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Review

Effects of Hormonal Regulation on Cell Number and Cell Size in Determining Fruit Size: A Mini-Review

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ABSTRACT

Fruits are sold by weight, and hence, fruit size is a central indicator of fruit yield and quality. In horticultural industries, fruit growers and researchers continually search for and improve cultivation methods to enhance fruit size. By providing a fundamental understanding of how fruit size is regulated in plants, the process of cell number production followed by the increase of cell size has been widely studied. Molecular and cellular approaches provide direction to both scientists and breeders in fruit quality enhancement. This mini-review discussed the interplay among major plant hormones in regulating cell number production and cell size in horticultural plants. We focused on hormones that are mainly involved in determining cell proliferation and cell size and on their interaction during genetic regulation and their signaling pathways, which in turn, influence final fruit size. We also deliberated the current findings around this research niche at cellular and molecular levels. This will ultimately assist breeders in improving the fruit quality, and yield and increase profit.

Key words: Cell division, cell expansion, fruit development, fruit size, plant hormones, ripening

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INTRODUCTION

Fruit development is controlled by plant hormones. It progresses with the effects of hormones through fruit set, cell division, cell expansion, maturation, and ripening, forming the fruit (Janssen *et al*. 2008; McAtee *et al*. 2013; Zhao *et al*. 2021).

During the fruit development, the hypanthium cells divide rapidly after fertilization and fruit set, lasting until 30 Days After Full Bloom (DAFB) while reaching the peak at 14 DAFB (Janssen *et al*., 2008; McAtee *et al*., 2013; Karim *et al*., 2022b). At this dividing stage, flower petals fall, and the hypanthium grows wider. The cells then expand beginning at 20 DAFB until the end of ripening while reaching the peak at 60 DAFB. In apples, the hypanthium continues to grow into a fruit, reaching maturity at 90 DAFB, and it becomes ripe at 120 - 145 DAFB (Janssen *et al*., 2008; Figure 1).

Horticultural industries are increasingly crucial in providing livelihoods, food quality, profits, and economic growth. In many horticultural plants, extensive studies were conducted to study the roles of hormones and genes in regulating the development of cell number, cell size, fruit size, fruit weight, and endo-reduplication primarily via a gene-mapping technique known as quantitative trait loci (QTL). In general, these plants encompassed those with full-genomes sequenced, such as the apple, tomato, strawberry, and bananas (Foolad, 2007; Janssen *et al*., 2008; Kang *et al*., 2013; Čermák *et al*., 2015; Tripathi *et al*., 2019; Qiao *et al*., 2021; Su *et al*., 2023). However, the genome sequences

of many other plants, particularly highly profitable tropical fruits, such as mangoes, pineapples, durians, and coconuts are not yet available. This mini-review describes the interplay of plant hormones alongside genome regulation in determining fruit cell number and cell size, which, in turn, affects the final fruit size in horticultural plants.

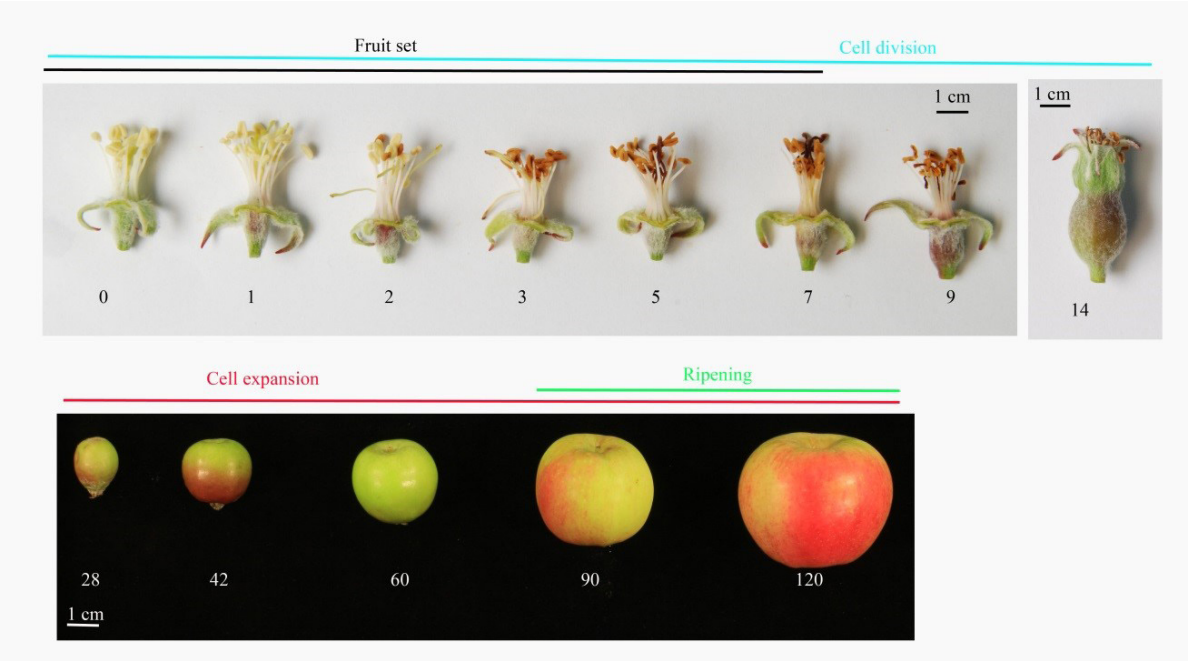

Fig. 1. 'Royal Gala' fruit morphology on various timepoints of days after full bloom (DAFB) throughout fruit development stages which are fruit set, cell division, cell expansion, and ripening.

The role of hormones in promoting cell division and expansion, and their signaling pathways

Hormones are low molecular weight substances that act at micromolar concentrations to regulate growth (Rodriguez-Gacio Mdel *et al*., 2009; Karim *et al*., 2022b). Hormones mediate their actions through signaling pathways in response to biotic and abiotic stresses, such as diseases, pests, and temperature. In general, there are six groups of plant hormones: auxins, gibberellins (GAs), cytokinins (CKs), ABA, brassinosteroids (BRs), and ethylene (Davies, 2010; Karim *et al*., 2022a). Hormones synthesized by a plant are called endogenous hormones, while exogenous hormones are synthetic substances that mimic endogenous hormones. Many hormones are synthesized by cells to carry out their functions; others are produced by various organs and transported to other plant parts for a specific action (Davies, 2010; McAtee *et al*., 2013; Kumar *et al*., 2014; Karim *et al*., 2022a).

