Scientia Horticulturae 318 (2023) 112103

Contents lists available at ScienceDirect

Scientia Horticulturae

journal homepage: www.elsevier.com/locate/scihorti

The impact of PGRs applied in the field on the postharvest behavior of fruit crops

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ARTICLE INFO

Keywords:
Vegetative growth control
Reproductive activity
Hormones
Storage
Quality
Ripening

ABSTRACT

In horticulture, Plant Growth Regulators (PGRs) are applied during cultivation in the field to control and regulate different processes with positive effects on stress responses and general performance, including yield, composition, and quality of the harvested produce. Both vegetative and reproductive activities may be affected by PGRs and, considering specifically fruit crops, the effects of these field treatments can also be observed in terms of storage behavior and postharvest physiology. The postharvest effects of inhibitors, antagonists, promoters or releasers of gibberellins, cytokinins, auxins and ethylene depend on the concentration, chemical formulation and plant developmental stage at the time of treatments. Ethylene-related PGRs in particular, applied to control ripening and optimize harvesting, have marked residual effects observed during the storage life. In addition to these hormonal categories, other substances such as salicylic acid, brassinosteroids and jasmonates, recognized as having physiological effects in developing plants and inducing compositional changes in fruits at harvest, are effective in altering specific postharvest ripening processes, such as firmness loss and ethylene physiology. The stimulation of antioxidant enzymes activity and the maintenance of cell membrane integrity during storage, resulting in a reduction of chilling injury incidence, appear to be among the main effects of the field application of these PGRs. This review emphasizes the implications of PGR applications during cultivation on fruit postharvest.

1. Introduction

In nature, plants and plant organs progress through specific and genetically controlled developmental processes culminating in senescence followed by death. This is also true for horticultural products, characterized by different and specific processes depending on genotype and type of organ, as in the case of fleshy fruits that undergo the ripening syndrome before entering senescence. However, in many crop plants the natural developmental cycle is interrupted before its completion due to the harvest. Timing of harvest maturity within the normal developmental cycle markedly varies depending on the commodities: for some products it occurs while they are still growing, while for others it is at more advanced stages, when they have reached mature/full development.

Among the factors that control and affect plant growth and development, hormones represent a major player. The concentration, availability, presence of active forms, balance and interplay between different hormones coupled with the tissue/organ sensitivity have a pronounced influence on the whole plant cycle. In this context, endogenous (specific hormone synthesis, conjugation/deactivation, perception, transport, intra- and inter-organ correlative relationships) and exogenous (environment, agronomic practices) factors modulate the hormonal metabolism affecting morphological development and physiology of the plant/organ during cultivation. Indeed, most of the PGRs used in the field have the precise goal of altering endogenous levels or the action of specific hormones, thus affecting the general performance of the plants, and the yield and qualitative traits of the crop at harvest.

Horticultural products are consumed soon after harvesting only in a few cases. Most of these commodities undergo a more or less prolonged postharvest period aimed at extending shelf/commercial life, allowing transportation from the site of production to the site of utilization while maintaining quality. For fruit products, these are challenges addressed by applying specific protocols principally based on the use of refrigeration often coupled with other treatments/conditions (e.g. controlled/

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https://doi.org/10.1016/j.scienta.2023.112103
Received 20 January 2023; Received in revised form 14 April 2023; Accepted 18 April 2023

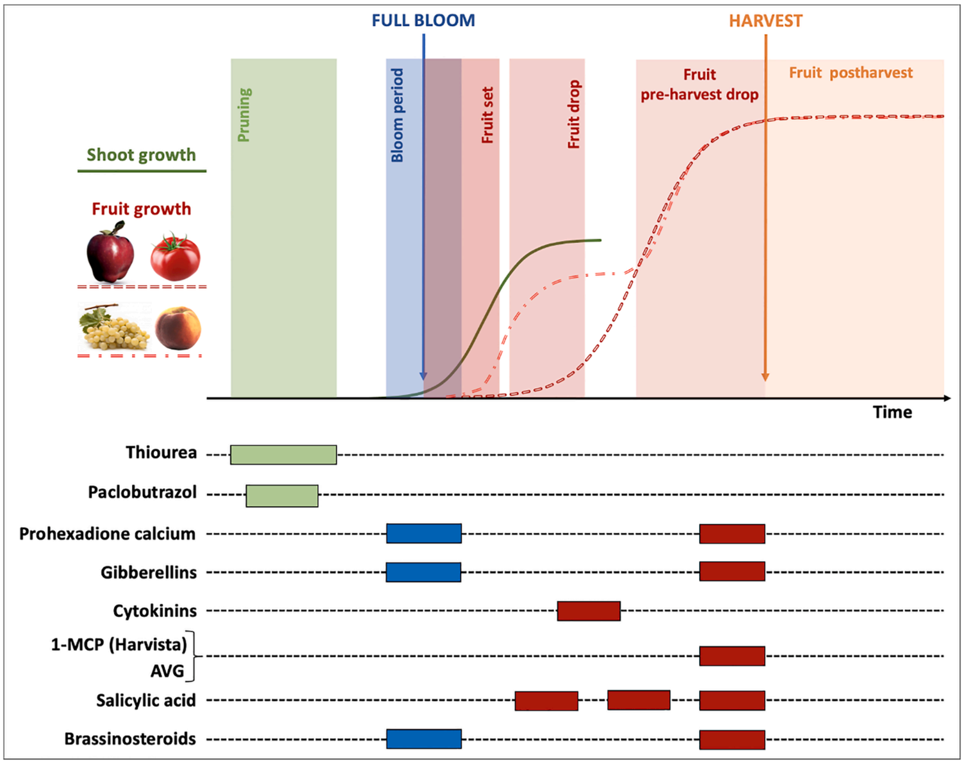

Fig. 1. Diagram showing when different PGRs are applied in the field in correspondence of different developmental stages, biological processes and agronomic/technical practices of fruit crops, indicated with boxes of different colors. The growth curves of shoots (single sigmoid, continuous green line) and fruits (simple and double sigmoid, dashed red lines), as well as full bloom (blue vertical line), and harvest time (orange vertical line) are reported.

