene 12 (SAG12) promoter. (Matsuo *et al*., 2012) [27]. this promoter drives the expression of many genes during senescence. The cysteine protease that the SAG12 gene encodes for was active during senescence and unrelated to the trigger events. The transit of amino acids, cell senescence, cell growth, and cell differentiation all include cytokinins in plants. Pear fruit size is improved by using CPPU at 10 ppm and BA at 30 ppm. The weight and size of the fruit of the pears Spadona and Coscia were significantly affected by the application of CPPU and BA. applied BA @11 m, followed by BA @4.4 m, produced the greatest amount of shoot multiplication on pear explants when different cytokinin concentrations were tested (Kumar *et al*., 2013). Like this, pears' leaves had more leaf chlorophyll after receiving a 10 ppm BA treatment, which delayed the start of leaf senescence. In prunus species explant, BA has a beneficial influence on the development of shoots. BA has a substantial impact on the GF-677 rootstock. The number of adventitious buds and the number of buds per explant increased in a medium containing TDZ or BAP. Application of CPPU 10 ppm promotes the maximum fruit retention, quantity of fruits per cluster, weight, and leaf area (Jameson & Song, 2015) [22], (Jain *et al*., 2023) [21].

Importance of Cytokinin in plant growth and development processes

Cytokinin's ability to drive cell division is their most crucial function, but their other roles are far more complicated and reliant on interactions with other plant hormones (Iqbal *et al*., 2011) [19-20]. Cytokinin and auxins can have opposing effects on root differentiation. For instance, auxin stimulates the formation of lateral roots whereas cytokinins prevent it. In addition to influencing the activity of other enzymes and the transport and accumulation of photosynthetic products, cytokinins have a significant influence on physiological and biochemical processes (Wang *et al*., 2022) [37]. Cytokinins are essential chemicals that control how chloroplasts grow and function. The earliest stage of leaf development is characterized by the greatest cytokinin concentrations, which are related to the activation of cytokinesis, membrane formation, plastid division, and intense protein synthesis that takes place at that time (Camas-Reyes *et al*., 2022).

Although they can also be generated in fruits and young leaves, cytokinin is mostly synthesized in root apical meristems (Camas-Reyes *et al*., 2022). Other phytohormones regulate their levels and have a substantial impact on both their production and breakdown. Auxins are powerful and quick suppressors of cytokinin production, and they play a significant role in reducing endogenous cytokinin levels. When cytokinins are produced, they are moved to different tissues via diffusion and active transport using transport protein, purine permease, and equilibrate nucleoside transporters (Sosnowski *et al*., 2023) [35].

Physiological effects of cytokinin

1. Cell division	Kinetin's principal biological effect in plants is to induce cell division. For instance, specifically in the callus of tobacco pith, carrot root tissue, soybean cotyledon, pea callus, etc.
2. Cell enlargement	Like auxins and gibberellins, kinetin may also promote cell growth. Significant cellular growth has been observed in a variety of plant tissues, including tobacco pith culture, pumpkin cotyledons, Phaseolus vulgaris leaves, and tobacco roots' cortical cells.
3. Concentration of apical dominance	Apical dominance is counteracted by the external application of cytokinin, which stimulates the formation of lateral buds.
4. Dormancy of seeds	Like gibberellins, some light-sensitive seeds like tobacco and lettuce, if we treat these light-sensitive seeds with kinetin treatment it can break the dormancy.
5. Delay of senescence	(Richmond - Lang effect) Due to the loss of chlorophyll and rapid breakdown of proteins the senescence of leaves takes place. By stimulating RNA synthesis and then protein synthesis, kinetin treatment can delay senescence by several days. Richmond and Lang (1957) It was discovered that kinetin might delay senescence for a few days by testing with detached Xanthium leaves.
6. Flower induction	We can apply cytokinin to short-day plants for the induction of flowers.
7. Morphogenesis	It has been observed that high auxin and low cytokinin promote only roots whereas high cytokinin and low auxin could promote the formation of shoot buds.
8. Accumulation and translocation of solutes	With the support of cytokinin, plants actively accumulate solutes and allow to translocation of solutes inside the phloem.
9. Protein synthesis	Osborne (1962) showed that the use of kinetin therapy can induce the rate of protein synthesis.
10.Other effects	In certain plants, cytokinin confers resistance to diseases, high temperatures, and low temperatures. Additionally, they promote flowering by taking the place of photoperiodic needs. In some cases, they promote the synthesis of many photosynthesis-related enzymes. In the dark, some light-sensitive seeds, including tobacco and lettuce, germination is poor. When exposed to light, especially red light, these seeds begin to germinate rapidly. When seeds, like tobacco and lettuce, are treated with an acid called gibberellic in the dark, their need for light is satisfied.
11.Commercial applications	To increase the shelf life of fruits, produce an efficient root system, quicken root induction and increase yield and oil contents of oil seeds like ground nut we use cytokinin.

