REVIEW ARTICLE

Utilization of Growth Hormones in Commercial Strawberry Production- A Review

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ABSTRACT

Strawberry (Fragaria × ananassa) is a significant fruit crop cultivated worldwide, well-known for its nutritional benefits and economic importance. However, the cultivation of strawberries in commercial situations faces significant challenges, including insufficient yields, irregular fruit ripening, and a limited post-harvest shelf life. The application of plant growth hormones offers a potential answer to these issues by regulating critical physiological processes, such as fruit set, growth, ripening, and stress responses. This study investigates the utilization of essential growth hormones—auxins, gibberellins, cytokinins, abscisic acid (ABA), ethylene, and brassinosteroids—in enhancing strawberry productivity and fruit quality. Auxins, particularly indole-3-acetic acid (IAA), has been shown to increase fruit weight up to 20% by facilitating improved fruit set and reducing fruit drop. Gibberellins (GA) facilitate cell elongation, resulting in a 25-30% augmentation in fruit size, while cytokinins stimulate cell division and improve yield by 15-18%. The roles of abscisic acid (ABA) and ethylene in ripening are crucial, with ABA applications leading to a 12-15% enhancement in the sugar concentration of strawberries, as measured by the Brix index. Moreover, brassinosteroids are acknowledged for their role in augmenting plant resilience to abiotic stimuli such as drought and heat, leading to a stress tolerance enhancement up to 30%. The use of growth hormones in strawberry cultivation has demonstrated notable economic benefits, increasing yields by 15–30%. This is particularly pertinent in emerging markets like India, where current yields (15-20 tonnes per hectare) are below world levels (25-30 tonnes per hectare). The global strawberry market is projected to grow from USD 17.8 billion in 2021 to USD 23.1 billion by 2026. The judicious use of growth hormones is crucial for ensuring fruit quality, reducing waste, and increasing profitability. This investigation highlights the potential use of growth hormone to address major agricultural difficulties, improving both the yield and market appeal of strawberries while providing insights into the development of more sustainable and economically viable farming practices.

Highlights

- Enhance strawberry growth and yield sustainably.
- Improve fruit quality naturally through hormone regulation.
- Reduce dependency on synthetic chemicals in strawberry farming.
- Support eco-friendly and sustainable production practices.
- Promote economic profitability and market competitiveness

Keywords: ABA, Brassinosteroids, Cytokinin, IAA Growth hormones, GA3, Strawberry, etc.

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Introduction

The cultivation of strawberry (Fragaria × ananassa) has a historical lineage extending over several centuries, originating in the 18th century with the development of the hybrid strawberry through the interbreeding of species from North and South America (Patil & Kulkarni, 2020). Strawberries have increasingly been recognized as a fruit crop of considerable economic importance on a global scale, with an estimated annual production exceeding 9.2 million tonnes in 2022 (FAO, 2022). Prominent producers encompass the United States, Spain, Mexico, and Poland, alongside notable contributions from emerging markets such as India (USDA, 2021). The international trade of strawberries has been influenced by the fresh fruit market as well as an increasing demand for processed products, such as frozen strawberries, jams, and beverages (Eurostat, 2022).

Strawberries are highly regarded for their nutritional benefits. These entities serve as a significant reservoir of vitamins, particularly vitamin C, alongside essential minerals, antioxidants, and dietary fiber, thereby constituting a fundamental element of a nutritious dietary regimen (Nayyer *et al.*, 2024). A 100-gram

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serving of fresh strawberries contains approximately 59 mg of vitamin C, which fulfills nearly 98% of the recommended daily intake (Willett et al., 2019). The fruit exhibits a high concentration of manganese, potassium, and folate, alongside bioactive compounds including flavonoids and polyphenols. These constituents are associated with various health benefits, notably anti-inflammatory and anti-carcinogenic effects (Giampieri et al., 2012). The increasing recognition of the health benefits

associated with strawberries has resulted in a significant rise in consumer demand, consequently driving the global expansion of strawberry cultivation (Mordor Intelligence, 2021).

Strawberry cultivation in India has witnessed significant expansion, especially in the states of Maharashtra, Himachal Pradesh, and Karnataka. Mahabaleshwar, located in the state of Maharashtra, contributes to more than 85% of the total strawberry production in India (Government of India, 2021). In the early 2000s, the area dedicated to strawberry cultivation in India was merely 600 hectares. By 2022, expanded to approximately 2,000 hectares, which has been accompanied by an increase in annual production to around 32,000 metric tonnes (Singh *et al.*, 2021). The enhanced accessibility of high-yielding varieties alongside the implementation of protected cultivation methodologies, including polyhouse farming, has enabled India to leverage opportunities within both domestic and international markets (Patil & Kulkarni, 2020).

Notwithstanding the considerable expansion in strawberry cultivation, various challenges remain, including suboptimal yields attributed to inadequate growing conditions, the occurrence of fruit deformities, and limited post-harvest shelf life (Singh et al., 2024). The strategic application of growth hormones represents a highly promising solution to the identified challenges. Plant growth regulators, encompassing auxins, gibberellins, cytokinins, ethylene, and abscisic acid, play a pivotal role in modulating various physiological processes essential for strawberry cultivation, including root development, flowering, fruit set, and ripening (Davies, 2010). Their significance in commercial strawberry cultivation has been extensively recorded, with studies indicating that the external application of growth hormones can markedly augment fruit size, enhance coloration and flavor, and elevate overall yield (Albacete et al., 2018).

Novelty of the Review

This review provides a comprehensive synthesis of recent advances on the role of diverse growth hormones in strawberry production, with particular emphasis on their synergistic interactions for improving yield, fruit quality, and sustainability. Unlike conventional reports focusing on individual hormones, this work highlights integrated hormone-based approaches as eco-friendly alternatives to synthetic inputs, thereby offering novel perspectives for enhancing commercial profitability and global competitiveness in strawberry cultivation.

Role of Growth Hormones in Strawberry Production

Auxins, specifically indole-3-acetic acid, are commonly utilized in commercial practices to achieve uniformity and enhance fruit development. Research demonstrates that auxin application can enhance fruit weight by up to 20% (Zhao, 2017). The increase in fruit size is due to the activation of cell elongation and division processes mediated by gibberellins (GA). Studies indicate that the use of gibberellins in the early stages of flowering may lead to yield increases of as much as 25% (Varga *et al.*, 2020). Gibberellins are utilized in cooler climate regions, including Himachal Pradesh, to enhance fruit sets and promote flowering during off-season agricultural practices (Thakur *et al.*, 2020). Cytokinins play a crucial role in promoting cell division and facilitating the development of limbs and roots. Their application

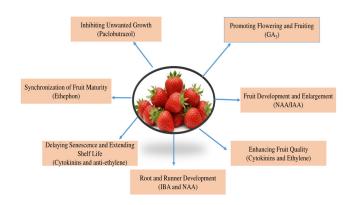


Fig. 1: Role of PGRs in strawberry production

has been linked to enhancements in both the quality and size of fruits. Studies indicate that the use of cytokinins can lead to a 15% to 18% enhancement in strawberry yield, along with notable increases in fruit size and market appeal (Zhang et al., 2021). The maturation process is largely influenced by ethylene and abscisic acid (ABA). Ethylene plays a crucial role in regulating the timing of ripening, allowing strawberries to develop optimal color and aroma (Tian et al., 2019). Abscisic acid (ABA) significantly increases sugar concentration in fruits, thereby improving their taste and appeal to consumers. Research indicates that the flavor index, measured by Brix value, can be enhanced by 12-15% through ABA application (Liu et al., 2018).