modified atmosphere, packaging, etc.). Detached fruits have a high water content and they consequently react to the above-mentioned postharvest conditions by slowing down their general metabolism. The postharvest responses depend on several factors, primarily genotype and applied conditions, and are the result of physiological mechanisms strongly involving plant hormones. Considering specifically fruits, ripening and senescence are the developmental stages affected and that must be delayed by the applied postharvest conditions. In this context the plant hormone ethylene plays a major role and, indeed, control of the synthesis and action of this hormone is a main goal in postharvest science (Graham et al., 2012; Pech et al., 2012). In addition to the applied physical methods (low temperature, low oxygen and high carbon dioxide concentrations), this result may be achieved, for specific crops, by applying (alone or in combination with other treatments/conditions) the ethylene antagonist 1-methylcyclopropene (1-MCP) one of the most effective postharvest-applied PGRs, which induces positive and strong responses in terms of ripening and senescence delay in different fruit species (Blankenship and Dole, 2003; Li et al., 2016b; Watkins, 2008).

In addition to storage protocols and conditions, the postharvest behavior of fruit crops also depends on preharvest factors and the developmental stage of the product at harvest. This implies that growth and development processes and the associated hormonal balance characterizing these processes in the field may affect the progress and evolution of the latest developmental stages, but also the responses of the specific crops to the imposed storage conditions and, more in general, postharvest life. The use of PGRs in the field for inducing resistance to biotic and abiotic stresses, regulating vegetative growth, fruit set and yield, crop quality and composition, fruit ripening and antioxidant properties, therefore has an impact on the general physiology throughout the life cycle, including the postharvest phase (Fig. 1). This review reports the observed effects on postharvest behavior and physiology of fruit crops after PGR application in the field during cultivation.

2. PGRs applied to control vegetative growth

Excessive vegetative growth limits fruit production as there is an inverse relationship between shoot growth and reproductive organs development (Greene, 2010). In several fruit species, excessive vegetative growth leads to an ineffective and unproductive tree structure (Greene, 2010; Primo-Millo and Agustí, 2020). This effect is the result of an unbalanced relationship between primary assimilation of photosynthetic “source” tissues and the metabolic needs of non-photosynthetic “sink” organs (Falchi et al., 2020). In addition to the need to establish a balance between vegetative and reproductive activities, the control of vegetative growth is strategic for the appropriate management of orchards in several fruit trees. PGRs such as paclobutrazol (PBZ) are effective in inhibiting gibberellins (GAs) biosynthesis and were applied from the mid- 1980s to early 1990s to reduce shoot growth and, at the same time, improve fruit number and their shape and composition in several species (Yadav et al., 2005). Specific studies on the effect of vegetative growth retardants on fruit postharvest are very few: Chen et al. (1989) observed that pears harvested from PBZ-treated trees were capable of ripening normally after cold storage. Treatments with prohexadione calcium (pro-Ca), another inhibitor of GAs biosynthesis, were able to reduce chilling injuries (CIs) in cold-stored peppers and tomatoes (Aghdam, 2013; Lurie et al., 1994). Possible explanations for PBZ ability to counteract CIs derive from the increase of antioxidant enzyme activities and free-radical scavengers’ content (Kopyra and Gwozdz, 2003; Lin et al., 2006), as well as the increment of soluble carbohydrates and proline levels (Ghasemi-Soloklui et al., 2014). Positive effects have been related to a delay in pulp firmness loss in PBZ-treated fruit, and the maintaining of membrane integrity in pro-Ca-treated fruit. These results suggest that in trees treated with PBZ or Pro-Ca, fruit ripening and senescence processes are delayed due to increases in cytokines and polyamines content (Basiouny, 1994; Hunter and Proctor, 1992)

Vegetative growth can also be controlled by strigolactones (SLs).

These carotenoid-derived plant growth regulators can induce secondary growth in stem and root tissues (Agusti et al., 2011), control shoot architecture (Brewer et al., 2009), promote seed carbohydrate metabolism (Li et al., 2016a) in Arabidopsis, and promote flower and fruit size of tomato (Kohlen et al., 2013). SLs also regulate the senescence process of plants in concert with ethylene (Ueda and Kusaba, 2015), anthocyanin biosynthesis in grapevine berries (Ferrero et al., 2018), and the response of pea and Arabidopsis to CIs (Cooper et al., 2018). The latter action seems to be related to the ability of SL to maintain the homeostasis of reactive oxygen species (ROS) (Decros et al., 2019). Similarly, cold-stored strawberries (Huang et al., 2021a) and oranges (Ma et al., 2022) treated with SLs showed a longer shelf-life as consequence of improvements in the antioxidative system and the metabolism of phenylpropanoids, nitric oxide and hydrogen sulfide. The same results can also be obtained by bagging fruits during their development. Zhang et al. (2015) reported that fruit bagging changes the microclimate (higher temperature and humidity) around the developing fruits which causes a ROS increase. To counteract this ROS increase, the antioxidative system is activated through the induction of superoxide dismutase and catalase enzyme activities as observed in cold-stored mangoes (Nadeem et al., 2022) and apples (Onik et al., 2021). It is still unclear if this behavior is caused by changes in the hormone profile, including SLs, as suggested by Aghdam et al. (2018).