Biosynthesis of Cytokinin

The metabolic origin of cytokinins in plants remains unclear, but the discovery of a cytokinin biosynthesis enzyme in Dictyostelium discoideum, which converts AMP and DMAPP into iPMP and iPA, led to the development of the idea that iPMP is the principal cytokinin intermediate in plants (Sosnowski *et al*., 2023) [35].

Abscisic acid

Site of production = Chloroplasts

For the regulatory effect on abscission and dormancy, ABA was previously called Dormin or Abscisin. This hormone is present in a wide variety of organs and tissues of higher plants, both old and young. A small sesquiterpene molecule known as abscisic acid is essential to many phenological and developmental processes in plants, such as the formation of lipids and storage proteins, senescence of leaves, stomatal movement, blooming, vegetative growth, seed dormancy and development. A wide range of plants' leaves and the fruits of some plant species shed their leaves when exposed to ABA (Emenecker & Strader, 2020) [12]. At least in certain temperature zones, woody plants' buds appear to go into dormancy because of an internal chemical called ABA. Additionally, ABA hinders or inhibits seed germination. A wide range of plant tissues and organs, including leaves, coleoptiles, stems, hypocotyls, and roots, are all slow to develop when exposed to ABA. Through leaf abscission, deterioration of removed leaves, and acceleration of chlorophyll deterioration, it induces senescence. The term "stress hormone" is widely used to describe ABA, which plays a part in controlling both biotic and abiotic stress responses. Despite these traditional definitions, auxin and ABA both play important roles in plant growth and development under non-stressful circumstances, as well as in response to different stressors (Xiong & Zhu, 2003) [39].

Discovery of Abscisic acid

ABA has been anticipated for some time, but it was the last important hormone to be discovered. Researchers led by Addicott discovered dormancy in woody perennials (Cornforth *et al*., 1965) [6] and Abscisin II in cotton, respectively, while examining hormonal interactions in cotton (Ohkuma *et al*., 1963) [28]. After it was found that the two substances were similar, they were given the name Abscisic acid in 1967 during a symposium on plant hormones that was held in Ottawa, Canada.

Functions of Abscisic Acid

Endogenous hormones and their balance have an impact on both the absorption of vitamins and minerals to the developing organs and the longevity of a bud. Since auxin transport by plants lasts a long time without seeming to be affected by ethylene, exogenous application of 2,4-D or NAA has shown that abscission is reliant on the endogenous auxin level (Xiong & Zhu, 2003) [39]. 2, 4-D and naphthalene acetic acid (NAA) have an impact on the reduction of fruit drops in the pummelo cv. Stops cell division, which limits plant growth, accelerates floral initiation, senescence, and abscission, reduces root growth, and promotes bud and seed dormancy. ABA also causes the shutting of stomata as a stress response in plants (Jain, 2013) [21].

