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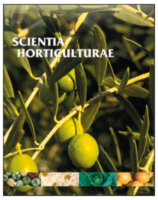

Review Article

Insights into the molecular regulation of premature fruit drop - what we have learned from mango (*Mangifera indica*) and other fruit crops

Sophie C. Jones [a,b,*], Ryan Orr [c], Gerhard C. Rossouw [c], Harley M. Smith [d], Christine A. Beveridge [a,b], Lindsay M. Shaw [b,e,*]

[a] *School of Agriculture and Food Sustainability, The University of Queensland, St Lucia, QLD, Australia*
[b] *ARC Centre of Excellence for Plant Success in Nature and Agriculture, The University of Queensland, St Lucia, QLD, Australia*
[c] *Queensland Department of Primary Industries, Mareeba, QLD, Australia*
[d] *CSIRO Agriculture and Food, Waite Campus, Glen Osmond, SA, Australia*
[e] *Queensland Alliance for Agriculture and Food Innovation, The University of Queensland, St Lucia, QLD, Australia*

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ABSTRACT

Fruit abscission is a complex physiological process influenced by the availability of carbohydrates, along with environmental, genetic, and hormonal cues. In perennial tree crops, such as mango (*Mangifera indica* L.), the abscission of fruitlets prior to maturity directly impacts yield and is a major hurdle for commercial production. Studies have demonstrated that five classes of phytohormones play a pivotal role in regulating the abscission process, including auxins, cytokinins, gibberellins (GA), ethylene and abscisic acid. Naturally occurring and synthetic hormones, known as plant growth regulators (PGRs), have been applied to manage fruit abscission in mango, with varying success. Here we performed a meta-analysis on available published PGR studies in mango, and found that individual applications of gibberellic acid (GA_3), or synthetic versions of auxin (1-naphthaleneacetic acid) or cytokinin (forchlorfenuron) improve fruit retention and yield. Applying combinations of these PGRs has been shown to further improve fruit retention in other species but requires further exploration in mango. Carbohydrate availability also plays a critical role in fruit abscission. Experimental manipulations resulting in carbon-limiting conditions, such as defoliation coupled with girdling, consistently increase fruitlet drop. This response is thought to be mediated by hormonal pathways with low carbohydrate levels reducing auxin signalling while enhancing ethylene biosynthesis and sensitivity, tipping the balance toward abscission. This review provides a comprehensive overview of the current understanding of the molecular mechanisms governing mango fruit abscission, highlighting the intricate interactions between hormones and their application for improvement of fruit retention. Understanding these interactions will enable future studies to develop targeted interventions for improved fruit retention.

1. Introduction

Mango (*Mangifera indica* L.) is widely regarded as one of the most popular and commercially valuable tropical fruits, cultivated extensively across tropical and subtropical regions worldwide. While many fruit trees produce more flowers and fruits than they can support to maturity, mango is an extreme case. A mature mango tree can produce hundreds of panicles, each bearing thousands of flowers, but typically fewer than 1 % of these flowers develop into mature fruit (Lobo and Sidhu, 2017). Many tree crops have developed an abscission process to facilitate the shedding of immature fruits in response to endogenous and environmental cues including climatic stress, pest infestation, and disease (Shi et al., 2023). From an evolutionary perspective, mature fruit abscission can be advantageous as it allows for the release and dispersal of seeds, whereas abscission of immature fruit can be used to eliminate damaged or infected organs, as well as shed excess fruit. Fruit abscission is also important to maintain a balance between vegetative and reproductive growth, to ensure an adequate supply of resources to support the development of the remaining fruits (Lakso et al., 2006). However, excessive immature fruit abscission can be a major limitation for crop

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* Corresponding authors.

E-mail addresses: sophie.jones@uq.edu.au (S.C. Jones), Ryan.Orr@dpi.qld.gov.au (R. Orr), Gerhard.Rossouw@dpi.qld.gov.au (G.C. Rossouw), Harley.Smith@csiro.au (H.M. Smith), c.beveridge@uq.edu.au (C.A. Beveridge), lindsay.shaw@uq.edu.au (L.M. Shaw).

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production leading to a reduction in crop quality and yield.

In mango, fruit abscission occurs throughout development, but three key stages have been identified as particularly sensitive: post-anthesis during early fruitlet formation, during fruit expansion, and pre-maturation (Yadav and Tripathi, 2022). These stages are associated with increased abscission rates and together can account for a substantial proportion of total fruit loss, often exceeding 90 % of initial fruit set (Hagemann et al., 2016; Nunez-Elisea and Davenport, 1986). The relative contribution of each stage to overall abscission varies depending on cultivar, environmental conditions, and management practices, but early fruitlet drop typically represents the largest proportion.

Fruit abscission is governed by the coaction of plant metabolites, particularly phenologically-driven phytohormone signalling and carbohydrate availability (Estornell et al., 2013). Phytohormones are chemical signalling molecules that play a crucial role in the growth and development of plants. These hormones accumulate at low concentrations and regulate developmental processes that occur throughout the lifespan of an organ including cell division, cell expansion, differentiation, senescence and abscission (Fenn and Giovannoni, 2021). A wide range of hormones regulate the development, setting and retention of fruit including auxins, gibberellins, cytokinins, brassinosteroids, abscisic acid (ABA), ethylene and jasmonic acids (Fenn and Giovannoni, 2021; Kumar et al., 2014).

Application of plant growth regulators (PGRs), such as gibberellic acid (GA_3), forchlorfenuron (CPPU) and 1-naphthaleneacetic acid (NAA), that are predicted to maintain growth of fruit, have been utilised with variable success to limit immature fruit abscission in mango (Gattass et al., 2018; Jiang et al., 2024). In addition, growth inhibitors, such as paclobutrazol, that act to reduce the expansion of vegetative shoots has also been used with variable results to reduce immature fruit abscission (Nafees et al., 2010). Results from mango fruit drop studies will be explored further in this review. However, few studies have focused on understanding the role of endogenous hormones during periods of immature fruit abscission in mango.

While most studies have focused on the use of PGRs to reduce fruit abscission and improve fruit retention, other PGRs have also been employed to intentionally increase fruit abscission as a method of chemical thinning. This approach is commonly used in other fruit crops and has been trialled in mango to manage excessive fruit set and improve fruit quality (Li et al., 2025; Shainika and Tambe, 2020). Ethylene-releasing compounds, such as ethephon are commonly applied during early fruit development to induce controlled fruit drop, thereby reducing competition among fruitlets and enhancing the size and sweetness of retained fruits (Chung et al., 2023; Kulkarni et al., 2017). The effectiveness of chemical thinning depends on the timing, concentration, environment and cultivar sensitivity, and while promising, it requires careful calibration to avoid excessive fruit loss. Including chemical thinning strategies in mango management may offer growers a flexible tool to balance yield and fruit quality under variable environmental conditions.

While the molecular mechanisms and signals governing plant growth and development in annual species have received extensive study (Vanstraelen and Benková, 2012; Wingler and Henriques, 2022), our knowledge about the molecular regulation of fruit abscission in perennial tree crops is expanding. This review focuses on the molecular signals associated with premature mango fruit abscission, in particular the role of hormones and the effects of applying commercially available PGRs to manage excessive fruit drop.

2. Mango fruit abscission occurs in the abscission zone

Plant organs abscise at a specific position, known as the abscission zone (AZ). This zone is differentiated early in development, and synchronised with the development of nearby organs, such as flowers, fruits and leaves (Roberts et al., 2002). There are two AZs in mango, one at the pedicel, where the fruit detaches and another at the panicle, where the entire panicle detaches (Fig. 1). Both mango AZs are formed at floral initiation and are often visibly distinct as a groove close to the base of the organ (Hagemann et al., 2016).

The AZ is composed of a group of highly differentiated cellular layers that undergo enzymatic cell wall degradation during abscission. This process involves the breakdown of pectin, cellulose, and hemicellulose, ultimately leading to the detachment of the organ (Bonghi et al., 2000; Estornell et al., 2013). When visualised using microscopy, AZ cells are morphologically and anatomically distinct from surrounding cells (Estornell et al., 2013; Roemer, 2011). The cellular composition of the AZ varies with species and plant organs (Sexton and Roberts, 1982), and can consist of up to 50 layers of AZ cells (Ito and Nakano, 2015; Shi et al., 2023).