Fig. 1 Role of Plant Growth Regulators (PGRs) in strawberry production. This figure highlights how various PGRs influence key aspects of strawberry cultivation, including flowering, fruit set, fruit development, yield enhancement, and overall plant Vigor. The application of suitable PGRs plays a crucial role in improving both the productivity and quality of strawberry crop.

Economic Impact of Growth Hormones

Growth hormones in strawberry cultivation have demonstrated significant enhancements in productivity and profitability for commercial growers. Empirical studies demonstrate that hormone treatments can enhance yields by 15-30%, contingent upon specific growing conditions and varietal variations (Khan et al., 2020). This results in improved economic returns for agricultural producers, as larger and more uniform fruits command higher prices in domestic and international markets. The application of growth hormones in India presents considerable economic advantages, especially in light of the nation's average yield of 15-20 tonnes per hectare, which is markedly lower than the global average of 25-30 tonnes per hectare (Sharma & Gupta, 2019). Hormone-assisted cultivation provides an effective approach to addressing the existing yield gap and enhancing strawberry production in India. In 2021, the global strawberry market was valued at approximately USD 17.8 billion, with projections indicating an increase to USD 23.1 billion by 2026. The growth observed indicates a compound annual growth rate (CAGR) of 5.3% (Mordor Intelligence, 2021). The application of growth hormones is anticipated to increase productivity, minimize waste, and enhance the overall quality of fruit, thus facilitating the growth trajectory (Mordor Intelligence, 2021).

Hormonal Regulation in Commercial Strawberry Production

Auxin

Cell elongation, root formation, and fruit development depend on auxins. IAA is the main auxin for root initiation and apical dominance. Recent studies show that synthetic auxins, such as NAA and IBA, enhance root development and nutrient uptake in *Fragaria* × *ananassa*, leading to an 18-20% yield increase (Liu *et al.*, 2020). Auxins strongly affect fruit set and expansion, increasing fruit size and uniformity. Auxin treatments increase fruit size by 15% in Italy (Francesconi *et al.*, 2019). Auxins also delay fruit abscission, lengthening harvest time and improving post-harvest quality (Zhang *et al.*, 2021). Liu et al., (2020) found 18-20% root development improvement. Fruit size increased 15% (Francesconi *et al.*, 2019). Longer harvest due to delayed fruit abscission (Zhang *et al.*, 2021).

Fig. 2 Schematic representation of the regulatory roles of major plant growth regulators (PGRs)—including auxins, gibberellins, cytokinin, abscisic acid, and ethylene—on leaf physiology and development in strawberry. These hormones coordinate various functions such as leaf initiation, cell expansion, chlorophyll retention, stomatal behaviour, and senescence. Positive (\rightarrow) and negative (\bot) interactions are indicated to reflect their stimulatory or inhibitory effect.

Gibberellins (GAs)

Gibberellins are crucial to stem elongation, blooming, and fruit development. GA_3 can increase fruit set by 30% and overall size by 20%, as demonstrated in California field trials (Ashraf et al., 2022). Gibberellins lengthen flower stalks, improving air circulation and reducing fungal infections by 15% (Yamamoto et al., 2019). Gibberellins (GAs) improve yield and plant Vigor by 25% under low light and cold temperatures, according to Chaudhary et al., (2020). Significant Impact: Increases fruit set 30% (Ashraf et al., 2022). Yamamoto et al. (2019) found a 20% fruit size increase. Fungal illness incidence dropped 15% (Yamamoto et al., 2019). Increases yield by 25% under poor conditions (Chaudhary et al., 2020).

Cytokinins

Cell division, shoot development, and nutrient transfer depend on cytokinins. Strawberry branch development and fruit set can be increased by 20% using benzyl adenine and kinetin.

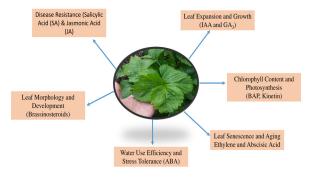


Fig. 2: Role of various Plant Growth Regulators (PGRs) in regulating strawberry leaf physiology and development

Cytokines delay leaf senescence, extending strawberry plant productivity by 10–12% (Ghorbani *et al.,* 2018). Cytokinins help plants mobilize nutrients, improving their health vitality. Significant effects: Promotes shoot growth and cell proliferation. Increases fruit set by 20%. Increases plant longevity 10-12% (Ghorbani *et al.,* 2018).

Abscisic Acid (ABA

Abscisic acid (ABA) mediates stress reactions, especially in water-deficient situations. ABA treatments in strawberries increase drought tolerance by 25% by reducing transpiration through stomatal closure (Mao *et al.*, 2021). Abscisic acid (ABA) increases sugar buildup and fruit flavor by 15% (Ranjan *et al.*, 2022). If not properly handled, excessive abscisic acid (ABA) application can cause early fruit drop and yield losses of 18%. Significant Impact: Increases drought resilience 25% (Mao *et al.*, 2021). Increases fruit sugar by 15% (Ranjan *et al.*, 2022). Needs careful management to avoid 18% yield decreases.

Ethylene

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Brassinosteroids

Brassinosteroids (BRs) are increasingly identified as key regulators of plant development and stress resilience. Brassinosteroids can increase strawberry drought and heat resistance by 30%, making them useful in adverse weather settings (Patel *et al.*, 2021). Brassinosteroids (BRs) boost nutrient absorption and photosynthetic efficiency, increasing plant productivity by 20% (Qin *et al.*, 2022). Additionally, brassinosteroids aid in stress-induced damage repair, reducing plant mortality by 15% (Rodríguez-Moreno *et al.*, 2021). Increases drought and heat resistance by 30% (Patel *et al.*, 2021). Increases productivity and nutrient absorption by 20% (Qin *et al.*, 2022). A 15% decrease in plant mortality was found (Rodríguez-Moreno *et al.*, 2021). Growth hormones are very important for commercial strawberry production as given in Table 1. This indicates the commercial applications of growth hormones.

Molecular Mechanisms of Growth Hormone Action in Strawberries

Strawberry growth hormone function involves complicated signaling networks and transcriptional control. Auxins activate auxin response factors (ARFs) to interact with cell division and elongation gene promoters for organogenesis and fruit set. Gibberellins degrade DELLA proteins via the GID1 receptor, activating transcription factors to promote growth and blooming. Cytokinins modulate mitosis-promoting cell cycle genes via stimulating histidine kinases (HKs) in a two-