Pruning techniques have been used to manipulate the flux of metabolites and hormones to modulate fruit ripening and, consequently, the fruit postharvest physiology. By means of a transcriptomic approach (RNA-seq), Peng et al. (2022) demonstrated that an upregulation of genes involved in ethylene biosynthesis and abscisic acid (ABA) and brassinosteroids (BRs) responses, as well as a downregulation of genes involved in indoleacetic acid biosynthesis occurred in grape berries following shoot girdling. These hormonal changes are necessary for starting the berry ripening (vèraison stage), as reported by several authors (Böttcher et al., 2013; Fortes et al., 2015; Ziliotto et al., 2012). Therefore, girdling promotes grape berry ripening by altering the hormonal status of berries at early vèraison stage. Recently, girdling and forchlorfenuron (CPPU) application, a cytokinin normally used to increase fruit size (Koprna et al., 2016), have been applied to improve the quality and storage life of Hayward kiwifruit (Ghasemnezhad and Aminifar, 2021). Summer trunk girdling combined with CPPU spray induced the production of fruit with higher dry matter percentage, soluble solids and SSC/TA at harvest time, and the lowest fruit weight loss with the highest fruit tissue firmness at the end of three months storage time. The postharvest effects of PGRs have also been evaluated in relation to different pruning times in Indian jujube (*Ziziphus mauritiana*) cultivated in arid conditions (Shashi et al., 2022). Results pointed out that the effects of the two applied technical protocols (different pruning time and the application of thiourea or salicylic acid, SA) did not display significant interactions, while a significant reduction of postharvest weight loss and fruit spoilage were observed when they were applied separately. To obtain the best results, pruning has to be timely, and thiourea should be preferred over SA. In fact, the application of thiourea, by altering carbohydrate metabolism, protein synthesis, and neutralization of organic acids appears to be more adequate for improving the shelf-life (Akladious, 2014).

3. Effects of PGRs employed for controlling flower and fruit thinning, fruit set and growth

Flower and fruit thinning PGRs are applied to ensure proper crop load and return bloom in the following year. In most cases their final effects on fruit storability after harvest largely depend on quality attributes imparted by these PGRs on fruits either indirectly by the reduction of crop load, and, consequently, of the competition between vegetative and reproductive growth, and/or directly by the promotion of fruit growth by the hormone-responsive stimulation of cell divisions and/or enlargement.

Chemical fruit thinning with PGRs has been most intensively studied on apple fruit thanks to the positive results obtained in this species compared to other fruit crops. Depending on the variety and time of application, active auxins (1-naphthaleneacetic acid,NAA; its amide, NAAm), cytokinins (6-benzylaminopurine, 6-BA; thidiazuron,TDZ; forchlorfenuron, CCPU) and gibberellins ($GA3+4+7$), as well as ethylene promoting compounds (e.g. 1-aminocyclopropane-1-carboxylate, ACC; ethephon), act as thinners when they are applied after petal fall or at an early fruit developmental stage, immediately after fruit set and before the “june drop”. Conversely, GA inhibitors such as Pro-Ca, when applied in the same developmental window may act as fruit set enhancers through the control of vegetative growth (as reported in the previous section), therefore, leading to a more balanced allocation of carbohydrate resources between vegetative and reproductive activities (Greene, 2007).

Link (2000) categorized the fruit quality attributes that may be impacted by thinning PGRs into two major groups. The first includes size, color and skin performance, firmness, sugar content and acidity. The second group includes inorganic compounds, in particular calcium and potassium content.

The increase in size linked to chemical thinning has often been associated with lower calcium levels and consequently to an impaired potassium/calcium ratio. These latter compositional changes are often accompanied by higher susceptibility to calcium-dependent postharvest disorders such as bitter pit and internal breakdown (Elfving and Cline, 1993; Koukourikou-Petridou et al., 2007). The effects of thinning PGRs are diverse and cannot be generalized. Koukourikou-Petridou et al. (2007) showed that the combined use of cytokinins (CKs) and GAs, applied on early developing Red delicious apples, delayed fruit senescence during postharvest, and led to increased flesh firmness and acidity and to a lower incidence of internal breakdown after storage. Consistently, Basak (1999) reported that the application of benzyladenine as a fruit thinner increased fruit firmness and reduced rotting and shriveling of apples during storage, while it increased the incidence of brown core. On the other hand, treatments with CPPU or GA4 and GA7, applied to enhance fruit set, stimulated and reduced, respectively, the russeting of apple parthenocarpic fruits. These PGRs increased the frequency of Ca-deficiency symptoms (Bangerth and Schröder, 1994). In agreement with these findings, the post-bloom application of the shoot growth retardant Pro-Ca resulted in an increased calcium content of Braeburn fruits and decreased incidence of bitter pit and skin cracking at the end of their postharvest storage (Do Amarante Et Al., 2020).