While the formation of the AZ appears early in organ development, Ito and Nakano (2015) suggested that the AZ is not always active throughout the organ's life and can remain in a quiescent state until they receive abscission signals.

There are many factors, both exogenous and endogenous, that influence the initiation of these AZ development steps. It has been hypothesized that dominance among developing fruits, as well as with expanding vegetative shoots, is a major factor that induces immature fruit abscission in tree crops (Sadka et al., 2023). According to this hypothesis, developing fruits and/or vegetative shoots with a high growth potential act to induce abscission of immature fruits with a low growth potential. In this model, the dominant fruit or shoot induces abscission by suppressing auxin export from immature fruit with a low growth potential. As a result of decreased auxin transport through the pedicel, the AZ becomes sensitized to ethylene. Ethylene influences fruit abscission by regulating the expression of genes involved in cell wall degradation, such as polygalacturonase, cellulase and pectin methylesterases, which aid cell separation (Payasi et al., 2009; Perini et al., 2017), causing the fruit to detach from the tree (Estornell et al., 2013). Studies in apple (*Malus domestica*) suggest that abscission is initiated in the cortex of the fruit by a sugar signalling event that triggers ethylene and ABA biosynthesis (Botton et al., 2011). Following the burst of ethylene in the cortex, it has been suggested that this hormone diffuses to the seed to induce embryo abortion via an ethylene signalling event (Eccher et al., 2015). It has been speculated that embryo abortion is a critical event that reduces auxin transport out of the fruit and through the pedicel (Botton et al., 2011). Ethylene produced in the cortex could also diffuse to the pedicel to initiate cell separation in sensitized cells of the AZ (Sawicki et al., 2015). Other hormones that influence auxin activity or act as secondary signals to influence the growth potential of fruits could also play a role in modulating dominance mediated abscission (Sadka et al., 2023).

3. The role of phytohormones in mango fruit development and abscission

Studies have shown that auxins, cytokinins, gibberellins, ABA and ethylene interact in a delicate balance to regulate the fruit development and abscission processes, ensuring proper growth, and ultimately determining crop yield (Fenn and Giovannoni, 2021; McAtee et al., 2013). It is important to understand the individual effects of these hormones and their crosstalk throughout the growth and abscission of developing fruits.

A summary of changes in hormonal and cellular activity throughout mango fruit development, based on available published data is depicted in Fig. 2 with the role of individual phytohormones discussed in this review. Growth promoting hormones, such as auxins, cytokinins and gibberellins, are more prominent early in mango fruit development, whereas ethylene and ABA increase during the later stages of fruit growth to promote ripening. It should be noted that variations in the observed hormonal activity during fruit development may be attributed to cultivar differences, the timing and location of sample collection, and the diverse methods used for hormone quantification. While we have

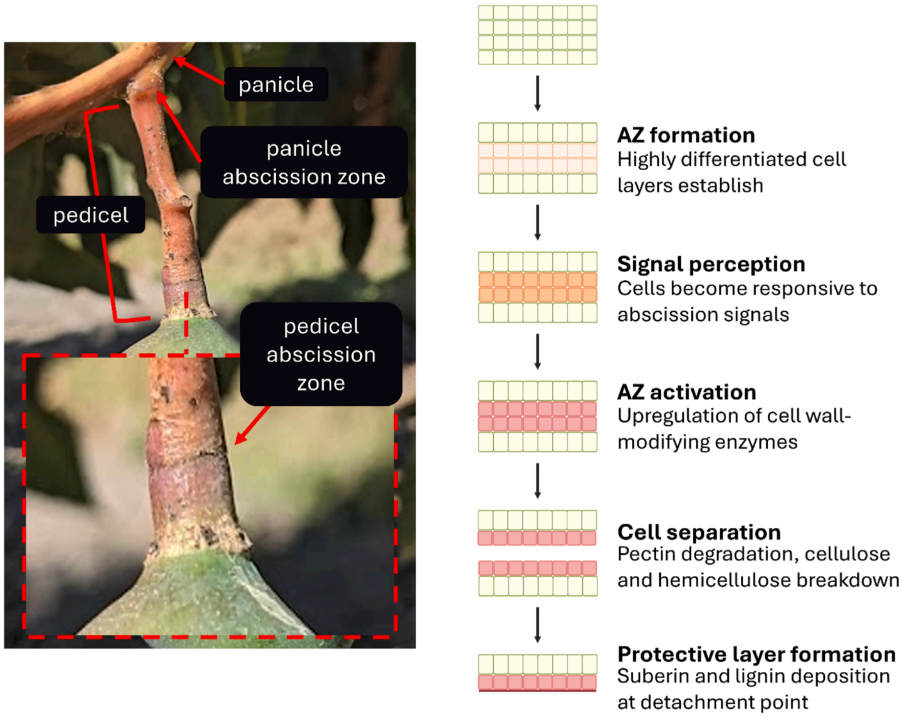

Fig. 1. Mango abscission zones (AZs) are morphologically and anatomically distinguishable. The pedicel of an immature mango fruit displays distinct grooves corresponding to the panicle and pedicel abscission zones, as shown in the image on the left. On the right, a schematic illustrates the sequential stages of abscission in tree crops: (1) AZ formation with highly differentiated cell layers (light orange); (2) signal perception, where cells becomes responsive to abscission cues (dark orange); (3) AZ activation involving the upregulation of cell-wall modifying enzymes (red); (4) cell separation driven by pectin degradation and cellulose/hemicellulose breakdown (red); and (5) protective layer formation through suberin and lignin deposition at the detachment point (dark red). This figure is adapted from Estornell et al. (2013), Patharkar and Walker (2017) and Shi et al. (2023).

some understanding of the role of these phytohormones in fruit development, to date, limited studies have observed the activity of major hormone classes throughout the multiple abscission events that occur during the mango fruiting season. Given the interconnected nature of these hormones, studies that encompass all aforementioned hormones during key abscission periods are essential to developing solutions to manage immature fruit abscission.

3.1. *Ethylene*

Ethylene is a major plant hormone that promotes abscission and regulates organ senescence and the ripening of climacteric fruits (Iqbal et al., 2017). Ethylene influences climacteric fruit development by regulating cell division and suppressing expansion (Dubois et al., 2018). Climacteric crops, such as mango and tomato (*Solanum lycopersicum*), are characterised by an increased rate of respiration and a burst in ethylene biosynthesis during ripening. The activation of the AZ appears to be induced by ethylene and delayed by the basipetal flux of auxins through the AZ (Estornell et al., 2013; Meir et al., 2015).

The biosynthesis and signalling of ethylene in mango have been briefly characterised during later stages of fruit ripening (Akamine and Goo, 1973; Malik, 2003). Studies indicate that high ethylene production occurs early in mango fruit development, declines as fruit develop and then spikes at abscission and ripening (Akamine and Goo, 1973; Malik, 2003; Nunez-Elisea and Davenport, 1986; Wu et al., 2022). Malik (2003) found higher levels of ethylene in abscising fruitlets and their pedicels compared to those retained. Nunez-Elisea and Davenport (1986) also found enhanced ethylene production in fruitlets prior to abscission. However, most ethylene studies are focused on changes after harvest, limiting information regarding ethylene activity during fruit development and abscission.

As mango fruit abscission has been correlated with high ethylene production (Nunez-Elisea and Davenport, 1986), some studies have focused on inducing fruit abscission using the ethylene-releasing compound, ethephon, to identify ethylene signalling genes involved in AZ activation (Hagemann et al., 2015; Ish-Shalom et al., 2011; Rai et al., 2021). Using this approach, ethephon induced abscission is associated with strong upregulation of *ETHYLENE RESPONSE SENSOR 1* (*ERS1*) in fruitlet AZs, an increase in the *ERS1*/ *ETHYLENE RECEPTOR 1* (*ETR1*) ratio in the AZs of abscising mango fruitlets (Hagemann et al., 2015; Ish-Shalom et al., 2011), and decreased expression of auxin-related genes, including *AUXIN RESISTANT* (*AUX*) and *PIN-FORMED* (*PIN1*), in the treated AZs (Denisov et al., 2017). Ethephon treatment has also been shown to induce *INFLORESCENCE DEFICIENT IN ABSCISSION* (*IDA*)-like genes in mango (Rai et al., 2021). These genes encode signalling peptide that promotes cell separation in the AZ by activating receptor-like kinases such as HAESA (HAE) and HAESA-LIKE2 (HSL2), which trigger downstream transcriptional changes involved in cell wall degradation (Lalun et al., 2024).