Hormone	Primary Roles	Commercial Applications	Effects on Fruit Quality & Yield	References	
Auxins (IAA, NAA)	- Stimulates root growth	- NAA application at 19.97–49.94 mg/L	- Increases berry width, length, and weight		
	- Regulates cell elongation and division	- Foliar spray of 125 mg/L NAA	- Enhances fruit firmness		
	- Controls early fruit development	- Early application enhances mechanical support	- Increases sugars and acidity	Singh et al., 2022; Kumar et al., 2020	
	- Delays fruit ripening		- Promotes longer petioles		
	- Promotes vascular tissue differentiation		- Prevents premature fruit drop		
Gibberellins (GA ₃)	- Promotes flowering in non-chilled plants	- GA₃ at 80 ppm for vegetative growth	- Shortens the cropping season		
	- Increases vegetative growth	- Combined with PSB at 6 kg/ha + GA_3 at 100 ppm	- Increases plant height and leaf area	Kumar et al., 2020; Liao et al., 2018	
	- Enhances runner formation	- Application to replace chilling	- Improves plant Vigor		
	- Inhibits fruit ripening		- Enhances runner production	ai., 2010	
	- Breaks dormancy		- Shortens time to first bloom		
Abscisic Acid (ABA)	- Critical regulator of fruit ripening	- Externally applied to enhance ripening	- Promotes color development		
	- Controls color development	- Monitored for post- harvest management	- Regulates ripening	Jia et al., 2011; Medina-Puche	
	- Influences senescence		- Increases during storage	et al., 2016	
	- Key in non-climacteric ripening		- Influences senescence		
Cytokinins	- Counteracts apical dominance	 Used with low auxin for shoot generation 	- Enhances fruit set and growth		
	- Promotes cell division	- Applied to promote reproductive growth	- Promotes reproductive growth	Kumar et al.,	
	- Influences shoot regrowth		- Increases flower development	2020; Liao et al., 2018	
	- Shifts growth to the reproductive phase				
Brassinosteroids	- Highest at anthesis	- Limited commercial use in strawberries	- Not important for ripening	Medina-Puche et al., 2016	
	- Drop before ripening		- Levels drop before ripening		
	- Limited role in ripening				
Ethylene & Methyl Jasmonate	- Limited role in ripening (non- climacteric)	- Post-harvest management	- Affect senescence and storage life	Medina-Puche et al., 2016; Jia et al., 2011	
	- Influence post-harvest senescence	- Less important than in climacteric fruits	 Impact biochemical metabolism during storage 		

component system. ABA inhibits PP2C phosphatases via binding to PYR/PYL receptors, allowing SnRK2 kinases to activate stress-responsive genes. Ethylene activates a MAPK cascade that affects ripening transcription factors like EIN3 via ETR receptors. Hormonal mechanisms regulate gene expression and protein interactions at numerous transcriptional and post-translational stages, affecting strawberry growth, fruit quality, and stress adaptation.

Growth Hormone Biosynthesis and Signal Transduction in Strawberry

Growth hormones play a crucial role in controlling physiological processes such as growth, development, and ripening in *Fragaria* × *ananassa*. Auxins, gibberellins, cytokinins, ABA, ethylene, and brassinosteroids are detected. Strawberry growth hormone biosynthesis and signal transduction systems provide promising regulatory options to improve fruit quality and yield.

Auxins

Auxins, primarily indole-3-acetic acid (IAA), are synthesized in the apical meristems and juvenile leaves of strawberry plants. Indole-3-acetic acid (IAA) production relies on tryptophan, which is transformed into IAA via many intermediates, including IPyA and IAAId (Zhao, 2017). Polar auxin transport systems transfer indole-3-acetic acid (IAA) throughout the plant via AUX1 and PIN proteins (Zhao, 2017). Indole-3-acetic acid (IAA) binding to the TIR1 receptor starts auxin signaling. This link degrades AUX/IAA repressor proteins, activating ARF transcription factors. These molecules regulate auxin-responsive genes necessary for cell division and proliferation (Bao *et al.*, 2017).

Gibberellins

Strawberry plastids synthesize bioactive gibberellins (GA) from geranylgeranyl diphosphate (GGDP) through enzyme conversions. Strawberry stem elongation, flowering, and fruit enlargement require hormones (Varga *et al.*, 2020). The GA signal transduction pathway begins when gibberellins bind to their receptor, GID1. DELLA proteins, which inhibit GA signaling, degrade after this link. GA-responsive genes activate during degradation, increasing cell elongation and division (Wang *et al.*, 2020).

Cytokinin

Plant hormones called cytokinins are needed for cell division, growth, and differentiation. They control plant growth and environmental reactions. Cytokinins, produced in the root system and transported through the xylem, regulate cell division, stimulate shoot development, and delay senescence. AMP is converted to cytokinins via isopentenyl transferases (IPTs) (Zhang et al., 2021). Cytokinins and auxins influence physiological processes, including strawberry fruit development. In a two-component system, cytokinin molecules interact with histidine kinase receptors like CRE1 to signal. Activation of response regulators (ARRs) by phosphorylation cascades regulates cytokinin-responsive gene expression (Zhang et al., 2021).

Abscisic Acid

ABA, a plant hormone, regulates seed dormancy, stomatal closure, and stress responses. Plants need synthesis and

signaling channels to adapt to environmental changes. In plastids, zeaxanthin is converted into abscisic aldehyde, which is oxidized to ABA (Liu *et al.*, 2018). Strawberry fruit ripening depends on abscisic acid (ABA), which affects anthocyanin formation, sugar accumulation, and stress response (Liu *et al.*, 2018; Arteca & Arteca, 2016). ABA binds to PYRABACTIN RESISTANCE1 (PYR1) receptors to start signaling. SnRK2 is activated by inhibiting protein phosphatase 2C (PP2C). Nishimura et al., (2020) found that these kinases phosphorylate ABA-responsive transcription factors.

Ethylene

Many chemical processes and applications require colorless ethylene. It is mostly used to synthesize polyethylene and other important chemicals. The qualities and responses are important in industry and research. In the Yang cycle, S-adenosylmethionine (SAM) is converted into 1-aminocyclopropane-1-carboxylic acid (ACC) by ACC synthase to produce ethylene. ACC oxidase (ACO) oxidizes ACC to ethylene (Hu & Ding, 2019). Strawberry ripening depends on ethylene, which softens and enhances the flavour (Chai & He, 2018). When ethylene interacts with receptors like ETHYLENE RESPONSE1 (ETR1), EIN2 activates and enhances ethylene-responsive gene transcription (McAtee *et al.*, 2018).

Brassinosteroids (BRs)

The most potent brassinosteroids (BRs) are bioactive brassinolide (BL), which is formed from campesterol through oxidation and hydroxylation processes (Zhu *et al.*, 2017). Brassinosteroids (BRs) play a critical role in supporting cellular growth, division, and differentiation in *Fragaria* × *ananassa*, enhancing fruit development and stress tolerance (Vishal & Kumar, 2018 Brassinosteroids bind to the cell membrane's BRI1 receptor to start BR signaling. This link activates BZR1 transcription factors by inducing a phosphorylation cascade that inhibits BIN2 kinase. These chemicals increase BR-responsive genes needed for cell growth (Clouse, 2021).

Brassinosteroids (BRs) interact with several phytohormones, such as auxins and gibberellins, which are essential for regulating strawberry growth and development, thus improving fruit size and quality (Vishal & Kumar, 2018; Bajguz & Tretyn, 2017). Research suggests that the use of BR can improve strawberry output by promoting cell elongation and expansion, similar to effects noted in other plant species (Arteca & Arteca, 2016; Clouse, 2021).

Cellular Expansion and Turgor Maintenance in Strawberry (Fragaria × ananassa)

Strawberry plant growth and fruit development depend on cellular expansion and turgor maintenance. A complex combination of hormonal signals regulates cell wall dynamics, water absorption, and intracellular pressure. Strawberry plants' auxins, gibberellins, cytokinins, brassinosteroids, and abscisic acid (ABA) regulate physiological processes to coordinate cellular expansion for optimal fruit size and texture.

Turgor Pressure and Its Role in Cellular Expansion

Turgor pressure is the vacuole fluid's hydrostatic pressure against the cell wall. Maintaining cell stiffness and promoting cell growth is crucial. Enzymatic cell wall loosening increases flexibility, allowing turgor pressure to expand cells. In fast-growing tissues like strawberry fruits, cell size increases significantly to enlarge the fruit (Zhu *et al.*, 2017). Turgor pressure is crucial for fruit firmness and wilting prevention, especially in response to environmental changes (Wang *et al.*, 2020).