Auxin

Auxins feature prominently during the entire life span of a plant. Typically, auxin stimulates cell expansion. It also promotes cell division and a wide range of growth and development responses (Naqvi, 2001; Fenn & Giovannoni, 2021). At the cellular level, it acts on both division and expansion. Regulation of auxin concentration (homeostasis) is crucial for its action because activating a signaling pathway is exclusively dependent on a precise auxin level. Auxins occur naturally in plants as indole-3-acetic acid (IAA) (Fenn & Giovannoni, 2021). In the auxin signaling, auxin-specific responses are regulated by the transcription of auxin-responsive genes, and they comprise three groups: Gretchen hagen3 (*GH3*), auxin/indol-3-acetic acid (*Aux/IAA*), and small auxin-up RNA (*SAUR)*(Abel & Theologis, 1996; Guilfoyle, 1999; Hagen & Guilfoyle, 2002; Yang *et al*., 2015; Feng *et al*., 2019; Baranov *et al*., 2024). Two primary pathways are mediating the auxin response: proteasome-dependent and proteasome-independent signalings (summarised in Figure 2).

In the proteasome-dependent pathway, the IAA molecule binds to its receptor, the Transport Inhibitor Response 1/Auxin-Signaling F-Box protein (TIR1/AFBs) (This F-box protein forms a part of the SCF^{TIR1} complex which consists of four subunits which are TIR1/AFB, ASK1, CUL1, and RBX) and to the Aux/IAA proteins. This complex function is also regulated by an additional protein, RUB. When IAA levels are high, it binds to the TIR1/AFBs complex, and Aux/IAA proteins are ubiquitinated (tagged) to be degraded by 26S proteasome which releases Auxin Responsive Factors (ARFs) resulting in the transcriptional of auxin-responsive genes. When IAA levels are low, Aux/IAA and TOPLESS (TPL) proteins form heterodimers with ARFs to repress gene transcription. Another auxin-responsive pathway

is through the proteasome-independent pathway. Auxin Binding Protein 1 (ABP1) which is located at the endoplasmic reticulum (ER) or the plasma membrane acts as an IAA receptor to mediate cell wall loosening during cell expansion.

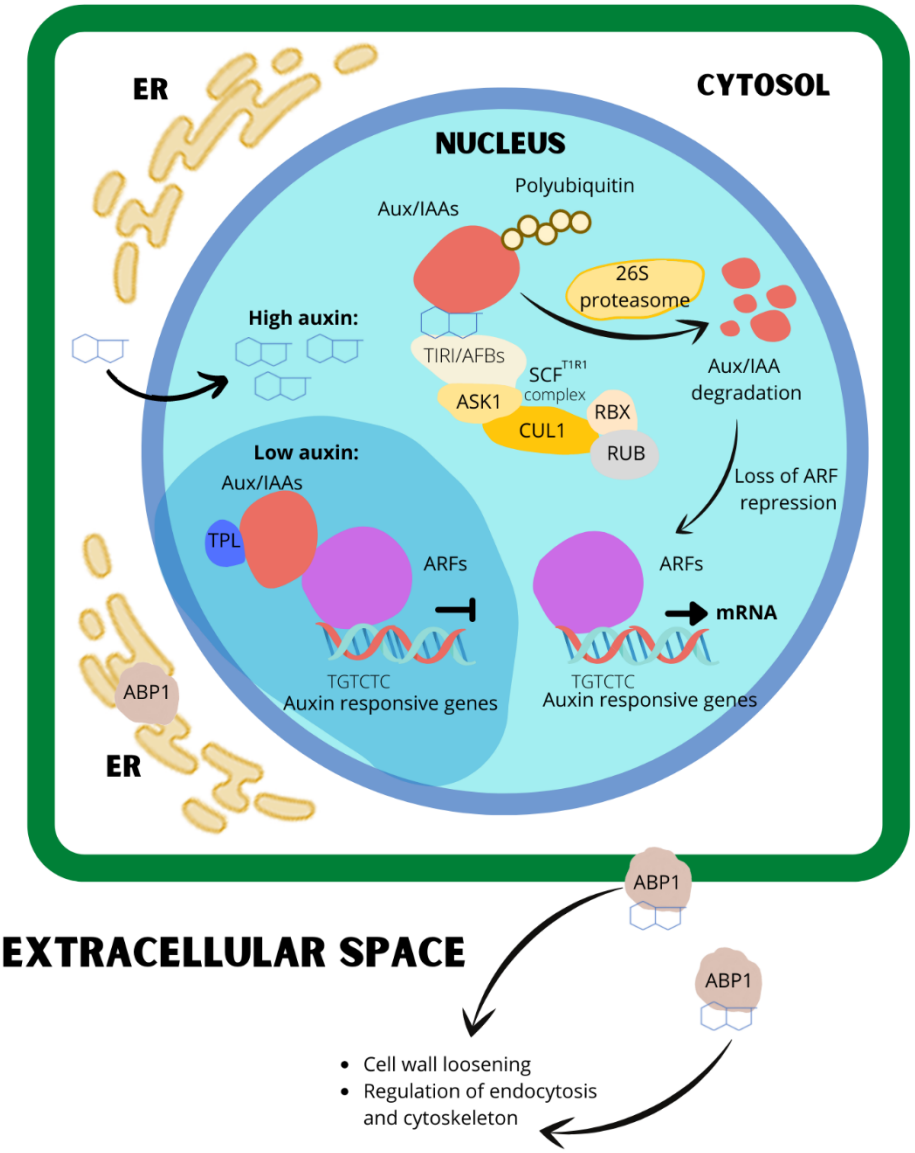

Fig. 2. Auxin signaling pathway showing both proteasome-dependent and proteasome-independent auxin pathways.

The proteasome-dependent signaling pathway degrades the Aux/IAA proteins via the 26S proteasome. The Aux/IAA proteins repress the activity of auxin response factors (ARF), i.e., transcription factors that bind to the promoters of auxin-regulated genes. In this pathway, an F-box protein called transport inhibitor response 1 (TIR1) binds to IAA, degrading the Aux/IAA transcriptional repressors for ARFs to control the transcription of the auxin-related genes (Doonan & Sablowski, 2010; Feng *et al*., 2019). TIR1 is a nuclear receptor for auxin and part of a multi-gene family, including the auxin F-box receptor (AFBs). TIR1/AFBs are F-box proteins that form the ubiquitin-protein ligase complex, known as the Skp, Cullin, F-box-containing complex (SCF^{TIR1} complex), where the F-box complexes with ASK1, CUL1, and RBX. At high auxin concentrations, IAA molecules diffuse into the cytoplasm through the plasma membrane. They then bind with TIR1/AFBs proteins, forming a co-receptor complex with the negative regulators, Aux/IAAs (Ljung, 2013; Blázquez *et al*., 2020). Aux/IAA is then ubiquitinated (tagged) and degraded, freeing the ARFs to activate or repress the transcription of auxin-regulated genes. By contrast, at low auxin concentrations, Aux/IAA binds with the co-repressor protein, TOPLESS (TPL), which then binds at the ARF sites to block or repress the protein transcription (Szemenyei *et al*., 2008; Causier *et al*., 2012; Blázquez *et al*., 2020).