3.2. *Abscisic acid (ABA)*

ABA plays a regulatory role in plant growth, development, stress response, seed dormancy, and fruit ripening processes, including abscission (Shen and Rose, 2014). In climacteric species, including mango, ethylene is expected to play a larger role in fruit development than ABA. However, in non-climacteric crops, like grapevine (*Vitis vinifera*) and strawberry (*Fragaria x ananassa*), ABA is considered the key hormone regulating the onset of ripening (Bai et al., 2021; Shen and Rose, 2014). ABA levels increase during fruit maturation in climacteric fruit, as shown in peach (Zhang et al., 2009a), tomato (Zhang et al., 2009b) and mango (Wu et al., 2022), and to an even greater extent in non-climacteric fruit, including grapevine and citrus (McAtee et al., 2013; Setha, 2012). In mango fruit peel and pulp, ABA levels increase

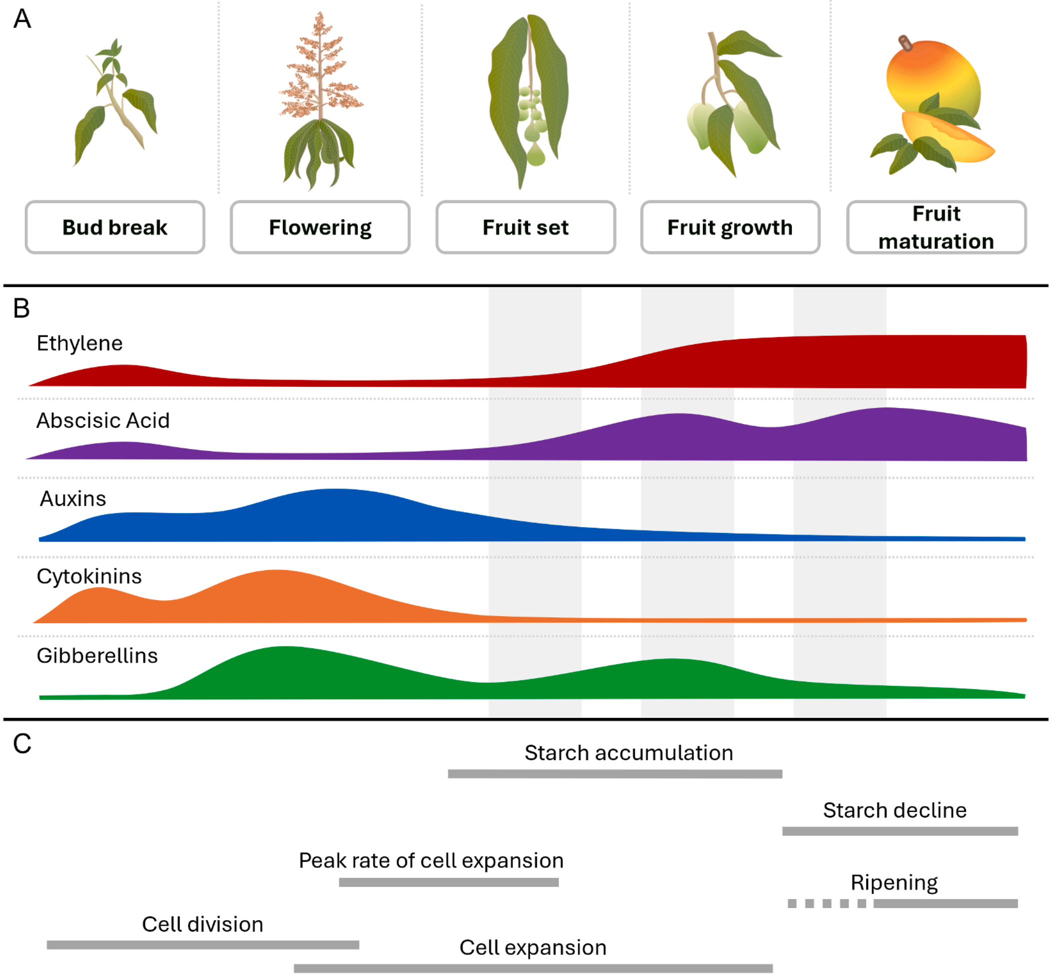

Fig. 2. Hormonal changes that occur during mango fruit development and ripening.

The average mango fruiting season takes five to six months from the point of bud break to fruit maturation as depicted in panel A, with periods of fruit abscission depicted by shaded grey areas. Throughout this process there are numerous changes in hormone (B) and cellular (C) activity that correlate with developmental changes. Early stages of mango bud break involve increased cell division, as well as rises in ethylene, abscisic acid, auxin and cytokinin content. During flowering, ethylene and abscisic acid remain low, whereas plant growth promoting hormones (auxin, cytokinin, and gibberellins) peak in conjunction with higher rates of cell expansion. As mango fruits develop, gibberellin activity and starch levels increase before lowering for the duration of maturation, and ripening hormones (ethylene and abscisic acid) peak. This figure was inspired by McAtee et al. (2013), Fenn and Giovannoni (2021), and Perotti et al. (2023), and used published studies in mango to depict changes in hormones, sugars and cellular activity (Akamine and Goo, 1973; Bains et al., 1997; Chen, 1983; Kondo et al., 2004; Malik, 2003; Murti and Upreti, 1995; Nunez-Elisea and Davenport, 1986; Pal and Ram, 1978; Prakash and Ram, 1984; Ram, 1983; Silva et al., 2008; Tandon and Kalra, 1983; Wu et al., 2022; Zaharah et al., 2012). BioRender.com was used for illustrations.

towards harvest, as shown in Fig. 2, whereas the content in the seed is higher during the early stages of fruit development and decreases as the fruit matures (Kondo et al., 2004; Wu et al., 2022). Bains et al. (1997) found ABA content to be higher in the fruitlets and pedicels of fruit about to abscise compared to intact fruitlets. This is similar to changes in ethylene associated with fruit development and abscission.

ABA has been suggested to regulate changes in fruit development by activating transcription factors such as basic leucine zipper (bZIP), which then target hormone response elements in the promoters of multiple genes (Pilati et al., 2017). For example, increased expression of ABA-response bZIP transcription factor gene *ELONGATED HYPOCOTYL 5* (*MiHY5*) was found during late-stage fruit development in mango (Wu et al., 2022). An upregulation of most bZIP family genes, particularly *HY5,* has also been observed in the AZ of tomato (Sundaresan et al., 2016), melon (*Cucumis melo*) (Corbacho et al., 2013) and olive (*Olea europaea*) (Gil-Amado and Gomez-Jimenez, 2013). bZIP transcription factors, such as HY5, are hypothesised to contribute to fruit abscission by regulating stress-responsive and hormone-related gene expression in the AZ. Their upregulation in multiple fruiting crops suggests a potential role in coordinating ABA and ethylene signalling during the activation of cell separation processes.

In climacteric crops, ABA content has been shown to accumulate prior to the main burst of ethylene (Leng et al., 2009; Mou et al., 2016), and mediate the transformation of the ethylene precursor, 1-aminocyclopropane 1-carboxylic acid (ACO), into ethylene during fruit ripening (Zaharah et al., 2013). It has been suggested that ABA can promote fruit ripening and abscission in climacteric fruits by regulating ethylene biosynthesis and signalling (Gupta et al., 2022), however the mechanism controlling the interactions between ABA and ethylene leading to the activation of the abscission process has not yet been determined.

ABA is widely recognised as a stress-responsive hormone, and its role in fruit abscission is often intertwined with its function in mediating plant responses to environmental stress. This overlap makes it hard to disentangle the direct involvement of ABA in abscission from its broader role in stress signalling. For example, Zhu et al. (2011) reported significant upregulation of the ABA biosynthesis gene *NINE-CIS-EPOXYCAROTENOID DIOXYGENASE 9* during shade-induced abscission in apple, suggesting that ABA accumulation under resource-limiting conditions can trigger abscission pathways. In this context ABA acts as an integrator of stress signals by coordinating responses to environmental cues such as drought, shading and nutrient limitation, and by modulating downstream hormonal interactions, particularly with ethylene and auxin. This integrative role involves ABA-mediated transcriptional regulation of stress-responsive genes and hormonal crosstalk that collectively influence the activation of cell separation processes in the AZ.