Auxins: Modulating Cell Wall Loosening and Turgor-Driven Expansion

Strawberry cell expansion is promoted by auxins, particularly indole-3-acetic acid (IAA), which weaken cell walls and stimulate turgor-driven development. The auxin-mediated acid growth theory states that auxins increase plasma membrane proton (H⁺) pump activity, resulting in cell wall acidity (Zhao, 2017). Expansins and xyloglucan endotransglucosylase/hydrolases activate when pH drops. These enzymes disrupt hydrogen bonds between cellulose fibers and matrix polysaccharides, weakening the cell wall (Bao et al., 2017). Turgor-driven expansion, crucial during rapid growth, is enabled by cell wall relaxation, especially in strawberry fruit development (Zhao, 2017). Auxins regulate aquaporin gene expression, which encodes water channel proteins that carry water into vacuoles and maintain high turgor pressure (Zhang et al., 2021). Water is essential for cellular expansion, as cell wall relaxation and turgor pressure help the fruit expand

Gibberellins: Promoting Cell Elongation and Turgor Maintenance

Gibberellins (GA) affect cell elongation and turgor pressure, affecting cellular expansion. Gibberellins increase cell wall extensibility by upregulating genes that encode expansions and XTHs (Varga et al., 2020). Strawberry growth depends on hormone-induced cell wall relaxation, which increases turgor pressure and cell elongation. Gibberellins upregulate aquaporin, which increases water absorption and vacuolar turgor for cellular growth (Wang et al., 2020). Strawberry fruit growth relies on gibberellins, notably during vigorous cell division and elongation (Wang et al., 2020). The manufacture of these enzymes requires gibberellin signaling regulation, which affects cellular expansion capacity and fruit size (Varga et al., 2020).

Cytokinins: Regulation of Water Transport and Turgor Pressure

Strawberry cell division and growth depend on cytokinins, which control water transport and turgor pressure. Cytokinins increase aquaporin activity, which increases water influx into cells and maintains high turgor pressure for growth (Zhang et al., 2021). This group of hormones also increases fruit tissue cell proliferation, which boosts turgor-driven growth. Strawberry cytokinins promote cell proliferation and water balance to sustain turgor pressure during rapid fruit growth (Zhang et al., 2021). When cytokinins and auxins interact, cell division and expansion occur simultaneously, boosting fruit size and texture.

Brassinosteroids: Enhancing Cell Wall Extensibility

Brassinosteroids (BRs) have a crucial role in maintaining cell wall dynamics and turgor in *Fragaria* × *ananassa*. Brassinosteroids (BRs) upregulate expansions and other cell wall-modifying enzymes, such as pectin methylesterases (PMEs), which break

down pectin (Zhu et al., 2017). Deterioration reduces cell wall rigidity, facilitating cellular expansion in response to turgor pressure. Brassinosteroids (BRs) also impact water transport genes, including aquaporins, allowing enough water to enter vacuoles to sustain turgor pressure (Vishal & Kumar, 2018). Strawberry brassinosteroids increase cellular proliferation and growth, resulting in larger and better fruit. Research shows that brassinosteroids (BRs) increase strawberry fruit size by promoting cellular expansion and water absorption, underlining their role in turgor pressure (Bajguz & Tretyn, 2017).

Abscisic Acid (ABA): Balancing Turgor Under Stress Conditions

Turgor maintenance requires ABA, especially in droughts. Abscisic acid (ABA) signaling enhances stomatal closure, reducing water loss and preserving internal water levels, which maintain cell turgor pressure (Liu et al., 2018). ABA also promotes cell wall breakdown genes during fruit ripening, facilitating turgor-driven expansion during this important time (Nishimura et al., 2020). In strawberry plants, abscisic acid (ABA) regulates ion transport gene expression to maintain osmotic balance and stabilize turgor pressure during water stress. This regulation helps keep fruit solid and reduce wilting, especially in later stages (Liu et al., 2018).

Growth Hormones and Secondary Metabolite Synthesis in Strawberry (*Fragaria* × *ananassa*)

Growth hormones (GHs) regulate strawberry secondary metabolites, which are critical for plant defence, pigmentation, flavor profiles, and scent. Fruit quality and durability depend on secondary metabolites like phenolics, flavonoids, anthocyanins, and VOCs. These compounds are regulated by auxins, gibberellins (GA), cytokinins, abscisic acid (ABA), ethylene, and brassinosteroids (BRs), which coordinate growth and biosynthesis for optimal fruit development.

Auxins and Phenolic Compound Biosynthesis

Strawberry phenolic compound synthesis requires auxins like IAA. Phenylalanine ammonia-lyase (PAL), cinnamate-4-hydroxylase (C4H), and 4-coumarate-CoA ligase (4CL) are regulated by auxins. This regulation encourages the production of phenolic compounds such as hydroxycinnamic acids, lignin, and flavonoids (Zhao, 2017). These metabolites boost antioxidant activity and disease resistance in plants (Sharma et al., 2019). Auxins increase phenolic compound production by modulating phenylalanine ammonia-lyase (PAL) expression in early fruit development. Increasing lignin synthesis improves fruit firmness and structure (Zhang et al., 2021). Auxins and other hormones, notably gibberellins, increase flavonoids and phenolic acids, boosting the fruit's antioxidant potential (Yoon et al., 2020).

Gibberellins and Flavonoid Synthesis

Gibberellins (GA) regulate flavonoid production, especially anthocyanins, which give strawberries their red color. Anthocyanin formation requires enzymes including chalcone synthase, flavanone-3-hydroxylase, and dihydroflavonol-4-reductase, which gibberellins regulate (Varga *et al.*, 2020). Strawberry nutrition is improved by flavonoids, which boost

color and antioxidants (Molina-Hidalgo *et al.*, 2020). Research shows that using GA increases anthocyanin and flavonoid concentrations, leading to better fruit quality and colour (Martínez-Rivas *et al.*, 2019). Gibberellins also synergistically modulate the phenylpropanoid pathway with ethylene and auxins, increasing flavonoid synthesis (Vishal & Kumar, 2018). Gibberellin signaling increases strawberry fruit flavanol production, including quercetin and kaempferol, which boost antioxidant activity and stress resilience (Wang *et al.*, 2020).

Cytokinins and Terpenoid Biosynthesis

Cytokinins regulate terpenoid synthesis, especially the production of volatile terpenoids like linalool and nerolidol, which give strawberries their distinctive smell (Lal et al., 2018). Cytokinins modulate GPPS and FPPS, which are essential for monoterpene and sesquiterpene production, to regulate the isoprenoid pathway (Zhang et al., 2021). Terpenoids affect fruit taste and prevent herbivores, and attract pollinators (Dudareva et al., 2018). Cytokinins increase glycosylated terpenoids, which are precursors to volatile compounds produced during fruit ripening, making fruit smell and sell better (Zhang et al., 2021). Cytokines, auxins, and brassinosteroids regulate primary growth and secondary metabolite production, boosting fruit development and flavour.

Abscisic Acid (ABA) and Anthocyanin Accumulation

Abscisic acid (ABA) regulates anthocyanin production, especially during fruit ripening. Abscisic acid (ABA) increases strawberry anthocyanin concentrations via increasing the transcriptional activity of anthocyanin biosynthesis genes such as ANS, UFGT, and MYB (Liu et al., 2018). Anthocyanins give fruit red color and antioxidant capacity, improving its nutritional value and appearance (Ma et al., 2021). ABA also impacts the manufacture of antioxidants such as caffeic acid and ferulic acid, which help reduce oxidative stress (Zhu et al., 2017). Later fruit development requires ABA to modulate secondary metabolites, improving fruit quality and stress resilience (Liu et al., 2018). Abscisic acid (ABA) also interacts with phytohormones like ethylene to regulate fruit ripening and sync secondary metabolite synthesis with the optimal stage (McAtee et al., 2018).