Meanwhile, the alternative proteasome-independent signaling pathway involves the auxin-binding protein 1 (ABP 1), i.e., an auxin receptor located in the endoplasmic reticulum (ER) and at the plasma

membrane. ABP1 is an essential protein for plant development and is crucial for cell division and expansion, indicating its importance in wall loosening (Ljung, 2013; Blázquez *et al*., 2020). ABP1 binds the auxin molecule and transports it into the cytoplasm. Auxin may then regulate the cell cycle protein cyclin-dependent kinase (CDK), crucially linking to the progression of the cell cycle (Himanen *et al*., 2002; David *et al*., 2007; Torii *et al*., 2020). Overall, ABP1 is involved in quicker responses at the plasma membrane, such as modifying ion fuses and regulating the endocytosis of the auxin transporter known as PIN1 (Sauer & Kleine-Vehn, 2011; Löfke *et al*., 2013; Torii *et al*., 2020) (Figure 3).

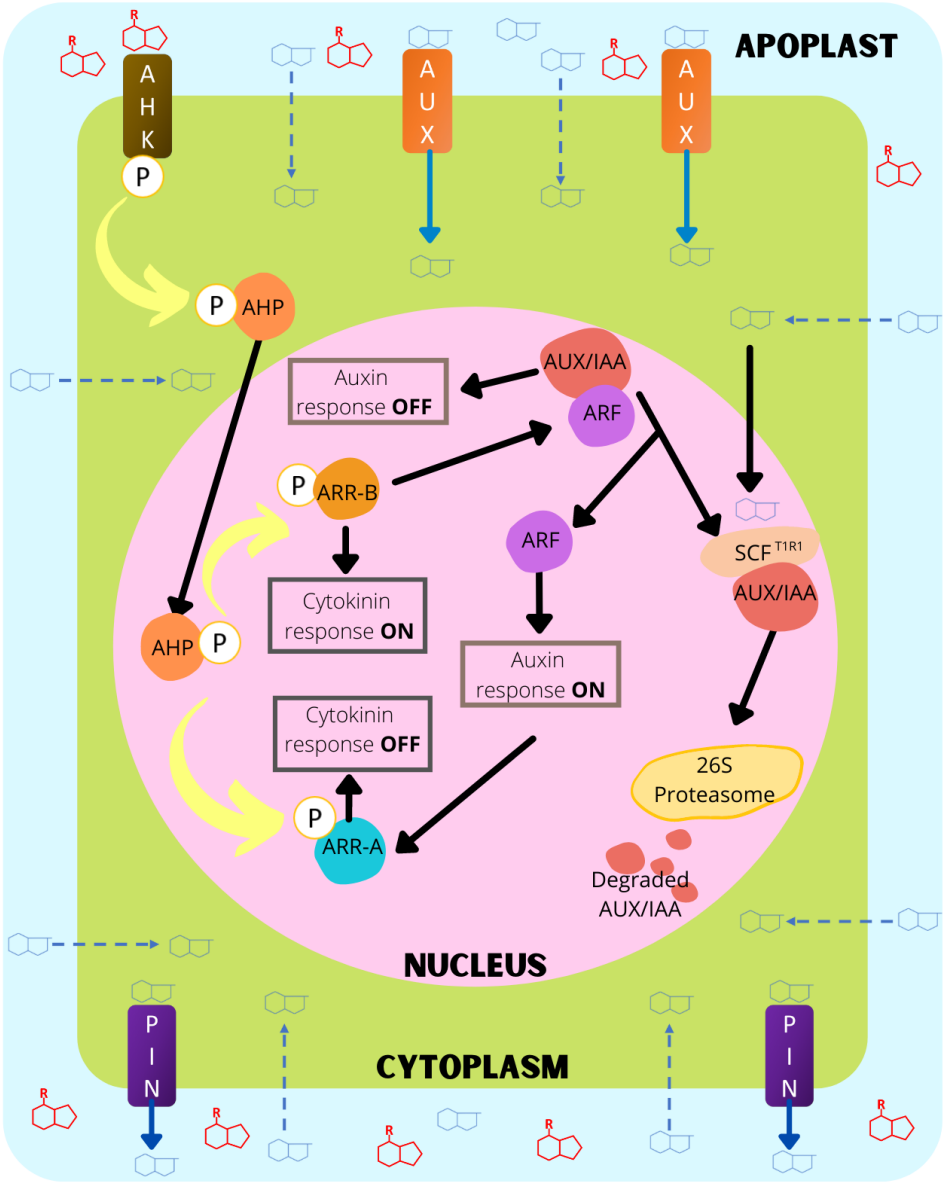

Fig. 3. The auxin and CK signaling interaction.

Arabidopsis Histidine Kinases (AHKs) act as cytokinins (red molecules) receptors, which act as a histidine kinase. The phosphoryl group (P) on the His of the receptor is transferred to ARABIDOPSIS HIS PHOSPHOTRANSFER PROTEIN (AHP) in the cytoplasm (yellow arrows indicate the phosphotransfer) which then transfer the phosphoryl group to the type-A or type-B ARR (ARABIDOPSIS RESPONSE REGULATORS) cytokinin primary response gene. The type-B ARRs activate the transcription of the cytokinin-regulated genes, including the type-A ARRs (cytokinin response ON). Type-A ARRs suppress cytokinin signaling through as yet unknown mechanisms (cytokinin response OFF). Apart from freely diffusing across the plasma membrane, auxin (blue molecules) can also be actively taken up from the apoplast by the action of influx transporters AUX/LAX (AUXIN-RESISTANT MUTATION 1/LIKE AUX1) and actively transported out of the cell by auxin efflux carriers, the PIN proteins which direction (solid

blue arrows) is depending on the PIN subcellular asymmetric localization. When auxin concentration is low, the Aux/IAA protein heterodimerizes with the ARF (AUXIN RESPONSE FACTOR) transcription factors, repressing the transcription of the auxin-response genes (auxin response OFF). When auxin concentration is high, auxin binds to the TIR1 (TRANSPORT INHIBITOR RESPONSE 1) receptor, stimulating the interaction of the Aux/IAAs proteins with the SCF^{TIR1} ubiquitin-ligase complex (SKP1, CDC53/ CULLIN, F-box) to promote their degradation by the 26S proteasome resulting in the release of ARFs, inducing the expression of auxin-responsive genes (auxin response ON).