3.3. Auxins

Auxins are a class of hormone that regulates fruit development in many fleshy fruits through modulation of cell division, cell expansion and embryogenesis (Godoy et al., 2021). The activation of auxin signalling is believed to occur early in fruit development, soon after pollination, with auxins typically accumulating in developing seeds and to a lesser extent in the pericarps of fruits (Devoghalaere et al., 2012; Godoy et al., 2021). This activation then triggers fruit set, possibly through gibberellin biosynthesis, as observed in model plant species such as *Arabidopsis thaliana* and tomato (Dorcey et al., 2009; Serrani et al., 2007). Experimental results suggest that a decrease in auxin levels and a concurrent rise in ethylene and ABA is critical for promoting fruit maturation (Fenn and Giovannoni, 2021). Auxins are involved in regulating sugar metabolism during fruit development, particularly through degradation of sucrose into glucose and fructose, both of which are essential for fruit growth (Durán-Soria et al., 2020). Auxins do this by enhancing the enzymatic activity of sucrose synthases and invertases which hydrolyse sucrose into glucose and fructose, helping to maintain sink strength and promote cell division (Wang and Ruan, 2013). The interaction between auxins and sugars, particularly glucose, plays a fundamental role in regulating fruit growth, but requires further study.

Auxins play a major role in the control of organ abscission through interactions with ethylene. The reduction of auxins within the pedicel influences the sensitivity of the AZ to ethylene, causing AZ activation and fruit abscission (Denisov et al., 2017; Dong et al., 2021). Fruitlets and pedicels of abscising mango fruits have lower indole-3-acetic acid (IAA), the most common occurring auxin, and increased ABA relative to retained organs, suggesting that changes in ABA and IAA levels are associated with ethylene production and consequently fruit abscission (Bains et al., 1997). Auxins and ethylene have an antagonistic relationship, and reduced IAA may contribute to increased ethylene biosynthesis. This relationship has been observed in mango fruit pulp, where IAA was found to gradually decline after an increase in respiration and subsequent ethylene peak during an eight-day ripening period (Fig. 2) (Zaharah et al., 2012). This crosstalk between auxins and ethylene has been observed in numerous species, including apple, avocado, and tomato (Jones et al., 2002; Lieberman et al., 1977). Additionally, exogenous application of auxins at a pre-climacteric phase lowered ethylene production. In grape, application of auxin at pre-veraison delays ripening (Davies et al., 1997). Conversely, auxins enhance ethylene biosynthesis when applied at relatively high levels to apples, avocado and tomato in the climacteric stage (Lieberman et al., 1977). Experimental results suggest that this crosstalk is mediated in part through the stimulation of 1-aminocyclopropane-1-carboxylic acid synthase (ACS), a key enzyme in the ethylene biosynthesis pathway (Iqbal et al., 2017).

3.4. Cytokinins (CKs)

Like auxins, CKs are another class of hormones involved in the development of plant growth by promoting cell division in roots and shoots, as well as affecting axillary bud growth and leaf senescence (Haas, 2019; Tan et al., 2019). Some types of CKs, such as *trans*-zeatin are predominantly root-derived and travel acropetally through the vascular tissue, whereas isopentyl adenine type CKs are mainly produced in the shoots (Zhao et al., 2024).

Increased content of CKs early in fruit development suggests they play an important role in fruit set, however their contribution to the abscission process is less understood. During early mango fruit development, the levels of endogenous CKs within the seed and pericarp fluctuate (Fig. 2). CK content is high proceeding the period of rapid cell division, reduced for a brief period before peaking again and then becoming quite low for the remainder of fruit maturation (Chen, 1983; Murti and Upreti, 1995; Ram, 1983; Ram et al., 1983). This additional peak later in fruit development could be connected to a secondary period of fruit drop, although details on timing of fruit drop were not reported. Similar patterns have been observed in tomato, where a secondary CK increase was linked to developmental transitions and fruit abscission (Matsuo et al., 2012). CKs are known to interact with auxin and ethylene pathways, which are central to abscission regulation (Tipu and Sherif, 2024). A late-stage increase in CKs may reflect a shift in resource allocation or stress signalling, potentially weakening sink strength or hormonal support for developing fruit. No research has yet examined endogenous CK levels in direct relation to defined periods of mango fruit abscission, highlighting a gap in understanding the potential regulatory role of CKs during fruit development (Aremu et al., 2020).

3.5. Gibberellins (GAs)

GA is an important class of hormones that promotes plant growth and development (Gao et al., 2017) and has been shown to promote cell expansion. In addition, they also stimulate seed germination, regulate flowering in perennial species, and promote the production of enzymes that break down starch reserves, which is necessary for the growth of fruits, shoots, and roots (Gupta and Chakrabarty, 2013; Jong et al., 2009; Wu et al., 2023; Zahid et al., 2023). GAs interact with other hormones, particularly auxins, during fruit set to co-regulate pollination and fertilisation (Fenn and Giovannoni, 2021). Carbohydrate source tissue, such as leaves and storage organs, have been identified as major sites of endogenous GA production in mango (Davenport et al., 2001). While GAs' role in flower and fruit set are known, their impact on fruit abscission is ambiguous.

There are currently over 136 GAs identified in plants, fungi and bacteria (Hedden, 2020; MacMillan, 2001), however only a few are biologically active, including GA_1, GA_3, GA_4 and GA_7 (Sun, 2008), all of which have been identified in mango (Cavalcante et al., 2020; Davenport et al., 2001). The other GAs are generally metabolites in the biosynthesis and degradation pathways of active GAs. Studies in pea (*Pisum sativum*) and tomato demonstrated that GA_1 plays a role in fruit development (Ozga et al., 2009; Serrani et al., 2007), however this has not been confirmed in mango.

As depicted in Fig. 2, studies in mango demonstrated that GAs accumulate within the seed and pericarp of developing fruits during the early stages of fruit development, before rapidly decreasing and remaining low for the duration of fruit maturation, consistent with a role in cell expansion (Ram, 1983, 1992). This change in endogenous GA content during fruit set and early development is consistent with findings in macadamia (*Macadamia integrifolia*) and tomato (Trueman, 2011; Wu et al., 2023). Bains et al. (1997) observed a decrease in GA_3 in fruitlets and pedicels of abscising mango fruits compared to intact ones. The potential role of GAs in the activation of fruit abscission has not been well investigated, however they are known to interact with other regulators of abscission, such as auxins and sugars.

The role of GAs in fruit abscission may involve interactions with carbohydrate availability, although this relationship has not yet been experimentally validated in mango. In peach, bioactive GAs (GA_1 and GA_3) were significantly reduced in girdled trees compared to ungirdled control trees (Cutting and Lyne, 1993), indicating that disruption of phloem transport, and thus carbohydrate supply, may influence GA levels. Similarly, defoliation in citrus led to reduced GA_1 content in immature fruits and complete fruit abscission (Gómez-Cadenas et al., 2000), while shading in apple downregulated genes involved in GA signalling pathways in apple (Zhu et al., 2011). These findings indicate a potential link between carbohydrate limitation and reduced GA biosynthesis or signalling, which may contribute to fruit abscission.

Based on this evidence, we hypothesise that carbohydrate depletion may suppress GA activity in mango, thereby promoting abscission. To test this, future studies could experimentally manipulate carbohydrate availability through girdling, defoliation or shading, and measure corresponding changes in GA levels and abscission rates. Such research would help clarify whether GA-mediated signalling is responsive to carbon status and whether this contributes to fruit retention outcomes in mango.