Ethylene and Volatile Organic Compounds (VOCs)

Fruit ripening requires ethylene to produce volatile organic compounds (VOCs). Ethylene modulates the production of enzymes, including alcohol acyltransferase (AAT) and lipoxygenase (LOX), which are needed to make esters, alcohols, and aldehydes, which give strawberries their scent and flavor (Chai & He, 2018). Methyl hexanoate and ethyl butanoate contribute to the delightful smell of ripe strawberries (Hu & Ding, 2019). During late ripening, ethylene greatly increases strawberry VOC biosynthesis gene expression, influencing the fruit's fragrance and sensory profile (McAtee *et al.*, 2018). Changing ethylene's role in volatile production can enhance fruit flavour and appeal to consumers (Martínez-Rivas *et al.*, 2019).

Brassinosteroids and Phenolic Biosynthesis

Brassinosteroids (BRs) modulate the phenylpropanoid pathway to regulate strawberry phenolic component production. BRs activate PAL, C4H, and 4CL enzymes to biosynthesize

phenolic acids, flavonoids, and lignin (Zhu et al., 2017). The chemicals retain structural integrity, display antioxidant action, and boost plant defences (Vishal & Kumar, 2018). BRs also increase anthocyanin and flavonoid accumulation, improving fruit color and antioxidant properties (Sharma et al., 2019). External brassinosteroids increase lignin synthesis, enhancing fruit firmness and post-harvest shelf life (Lal et al., 2018). The interaction between brassinosteroids, auxins, and cytokinins affects secondary metabolite biosynthesis, promoting optimal growth and metabolite accumulation during fruit development (Martínez-Rivas et al., 2019).

Growth Hormone's Role in Enhancing Strawberry Quality

Gibberellins (GAs), key growth hormones, regulate strawberry fruit development and quality. Gibberellins (GAs) increase fruit size by promoting cell elongation and division, leading to greater bulk and commercial value (Rodríguez et al., 2019). Their regulation of cell wall integrity improves firmness, which extends postharvest shelf life and reduces transportation damage (Mazur et al., 2017). Gibberellins (GAs) interact with abscisic acid (ABA) and ethylene to generate color in strawberries, resulting in the unique red pigmentation seen in fully mature fruits (Li et al., 2020; Hu & Ding, 2015).

Gibberellins and cytokinins also affect sugar metabolism, promoting soluble sugar accumulation and sweetness, which customers value (Gao *et al.*, 2018). The fruit's aroma and flavor are likewise affected by flavor volatile biosynthesis regulation (Shi *et al.*, 2016). By boosting the plant's physiological defences, gibberellins (GAs) help ripen and protect fruit quality from stress and disease (Khan *et al.*, 2020).

Gibberellins regulate fruit set and seed development, ensuring correct fruit morphology and decreasing malformations and asymmetrical growth (Tian *et al.*, 2019). Thus, accurate gibberellin control and their interactions with other phytohormones are essential for maximizing strawberry size, firmness, color, sweetness, and stress resilience, improving fruit quality.

Inhibition of Cell Wall-Degrading Enzymes

Gibberellins (GAs) and auxins regulate cell wall-degrading enzymes such as pectinases, polygalacturonases, and cellulases to disintegrate the cell wall matrix, a vital phase in fruit softening. Research suggests that gibberellins inhibit enzyme activity, delaying cell wall dissolution and softening (Rodríguez et al., 2019). Polygalacturonases soften cell walls by degrading pectin. Gibberellic acid reduces this enzyme, increasing fruit firmness (González et al., 2019). Auxins strongly regulate cell wall integrity and growth genes. Auxin-responsive genes regulate cellular elongation and breakdown, stabilizing cell wall components including pectin and cellulose throughout ripening and maintaining fruit firmness (McAtee et al., 2013).

Delayed Softening and Extended Shelf Life

By retaining cell wall integrity, GAs delay strawberry ripening and softening. The hormone slows fruit softening by reducing cell wall-degrading enzymes and modulating cell wall component synthesis (Mazur *et al.*, 2017). Gibberellins modulate cell wall metabolism to harden strawberries,

increasing shelf life and enhancing postharvest management. Cytokinins are synergistic with gibberellins, prolonging fruit softening. This interaction keeps the fruit solid during storage.

Interactions with Other Hormones: Balancing Ripening and Firmness

Abscisic acid (ABA) softens and changes fruit texture to start ripening. Gibberellins reduce abscisic acid's effect by delaying ripening genes, resulting in firmer fruit. Gibberellins and abscisic acid work together to manage firmness and ripening, allowing for controlled softening and excellent fruit texture (Li et al., 2020). While less important in non-climacteric fruits like strawberries, ethylene nevertheless affects ripening and softening. Ethyleneresponsive genes involved in cell wall breakdown can be regulated by gibberellins and auxins to reduce softening (Tian et al., 2019). Gibberellins, auxins, abscisic acid, and ethylene optimize firmness and ripening, improving postharvest quality.

Postharvest Quality: Resistance to Mechanical Damage

Strawberry mechanical damage during handling and transit depends on firmness. Gibberellins increase strawberry firmness, making them more resistant to bruising and compression (Shi *et al.*, 2016). Since firmer strawberries are less susceptible to transportation damage, this trait improves shelf life and marketability in local and export markets.

Consumer Perception and Market Value

Fruit firmness and texture strongly influence consumer preference. Firmer strawberries are associated with fresher and higher-quality strawberries, which affects their market value. Strawberry demand and marketability rise due to growth hormones' firmness-boosting properties (McAtee *et al.*, 2013). The hardness also affects strawberries' packaging and appearance, increasing their commercial viability.

Flavor and Aroma Enhancement

Strawberry flavor and scent depend on growth hormones such as gibberellins, auxins, and cytokinins. These hormones regulate sugar buildup, organic acid breakdown, and volatile chemical production. The metabolic mechanisms in question affect sensory qualities, including sweetness, tartness, and scent, which determine fruit quality and customer acceptance.

Regulation of Sugar Metabolism and Sweetness

Gibberellins (GAs) increase glucose and fructose buildup, which gives strawberries their sweetness. Gibberellins (GAs) upregulate sucrose synthase (SUS) and invertases, affecting sugar metabolism. These enzymes convert sucrose into glucose and fructose, which give the fruit its sweet taste. Strawberry sugar content increases due to hormone regulation, which affects consumer preference and market valuation. Sugar metabolism depends on auxins, such as indole-3-acetic acid (IAA), which help sugar transporters move glucose from leaves to fruit. Strawberry sweetness increases due to sugar input during ripening (Li *et al.*, 2020). Cytokinins and gibberellins work together to regulate sugar buildup by modulating sugar transport and metabolic gene expression. Cytokines increase the sugar-to-acid ratio, making strawberries sweeter (Herrera *et al.*, 2018).

Organic Acids and the Balance of Sweetness and Tartness

Strawberry sweetness and tartness depend on organic acid concentrations, especially citric and malic acids. These acids define the fruit's acidity, which, when combined with sweetness, creates a better-tasting profile. Auxins and cytokinins regulate organic acid metabolism by modulating the production and degradation of enzymatic activity (Rodríguez et al., 2019). Auxins break down organic acids during ripening, reducing acidity and improving the sweetness-tartness balance. This management helps strawberries achieve the ideal flavor profile because too much acidity reduces sweetness and affects customer perception (Gao et al., 2018).