Auxin-CK crosstalk

CK promotes cell division in the tobacco tissue culture and was named for its role in cytokinesis. Plants respond to CK via its signaling pathway. In *Arabidopsis* sp., three histidine kinases (HIS KINASES), termed AHK2, AHK3, and AHK4/Woodenleg 1 (WOL1)/Cytokinin response 1 (CRE1), act as transmembrane CK receptors (Milhinhos & Miguel, 2013). They transfer the signal to the nucleus, activating two primary *Arabidopsis* response regulators (ARRs) classes, i.e., type A and type B. The type-B ARRs function as transcription factors and induce the transcription of CK response genes, including the type-A ARRs that trigger downstream cellular changes and negatively regulate CK signaling in a feedback loop (Moubayidin *et al*., 2009).

Auxin and CK act either antagonistically or synergistically during plant development, particularly in regulating cell division and expansion. In the presence of auxin, the type-A ARRs are activated, causing CK signaling for the repression and activation of auxin signaling (Milhinhos & Miguel, 2013; Tyagi *et al*., 2023). In general, CK and auxin act antagonistically in regulating the development of the root stem by activating the type-A ARR genes, i.e., ARR7 and ARR15.

When these negative regulators of CK signaling become dysfunctional, they deactivate the auxin signaling, resulting in a defective root stem cell system (Ioio *et al*., 2007). Another type of CK response transcription factor, known as the type-B ARR(e.g., ARR1), negatively regulates PIN auxin transport by activating an auxin-signalling repressor gene, *SHY2/IAA3*. Conversely, auxin initiates cell division and sustains PIN activities by degrading the SHY2 protein (Ioio *et al*., 2007). In meristem growth, the expression of the *SHY2* gene is driven by ARR12 (Moubayidin *et al*., 2009). Activating ARR1 also switched on the transcription of another type-B protein, i.e., ARR6, which responds to CK (Sakai *et al*., 2001; Zhao *et al*., 2024). In roots, shorter root growth showed expression of 35S: ARR1 in the absence of CK (Sakai *et al*., 2001; Zhao *et al*., 2024).

Muraro *et al*. (2013) used multi-cellular mathematical models to study the interactions between auxin and CK in shaping the size and location of division and differentiation within the primary root. They showed that overexpression of auxin signaling genes reduced the total length of the root by diminishing the expansion zone of the root but increasing the length of the division zone. Other than the crosstalk between auxin and CK in regulating PIN activities in *Arabidopsis* sp, GAs might play a role in supporting cell division through their involvement in PIN activities (Milhinhos & Miguel, 2013). In GA-deficient plants, the auxin efflux facilitator protein decreased in x, resulting in less auxin transport. However, the defect was abated in wild-type plants with GA treatment (Willige *et al*., 2011; Shah *et al*., 2024).

Gibberellins

More than 136 naturally occurring GAs are identified. However, only a few are biologically active (Olszewski *et al*., 2002; Wang *et al*., 2018). There are two fundamentally different forms of GA based on the number of carbon atoms they contain: one with 19 carbon atoms and the other with 20. They are divisible into three different types: GA_1, GA_2, and GA_3 (Taiz & Zeiger, 2010; Wang *et al*., 2018). GA_3 is generally referred to as gibberellic acid due to its structural resemblance. The molecular characterization of GA response has led to the finding of gibberellin-insensitive dwarf 1 (GID1) and DELLA proteins, which are the key components of the GA-GID1-DELLA mechanism that enables plants to react to GA (Harberd *et al*., 2009). The DELLA protein represses the GA signaling pathway by acting as a downstream GID1 receptor (Milhinhos & Miguel, 2013). GID1, i.e., the GA receptor, is located in the nucleus and has a high affinity to GA. The binding of GA to GID1 will cause conformational changes for GID1 to interact with DELLA proteins, which belong to the GRAS (GA-insensitive (GAI), Repressor of ga1-3 (RGA) and Scarecrow (SCR)) family (Taiz & Zeiger, 2010). They are regulatory domain proteins of GA transcriptional regulator genes and function as repressors of growth that cause dwarfism in a plant because of the expression of GAI (Taiz & Zeiger, 2010).

As discussed earlier, the roles of auxin, CK, and GAs in fruit growth have been investigated before (Mariotti *et al*., 2011; McAtee *et al*., 2013). Auxin and CK are primarily involved in cell division and cell expansion during fruit development (Swarup *et al*., 2002). Since each stage of fruit development is

successive to the next, it is hard to separate the fruit set from the subsequent stages of fruit growth (i.e. cell expansion and ripening). This suggests that auxin and CK are also involved in both cell division and cell expansion (Swarup *et al*., 2002). However, understanding the roles plant hormones play in the transition between cell division and cell expansion is scarce (McAtee *et al*., 2013). Reports on these hormones functioning in promoting fruit set also imply a role in maintaining the subsequent stages. For example, the function of GA_3 in cell expansion is supported by the observation of larger cells existing in GA_3-induced fruit (parthenocarpic) than in seeded fruit, even though the overall size of GA_3-induced fruit was smaller than that of seeded fruit (de Jong *et al*., 2009a).

In whole plant systems, GA's role in controlling the growth of plant organs is well understood, typically promoting elongation in growth (Gillaspy *et al*., 1993; Hedden & Kamiya, 1997; Asahina *et al*., 2002; Olszewski *et al*., 2002; Serrani *et al*., 2007; de Jong *et al*., 2009a; Hedden & Thomas, 2012; McAtee *et al*., 2013). GA has also been reported to induce cell expansion by increasing auxin biosynthesis (Law & Hamilton, 1984; Saibo *et al*., 2003) and acts to maintain cell expansion when auxin levels decrease (Hayashi & Tanabe, 1991; Gillaspy *et al*., 1993; Ozga & Renecke, 2003; Zhang *et al*., 2005, 2007; Zhang, 2007). In fruit, when applied early in the cell expansion stage, GA supports cell division and helps maintain cell expansion in Japanese pears (*Pyrus pyrifolia* Nakai) (Zhang *et al*., 2007). This results in larger fruits than those grown without additional hormones (Hayashi & Tanabe, 1991; Zhang *et al*., 2005; Zhang *et al*., 2007). The cooperative action of GAs with auxin has also been observed in tomato fruits where both GA_3 and NAA are involved in regulating cell division and cell expansion (Srivastava & Handa, 2005).