Considering that fruit skins with russet symptoms or poorer wax layers are more permeable to water vapor, the preharvest use of PGRs to control russet may have an important impact on the subsequent postharvest life of fruits due to reduced water loss and shriveling. In fact GAs, commonly used to reduce russet formation on apple (Barandoozi and Talaie, 2009), pear (Yuri and Castelli, 1998), and grapes (Xu et al., 2019) (reviewed by Winkler et al., 2022), when applied on self-pollinated early developing apple fruits to improve size and shape resulted in increased thickness of the wax layer and lower postharvest fruit water loss and higher storability (Liu et al., 2022a). Consistently with these findings, in seedless grape varieties, the CK-like substituted phenylurea compounds CPPU and TDZ, used at fruit set to increase berry and cluster size, have been reported to increase storability by delaying maturity and senescence and by reducing rachis drying and berry shrivel during postharvest (Reynolds et al., 1992). The combined use of GA and CPPU after full bloom was shown to prevent russet development in table grapes and may exert similar postharvest effects (Xu et al., 2019).

Thus, some fragmentary evidence exists linking the use of PGRs, applied after petal fall with the purpose of controlling fruit thinning, fruit set or shape/appearance, with the subsequent storability and quality of fruits during postharvest. However, the effects of such PGRs on postharvest life of fruits have not been systematically studied. While a large body of literature is available on the influence of thinning on fruit quality at harvest, information concerning the postharvest storage consequences is very limited and sparse, especially concerning physiological and biochemical aspects.

4. PGRs applied to control ripening and improve fruit composition at harvest

The PGRs that are applied to accelerate or delay fruit ripening, control abscission and the composition and biochemical features of mature fruit at harvest are based on different hormones and their interplay/cross talk.

4.1. Ethylene-related PGRs

Among the different PGRs effective in inducing physiological responses in fruit crops, those related to ethylene are of particular interest, also considering the effects occurring during the postharvest phase.

An ethylene-releasing compound is Ethrel® (containing ethephon as active compound), while commercial products inhibiting ethylene biosynthesis and perception are ReTain® and Harvista®, containing AVG (aminoethoxyvinylglycine) and 1-MCP as active compounds, respectively. In plant tissues ethephon is directly transformed to ethylene, while 1-MCP is an antagonist of ethylene receptors, and AVG is a potent inhibitor of ACC synthase enzyme activity, which catalyzes the formation of ACC, the precursor of ethylene. By applying these PGRs to fruit crops in the field is possible to achieve a better management of harvest procedures in species requiring a limited/delayed natural drop, and in other species that benefit from a mechanical harvesting facilitation. Ethylene is involved in organ abscission by activating the abscission zone (AZ) and inducing cell wall and middle lamella degradation that results in fruit detachment (Bonghi et al., 2000; Roberts et al., 2002; Arseneault and Cline, 2016). In some apple varieties the early activation of the AZ leads to the preharvest drop (PHD) of mature fruit. When applied within one or two weeks before the anticipated harvest date, AVG (ReTain®) can reduce PHD in different varieties (Greene, 2005; Liu et al., 2022b; Özkan et al., 2016; Yildiz et al., 2012; Yuan and Carbaugh, 2007). Similarly, 1-MCP (Harvista®) treatment can effectively prevent apple PHD, with an optimization of harvest time up to two weeks and outperforming AVG-driven PHD control in some cultivars (Liu et al., 2022b; Sakaldas and Gundogdu, 2016; Yuan and Carbaugh, 2007; Yuan and Li, 2008).

These preharvest treatments aimed to limit fruit abscission may have specific postharvest effects on fruit quality traits. In apples, they can maintain higher firmness levels (Lee et al., 2019; Özkan et al., 2016; Sun et al., 2021; Tomala et al., 2022, 2020; Yildiz et al., 2012). This is the result of the recognized effect of ethylene suppression on the expression and activity of specific cell wall enzymes (e.g. polygalacturonases) (Tacken et al., 2010). A hypothesis of the presence of a developmental clock measuring cumulative ethylene effective in controlling apple fruit cell wall disassembly and softening was proposed by Ireland et al. (2014). According to this hypothesis, treatment limiting ethylene biosynthesis and /or perception in the field are also effective in altering the ethylene-dependent postharvest ripening processes.

Generally, higher acidity levels have also been observed both at harvest, and during storage and shelf-life, as a result of a general delay in ripening. In some cases, however, these effects recorded at harvest disappear during storage (Yoo et al., 2019). The effectiveness of these treatments appears to be strongly related not only to the specific apple cultivar, but also to the time gap between the treatment and harvest (Małachowska and Tomala, 2022).

Both AVG and 1-MCP treatments applied before harvest have been reported to significantly affect apple ripening, decreasing the respiration rate and increasing the starch index (Al Shoffe et al., 2021; Doerflinger et al., 2019; Elfving et al., 2007; Lee et al., 2019; Sun et al., 2021). The reported results clearly demonstrate the effects of such field treatments on postharvest carbohydrate metabolism via modulation of the activity of both gene and enzymes related to sugar metabolism, such as amylases, sucrose-phosphate synthases, and invertases, down-regulated/inhibited by the treatments. However, based on the ripening index of the treated fruit the effect on sugars can be negligible, with lower effect on less ripe fruit (Thammawong and Arakawa, 2007).

Positive effects of 1-MCP and AVG field treatments on reduction of storage physiological disorders have been reported. Treated apples developed less watercore, greasiness, wrinkly skin defect, cracking, mealiness and soft scald symptoms (Algul et al., 2021; Argenta et al., 2018; DeEll and Ehsani-Moghaddam, 2010; Lee et al., 2019; Soethe et al., 2022; Steffens et al., 2005; Yuan and Li, 2008). However, preharvest 1-MCP treatments also increased the onset of shriveling defect in ‘Fuji’ apple (Lee et al., 2019) and bitter pit in ‘Honeycrisp’ (Al Shoffe et al., 2021).