Biosynthesis of Aroma Volatiles

Strawberry aroma depends on volatile chemical molecules. Terpenoids, esters, alcohols, and aldehydes are being studied. Gibberellins (GAs) and auxins regulate volatile chemical biosynthesis genes such as alcohol acyltransferase (AAT), lipoxygenase (LOX), and acyl-CoA oxidase (ACO) (Shi et al., 2016). Gibberellins increase AAT activity, which helps synthesize volatile esters that give strawberries their sweet and floral scents. Strawberry esters like methyl butanoate and ethyl hexanoate give them their pleasant, fruity smell (McAtee et al., 2013). Fatty acid metabolism, which produces aroma-related volatiles such as aldehydes and alcohols, requires auxins. The compounds affect strawberry scent richness and intensity, improving the sensory experience (Tian et al., 2019). Cytokinins promote terpenoids, which increase strawberry scent complexity by influencing volatile organic compound (VOC) production (Herrera et al., 2018).

Cross-talk Between Hormones: GA, ABA, and Ethylene

Gibberellins, abscisic acid (ABA), and ethylene strongly affect strawberry taste and aroma production. Abscisic acid (ABA) regulates ripening, boosting sugar accumulation and volatile chemical production. Gibberellins (GAs) considerably affect these physiological processes' timing and intensity (Mazur *et al.*, 2017). Although less important in non-climacteric fruits like strawberries, ethylene helps ripen them. Gibberellins and auxins regulate ethylene's effect on volatile compound production, preventing premature ripening and ensuring fruit has the proper flavor and scent (Li *et al.*, 2020).

Postharvest Aroma Preservation

GAs in postharvest processing maintain scent throughout storage. GAs slow volatile component degradation, preserving the fruit's fresh scent during storage or transit (Shi *et al.*, 2016). Maintaining fruit quality and marketability is crucial, with scent determining customer approval.

Impact on Consumer Preference and Marketability

Sweetness, acidity, and a rich, nuanced fragrance profile greatly influence consumer preference. Gibberellins, auxins, and cytokinins improve sugar metabolism, organic acid breakdown, and volatile compound synthesis. Thus, hormonally treated strawberries are more appealing and valuable (McAtee *et al.,* 2013).

Growth Hormones and Stress Tolerance

Strawberry growth, yield, and quality are greatly affected by abiotic stresses such as drought, salinity, and extreme temperatures. Gibberellins (GAs), abscisic acid (ABA), auxins, cytokinins, brassinosteroids (BRs), ethylene, and salicylic acid (SA) are used by plants to respond to environmental stressors. Stomatal regulation, root growth, antioxidant defense, and osmotic equilibrium are regulated by these hormones, which improve stress tolerance. This article examines how brassinosteroids and ethylene regulate strawberry plant abiotic stress responses.

Gibberellins (GAs) and Stress Regulation

Gibberellins (GAs) are best known for promoting cell elongation and flowering. Gibberellins (GAs) decrease under abiotic stress, helping plants conserve energy and allocate resources to adaptation mechanisms (Shu *et al.*, 2018). In strawberries, low gibberellin levels restrict vegetative growth, promoting root development and water uptake during drought stress (Tian *et al.*, 2019). Under stress, abscisic acid (ABA) inhibits development by downregulating GA production in gibberellins (GAs). The hormonal homeostasis helps strawberry plants slow their development for survival, including water preservation (Miao *et al.*, 2021).

Abscisic Acid (ABA) and Drought Tolerance

ABA is the main hormone that regulates drought tolerance. Strawberry plants' abscisic acid (ABA) levels rise during drought stress, closing stomata. This physiological response lowers transpiration and conserves water (Yang *et al.*, 2019). Abscisic acid (ABA) regulates stomatal function to reduce transpiration under water constraints. Osmoprotective molecules, including proline and carbohydrates, which maintain cellular turgor and prevent dehydration, are also affected by ABA (Liu *et al.*, 2021). Abscisic acid (ABA) also increases stress response genes, which produce proteins like dehydrins that protect cells from dry circumstances.

Auxins and Root Development under Stress

Auxins are essential for the regulation of root architecture, a crucial element for enhancing water and nutrient uptake under stressful circumstances. Auxins in strawberries promote the development of lateral roots and root hairs, hence increasing the root surface area, which is essential for enhanced water absorption during drought or salinity stress (Kaya et al., 2020). Auxins are essential for maintaining ion homeostasis under salt stress by modulating the function of ion transporters, thus preventing the accumulation of harmful sodium ions (Na+), which can cause cellular damage. This process enhances the salt tolerance of strawberries by alleviating osmotic stress (Ahanger et al., 2020).

Cytokinins and Antioxidant Defense

Cytokinins help cell division and shoot development under ideal conditions, but abiotic stress lowers their concentrations, inhibiting shoot growth and promoting root formation. Strawberry adaptation optimises water acquisition during drought stress (Zwack & Rashotte, 2015). Cytokinins increase SOD, CAT, and peroxidase activity to modulate plant antioxidant

defence mechanisms. This increase reduces stress-induced ROS accumulation. This method protects cells from oxidative damage, increasing stress tolerance.

Brassinosteroids (BRs) and Stress Adaptation

Plant development and stress resilience depend on brassinosteroids (BRs). By regulating antioxidant enzymes that detoxify reactive oxygen species (ROS) produced during drought and salinity, BRs boost cellular defences against abiotic stresses (Ahammed *et al.*, 2020). Strawberry brassinosteroids improve stress tolerance by remodelling cell walls, which increases cell integrity and lowers water loss. Brassinosteroids, abscisic acid, and gibberellins govern growth and stress responses, balancing growth suppression and survival in demanding situations (Anwar *et al.*, 2020).

Ethylene and Stress Response

Although ethylene is associated with fruit ripening and senescence, it also plays a key function in stress reaction signaling pathways. Ethylene increases during abiotic stress, which promotes stress response gene expression and tolerance (lqbal et al., 2017). Plants can conserve energy on non-essential organs and focus resources on root development for water absorption by promoting leaf senescence and root elongation with ethylene. ABA and brassinosteroids (BRs) interact with ethylene to regulate stress response. In droughts, ethylene balances abscisic acid (ABA)-induced stomatal closure and root elongation. This regulating mechanism ensures strawberry plant water conservation and root access to deeper water sources (Shi et al., 2016).

Salicylic Acid (SA) and Oxidative Stress Management

Salicylic acid (SA) is essential in mitigating oxidative stress by stimulating the synthesis of antioxidant enzymes that neutralize reactive oxygen species (ROS) generated by abiotic conditions such as drought and salinity (Kaya *et al.*, 2020). SA facilitates the synthesis of heat shock proteins (HSPs) and other stress-related proteins, essential for preserving cellular integrity and averting protein denaturation during heat and drought stress (Larkindale & Huang, 2004).

Crosstalk Between Hormones for Integrated Stress Response

Fragaria × ananassa regulates abiotic stress responses through hormonal interactions that balance growth and survival strategies. Abscisic acid (ABA) closes stomata to conserve water, whereas gibberellins (GAs) are downregulated to limit growth. Brassinosteroids and ethylene boost root growth and oxidative stress defences, while auxins increase root architecture. Since cytokinins boost antioxidant defences and ABA conserves water and activates stress-responsive genes, their interaction is critical. Strawberry plants can respond to many stimuli simultaneously due to hormonal coordination (Zhang et al., 2021).