Brassinosteroids

BRs are unique plant steroids essential throughout plant development (Li & Nam, 2002). They were first found in the pollen of the *Brassica napus* (Mitchell *et al*., 1970; Bajguz & Tretyn, 2003; Hasan *et al*., 2011). Among BRs, brassinolide (BL) was the first identified compound (Hasan *et al*., 2011). Similar to animal steroids, many BL-like substances occur throughout the plant kingdom. Thus, the term steroid is included in the name of BR (Clouse & Sasse, 1998; Chai *et al*., 2013). In general, BR promotes cell division and cell expansion while facilitating germination by stimulating embryonic growth (Clouse, 2011). Plants with BR deficiency are dwarf-like, with delayed flowering and senescence.

BR and GA cause dwarfism in plants, thus, indicating their role in organ elongation. They synergistically induce cell expansion in the hypocotyls of *Arabidopsis* sp. (Gallego-Bartolomé *et al*., 2012). Applying BRs to cucumber cultivars without parthenocarpic capacity produced parthenocarpic fruits (Fu *et al*., 2008). This finding shows that BR was essential to induce fruit set by stimulating parthenocarpic growth (Li *et al*., 2014), in addition to other fruit set-promoting hormones, such as auxin, CK, GA, and ABA. Fig. 4 shows the interaction of plant hormones during fruit development.

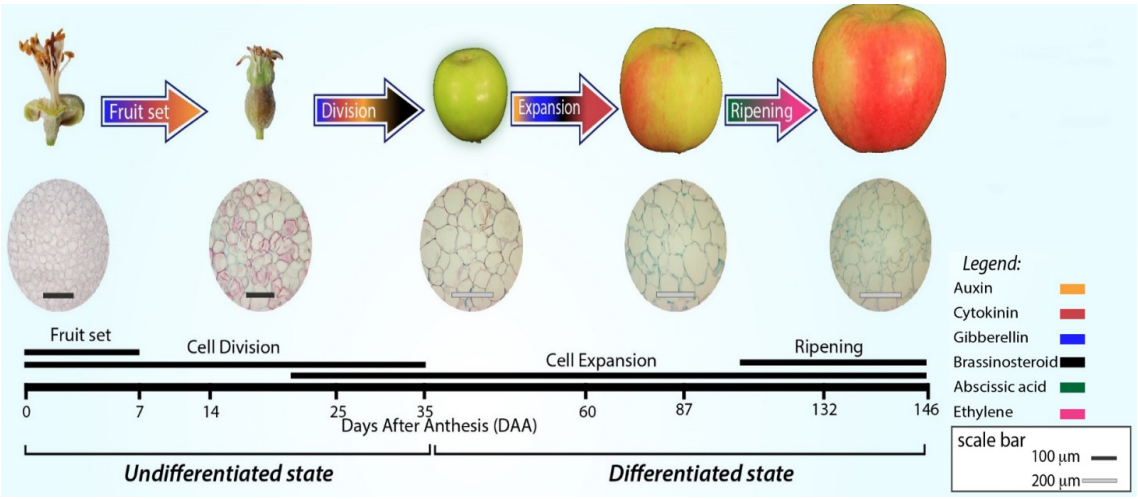

Fig. 4. Hormonal changes in a fleshy fruit during fruit development and ripening. Various studies have shown the presence of auxin, CKs, GAs, and BRs during fruit set, cell division, and cell expansion. For ripening, ABA and/or ethylene biosynthesis occur to trigger the ripening process.

Genetic regulations on cell division, expansion, and fruit size

The final fruit size relies on the contribution of cell division and cell expansion during fruit development. Several genetic regulations are involved in determining the fruit size, including plant hormone interactions and signaling pathways, microRNA, endoreduplication, and epigenetics. Much research has been reported on these factors that contribute to final fruit size. At the cellular level (histology), melon fruits shared a similar cell size before bloom and at ripening, which is suggestive of cell division controlling final fruit size among the cultivars (Higashi *et al*., 1999). In an apple fruit size study, a positive relationship between cell size and fruit width gives credence to the idea that cell expansion may affect final fruit size (Karim *et al*., 2022a). In blueberry fruit size studies, even though cell expansion is the major cause of cell growth, the contribution of cell expansion in determining fruit size among genotypes is not clear (Johnson *et al*., 2011). Cell division was also found to influence fruit size in many plant types, such as Japanese pear (Zhang *et al*., 2005; 2006), rabbiteye blueberry (Johnson *et al*., 2011), tomato (Bertin *et al*., 2003), sweet cherry (Olmstead *et al*., 2007), plum (Cerri *et al*., 2019) and wheat (Reale *et al*., 2017). Meanwhile, in other plants, cell division and a degree of cell expansion were described to control final fruit size, such as in sweet cherries (Yamaguchi *et al*., 2004) as well as in apples (Bain & Robertson, 1951; Harada *et al*., 2005). Reports on sweet cherries have concluded that cell division and cell expansion were both involved in controlling final fruit size, even though the fruit weight and cell number were consistently high (Yamaguchi *et al*., 2004; Olmstead *et al*., 2007). Table 1 summarizes the findings on the cell division that controls fruit development.

Table 1. List of findings on the cell division control during fruit development

Plant names	Findings	References
Melon	similar cell size before bloom and at ripening	Higashi *et al*., 1999
Apple	Cell size correlates with fruit width	Karim *et al*., 2022a
Blueberry	Cell division and cell expansion contribute to the final fruit size	Johnson *et al*., 2011
Japanese pear	Cell division increases fruit size	Zhang *et al*., 2005, 2006
Tomato	Cell numbers correlate with fruit width	Bertin *et al*., 2003
Sweet cherry	cell division improves fruit size	Olmstead *et al*., 2007
Plum	Cell division contributes to the final fruit size	Cerri *et al*., 2019
Wheat	Cell division	Reale *et al*., 2017

In apples, fruit size in three apple cultivars was reported to correlate best with cell division, indicating that variation in cell number was the main cause of fruit size differences between the cultivars studied. Fruit size measurements across fruit development showed that ‘Twenty Ounce’ (large-sized cultivar) grew faster than Crab apple (small-sized cultivar) and ‘Royal Gala’ (medium-sized cultivar). These observations were correlated with a greater cell number of ‘Twenty Ounce’ than Crab apple and ‘Royal Gala’, suggesting a positive correlation between fruit size and cell number (Karim *et al*., 2022a). The final cell number in fruit is determined by cell production before bloom and/or the cell production during fruit development (Johnson *et al*., 2011; Karim *et al*, 2022a). The study also reported that similar cell numbers and hypanthium width before bloom were found in these three apple cultivars, inferring that final cell number and fruit size differences between the cultivars occurred during fruit development (Karim *et al*., 2022a). Cell numbers in large-sized cultivars of blueberry (*Vaccinium ashei*) are higher than the small-sized cultivars before bloom, which means that cell production before bloom may influence the variation in final fruit size between cultivars (Johnson *et al*., 2011).