The evaluation of the effects of these ethylene inhibitors/antagonists applied in the field on the appearance of physiological disorders or alterations during/after storage must always consider the effects that these treatments induce on fruit development and ripening physiology. Any deviation from the optimal ripening stage at harvest has profound effects on the incidence of postharvest behavior (Prange et al., 2011), and this may explain some of the contrasting effects of the ethylene-related PGRs application on apple trees reported in the literature.

Fruit color is often negatively affected by these PGRs, which can cause both a reduced pigment accumulation and/or an altered chlorophyll degradation (Argenta et al., 2018; do Amarante et al., 2022; Doerflinger et al., 2019). A decreased accumulation of anthocyanins has been reported in the apple peel of several cultivars treated with AVG (Özkan et al., 2016; Steffens et al., 2006), although this is not true for all varieties and can be avoided by applying optimized concentrations (Greene, 2005; Yildiz et al., 2012; Yuan and Li, 2008). The combination of AVG and NAA treatments, or the subsequent treatment with ethephon, appeared to mitigate this negative effect in some cultivars (Li and Yuan, 2008; Steffens et al., 2006; Whale et al., 2008; Yuan and Carbaugh, 2007; Yuan and Li, 2008).

Ethylene has been recognized to be a key regulator of the biosynthesis of different volatile compounds, including esters (Schaffer et al., 2007). Decreased emission of volatile organic compounds (VOCs) such as alcohols and esters, has been reported after preharvest AVG application (Schultz et al., 2022). Also in this case, subsequent treatment with ethephon can mitigate VOCs deterioration by inducing, in particular, higher esters production (Schultz et al., 2022; Steffens et al., 2006).

Phenolic profile, together with total polyphenol content (TPC) and total antioxidant activity (TAA), can be negatively affected by these PGRs as well (Öztürk et al., 2013; Soethe et al., 2019). AVG application, when not performed at proper doses, may decrease TPC and TAA in apple skin due to reduced phenylalanine ammonia-lyase (PAL) enzyme activity (Öztürk et al., 2015; Soethe et al., 2022). A subsequent ethephon treatment can partly prevent this decrease of phenols.

Besides being useful to balance some negative effects of other PGRs, ethephon is normally applied in preharvest to optimize harvesting. In processing tomato, it can help synchronize ripening within fruit clusters, also inducing a more intense red color after the treatment and reducing the harvesting window to allow a single mechanical harvest (Logendra et al., 2004; Murray, 2001). However, despite only negligible effects being reported on quality parameters like pH and soluble solids, there is often a lower yield, and leaf senescence is also induced, making this protocol unsuitable for traditional greenhouse tomato that produces fruit clusters sequentially for months (Logendra et al., 2004; Renquist et al., 2001). Preharvest ethephon application has also been studied to optimize chili pepper harvest, improving the color by decreasing chlorophyll levels and increasing the concentration of the main carotenoid, namely capsanthin, while also enhancing spicy flavor by increasing capsaicin synthesis and reducing soluble solids accumulation (Krajayklang et al., 2000; Yang et al., 2011). Despite a strong effect of the cultivar having been observed, ethephon can also significantly modify non-climacteric fruit composition, such as in the case of olive and citrus.

In olive, where ethephon can be used to facilitate mechanical harvest, it can accelerate chlorophyll degradation, generally enhancing ripening while showing a negligible effect on oil acidity, peroxide levels and fatty acid profile (Royer et al., 2006; Touss et al., 1995; Tsantili and Pontikis, 2004; Zaen El-Daen, 2019). On the other hand, ethephon is applied to accelerate citrus peel color transition from green to orange, also increasing the peel lightness (Huang et al., 2021b; John-Karuppiah and Burns, 2010; Zhou et al., 2010). Lastly, ethephon application can enhance synthesis and accumulation of anthocyanins and soluble solids in grape (Ferrara et al., 2016; Shulman et al., 1985; Szyjewicz et al., 1984).

4.2. Salicylic acid, brassinosteroids and jasmonates

SA is an important phytohormone that serves as a critical signal molecule mediating immunity and plant growth. It regulates cell division and expansion also by interacting with other hormones such as auxin, GA and ethylene. In horticultural production, treatments with SA, or its conjugates acetyl salicylic acid (ASA), or methyl salicylate, in the field can induce fruit resistance against pathogens, which can also be maintained during the postharvest phase by eliciting systemic acquired resistance (SAR) (Romanazzi et al., 2016; Xiang et al., 2021). In addition, SA and its conjugates are effective in enhancing the antioxidant potential by stimulating the production of fruit total phenolics contents (Cui et al., 2020; Serna-Escolano et al., 2021), carotenoids (Martínez-Esplá et al., 2017) and ascorbic acid (Alrashdi et al., 2017), with benefits for consumers in terms of nutraceutical properties. The enhanced content of these metabolites and the increased antioxidant potential and activity of antioxidant enzymes (catalase, ascorbate peroxidase and peroxidase) induced by SA treatments in the field in pomegranate and plums is maintained after harvest (García-Pastor et al., 2020b; Martínez-Esplá et al., 2018, 2017). These observed effects could explain the better postharvest performance reported in several fruit species after SA treatments in the field (Gong et al., 2022). In addition, the positive postharvest effects induced by SA treatments could be the result of increased cell membrane integrity, a condition recognized to improve the tolerance of fruit to cold stress during storage. Indeed, reports of reduced CI incidence following refrigerated storage have been reported in SA-treated apricots (Cui et al., 2020; Fan et al., 2021), peaches (Ali et al., 2021), and pineapples (Lu et al., 2011). Other positive aspects in postharvest performance of SA-treated fruit, such as the maintenance of flesh firmness values as observed in peaches (Ali et al., 2021) and grapes (Champa et al., 2015), could be related to the interaction between SA and ethylene.