Applications in Abiotic Stress Management in Strawberry Cultivation

Exogenous treatments of abscisic acid, brassinosteroids, salicylic acid, and ethylene inhibitors enhance stress tolerance in

Fragaria × ananassa. These treatments improve the plant's stress tolerance by triggering physiological responses like osmotic adjustment, antioxidant defence, and stomatal regulation (Miao et al., 2021). New biotechnology and genetic engineering techniques manipulate hormone production and signalling pathways to create strawberry cultivars that are more resistant to harsh conditions. Overexpressing genes that increase ABA or BR signalling pathways improves drought and salinity tolerance (Shu et al., 2018).

Auxin and Gibberellin in the Process of Fruit Development

Auxins and gibberellins synergistically regulate strawberry fruit growth. Auxin, mostly indole-3-acetic acid (IAA), is synthesized in achenes (seeds) and promotes fruit development by promoting cell division and expansion. Cell elongation stimulated by GA biosynthesis aids fruit growth in later stages (Dorcey *et al.*, 2009; Chai & He, 2014). Fruit development depends on auxingibberellin interaction. Auxin deficit reduces GA signaling, affecting fruit development. Auxin activates GA biosynthetic genes, including GA200x, in Arabidopsis and strawberries, enabling coordinated fruit development (Chai *et al.*, 2014). Auxin promotes strawberry growth, and gibberellins maintain fruit size (Dorcey *et al.*, 2009).

Abscisic Acid and Ethylene in Fruit Ripening

In strawberry ripening, abscisic acid (ABA) and ethylene work synergistically. Because strawberries are non-climacteric, ABA has a greater effect. Abscisic acid (ABA) helps anthocyanin accumulation, sugar production, and fruit softening during ripening. Ethylene modulates fragrance volatiles and enhances softening later in ripening (Li et al., 2020; McAtee, 2013). The interplay between ABA and ethylene helps the ripening progress orderly. ABA starts the metabolic pathways of color-developing genes like FvMYB10. In contrast, ethylene upregulates polygalacturonase and pectin methylesterase genes to degrade cell walls, softening fruit (Tian et al., 2019). This interplay produces strawberries with aesthetic and flavour features that satisfy customer desires.

The Interplay of Cytokinins and Auxins in Root and Shoot Development

Root and shoot growth depend on cytokinin-auxin interactions. Auxins help roots develop and elongate, while cytokinins stimulate meristematic tissue cell division to promote shoot growth. Strawberry root-to-shoot balance depends on the cytokinin-auxin ratio, especially in various environmental situations (Zwack & Rashotte, 2015). Recent studies show that hormonal interactions promote auxin in dryness, boosting root growth but reducing shoot development. Strawberry survival under water scarcity is improved by this adaptation mechanism (Peleg & Blumwald, 2011).

Interaction of Brassinosteroids and Salicylic Acid in Abiotic Stress Response

Brassinosteroids (BRs) and salicylic acid (SA) synergistically regulate abiotic stress responses, especially in drought and salinity. Brassinosteroids reduce stress by improving cell wall stability, antioxidant defence, and hydration retention (Ahammed *et al.*, 2020). Salicylic acid (SA) activates defense-related genes, which boosts antioxidant enzyme activity and the plant's ability to fight oxidative damage (Kaya *et al.*, 2020). Research on strawberry plants shows that brassinosteroids (BRs) and SA aid osmotic adjustment and reduce ROS buildup, improving plant resilience to stress. Research shows that exogenous application of BRs and SA together improves drought tolerance in strawberries more than either component alone (Anwar *et al.*, 2020).

Interaction Between Abscisic Acid and Gibberellins in Seed Dormancy and Germination

The antagonistic relationship between abscisic acid and gibberellins plays a crucial role in the regulation of seed dormancy and germination processes in strawberry plants. Abscisic acid (ABA) plays a crucial role in the maintenance of seed dormancy through the inhibition of germination processes. Conversely, gibberellins (GAs) facilitate the breaking of dormancy by enhancing the expression of enzymes responsible for the mobilization of seed reserves (Liu et al., 2021). The interaction between ABA and GA is essential for regulating the germination of strawberry seeds, ensuring that this process occurs solely under optimal environmental conditions. Recent investigations have demonstrated that abscisic acid (ABA) inhibits gibberellin (GA) biosynthesis through the downregulation of GA biosynthetic genes, whereas gibberellins enhance their biosynthetic pathway by suppressing the activity of ABA. This antagonistic relationship facilitates accurate regulation of germination timing, an essential characteristic for survival in fluctuating environments (Shu et al., 2018).

Interactions Between Ethylene and Auxin in the Context of Senescence and Stress Adaptation

Ethylene and auxins regulate leaf senescence and stress responses cooperatively and antagonistically. Ethylene activates genes involved in cell death and nutrient remobilization, while auxins decrease ethylene production and signalling to delay senescence (lqbal et al., 2017). Ethylene levels rise during abiotic stress, particularly drought, promoting leaf senescence to preserve water. Auxins fight ageing, extending photosynthetic activity. Ethylene and auxin cooperate to optimise growth and survival, allowing strawberry plants to adapt to changing environmental conditions while sustaining critical physiological functions (Zhang et al., 2021).

Interaction between Cytokinins and Brassinosteroids in Growth Regulation

Strawberry growth regulation depends on cytokinins and brassinosteroids (BRs), which affect cellular division and elongation. Cytokinins increase shoot apical meristem cell proliferation, while brassinosteroids modulate cell wall loosening enzymes like expansions to elongate cells (Anwar et al., 2020). Cytokinins and brassinosteroids balance cellular proliferation and elongation, promoting vegetative and reproductive development. Strawberry contact helps fruit grow to the right size and form (Zhang et al., 2021).

Table 2: Influence of Plant Hormones on Physiological and Related Parameters of Strawberry.

Plant Hormone	Specific Physiological Roles in Strawberry	Regulated Parameters	References
Auxins (IAA, NAA)	Stimulate vascular differentiation, apical dominance, and early fruit morphogenesis.	Fruit initiation, cell elongation, sink strength enhancement	Li et al., 2021; He et al., 2022
Gibberellins (GA ₃ , GA ₄₊₇)	Trigger stolon development, delay leaf senescence, and promote floral induction	Runner formation, flowering time regulation, and peduncle elongation	Wang et al., 2021; Xu et al., 2022
Cytokinins (BA, kinetin)	Support apical meristem activity and cytokinesis in fruit tissue	Shoot proliferation, chlorophyll retention, and delayed senescence	Zhang et al., 2022; Ren et al., 2021
Abscisic Acid (ABA)	Control water stress signalling and anthocyanin biosynthesis during ripening	Color development, osmotic adjustment, and firmness	Liang et al., 2021; Chen et al., 2023
Ethylene	Modulates volatile synthesis and accelerates texture softening	Aroma compound release, cell wall enzyme activation	Gao et al., 2021; Huang et al., 2022
Salicylic Acid (SA)	Activates systemic acquired resistance and antioxidant systems	Disease resistance, enzymatic antioxidant activity, and firmness retention	Zhou et al., 2021; Meena et al., 2023
Jasmonic Acid (JA)	Regulates phenolic biosynthesis and defence responses	Bioactive compound production, tolerance to abiotic/biotic stress	Fang et al., 2022; Zhu et al., 2017
Brassinosteroids (BRs)	Enhance sugar transport and plant Vigor under stress	Soluble sugar accumulation, photosynthetic efficiency, stress resilience	Liu et al., 2021; Sharma et al., 2024

Future Directions in Growth Hormone (GH) Research and Applications for Commercial Strawberry Cultivation

Strawberry (Fragaria ananassa) plant growth, development, and stress responses are regulated by phytohormones like auxins, gibberellins (GAs), abscisic acid (ABA), cytokinins, ethylene, brassinosteroids (BRs), and salicylic acid (SA). Phytohormonal crosstalk regulates fruit development, ripening, stress tolerance, and senescence through complicated signaling networks. To maximize strawberry output, fruit quality, and stress resilience in commercial agriculture, one must understand the molecular and physiological mechanisms that drive these relationships.