Apple fruit size studies have found that an increase in fruit weight can be attributed to an increase in cell number rather than cell size (Bain & Robertson, 1951; Denne, 1963; Harada *et al*., 2005; Dash *et al*., 2013). Although it was stated that cell expansion also contributed to the final fruit size, the magnitude was not determined as it was only a very small contribution. A similar relationship has also been seen with peach, apricot, tomato, olive, Japanese pear, melon, rabbiteye blueberry, and sweet cherry (Scorzal *et al*., 1991; Higashi *et al*., 1999; Rapoport *et al*., 2002; Bertin *et al*., 2003; Yamaguchi *et al*., 2002; 2004; Zhang *et al*., 2006; Olmstead *et al*., 2007; Johnson *et al*., 2011; Rosati *et al*., 2011; 2012; 2020). In addition, a decrease in the expression of cell division-related genes when cropped at a high fruit load resulted in a decrease in fruit size, suggesting the role of cell division in determining fruit size (Dash *et al*., 2013). A comparison of cell size between the normal-sized ‘Gala’ and the induced large-sized (mutant) ‘Grand Gala’ showed a considerable enhancement of cell size in the mutant (Malladi & Hirst, 2010). This may indicate that cell expansion does not solely influence fruit size unless it is triggered by endoreduplication and an increase in ploidy because of G2 cell cycle arrest (Malladi & Hirst, 2010). Cell

size differences did not contribute to fruit size differences among kiwifruit (*Actinidia deliciosa*) cultivars (Nardozza *et al*., 2011). Therefore, cell division regulates final fruit size across many plant cultivars.

After the fruit set, a fruit undergoes rapid cell division and subsequent expansion. In general, fruit set is inseparable from later stages of fruit development, though auxin and GA are indeed keys in the sustained growth of fruit. Hormones such as CK and auxins are involved primarily in cell division and expansion during fruit development (Swarup *et al*., 2002) by stimulating cell cycle activity (McAtee *et al*., 2013). Auxin and GA co-regulate fruit sets via the auxin activation of GA synthesis (Kumar *et al*., 2014). Therefore, auxin and GA are widely used to increase fruit sets by inducing parthenocarpic growth in many crops (Fu *et al*., 2008). For example, GA or auxin treatments on tomatoes lead to the development of parthenocarpic fruits (Serrani *et al*., 2007; de Jong *et al*., 2011). Silencing *SlARF7*, an auxin-negative regulator, caused the production of parthenocarpic fruits following an increment in auxin and GA concentrations, indicating an interaction between these hormones in regulating fruit set (de Jong *et al*., 2009b; Kumar *et al*., 2014). Early studies showed that auxin concentrations increased during seed development, and then GA concentrations increased in the ovaries during fruit set (Olimpieri *et al*., 2007; Jianhon *et al*., 2008; McAtee *et al*., 2013), and this is evidenced by the application of GA inhibitors to tomato, which resulted in a decreased in fruit set. In parthenocarpic tomato fruit (*pat*) mutants, high expression of GA-related gene, i.e., a gene derived from a recessive mutation conferring parthenocarpy in tomato, supports that GA controls tomato fruit set in parthenocarpic fruit (Olimpieri *et al*., 2007).

In normal fruit development, successful pollination and fertilization induce an increase in both auxin and GA concentrations within the ovary (Mapelli *et al*., 1978; Sjut & Bangerth, 1982; Koshioka *et al*., 1994; de Jong *et al*., 2009a; Hoagland & Boyette, 2024). For example, the Japanese pear produced larger fruits following hand pollination, indicating an increased number of fertilized stigma with higher levels of GA produced by the pollen and subsequently enhanced cell division (Zhang, 2007). Thus, GA is crucial for pollination and fertilization (Jianhon *et al*., 2008). Treating tomato ovaries with auxin could produce fruits with more pericarp cells. In comparison, GA-induced tomatoes consisted of fewer but larger cells because GA enlarged cells during fruit growth (McAtee *et al*., 2013).

Normal-sized fruits undergo a balance between cell division and expansion following stable concentrations of auxin and GA (Vriezen *et al*., 2008). Besides, in certain fruits, GA is involved in the growth without auxin, producing fruit with sizes that are twice as large, as shown in transgenic tomatoes (*S. lycopersicum* L.) with low levels of auxin response factor 7 (*Sl*ARF7) (de Jong *et al*., 2011). Commercially, GA enhances fruit size and fruit cluster in parthenocarpic fruits by increasing carbohydrate import to the fruits. Consequently, parthenocarpic fruits are usually smaller and in compact fruit clusters. Examples include grapes, citrus, and berries (Taiz & Zeiger, 2010). Also, GA overcomes fruit set problems in apple and pear, particularly during biennial bearing (a phenomenon where the high production of fruits one year suppresses flower production of the coming year, hence lower yield production) to promote flower production thereby increasing fruit set and yield (Taiz & Zeiger, 2010).

Another crucial function of GA in fruit development is to stimulate organ growth (Hedden & Thomas, 2012; Hoagland & Boyette, 2024). GA also features in germination, flowering, and fruit set in many plant species (Hedden & Kamiya, 1997; Serrani *et al*., 2007; Olszweski *et al*., 2002). During fruit development, GA concentration increases twice: once in early fruit growth to trigger cell division and then during cell expansion (Gillaspy *et al*., 1993). During early development, the pollen produces GA to facilitate the growth of pollen tubes and germination (de Jong *et al*., 2009a). In tomatoes, the pollen will transfer some GA into the ovary to trigger fruit growth (de Jong *et al*., 2009a). Thus, an elevated GA concentration in the ovaries following pollination (which later causes auxin levels to increase (Gillaspy *et al*., 1993) suggests that both are involved in fruit set and growth (Serrani *et al*., 2007; Hoagland & Boyette, 2024).

Also, GA could induce and maintain cell expansion (Gillaspy *et al*., 1993; Ozga & Reinecke, 2003; Zhang, 2007; Olmstead & Iezzoni, 2007) when auxin concentrations decreased (Gillaspy *et al*., 1993). Compared to seeded fruit, GA_3-induced fruit (parthenocarpic) produced larger cells despite a smaller fruit size, further supporting that GA was responsible for cell expansion (de Jong *et al*., 2009a). Applying 2, 4-D, and GA_3 together produced parthenocarpic fruits with cells similar in size and shape to seeded fruits (de Jong *et al*., 2009a). In the Japanese pear, GA maintained cell expansion when used during the early stage of cell expansion, yielding pears larger than untreated fruits (Hayashi & Tanabe, 1991; Zhang *et al*., 2005, 2007; Zhang, 2007). Meanwhile, applying GA_3 and auxin yielded substantial tracheid expansion in the differentiation of the tracheid element since GA caused the cell to expand. In comparison, an auxin only produced short tracheid growth (Kalev & Aloni, 1998). This finding showed that auxin and GA played a coordinating role in regulating cell division and expansion, probably based on a common response pathway. Early hypotheses speculated that GA might increase

auxin biosynthesis or transport (Law & Hamilton, 1984).