In kiwifruit ASA applications resulted in the suppression of ACC synthase and ACC oxidase activities and biosynthesis of ethylene, leading to a retarded climacteric rise in ethylene production and delayed fruit ripening and senescence (Zhang et al., 2003). This inhibitory effect of SA on ethylene biosynthetic gene expression and enzyme activity has also been observed in other fruit species, such as mango and apricot (Hong et al., 2014; Li et al., 2022b). Based on transcriptional and post-transcriptional analyses, a multidimensional system for inhibition of ethylene biosynthesis by ASA, inducing differential expression of some ethylene biosynthesis genes, as well as differential effects on protein activity on other targets has recently been proposed in kiwifruit (Wang et al., 2022).

BRs are a class of natural plant hormones that play important roles in regulating plant development, growth and stress resistance (Peres et al., 2019). The exogenous application of BR has increased the growth, yield and has reduced stress effects in different plant species. Considering fruit crops, most papers dealing with BRs report the effect of treatments (by dipping, immersion, spraying) on harvested produce, showing dual effects on fruit ripening. An acceleration of the process has been observed in tomato (Zhu et al., 2015), mango (Zaharah and Singh, 2011) and persimmon (He et al., 2018), mainly due to an enhanced ethylene biosynthesis, while in carambola fruit BR postharvest treatments effectively delayed ripening and senescence due to the inhibition of respiration rate and enhanced antioxidant system (Zhu et al., 2021), and in table grapes the firmness was maintained during storage (Liu et al., 2016). Considering field treatments, trials conducted on species other than fruit crops indicate that the physiological and biochemical effects of exogenous BR application are often concentration dependent. Very limited information is available concerning the effects of field treatments with BR or the synthetic analog brassinolide on the ripening and postharvest behavior of fruits. Foliar spray with 24-epibrassinolide during growth stages of strawberry plants enhanced fruit total antioxidant activity, total phenolics, and total anthocyanin contents of fruit at harvest. Treated fruits showed less decay, microbial count, weight loss and a longer postharvest life (Sun et al., 2020). If this effect induced by field treatments with BRs is also present in other fruit crops remains to be elucidated.

In the last decade jasmonates (Jas), particularly methyl jasmonate (MeJa), have frequently been applied as modulators of ripening and senescence processes in fruits (Wang et al., 2021). However, MeJA is mainly known for its ability to enhance the innate disease resistance of plants against pathogen infection and abiotic stress, such as cold (Singh et al., 2019). These actions are also a consequence of Ja capacity to modulate the biosynthesis of other phytohormones (Ahmad et al., 2016). Differently from BRs, application of MeJa in the field to modulate ripening is well documented, with effects that may be different in relation to the concentration used (García-Pastor et al., 2020a; Wang et al., 2021). Early applications of MeJa on peach fruit (56 days after full bloom) profoundly interfered with seed and mesocarp development, ultimately slowing down ripening (Ruiz et al., 2013). This effect is the result of a MeJa-modulation of biosynthesis and perception of ethylene and, to a lesser extent, with auxin, ABA and GAs. Later applications (two weeks before harvest) in plum resulted in fruit with higher firmness and antioxidants content (Karaman et al., 2013). Preharvest applications of MeJa reduced postharvest CI symptoms in pomegranate by 70% and increased the aril color (García-Pastor et al., 2020a).

MeJa effects seem to be the combined result of its direct and indirect actions. The maintenance of fruit firmness is a direct effect of MeJa because this molecule can enhance cell wall integrity (Chen et al., 2019; Li et al., 2017), while a longer color maintenance is an indirect effect due to more stable content of pigments such as anthocyanins or betacyanins (Mustafa et al., 2018; Yang et al., 2011). More recent investigations have increased the number of species in which MeJa delays fruit softening, including persimmon (Bagheri and Esna-Ashari, 2022), peach (Meng et al., 2009) and apple (Fan et al., 2022; Öztürk et al., 2014). However, other articles reported no or slight effect in mango (González-Aguilar et al., 2000), papaya (Bron et al., 2023; González-Aguilar et al., 2003) and tomato (Li et al., 2022a). All these results suggest that the MeJa effect on fruit firmness is species/cultivar-specific and dose-dependent. The initial idea that observed color was only due to a longer maintenance of pigments level has been revised. Combined treatment of MeJA and UV-B induced an increase of idaein (cyanidin-3-O-galactoside) content in apple fruit throughout a positive transcriptional control of anthocyanins biosynthetic genes (Ryu et al., 2022). A similar result was reported for peaches, where MeJa or prohydrojasmon treatments promoted anthocyanins biosynthesis by regulating sucrose metabolism during postharvest storage (Tang et al., 2022).

The mitigation of CIs in MeJa-treated fruit has been reported for several species (e.g. peach, lemon, orange, pomegranate, tomato and pepper (Wang et al. (2021) references therein) and it was attributed to the enhancement of antioxidant capability and membrane integrity as well as to the alteration of amino acids and fatty acids metabolism. These effects were magnified by the combination of MeJa and SA which can increase cell membrane stability in cherries by reducing the activity of membrane lipid degradation related-enzymes (Gu et al., 2022). Despite this large body of evidence of MeJA treatment on alleviation of CI after cold storage, the molecular mechanism of MeJA amelioration of postharvest fruit ripening and quality remains largely unknown. A

Table 1
PGRs field-used for fruit production and main effects in postharvest.