Auxin and Gibberellin Interplay in Strawberry Fruit Development

Strawberry growth is regulated by auxins and gibberellins. Achenes (seeds) release auxins, mainly indole-3-acetic acid (IAA), which promote cell division and expansion in early fruit development. This mechanism starts gibberellin production, which lengthens fruit cells later on (Chai & He, 2014). According to Dorcey et al., (2009) and Chai et al., (2014), auxin increases the expression of GA20ox, an important gibberellin biosynthesis enzyme, facilitating coordinated fruit growth. Strawberry plants with auxin signaling insufficiency have lower gibberellin activity, which hinders fruit growth. Varga et al., (2020) found that optimized auxin and gibberellin can increase fruit size by 20%. This relationship is crucial for optimal fruit size and quality in high-yield commercial production.

Abscisic Acid (ABA) and Ethylene Regulation in Ripening

The relationship between abscisic acid (ABA) and ethylene regulates strawberry ripening, a non-climacteric fruit. ABA

promotes anthocyanin buildup, sugar production, and fruit softening to start ripening. In ripening strawberries, ABA increases Brix index by 12-15% (Liu *et al.*, 2018). Though less important than in climacteric fruits, ethylene regulates aroma volatile synthesis and promotes color development by modulating cell wall softening genes, polygalacturonase and pectin methylesterase. Recent data reveal that ABA and ethylene balance can improve post-harvest quality by 10-15%, postponing over-ripening and enhancing flavor (Tian *et al.*, 2019).

Hormonal Optimization to Enhance Yield and Quality

Auxins and gibberellins are crucial hormones for early and midfruit growth. Gibberellins lengthen cells, while auxins divide them (Kang et al., 2021). Hormonal imbalances can affect fruit size and quality. Studies show that strategically timing auxin and gibberellin sprays can improve fruit size by 15-20% and yield by 20-30%, depending on environmental conditions (Varga et al., 2020). ABA increases sugar buildup and fruit colour by 10-15% during ripening (Li et al., 2020). Precision agriculture technology includes automated spraying systems and hormone-sensing devices that optimise growth regulator applications and reduce input costs (Seidl et al., 2021).

Enhancing Stress Resilience Through Hormonal Crosstalk

Drought, salt, and heat greatly affect strawberry productivity and quality. ABA, BRs, and SA are important regulators that boost plant stress resistance. In drought, ABA closes stomata, reducing transpiration and water loss. BRs and SA increase antioxidant enzyme activity, including SOD and CAT, to fight oxidative stress. ABA treatment increases strawberry drought tolerance by 20-30%, while BR treatments increase heat and

drought resilience by 10-15%. Ethylene and ABA regulate leaf senescence in water-limiting situations (Peleg & Blumwald, 2011). Future research on the molecular underpinnings of hormone crosstalk may help generate more hardy strawberry types.

Genetic Modification for Enhanced Hormonal Regulation

New genetic engineering methods, like as CRISPR/Cas9, improve strawberry hormone regulation. Genetic alterations to gibberellin production pathways can increase fruit size by 25%, whereas ABA signaling adjustments can improve drought tolerance by 30% (Shu *et al.*, 2018; Xiong, 2016). Overexpressing gibberellin biosynthetic genes such as GA20ox increases fruit size, uniformity, and quality. Genetic interventions that reduce ethylene sensitivity in post-harvest strawberries can increase shelf life by 15-20%, lowering post-harvest losses (McAtee *et al.*, 2013). Genetically engineered strawberry plants that can self-regulate hormone levels in response to environmental variables will reduce the need for hormone treatments and benefit large-scale commercial production (Li *et al.*, 2020).

Synergistic Effects of Brassinosteroids and Cytokinins on Growth and Yield

Brassinosteroids (BRs) and cytokinins are essential in regulating vegetative growth and fruit yield. BRs facilitate cell elongation and enhance stress resistance, whereas cytokinins stimulate cell division and promote shoot development (Anwar *et al.*, 2020). Research indicates that the combined application of brassinosteroids and cytokinins can enhance fruit yield by 15-25% through the improvement of vegetative growth and fruit set (Vandenbussche *et al.*, 2012). Research on the interactions among brassinosteroids, cytokinins, and auxins is crucial for optimising hormonal treatments. The formulation of BR-cytokinins designed for particular environmental conditions may enhance yield and stress resilience (Gupta *et al.*, 2017).

Postharvest Management Through Hormonal Interventions

Postharvest losses present a considerable challenge in strawberry production, with hormonal interventions potentially playing a crucial role in prolonging shelf life. Ethylene inhibitors, including 1-methylcyclopropene (1-MCP), effectively delay ripening and decrease spoilage by 25-30% (Asghari & Aghdam, 2010). ABA necessitates careful management to achieve a balance between colour development and sugar accumulation while preventing premature softening. Studies indicate that the use of ethylene inhibitors in conjunction with ABA can extend shelf life by 20-25%, thereby preserving fruit quality throughout transport and storage (Asghari *et al.*, 2010). Future research should examine the interactions among ethylene, ABA, and salicylic acid during the postharvest period to formulate more effective strategies for minimizing losses (McAtee *et al.*, 2013).

Table 2 illustrates the influence of major plant hormones on specific physiological processes in strawberry, highlighting their roles in fruit initiation, runner formation, stress signalling, and metabolite regulation (Li et al., 2021; Wang et al., 2021; Liang et al., 2021; Chen et al., 2023; Gao et al., 2021; Zhang et al., 2022; Meena et al., 2023; Sharma et al., 2024).

CONCLUSION

The thoughtful application of plant growth regulators including auxins, gibberellins, cytokinins, abscisic acid (ABA), ethylene, and brassinosteroids presents significant opportunities to enhance productivity, fruit quality, and abiotic stress tolerance in commercial strawberry cultivation (Fragaria × ananassa). It highlights the integral roles these hormones play in tempering key physiological processes such as fruit set, development, ripening, and adaptive responses to environmental stress.

- Auxins have been shown to increase fruit weight by up to 20%.
- Gibberellins promote cell elongation, contributing to a 25–30% increase in fruit size.
- Cytokinins stimulate cell division, raising yields by 15–18%.
- ABA enhances sweetness, elevating sugar levels by 12–15%.
 Brassinosteroids strengthen resilience to abiotic stressors like drought and heat, with up to 30% improvement.

Such findings emphasize the potential of hormone-mediated interventions to slender the productivity gap, predominantly in regions like India, where average yields (15–20 tonnes/hectare) fall short of global benchmarks (25–30 tonnes/hectare). Economic predictions further reinforce this promise, forecasting growth in the global strawberry market from USD 17.8 billion (2021) to USD 23.1 billion by 2026.

Realizing these benefits will require targeted research focused on augmenting hormone dosage and timing, exploring genetic avenues to improve endogenous hormone regulation, and developing post-harvest solutions that enhance shelf life and minimize waste. Harnessing the power of growth regulators thus offers a viable pathway to achieve higher yields, superior fruit quality, and improved productivity—positioning hormone-assisted cultivation as a support of sustainable and scalable strawberry production.

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AUTHOR'S CONTRIBUTION

Kinker Singh, Conceptualization of the idea and writing the original draft of the Manuscript and collection of review literature and compilation.

DECLARATION OF COMPETING INTEREST

The authors have no conflict of interest.

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