4. Use of hormones and their inhibitors to regulate fruitlet abscission

Application of plant hormones, such as auxins, cytokinins and gibberellins, has been reported to improve flowering, fruit set, and fruit retention in mango (Kulkarni et al., 2017; Zahid et al., 2023). These hormones are part of a broader group known as plant growth regulators (PGRs), which also includes synthetic analogues and other growth-modifying compounds such as growth retardants, like paclobutrazol and uniconazole. The effectiveness of PGR application to control fruit retention in mango production has been highly variable. PGRs are primarily applied as a foliar spray, except for GA antagonists like paclobutrazol and uniconazole which are typically applied as a soil drench (Zahid et al., 2023). Each method has limitations, with soil drench likely to lead to soil adsorption, loss to the environment, and microbial degradation, while foliar application is susceptible to spray drift and photodegradation. Research in pear (*Pyrus communis*) and apple suggests that environmental factors, such as temperature and humidity affect the rate that hormones penetrate through the leaf cuticle (Black et al., 1995; Luckwill and Lloyd-Jones, 1962; Schönherr et al., 2000). It can be assumed that these environmental factors would also influence PGR uptake in mango leaves, despite their more pronounced waxy coating compared to pear leaves. Waxy cuticles act as a physical barrier to foliar absorption, reducing the permeability of aqueous solutions and limiting the diffusion of chemicals into the leaf tissue (Fernández et al., 2017). However, this has not been specifically investigated in mango. To the best of our knowledge, no research has explored the permeability of the mango panicle, and consequently how applying PGRs at flowering may potentially influence fruit retention due to improved chemical penetration. The variable performance of foliar-applied PGRs may be linked to their penetration into plant tissues and target cells, yet most mango PGR trials have focused on effects on phenotype rather than testing chemical permeation or its effects on endogenous hormones and gene expression.

Exogenous application of PGRs affects endogenous hormone activity either by supplementing low hormonal levels or interacting with hormone biosynthesis and signalling through crosstalk or feedback inhibition (Chen et al., 2022; Zhou et al., 2023).

To evaluate the effect of PGRs on reducing fruit abscission in mango, we conducted two random-effects meta-analyses incorporating data of field trials reporting fruit retention (%) and tree yield (kg of fruit/tree) responses to three commonly used PGRs: NAA, GA_3 and CPPU.

Studies were identified through a systematic search of databases including Web of Science, Scopus and Google Scholar. Inclusion criteria were: (i) field-based trials on mango, (ii) quantitative data on fruit retention or yield, (iii) presence of a control group, and (iv) clear reporting of treatment replication. Studies were excluded if they lacked control comparisons, did not report replication, or did not provide quantitative data on fruit retention or yield.

A total of 45 studies met the inclusion criteria: NAA (22), GA_3 (14), and CPPU (9). Data were extracted for each PGR treatment and grouped by application stage: pre-fruit set (applications at or near flowering, before visible fruitlets formed), post-fruit set (applications on small developing fruitlets, typically at pea or marble stage), or multiple applications (treatments applied at two or more distinct timepoints spanning both stages.

Effect sizes were calculated as log response ratios (lnRR), comparing normalised treatment means to their corresponding control means within each study and application stage (pre-fruit set, post-fruit set, or multiple applications). Sampling variance was estimated using the standard formula provided in the *metafor* package in R, which counts for within-study replication (Viechtbauer, 2010). Both combined and individual PGR analyses used the same modelling approach. In the combined analysis, data from all three PGRs were pooled and grouped by PGR and application timing to estimate overall and subgroup effects. In the individual PGR analyses, separate datasets were used to model yield or retention effects for each compound independently.

All models were fitted using random-effects meta-analysis with the restricted maximum likelihood (REML) estimator in the *metafor* package. Potential sources of heterogeneity, such as cultivar differences, climatic conditions, and PGR application protocols, were acknowledged but not explicitly modelled due to limited reporting in the primary studies. However, subgroup analyses by PGR type and application timing were performed to partially account for treatment variability.

Results are presented as forest plots grouped by application stage, with 95 % confidence intervals. A positive lnRR indicates a beneficial impact of PGRs, and the confidence intervals that do not include zero suggest statistical significance.

The combined meta-analysis (Fig. 3) revealed that all three PGRs improve fruit retention and yield in mangoes compared to untreated controls. Specifically, the overall effect estimate for fruit retention was 0.45 [95 % CI: 0.35, 0.55], and for yield it was 0.37 [95 % CI: 0.26, 0.47). Multiple applications of each PGR consistently resulted in greater improvements than single pre- or post-fruit set applications. Among the PGRs, NAA showed the most reliable increase in fruit retention, particularly when applied multiple times (lnRR of 0.78 [95 % CI: 0.42, 1.14]), while GA_3 and CPPU showed greater variability and confidence intervals. These results suggest that while PGRs are broadly beneficial, the intensity and consistency of treatment effect depend on both the chemical used and its application strategy. It is worth noting that studies showing a significant, positive treatment effect are likely to be overrepresented in the literature, potentially skewing these findings (Easterbrook et al., 1991; Møller and Jennions, 2001). Detailed classification of each PGR is provided below.

4.1. Naphthaleneacetic acid (synthetic auxin)

NAA is a synthetic auxin used to promote plant growth by stimulating cell division, photosynthesis, and water uptake. NAA has previously been used to improve fruit quantity and quality of many tree crops, including avocado, citrus and mango (Ma et al., 2021; Mostafa et al., 2008; Tripathi et al., 2019).

Our analysis indicated that NAA treatment consistently enhanced fruit retention (%) and tree yield (kg of fruit per tree) in mango across the reviewed trials with an overall random-effects estimate of 0.54 [95 % CI: 0.39, 0.70] and 0.39 [95 % CI: 0.24, 0.55], respectively (Supplementary Figure 1 and 2).

Overall, NAA treatment response varied by application timing (Fig. 3), with significant increases in fruit retention and yield observed from multiple applications (pooled log response ratio of 0.78 [95 % CI: 0.42, 1.14; p value: $2.62e^{-5}$] and 0.52 [95 % CI: 0.15, 0.89; p-value: 0.006], respectively) compared to single pre- or post-fruit set sprays, which resulted in non-significant yield increases (0.32 and 0.31, respectively). These findings support the hypothesis that repeated auxin applications during the fruit development period help to sustain higher auxin levels, which likely suppressed abscission-related ethylene signalling in the AZ, resulting in greater retention of developing fruits. Despite some variability among studies, likely due to differences in