	Plant growth regulators	Active compound	Species (cultivars)	Time and dose of application	Effect in postharvest	Reference
PGRs applied to control vegetative growth	**Growth inhibitors**	paclobutrazol	Pears (d'Anjou and Bosc)	soil drench - 6 and 10 g/tree	Normal ripening after cold storage	Chen et al., 1989
		prohexadione calcium	Apple (Braeburn)	15 days after full bloom (FB) or five weeks before harvest (pH)- 300 mg/L	FB treatment induced a decrease of bitter pit and skin cracking Reduction of pigment accumulation	do Amarante et al.,2000
		prohexadione calcium	Tomato	attached berries mature green stage - 50–100 μM	Reduction of chilling injuries	Aghdam et al., 2013
	Cytokinins	forchlorfenuron (CPPU) and trunk girdling	Kiwifruit (Hayward)	summer girdling and CPPU 10 mg L/L	Reduction fruit weight loss and maintaining of fruit tissue firmness after three months storage time	Ghasemnezhad and Aminifar, 2021
	Thiocarbamide	thiourea and pruning	Indian jujube (Gola)	pruning and Thiourea (1000 PPM)	Reduction of weight loss and spoilage	Shasi et al., 2022
PGRs applied to control flower and fruit thinning, fruit set and growth	**Cytokinins**	forchlorfenuron (CPPU) and thidiazuron (+/- GA)	Grapevine (Sovereign Coronation and Summerland Selection 495)	shoots with berries (5–6 mm of diameter) - levels of CPPU or thidiazuron (1 mg/L)	Delay of fruit maturity and senescence	Reynolds et al., 1992
	Gibberellins	GA3, GA4/7 (Novagib)	Apple (Red Chief Delicious)	petal fall (for concentration see producers	Increase of total sugar, delay of decrease of total acidity and lower incidence of internal breakdown after 4 months of cold storage	Koukourikou-Petridou et al., 2007
		GA	Apple (Hanfu)	at central flower opened, and again 10 days later, 20 or 100 mg/ L	Increase of the wax layer thickness and reduction of the fruit water loss rate during storage	Liu et al., 2022a
		GA4/7 or Pro-Ca	Apple (Braeburn)	15 days after full bloom (FB) or five weeks before harvest (pH)- 300 mg/L	GA4+7 at FB increased while Pro-Ca inhibited the incidence of skin cracking and decay in the fruit	do Amarante et al., 2020
	Gibberellins + Cytokinins	GA4/7 and Benzyladenine (promalin and perlan) or kinetin	Apple (Red Chief Delicious)	petal fall (for concentration see producers)	Increase of total sugar, delay of decrease of total acidity and lower incidence of internal breakdown after 4 months of cold storage	Koukourikou-Petridou et al., 2007
PGRs applied to control ripening and improve fruit composition at harvest	**Ethylene biosynthesis and ethylene perception inhibitors**	1-methylcyclopropene −1MCP (Harvista)	Apple (Szampion)	7 days before harvest - 150 g/ha storage in 1.2% CO2, 1.2% O2 at 1 °C	Delay of fruit firmness loss	Tomala et al., 2020
		1-methylcyclopropene −1MCP (Harvista)	Apple (Starkrimson)	7 days before harvest - 1.8% 1-MCP	Inhibition of the starch degradation, delay of the increase of soluble sugar, reducing sugar, sucrose, glucose and fructose contents before 120 d of fruit storage	Sun et al., 2021
		1-methylcyclopropene −1MCP (Harvista) or Aminoethoxyvinylglycine (AVG)	Apple (Mcintosh, Empire)	Harvista 2 weeks before harvest (125 μL/L) AVG 4 weeks before harvest (823 g/ha)	Harvista more efficient in the delaying of the increase of internal ethylene concentration in comparison to AVG Reduction of pigment accumulation	Doerflinger et al., 2018
		1-methylcyclopropene −1MCP (Harvista) or Aminoethoxyvinylglycine (AVG)	Apple (Honeycrisp, Gala, Golden Delicious, JonaGold, Fuji, Soigent)	Harvista 1–2 weeks before harvest AVG 4 weeks before harvest	Variable effects of postharvest physiology disorders	Al Shoffe et al., 2021; Steffens et al., 2005; Yuan and Li, 2008; DeEll and Ehsani-Moghaddam, 2010; Argenta et al., 2018; Lee et al., 2019; Algul et al., 2021; Soethe et al., 2022

(*continued on next page*)

Table 1 (*continued*)