Physiological effects of Abscisic acid

1. Stomata Closure	If there will be water shortage ABA levels will be increase, then due to response of water stress it will lead to stomata closure.
2. Growth Inhibitors	ABA has less effect on root growth but inhibits the shoot growth.
3. GA Counteracts	Gibberellins' impact on alpha-amylase production in germinating seeds is reduced by ABA.
4. Induced Dormancy	ABA has an impact on a seed's ability to maintain or induce dormancy.

Biosynthesis pathway of Abscisic acid

The 15-carbon terpenoid molecule known as abscisic acid was first discovered in the 1960s and is now known as an inhibitor of growth (abscisin II) linked to cotton fruit abscission and maple bud dormancy. Later research showed that ABA modulates plant responses to abiotic stress and has a significant role in several developmental and physio-biochemical (Xiong & Zhu, 2003) [39]. All cells with chloroplasts or amyloplasts produce ABA, which is found in major organs and tissues. Seo and Koshiba (2002) state that the cytoplasm is where ABA is produced once it starts in the chloroplast. Isopentenyl diphosphate (IPP) is produced in the plastids by pyruvic acid and glyceraldehyde 3-phosphate. Geranylgeranyl diphosphate (GGPP) is subsequently produced by the methylerythritol 4-phosphate (MEP) pathway. Zeaxanthin is produced by GGPP from lycopene and beta-carotene when phytoene (C40) is formed.

Zeaxanthin epoxidase (ZEP) transforms zeaxanthin into all-trans-violaxanthin (C40). Next, the 9-cis-epoxy carotenoid dioxygenase enzyme (NCED) converts the all-trans-violaxanthin (C40) to 9-cis-neoxanthin (C40), which is then further broken down into xanthoxin (C15) and a C25 metabolite. Because NCED is a necessary enzyme, this reaction represents a rate-limiting step in the synthesis of ABA. Xanthoxin is transported to the cytoplasm by an enzyme belonging to the short-chain dehydrogenase/reductase family, where it is transformed into ABA-aldehyde. The conversion of ABA aldehyde into ABA is catalysed by ABA-aldehyde oxidase (AAO), according to multiple studies (Xiong and Zhu, 2003) [39]. ABA is produced by a variety of enzymes that are encoded by several genes (Emenecker & Strader, 2020) [12].

Ethylene

Methionine breaks down into a gas called ethylene. This is a straightforward gas that many plant tissues make in modest amounts, and it acts as a potent regulator of growth and development. They are abundantly present in ripening physiologically developed fruits**.** Ethylene is only very weakly soluble in water, it diffuses out of the cell and leaves the plant. The ratio of its synthesis rate to its rate of evaporation into the atmosphere determines how effective it is as a plant hormone. Particularly in the absence of light, rapidly dividing and developing cells release ethylene more quickly. Increased ethylene levels prevent leaf development because new growth and newly sprouted seedlings create more ethylene than the plant can handle (Dubois *et al*., 2018) [10]. Phytochrome reactions in the plant's cells provide a signal that tells ethylene synthesis to stop, enabling leaves to expand, when the new shoot is exposed to light. Cell elongation is inhibited by ethylene synthesis, which also causes the stem to enlarge. Studies seem to show that ethylene has an impact on the diameter and height of tree stems (Hajam *et al*., 2017) [17].

Discovery of Ethylene

Nejublov, who claimed that coal gas may accelerate leaf abscission, first identified the growth-regulating abilities of ethylene in 1901. Then, in 1935, Denny and Miller revealed that ethylene could induce pineapple flowering, accelerate fruit ripening, and break dormancy, as well as that it was naturally generated by a variety of organs in plants (Abeles, 1973) [1]. The scientific community overwhelmingly rejected the claim that ethylene should be given hormone status. It was difficult to see how a two-carbon chemical that was freely floating in the air could be taken seriously as a hormone. The physiological relevance and importance of ethylene were not understood until 1959 when the gas chromatograph was established as the principal method to measure endogenous ethylene. The position of ethylene was thus raised to that of a hormone (Burg and Thimann, 1959) [5].