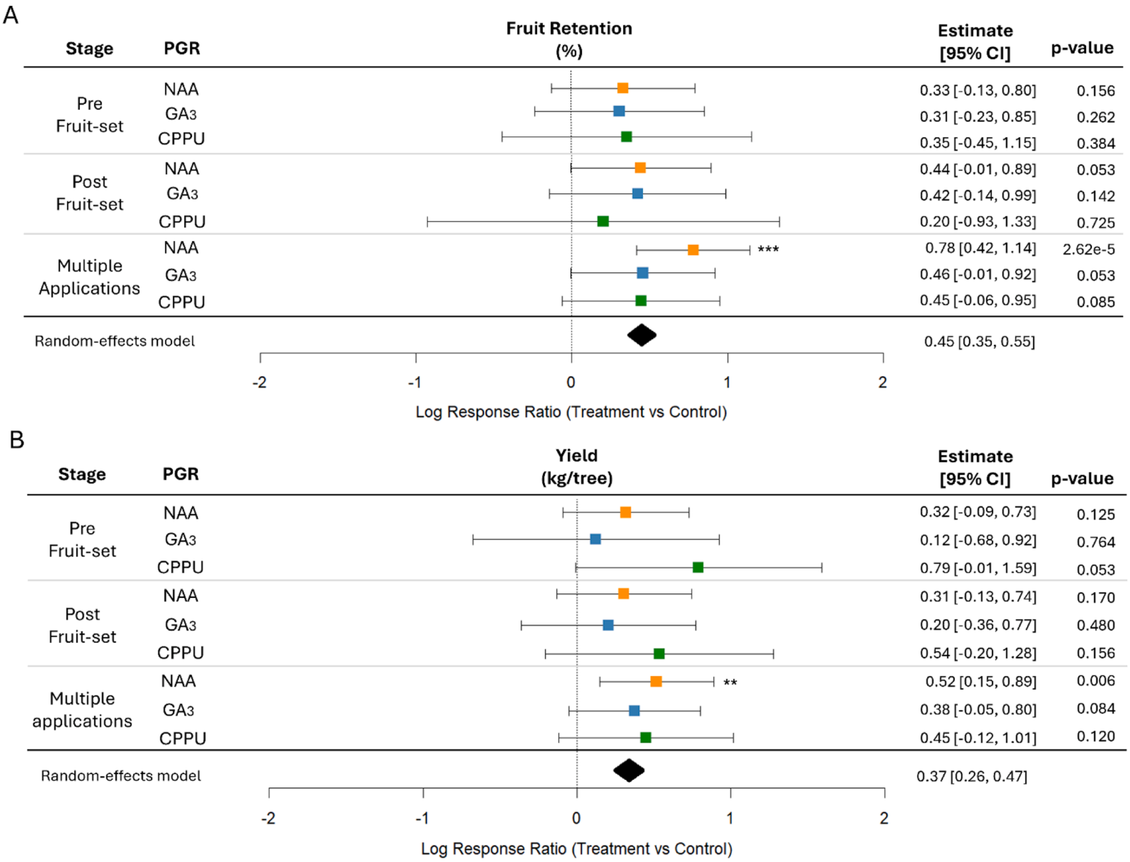

Fig. 3. The effect of plant growth regulator (PGR) treatments on mango fruit retention and yield.
Meta-analysis of field trials assessing the impact of three PGRs (NAA, GA_3, CPPU) on fruit retention (A) and yield (B), expressed as log response ratios (lnRR) relative to untreated controls. Data are grouped by PGR and application timing: pre-fruit set, post-fruit set, and multiple applications. The overall effect across all PGRs and stages is shown at the bottom of each panel. Positive values indicate an improvement in fruit retention or yield compared to untreated trees. Error bars represent 95 % confidence intervals. A random-effects model (REML) was used to estimate effect sizes. Pooled estimates were derived from normalised mean values across independent field trials ($n = 1$–10 per subgroup). Effect sizes are reported in the format: estimate [lower CI, upper CI], with p-values calculated using a Wald-type-z-test from the model estimate and standard error. Significance levels: *** $p < 0.001$, ** $p < 0.01$.

cultivar, climate, and dosage, NAA consistently shifted the balance toward fruit retention and yield gain, making it a viable option for managing abscission in commercial mango orchards.

4.2. Gibberellic acid

GA_3 is a naturally occurring gibberellin that is exogenously applied to promote plant growth and reduce preharvest fruit drop (Gao et al., 2017). It does this by stimulating cell division and differentiation (Gupta and Chakrabarty, 2013). In olive, the application of GA_3 affected endogenous hormone contents in the leaf, node and fruit, with increased ABA, IAA, GA_3, and CK zeatin content, as well as increased sugar contents in the fruits (Ülger et al., 2018). In sweet cherry (*Prunus avium*), GA_3 application delayed the accumulation of ABA at the onset of ripening, highlighting its potential as a management tool (Kuhn et al., 2020).

Our analysis found that GA_3 treatments resulted in small improvements to mango fruit retention (%) and tree yield (kg of fruit per tree), with an overall random-effects estimate of 0.38 [95 % CI: 0.22, 0.54] and 0.27 [95 % CI: 0.11, 0.44], respectively (Fig. 3; Supplementary Figure 3 and 4). Multiple applications produced a moderate increase in retention (0.46 [95 % CI: −0.01, 0.92) and yield (0.38 [95 % CI: −0.05, 0.80]), though this effect was not statistically robust (Fig. 3). Pre- and post-fruit set applications of GA_3 showed minimal improvements to fruit retention and yield, with wide confidence intervals crossing zero.

These findings align with the known role of GA_3 in enhancing cell expansion and delaying senescence but suggest that its contribution to fruit retention and tree yield may be limited by environmental interactions or cultivar sensitivity. The wide confidence intervals observed across application stages may indicate substantial variability in treatment outcomes, implying that the efficacy of GA_3 is highly dependent on cultivar, climate, and application protocol. GA_3 may be more effective when integrated with other PGRs or when targeting fruit retention rather than total yield.

4.3. GA inhibitors

There are several triazole PGRs that inhibit gibberellin biosynthesis, such as uniconazole and paclobutrazol (PBZ) (Desta and Amare, 2021; Rademacher, 2017). PBZ impacts gibberellin biosynthesis by inhibiting the oxidation of *ent*-kaurene to GA_{12} through inactivating the relevant P450 monooxygenase (Hedden and Graebe, 1985).

PBZ has been used in mango, applied as either a soil drench or foliar spray, to control vegetative growth, preserving carbohydrate resources for reproductive processes (Yeshitela et al., 2004b). The application of PBZ prior to flower bud differentiation improved mango fruit set and yield (Singh, 2000). PBZ application has also been shown to manage irregular bearing by balancing reproductive and vegetative energy consumption between years (Nafees et al., 2010; Protacio et al., 2000). As such, PBZ is widely used in commercial mango production (Burondkar et al., 2013; Yeshitela et al., 2004a). Despite its involvement in reducing vegetative growth within a tree (Yeshitela et al., 2004b), the effect of PBZ on premature fruit drop, as opposed to flowering and fruit set, has been only lightly explored in mango. One study found that applying PBZ as a foliar spray at 1000 ppm to panicles in the later stages of flowering was able to increase the percentage of fruit retained (16.58 %) compared to control (5.47 %) (Benjawan et al., 2006).

4.4. *Forchlorfenuron (CPPU; synthetic cytokinin)*

CPPU is a highly active and stable synthetic cytokinin that promotes cell division, cell expansion and chlorophyll biosynthesis by inhibiting cytokinin oxidases, which leads to an increase in endogenous cytokinins (Kopečný et al., 2010). CPPU has also been used to increase fruit set and size in a variety of horticultural crops, including apple (Curry and Greene, 1993; Greene, 2001), macadamia (Zeng et al., 2016), blueberry (*Vaccinium sect. Cyanococcus*) (Fujisawa et al., 2018), and kiwifruit (*Actinidia chinensis*) (Nardozza et al., 2017).

The meta-analysis of field trial results of CPPU treatment to improve mango fruit retention (%) and yield (kg of fruit per tree) indicated an overall positive effect, with an overall random-effects estimate of 0.46 [95 % CI: 0.22, 0.71] and 0.54 [95 % CI: 0.29, 0.79], respectively (Fig. 3; Supplementary Figure 5 and 6).

CPPU applications showed generally positive trends in increasing mango yield, with a pooled effect of 0.45 [95 % CI: −0.12, 1.01] for multiple applications, though confidence intervals indicate variability (Fig. 3). Pre-fruit set application had the highest observed estimate (0.79 [95 % CI: −0.01, 1.59]), suggesting that early stage cytokinin activity may support improved fruit set and early growth (Fig. 3). However, variability among trials reduced the statistical significance of these findings. The large confidence intervals observed across treatments suggest that CPPU's efficacy is highly variable and may depend on cultivar-specific responses, environmental conditions, and dosage precision. Further refinement of CPPU dose and timing is likely needed to optimize its impact on final yield.

4.5. *Ethylene inhibitors (1-MCP and AVG)*

4.5.1. *1-methylcyclopropene (1-MCP)*

1-MCP acts as an inhibitor of ethylene signalling by irreversibly binding to the ethylene-binding receptor (Li et al., 2020). Plants treated with 1-MCP cannot respond to ethylene, which is why it has traditionally been used as a post-harvest treatment to extend fruit quality during transport and enhance shelf-life (Sakhale et al., 2018; Zanella and Rossi, 2015).

1-MCP has been used to inhibit ethylene action in non-climacteric and climacteric fruits, including mango (Lalel et al., 2003; Li et al., 2020; Sakhale et al., 2018), apple (Elfving et al., 2007; Li et al., 2022), avocado (Hershkovitz et al., 2005; Olivares et al., 2020, 2022), and pear (Bai et al., 2022). By blocking ethylene perception, 1-MCP also disrupts the feedback regulation of ethylene biosynthesis (Nakatsuka et al., 1997). In climacteric fruit, this typically suppresses the autocatalytic ethylene burst by preventing the ethylene-induced upregulation of ACS and ACO genes, although in some cases a temporary increase in their transcript levels has been observed without restoring functional ethylene signalling (Yang et al., 2012). In mango, application of 1-MCP prior to harvest supressed further ethylene biosynthesis. 1-MCP treated mangoes lacked a second peak in endogenous ethylene, as well as less 1-aminocyclopropane-1-carboxylate (ACC), a precursor to ethylene (Israel et al., 2014). These results suggest that when 1-MCP is applied early in mango fruit development it may delay fruit maturity and increase fruit retention.