Plant growth regulators	Active compound	Species (cultivars)	Time and dose of application	Effect in postharvest	Reference
	1-methylcyclopropene −1MCP (Harvista) or Aminoethoxyvinylglycine (AVG)	Apple (Scarletspur Delicious)	Harvista 1–3 weeks before harvest (90 mg a.i./L) AVG 4 weeks before harvest (125 mg/L)	Harvista more efficient in the control fruit ripening during shelf-life in comparison to AVG	Elfving et al., 2007
	1-methylcyclopropene 1-MCP (Harvista and Smartfresh)	Apple (Fuji)	Harvista applied at 4 or 10 days before harvest combined with Smartfresh during postharvest - 12.6 kg/ha	Maintaining pulp firmness and total acidity Reduction of greasiness and watercore	Lee et al., 2021
Salicylic acid	salicylic acid (SA), acetylsalicylic acid (ASA), and methyl salicylate (MeSA)	Pomegranate (Mollar de Elche)	4 days before the first harvest - SA, ASA, or MeSa at 10 mM	Concentration of phenolics, anthocyanins, and ascorbic acid were maintained at higher levels in pomegranate fruit from treated trees than in controls during prolonged storage at 10 °C.	Garcia-Pastor et l., 2020b
	salicylic acid (SA), acetylsalicylic acid (ASA), and methyl salicylate (MeSA)	Plum (Black Splendor, Royal Rosa)	at pit hardening, (63 days after full blossom, DAFB), initial color changes (77 DAFB), onset of ripening (98 DAFB) - SA at 0.5 mM, ASA at 1 mM, and MeSA at 0.5 mM	During storage, fruit firmness, total acidity, and antioxidant compounds were at higher levels in treated, than in control plums	Martínez-Esplá et al., 2017, 2018
	salicylic acid (SA)	Pineapple (Comte de Poris)	Sprayed on fruit 15 days before harvest - SA 2	Reduction of Internal Browning	Lu et al., 2011
	salicylic acid (SA)	Peach (Flordaking)	at cell division, pit hardening or lag phase and cell enlargement stage - SA (1, 2 and 3 mM)	Reduction of fruit weight loss, soluble solid contents, membrane leakage, chilling injury, color development, disease and decay incidence	Ali et al., 2021
	methyl salicylate (MeSA)	Apricot (Kate)	72 and 74 DAFB - MeSA (0.05, 0.1, 0.2 mmol/l)	Reduction of Chilling Injuries	Fan et al., 2021
Salicylic acid and chitosan	salicylic acid (SA) and chitosan (COS)	Apricot (Xiaobai)	7 and 2 days before harvest - 0.05% COS or/and 1 mmol $L-1$ SA	Reduction of Chilling Injuries	Cui et al., 2020
Brassinosteroids	24-epibrassinolide (EBL)	strawberry (Sabrosa)	15 days after full bloom and at ripening stage just 2 days before harvest- EBL solution (0, 1, and/or 4 µM)	Lower decay, microbial count, weight loss, and a longer postharvest life	Sun et al., 2020

recent investigation carried out in peaches pointed out that MeJA treatment determines changes of methylation degree, at promoter level, for several genes involved in the onset of CIs (Duan et al., 2022). Although it is still not possible to attribute a causal relationship between DNA methylation changes and transcripts abundance, the authors suggest that the hypomethylation is associated with increased expression, which in turn contributes to ethylene production (PpACS1), fruit softening (PpExp1), volatile synthesis (PpAAT1 and PpCCD4) and fruit ripening (PpNAC1) after cold storage of peach fruit. This work provides new insights into the interplay between plant hormone, transcription regulation and epigenetic modifications, which can improve our understanding of physiological process occurring in stored fruit such as the development of CI after cold storage.

5. Conclusions and future perspectives

In this review we have reported the possible use of PGRs in preharvest and its impact on the fruit physiology during storage and a table summarizing the cited compounds and their main effects in postharvest is provided (Table 1).

The practical application of these PGR may vary in different countries, not only in relation to the effects on specific crops and the environmental conditions and cultivation practices, but also depending on the authorization released by the competent national authorities. For example, many of these substances cannot be used in organic farms. This aspect is a “hot spot” not only for the issues treated in this review, but also considering the general perspective for a more sustainable management of fruit crops. Promising and environmentally-friendly products could be those called natural plant biostimulants (PBs) that are defined “materials that, in minute quantities, promote plant growth”

(Rouphael and Colla, 2020). Few reports are so far available in the technical/scientific literature regarding the preharvest use of biostimulants to control the postharvest. After a foliar application of macroseaweed extract, B-group vitamins and alfalfa protein hydrolysate, Soppelsa et al. (2018) were able to significantly reduce the incidence of "Jonathan spot," the main postharvest disorder for this apple cultivar. Biostimulants containing hormones and minerals maintained the firmness higher in yellow melon, particularly when they were applied by fertigation (De Góes Et Al., 2021). These results are encouraging mainly in the view of the development of new generation of PBs able to effectively substitute chemical products.

In addition to PBs, other molecules can be interesting for preharvest applications, such as lysophosphatidylethanolamine (LPE). LPE has been reported to inhibit the activity of phospholipase D (PLD) in a highly specific manner (Ryu et al., 1997). PLD is known to be activated during ethylene-induced senescence and this activation leads to membrane breakdown (Wang, 2001). Based on this evidence, LPE has been applied to control ripening in several stored fruit such as banana (Ahmed and Palta, 2015), apple (Farag and Palta, 1991) and cranberries (Özgen et al., 2005). LPE has been used in preharvest to improve size and composition of cherries at harvest (Özgen et al., 2015), while no information is available on the effect of LPE application in preharvest on stored fruit. The identification of novel molecules for controlling postharvest physiological processes, more sustainable and with effects when applied in preharvest, is a mandatory step for improving the postharvest management and technology. In this context, a new approach has been developed for discovering new growth regulators based on a cross-species network analysis (Curci et al., 2022). Thirty potential novel growth regulators, isolated by comparing Arabidopsis, maize and poplar, have been confirmed to affect the leaf phenotype when mutated or overexpressed in *Arabidopsis*. These results could make it easier to transfer information and expand the PGRs toolbox from model plants to crops.

CRediT authorship contribution statement

E.J. Ordoñez Trejo: Writing – review & editing. **S Brizzolara:** Writing – review & editing. **V. Cardillo:** Data curation, Visualization. **B. Ruperti:** Conceptualization, Writing – review & editing. **C. Bonghi:** Conceptualization, Visualization, Writing – review & editing. **P. Tonutti:** Supervision, Conceptualization, Writing – review & editing.

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.

Data availability

No data was used for the research described in the article.

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