Meanwhile, the function of auxin during fruit set is demonstrated by its presence in pollen, its production in the stalk (style), and fertilization (de Jong *et al*., 2009a). In tomatoes, the loss-of-function of *IAA9* and *ARF7* yields parthenocarpic fruit growth, suggesting that auxin inhibits fruit growth until fertilization (de Jong *et al*., 2009b). *IAA9* is a tomato Aux/IAA transcriptional regulator linked to plant responses to auxin through the expression of auxin-responsive genes (Wang *et al*., 2005). The reduction of *IAA9* concentrations in tomato plants elicits pleiotropic phenotypes, indicating that *IAA9* acts as a transcriptional repressor of auxin signaling (Wang *et al*., 2005; de Jong *et al*., 2009b). Besides, another negative regulator of the fruit set, i.e., *ARF8,* also shows similar effects as the *Arabidopsis ARF8* mutant (Goetz *et al*., 2006), where *ARF8* suppresses the ovary growth through the repressive action of the *Aux/IAA-ARF* complex on auxin-responsive genes (Pandolfini *et al*., 2007).

Besides fruit set, auxin also promotes cell division and expansion (Anastasiou & Lenhard, 2008; Karim *et al*., 2022b). While CKs regulate cyclin activity during the transition phases from G_1 to S during the cell cycle, auxin's involvement in the cell cycle occurs much earlier by acting as a permissive signal for the onset of cell division (David *et al*., 2007). However, this process is not yet fully understood (den Boer & Murray, 2000; Stals & Inzé, 2001; David *et al*., 2007). The role of auxins in regulating cell differentiation in plants was studied extensively. For example, an auxin gene, known as the auxin response factor (*ARF106*), was expressed during cell division and expansion in the fruit development of the apple (Devoghalaere *et al*., 2012). This gene was also co-localized with a fruit-size QTL, suggesting that auxin could regulate fruit growth through cell differentiation (Dash & Malladi, 2012).

Another example is the auxin receptor ABP1 which modulated ion fluxes in response to the hormone, probably mediating auxin-dependent cell expansion and hence, was essential for cell division (David *et al*., 2007; Devoghalaere *et al*., 2012). In the culture of tobacco BY-2 cells, applying the antisense suppression of the *ABP1* gene yielded slow proliferation, eliminating the possibilities of auxin-induced cell expansion and reducing cell division (Chen *et al*., 2001). Moreover, a mutation in the *ABP1* gene of *Arabidopsis* sp. caused a lethal effect on cells (David *et al*., 2007). The loss of function of ABP1 in *Arabidopsis* sp. also resulted in the lethal embryo following cell expansion arrest, indicating the role of auxin in cell expansion during embryogenic development through the function of ABP1 (Chen *et al*., 2001).

Along with auxin and GA, CK and ABA might also play a role in fruit sets. However, the crosstalk among these four hormones during fruit development is only partly understood. ABA is also involved in long-term developmental plant growth. While auxins, CKs, and BR are involved in early development, ABA is mainly present in the later stage of development, where cell maturation transpires. During the pollination of tomato fruit with auxin and GA, ABA concentrations decreased while those of CK increased (Kojima *et al*., 1994). ABA concentrations continued to decrease shortly after pollination (Kojima *et al*., 1994) and were validated by a decrease in the mRNA levels of ABA biosynthesis genes (Vriezen *et al*., 2008) and the diminution of ABA concentrations in tomato pistils after pollination (Kojima *et al*., 1993). However, pollinated fruits showed a higher concentration of ABA than the parthenocarpic fruits (Srivastava & Handa, 2005). Despite the suppression during and shortly after pollination, the ABA levels of the tomatoes rose afterward to support the fruit set. ABA was detected five days after pollination and was enhanced in seed and pericarp until 30 -50 days after pollination, with increasing concentrations during cell expansion (Mariotti *et al*., 2011).

A less-dividing small fruit of the Japanese pear 'Shinkou' showed higher ABA concentrations than the large Japanese pear cultivar 'Atago' during early fruit development (Zhang, 2007). In tomatoes, ABA showed a broad peak during cell expansion and maturation, indicating that ABA was involved in cell expansion and reaching the peak during cell maturation (Gillaspy *et al*., 1993). The association of ABA with cell expansion was determined by the reduction of fruit size in ABA-deficient mutants (Nitsch *et al*., 2012). However, the exact role of ABA in fruit development remains unknown.

BRs play a crucial role in early fruit development by promoting cell division, cell expansion in the stem, ripening, and abscission while inhibiting root growth (Clouse, 2002; Nemhauser *et al*., 2004; Hasan *et al*., 2011) in tomato (Vidya & Rao, 2002; Lisso *et al*., 2006), grape berry (Symons *et al*., 2006), and cucumber (Fu *et al*., 2008; Chai *et al*., 2013). Treating the dwarf tomato mutants with BR restored the dry mass content, sugar, and amino acid levels, showing that BR was essential for tomato fruit development (Lisso *et al*., 2006; Chai *et al*., 2013). In cucumber, applying exogenous BR to a cultivar without parthenocarpic capacity induced parthenocarpic growth while increasing cell division via cell cycle-related gene expression (Fu *et al*., 2008). By contrast, applying a BR biosynthesis inhibitor (brassinazole (Brz)) to a cucumber cultivar with parthenocarpic growth blocked the fruit set. However, this inhibitory effect was subsequently reversed by applying exogenous BR (Fu *et al*., 2008).

Other internal factors that affect fruit size

Cellular content

Endoreduplication is the arrest in mitotic activity accompanied by a concomitant increase in nuclear DNA levels during fruit development. Presumably, it drives cell expansion and is regulated primarily by cell cycle genes (Chevalier *et al*., 2014). During endoreduplication, the chromatids are duplicated exponentially, while the number of chromosomes remains unchanged. Endoreduplication is initiated by the transition from the mitotic to a modified cell cycle, known as the endocycle. DNA replication occurs in this endocycle without subsequent chromosome separation and cytokinesis. The increment of ploidy is due to the reiteration of the endocycle (Kobayashi, 2019). During tomato fruit development, endoreduplication acts as a crucial morphogenetic factor to support cell growth and various physiological functions (Chevalier *et al*., 2014). Impairment in the expression of WEE1, which encodes the cell cycle-associated protein kinase in transgenic tomato plants, reduces the plant and fruit size due to a decrease in cell size that correlates with a decrease in the DNA ploidy levels (Gonzalez *et al*., 2007).