Functions of Ethylene

Apical dominance is stopped, lateral growth is stimulated, leaves, flowers, and fruits are abscised, blooming is induced, fruit ripening is aided, rooting is aided, chlorophyll is aided, female flowers are increased, and apical dominance is halted. The emergence, development, and shelf life of diverse fruit crops are affected in a few different ways by ethylene, a naturally occurring molecule that encourages plant growth (Dubois *et al*., 2018) [10]. During ripening in climacteric fruits, ethylene regulates firmness and colour changes involving chlorophyll reduction, an increase in carotenoids or anthocyanins, sugars, and biosynthesis of volatile organic compounds (VOCs). Ethylene's biological activity is influenced by both endogenous and extracellular sources, and it can be intentionally or unintentionally exposed to levels that are physiologically active in harvested fruits. The synthesis and sensitivity of ethylene are increased by several biotic and abiotic stresses as well as plant developmental phases (Khan *et al*., 2020) [23]. Ethylene, a naturally occurring chemical that promotes plant growth, has a variety of effects on the emergence, development, and shelf life of various fruit crops. Ethylene can be introduced to levels that are physiologically active in harvested fruits either purposefully or accidentally. Its biological activity is controlled by both endogenous and external sources. Numerous biotic and abiotic stressors, as well as certain plant developmental stages, enhance the production and sensitivity to ethylene (Khan *et al*., 2020) [23].

Physiological effects of ethylene

1.	Fruit Ripening	Under natural circumstances, ethylene helps ripen fruits in the form of gas.
2.	Flower Initiation	In pineapple, flower initiation is promoted by Ethrel (Ethephon) and ACC.
3.	Leaf and Fruit Abscission	Quicken up fruit abscission in fruit crops including citrus, grapes, and cherries so that they may be mechanically harvested.
4.	Inhibit Vegetative Growth	Grape vines can be treated with ethephon to stop their vegetative growth, which will increase production and improve quality.

Biosynthesis pathway of ethylene

In gaseous form, ethylene is engaged in several crucial morphophysiological processes, including the threefold response in seed germination, flower development, fruit ripening, and initiating plant responses to external stimuli (Yin *et al*., 2017) [40]. Additionally, ET controls several stress-related biochemical reactions in plants that are subjected to abiotic stressors such as heat, drought, freezing, salt, heavy metals, water logging, flooding, or submerged situations (Awan *et al*., 2017). Fruits can be categorized as climacteric or non-climacteric based on the link between fruit ripening and the ethylene/respiration pattern. While ethylene levels in non-climacteric fruits decrease with fruit ripening and senescence, they rise and reach a peak in climacteric fruits by the rhythm of respiration (Dubois *et al*., 2018) [10].

Conclusion

Research on plant hormones as growth regulators demonstrate their potential to enhance the cultivation of various plant species. Auxins and cytokinin's, when applied at appropriate concentrations, can significantly promote rhizosphere regeneration, improve plant dry matter yield and stability, and reduce disease incidence, albeit with some trade-offs such as reduced vitamin C levels and increased phenolic compounds. These hormones also contribute to better tillering, increased leaf growth, and enhanced flower quality. Ethylene, another key phytohormone, is involved in a complex network of signaling pathways, interacting with other hormones to regulate plant growth and senescence. The strategic manipulation of ethylene and its crosstalk with other phytohormones offers a promising avenue for tailoring specific plant responses. Abscisic acid (ABA) is highlighted for its critical role in enhancing plant resistance to abiotic stress and improving growth and productivity through various mechanisms, including the stimulation of phytochelatin synthesis, antioxidant activity, osmolyte production, and enzymatic activity. The application of ABA through soil treatment, foliar sprays, seed priming, or culture media is identified as a viable approach to boost the growth and yield of economically important crops, showcasing the importance of understanding and leveraging phytohormone interactions and applications in agriculture.

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