4.5.2. *Aminoethoxyvinylglycine hydrochloride (AVG)*

AVG is a naturally occurring chemical that blocks ethylene production in plants, through the reversible inhibition of ACC synthase, an essential enzyme in ethylene biosynthesis (Wang, 2021). AVG applied just prior to the natural increase of ethylene production in climacteric fruit prevents activation of the ethylene biosynthesis pathway and consequently influences the timing of fruit ripening (Dal Cin et al., 2008; Knoche and Petracek, 2014).

In mango, pre-harvest application of AVG influenced final fruit retention at higher doses, with 1.03, 1.33, 1.70, and 1.75 fruits retained per panicle when treated with AVG at 5, 50, 150, and 200 mg/L of AVG respectively compared to only 1.25 fruits per panicle on untreated trees (Singh and Agrez, 2002). AVG application also increased the firmness of treated mango fruits, essentially delaying the ripening process (Aguirre-Medina et al., 2024).

There have been numerous AVG studies on peach, apple, pear, and banana (*Musa acuminata*) (Argiriou and Nanos, 2010; Arseneault et al., 2018; D'Aquino et al., 2010; Van Toan and Thanh, 2011). These studies demonstrated that AVG treatment delays and temporarily reduces the production of ethylene in plant tissues, dependent on timing, dose, and species. In orange, the application of AVG at 100, 200, and 300 mg/L resulted in an average pre-harvest fruit drop value of 17.52 %, 15.22 %, and 12.61 % respectively, compared to the untreated control's 25.14 % (El- Khayat, 2019).

It is crucial to acknowledge that although AVG can defer the onset of internal ethylene production in plant tissues, it does not impede the plant's reaction to ethylene. This is in contrast to 1-MCP discussed above which does not interfere with ethylene biosynthesis but irreversibly binds to the ethylene-binding receptor, prohibiting ethylene signalling in the transduction pathway (Li et al., 2020). Therefore, any delay in maturation triggered using AVG can be reversed at a later stage by applying compounds that generate ethylene, such as ethephon or ACC. Furthermore, there is no translocation of AVG or its metabolites from leaves into fruit, rather AVG within fruit tissues result from absorption through the skin of the fruit (Altuntas and Burhan, 2013).

4.6. *PGR combinations*

While individual applications of PGRs have been shown to effectively improve mango fruit retention, treating with a combination of PGRs often has additive benefits, with greater fruit development and retention than individual PGRs alone.

Studies in kiwifruit found CPPU promotes fruit development by increasing the endogenous levels of cytokinins, gibberellins and auxins (Brown and Woolley, 2010; Wu et al., 2020). Preharvest application of CPPU increased fruit firmness and storage capacity by reducing ethylene production in kiwifruit and grape (Costa et al., 1995; Marzouk and Kassem, 2011). It appears the effectiveness of CPPU is increased when used in combination with GA_3 or NAA (Mostafa et al., 2008; Notodimedjo, 2000). To date, only one study has explored the combination of GA_3, NAA and CPPU on mango fruit retention (Roemer, 2011). Trees treated with these three PGRs retained three times as many fruits compared with control trees, but had fewer fruits than trees treated with single applications of CPPU and NAA. However, it is difficult to determine the effect of these treatments as they are confounded by differences in stage of application.

The use of NAA in combination with GA_3 and CPPU in peach and avocado increased the percentage of fruits set and retained to maturity, yield and fruit size (Mostafa et al., 2008; Sartori and Marodin, 2003). The early application of AVG and NAA together also reduced premature fruit abscission more than either chemical alone in apple (Arseneault et al., 2018; Robinson et al., 2010; Yuan and Li, 2008). In apple, AVG plus NAA resulted in a cumulative fruit drop of 23 % compared to 91.1 % in untreated trees, 45 % in AVG single treatments, and 53.3 % in NAA single treatments (Yuan and Li, 2008). This is likely due to the collaborative impact of these two substances on genes related to polygalacturonase, a major enzyme responsible for the softening of fruit tissue, that become active during the fruit-ripening phase (Bonghi et al., 2000; Zhu et al., 2008). These findings support the well-established role of auxins and ethylene in initiating fruit abscission. However, they also underscore significant gaps in our understanding of the complex interplay between PGRs and endogenous hormone signalling.

5. The role of carbohydrates in fruit retention

Non-structural carbohydrates, such as sugars and starch, are essential for the growth and development of all living organisms and play a significant role in fruit retention (Capelli et al., 2021). Sugars, such as glucose, fructose and sucrose, are a primary source of energy for plants during the period of early fruit development (Durán-Soria et al., 2020). During periods of limited growth, source tissue, such as mature leaves and green stems, produce sugars which are converted to starch and stored until required (Capelli et al., 2021). These starch reserves, which in trees are primarily stored in roots and woody tissues, are then utilised during growth stages within the tree, such as fruit development, when the demand for carbohydrates in sink tissue outweighs the supply provided by photosynthesising leaves (Rossouw et al., 2024).

Where the demand for energy outweighs the combined availability from leaf photosynthesis and reserve remobilisation, this may result in the cessation of growth in some organs and activation of abscission (Smith and Samach, 2013). In citrus and litchi (*Litchi chinensis*) limiting carbohydrate supply through tree shading (Zhu et al., 2011), defoliation (Gómez-Cadenas et al., 2000), and girdling plus defoliation (Yang et al., 2015) resulted in fruit abscission. Recent studies have shown that sucrose not only serves as an energy source but also modulates auxin metabolism and signalling. In apple, reduced sucrose availability was associated with a decline in polar auxin transport through the pedicel, contributing to fruit abscission (Zhu et al., 2011). In *Actinidia arguta*, transcriptomic comparisons between abscission-prone and resistant cultivars revealed that starch and sucrose metabolism genes were differentially expressed alongside auxin signalling components, suggesting a coordinated role in abscission regulation (Yuan et al., 2025). Defoliation also decreased auxin levels in poplar (*Populus tremula*) and pear leaves (Jin et al., 2015; Wei et al., 2022). Decreased auxin levels within litchi fruitlets was also observed after limiting carbohydrate supply (Kuang et al., 2012). These findings support the hypothesis that sucrose availability influences fruit abscission not only through energy supply but also by modulating auxin levels and signalling pathways.

While carbohydrates are used directly as energy for sink development, they also function as signals in regulating fruit drop (Lordan et al., 2019; Zhao and Li, 2020). Studies in mango, citrus and macadamia demonstrated that abscission of immature fruits is triggered when sugar concentration in the fruit drops below a critical threshold required to maintain fruit development (Hagemann et al., 2016; Iglesias et al., 2006; Yang and Xiang, 2022). Similarly, analysis of starch in avocado flowers at anthesis revealed a higher concentration in flowers that successfully developed into fruits compared to flowers that abscised (Alcaraz et al., 2011). Also in avocado, a reduction in carbohydrate availability, including glucose, sucrose, and starch, in the stem preceded the premature fruit drop period, indicating that tree carbohydrate status influenced immature fruitlet abscission (Smith et al., 2022). Molecular sensors in plant tissues detect fluctuations in sugar concentrations which then activate a series of downstream responses, including triggering gene expression, enzyme activity and alterations in hormone levels (Rolland et al., 2006).