Polyploids are organisms comprising more than two paired homologous sets of chromosomes. Polyploidy is crucial in the evolution and diversification of higher plants. Artificial polyploidization is induced using a few antimitotic chemicals, such as colchicine, trifluralin, and oryzalin. The type of mitotic inhibitors, their concentration, and duration are variable and species-dependent. This technique can be used ex or in vitro, and tissue culture is more efficient. Changes in nuclear DNA content, gene expression, and developmental processes due to ploidy manipulation can lead to changes in morphology, anatomy, and physiology in polyploid plants (Miri, 2019). A high ploidy level resulted in larger cell size with variability due to asynchronous cellular endoreduplication.

Meanwhile, in cultivars (each cultivar usually corresponds to a single genotype in the apple & other clonally propagated crops), genetic variation forms the basis for selection-mediated improvement, and the subsequent development of superior cultivars (Nybom *et al*., 2020). Large fruit size is a crucial trait for artificial selection during the development of new varieties in blueberry breeding programs (NeSmith, 2004). Although considerable variation in fruit size occurs among the rabbit-eye blueberry genotypes, the basis of this variation is not well understood. Understanding the cellular and molecular basis of such variation is essential to developing tools for enhancing fruit size either through breeding or through the manipulation of fruit growth using horticultural practices. In the rabbit-eye blueberry, the fleshy mesocarp constitutes the majority of the mature fruit (Johnson *et al*., 2011). Given that the growth of the mesocarp tissue is likely mediated by a coordinated progression of cell production and cell expansion, these processes may be the key factors determining fruit size. Dissecting the relative contribution of these factors is essential to develop a clear understanding of fruit size regulation.

Epigenetics

Epigenetics generally refers to a class of heritable molecular events involving a variety of protein complexes and regulatory mechanisms but without changes in the DNA sequence (Bender, 2002; Abdulraheem *et al*., 2024). It could also refer to phenotypic alterations, morphological or molecular, with no changes in the coding gene sequence or the upstream promoter region. Plants may evolve at a certain point in their life cycle when adapting to climate change, and biotic, and abiotic stress. Plants' behavior towards their environment determines how their genomes work. Within the framework of epigenetics, new findings of how genes worked and were expressed improved the breeding methods, providing a new source of variability originating from epialleles (Rajnović *et al*., 2020). Recently, more reports on the significant epigenetic modifications and particularities of plant species impacting epigenetic mechanisms became available. In general, epigenetic behavior is dependent on "Genetic Imprinting" (GI), i.e., reverse modifications could occur on particular gene activities caused by paternal inheritance.

GI in plants is largely inherited from the endosperm. In plants, DNA methylation and histone are the two key regulators of GI. In DNA methylation, the fifth carbon of the cytosine base is methylated to form methylcytosine, converting it to a highly stable and heritable epigenetic marker (Tariq & Paszkowski, 2004; Gallusci *et al*., 2017). These methylated cytosines are maintained through mitosis following the activity of specific enzymes, namely maintenance and de novo DNA methyltransferases. DNA methylation occurs through small RNAs, such as small interfering RNA (siRNA) and micro RNA (miRNA). Since the modification occurs in chromatin, the epigenetic marker is even more stable and inheritable. DNA reprogramming via the DNA methylation tool is used during germination and early embryogenesis (Choi & Lee, 2020; Gutzat *et al*., 2020). The production of DNA-methylated plants is increasingly reported in several economically profitable plants, such as maize (Zhang *et al*., 2021), rice (Li *et al*., 2020), and other higher plants (Vanyushin *et al*., 2011). DNA methylation has also been used to overcome pathogen that causes diseases in crucial crops, such as rice (Atighi *et al*., 2020; Hoang *et al*., 2020; Jiang *et al*., 2020; Li *et al*., 2020; Cui *et al*., 2021), soybean (Luo *et al*., 2018; Rambani *et*

al., 2020; Wang *et al*., 2020; Zeng *et al*., 2021), wheat (Savadi *et al*., 2018; Geng *et al*., 2019; Kong *et al*., 2020; Saripalli *et al*., 2020; Tini *et al*., 2021), barley (Qi *et al*., 2019; Kong *et al*., 2020; Cai *et al*., 2021; Drosou *et al*., 2021; Galli *et al*., 2022; Tini *et al*., 2021); potato (Kuźnicki *et al*., 2019; Elsherbiny *et al*., 2020; Fesenko *et al*., 2021; Ross *et al*., 2021), citrus (Sicilia *et al*., 2021), and mulberry (Xin *et al*., 2021).

In plants, epigenetic modifications extensively involve GI, seed development, vegetative growth, pattern formation, fruit ripening, responding to environmental stimuli, responding to biotic and abiotic stress, and the creation of heritable epialleles (Bouyer *et al*., 2017; Cao *et al*., 2024). Epialleles are heritable alleles that have been epigenetically modified. They are usually found in isogenic lines and rarely occur spontaneously. Epigenetics also involve gene expression, suppression of repetitive element transcription, chromosome interaction, and silencing of transposable elements (TEs), i.e., DNA sequences that copy themselves and move to other locations within the genome (Bourque *et al*., 2018; Choi & Lee, 2020; Wu *et al*., 2024). TEs are mutations that occur in germ-cell genomes, where they will be propagated to future generations. Studies on the role of TEs in germ cells have been reported in siRNAs of *Arabidopsis* sp. using the RNA silencing approach (Kuo *et al*., 2017; Tsuzuki *et al*., 2020; Long *et al*., 2021).

CONCLUSION

Over the years, the advancement of plant hormone interaction has been fascinating; it has become a topic of great interest with numerous investigations through various analytical methods. The use of modern techniques to boost crop varieties becomes indispensable. In addition, advanced breeding methods allow scientists to insert the gene of interest into the genome, which is not feasible in classical breeding methods.

This review discussed the central roles of hormone interplay for regulating proper plant growth and the current updates on molecular approaches in studying fruit size. However, many questions about their discrete regulation and functional interaction remain unanswered. Meanwhile, studies on fruit size, particularly at the molecular level, are scarce in tropical fruits compared to other temperate fruits and staple crops. Genomic databases for high-value tropical fruit crops such as mango, pineapple, and durian are yet available. Therefore, it would be a crucial contribution to science ty if these databases were fully developed, like apple, banana, pear, strawberry, and rice. Hormone interactions in plants are complex, varying in physiology and molecular responses even within the same species. However, most studies on tropical fruit crops focus on the physiology of improving the post-harvest fruit quality. We hope to see more research and developments on the interaction of hormones in regulating plant growth in more diverse plant species, notably in tropical fruits.

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ETHICAL STATEMENT

Not applicable

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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