Trehalose-6-phosphate (T6P) is a metabolite that serves as both a signal and regulator of sucrose availability in plants (Fichtner and Lunn, 2021). T6P is believed to act through the sucrose non-fermenting-related kinase-1 (SnRK1) pathway (Figueroa and Lunn, 2016). The involvement of T6P and SnRK1 in fruit development has been explored in cucumber (*Cucumis sativa*), where the pre-existing fruits inhibit the growth of subsequent fruits, a phenomenon known as “first-fruit inhibition” (Zhang et al., 2015). Higher T6P and sucrose concentrations and lower SnRK1 activity was reported in the peduncles of the first fruit than the second. It was also found in macadamia that inducing carbohydrate starvation stress by girdling and defoliation resulted in the significant upregulation of trehalose 6-phosphate (T6P) biosynthesis genes, *TREHALOSE 6-PHOSPHATE SYNTHASE* (*TPS*) and *TREHALOSE 6-PHOSPHATE PHOSPHATASE* (*TPP*), in the husk and pedicels (Yang and Xiang, 2022). In contrast, in longan and apple, *TPS1* was downregulated in the fruit AZ from shading but not from auxin application (Zhu et al., 2011). This could suggest that T6P plays a role in fruit abscission by modulating sucrose availability in times of deficiency, potentially through the SnRK1 pathway. However, the relationship between T6P/SnRK1 signalling and abscission remains correlative rather than causal, and further research is needed to determine whether these sugar-signalling pathways directly regulate abscission-related gene expression or hormonal response in the AZ, particularly in mango.

Sucrose also interacts with ethylene and has been observed to enhance expression of ethylene receptor (*ETR*) genes in tomato (Li et al., 2016). A feedback loop between ethylene and sucrose occurs during periods of fruit ripening and abscission, with ethylene promoting sucrose accumulation in strawberry, kiwifruit, and tomato (Fei et al., 2020; Li et al., 2016; Luo et al., 2019). While the outlined interactions between sugars, ethylene and auxins have not been established in mango, it is likely that a similar interplay of sucrose and auxin levels activates the abscission process through an influx of ethylene in the pedicel AZ.

Together, these findings underscore the dual role of carbohydrates - as both metabolic resources and signalling molecules - in regulating fruit abscission. They highlight the need for further research into sugar–hormone interactions, particularly in mango, to inform targeted strategies for improving fruit retention.

6. Integrative model of molecular regulation of fruit abscission

The integrative model presented in Fig. 4 summarises potential molecular interactions discussed throughout this review, highlighting the roles of phytohormones, carbohydrate signalling, and cell wall-modifying processes in mango fruit abscission. While the model focuses on endogenous regulatory pathways, it provides a valuable framework for interpreting how PGRs may influence these mechanisms. It also distinguishes between interactions currently proposed in mango and those inferred from studies in other species, supporting the need for future research aimed at improving fruit retention strategies.

7. Conclusion

Premature fruit abscission is a complex physiological process that involves the coordination of various metabolic and signalling pathways, including phytohormones, carbohydrates, and cell-wall modifying signals. Plant growth promoting hormones, such as auxins, cytokinin and gibberellin play an important role in the development and retention of mango fruits. Whereas plant growth inhibitors, ethylene and abscisic acid, play a large role in fruit ripening and abscission. The overall abscission process appears conserved across species, however, few studies have quantified the fluctuation of these hormones in mango throughout fruit development and during periods of fruit abscission. This gap presents a challenge in ascertaining their exact function in relation to fruit abscission.

As the primary source of carbon and energy within the plant, the metabolism and signalling of sugars greatly impacts fruit retention. It has been established that low sucrose within developing fruitlets and pedicels increases the rate of abscission, particularly if carbohydrate supply is limited due to shading or canopy defoliation. Studies suggest that changes in sucrose and auxin levels within the pedicel initiate an influx of ethylene which results in fruit abscission.

It is important to combine the understanding of molecular signals associated with fruit abscission with established management practices to ensure optimised mango production. The use of PGRs is one strategy that has shown promising results in improving mango fruit retention, however little is known about how these PGRs influence molecular signalling. A meta-analysis was performed on available published PGR

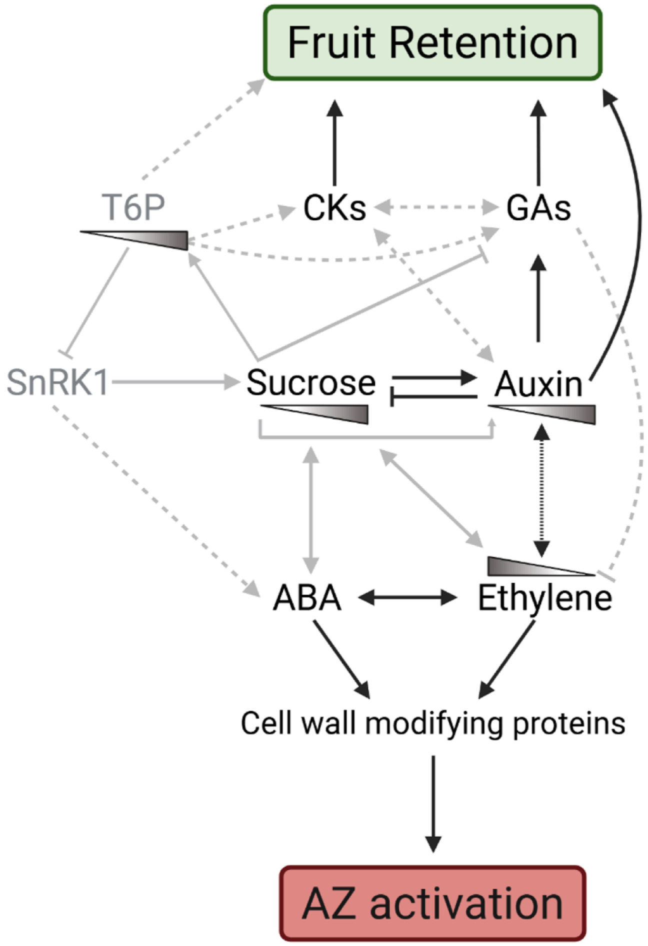

Fig. 4. Schematic representation of molecular regulators and interactions involved in fruit abscission and retention in mango.
This diagram illustrates potential interplay between key signalling molecules and metabolic regulators that influence fruit retention and abscission. Sucrose and trehalose-6-phosphate (T6P) modulate energy status and hormonal balance via sucrose non-fermenting-related kinase-1 (SnRK1), which in turn affects auxin and abscisic acid (ABA) levels. Auxin supports fruit retention through its interaction with cytokinins (CKs) and gibberellins (GAs), while ABA and ethylene promote cell wall degradation and abscission zone (AZ) activation. Crosstalk between auxin and ethylene is indicated by a dotted bidirectional line, reflecting evidence that indole-3-acetic acid (IAA) levels decline following or concurrently with ethylene increase, and that ethylene suppresses auxin-related gene expression. CKs and GAs support fruit retention and may interact with auxin and sugar signalling pathways Arrows indicate activation or promotion; blunt lines indicate inhibition; dotted lines represent hypothesised or indirect interactions. Black lines denote interactions or regulators supported by evidence in mango, while grey lines represent interactions known or hypothesised in other plant species. Created with BioRender.com.

studies in mango, and found that applications of NAA, GA_3 and CPPU were able to improve the final number of fruits retained and tree yield, particularly with multiple applications. While the meta-analysis demonstrated overall positive effects of PGRs on mango fruit retention and yield, notable variability was observed in the treatment outcomes, particularly for GA_3 and CPPU. The wide confidence intervals associated with these compounds suggest that their efficacy is highly context-dependent, influenced by factors such as cultivar, environmental conditions, and application protocols. This variability underscores the need for further research to refine dosage and timing strategies and to better understand the physiological and molecular mechanisms underlying these responses. Acknowledging this heterogeneity is essential for interpreting the reliability of PGR-based interventions and for guiding their practical application in diverse mango production systems. Applying combinations of these PGRs has been shown to further improve fruit retention in other species but requires further exploration in mango.

Existing research underscores the pivotal roles of hormones and carbohydrates in triggering fruit abscission, but gaps persist in the understanding of their precise mechanisms and crosstalk. Future research efforts focusing on elucidating these mechanisms and exploring the potential of PGRs as a management strategy offers avenues to enhance the efficiency and sustainability of mango production.

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Data availability

Supporting PGR field trial data that were analysed, but not generated, as part of this review are from previously published studies and datasets and are cited within the text at relevant places.

CRediT authorship contribution statement

Sophie C. Jones: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ryan Orr:** Writing – review & editing, Supervision, Conceptualization. **Gerhard C. Rossouw:** Writing – review & editing, Supervision. **Harley M. Smith:** Writing – review & editing, Supervision. **Christine A. Beveridge:** Writing – review & editing, Supervision. **Lindsay M. Shaw:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.scienta.2025.114572.

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