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Review

Physiological and molecular functions of brassinosteroids during fruit development, ripening, and postharvest damage of horticultural products: A review

Diego Alejandro Gutiérrez-Villamil, Stanislav Magnitskiy, Helber Enrique Balaguera-López *

Departamento de Agronomía, Facultad de Ciencias Agrarias, Universidad Nacional de Colombia, Bogotá 111321, Colombia

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A B S T R A C T

Fresh horticultural products satisfy the nutritional, and industrial needs of consumers worldwide. However, the lack of understanding of the fruit development process, the accelerated senescence process and the lack of postharvest technology in some regions, present a threat to the food and economic security of the food agribusiness. Brassinosteroids (BR) are plant hormones involved in the regulation of various physiological processes and have recently proven to be a viable post-harvest technology alternative to regulate the ripening and senescence of fruits and vegetables. In this review, the current state of BR research on fruit growth and development, physicochemical changes during ripening, and biotic-abiotic stress during the post-harvest life of horticultural products is presented. Furthermore, the review encompasses the effect of the application of exogenous BR and its relationship with molecular signaling on the processes mentioned above, including aspects such as methods, moments and BR analogues at the time of application, and the molecular mechanisms involved. This review proposes a basis for research of the physiological aspects of BR regulation in fruits and vegetables during their development and post-harvest period, and also points to a direction for in-depth investigation of the molecular mechanisms.

1. Introduction

Fresh horticultural products (fruits, vegetables, cut flowers, foliage) contribute to meeting the nutritional and industrial needs of consumers around the world. Fresh fruits and vegetables are rich in organic acids, carbohydrates, vitamins, minerals, and many phytochemicals that benefit health and are used to prevent consumer diseases (Yahia et al., 2019a); therefore, they represent an indispensable component of the daily human diet. The maturation process of horticultural products translates into physiological, biochemical, molecular, and structural modifications regulated by a hormonal signaling network to reach the optimal moment of consumption, or simply the deterioration and senescence of the product (Li et al., 2021). The process of senescence and deterioration occurs when optimal postharvest strategies are not in place to guarantee storage and preservation conditions for a long time.

Many horticultural products, especially those of tropical origin and located in developing countries, are lost and wasted in large quantities during post-harvest handling, leading to economic, food, nutritional and natural resource losses (Yahia et al., 2019b). According to FAO (2019), global losses of perishable horticultural products are estimated to reach up to 50% per year, of which between 20% and 40% are due to mechanical, microbial and physiological problems during postharvest operational techniques and the supply chain. Therefore, technologies, strategies and decisions must be implemented that reduce the loss of food and horticultural inputs. Recent research with some hormones and growth regulators has shown promising results in quality preservation, maturation and senescence delay, and generation of tolerance to physiological disorders in horticultural products (Wang et al., 2021; Castro-Cegrí et al., 2023; Chen et al., 2023; Zhang et al., 2023). Brassinosteroids (BR) are among the hormones that have achieved these results.

BR are polyhydroxylated steroids and plant hormones that signal during plant growth by regulating various physiological processes, including cell division, development and fertility, senescence, and tolerance responses to biotic and abiotic stress (Oh et al., 2020). Research in BR worldwide has increased in the last 20 years, and in some

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* Correspondence to: Departamento de Agronomía, Facultad de Ciencias Agrarias, Universidad Nacional de Colombia, Carrera 30 No 45-03, Bogotá A.A.14490, Colombia.

E-mail address: hebalagueral@unal.edu.co (H.E. Balaguera-López).

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countries the research development of this plant hormone has taken on great importance, which is reflected in the growing number of publications in specialized scientific journals (Fig. 1). Recently, more than 70 BR have been identified in plants, which can be classified according to the number of carbons in the side chain located at carbon number 17 of the main chain, such as C27, C28 and C29, with brassinolide, castasterone, and 24- epibrasinolide are the most representative and synthesized BR in plants (Bajguz et al., 2020). Furthermore, there are spirostane analogues of BR that arise from modifications in the steroidal core and side chain structure and can have biological activity (Duran et al., 2017).

In plants, three pathways lead to the production of BR, resulting in synthesis of types C_{27}, C_{28}, and C_{29} (Bajguz and Piotrowska-Niczyporuk, 2023). Early steps of the BR synthesis include formation of isopentenyl pyrophosphate (IPP), which can be produced via the MEP pathway and the MVA pathway (Wang et al., 2017). Later steps include synthesis of geranyl pyrophosphate and, further, of the isoprenoid squalene (Bajguz and Piotrowska-Niczyporuk, 2023). Squalene is converted by action of squalene epoxidases (SQE) and cycloartenol synthase (CAS1) to cycloartenol, which is the first committed precursor in sterol biosynthesis in plants (Rozhon et al. 2019). Cycloartenol is further metabolized to 24-methylenelophenol, where sterol biosynthesis divides in two parallel routs of BR formation, the late C-6 oxidation pathway and the early C-6 oxidation pathway (Rozhon et al., 2019; Parada et al., 2022). The C29 pathway generates β-sitosterol and stigmasterol as end products, while the C28 pathway leads to formation of campesterol, which serves as a precursor for hormone brassinolide (BL) (Rozhon et al., 2019; Vukašinović et al., 2021). Additionally, the early C-22 oxidation pathway could be the main route in BR biosynthesis in some species, such as *A. thaliana* (Rozhon et al., 2019).

According to Xia et al. (2023), the principal steps in the BR synthesis include the 5α-reduction, C-22 hydroxylation, C-3 oxidation, and C6-oxidation catalyzed by DEETIOLATED 2 (DET2), DWARF 4 (DWF4), CONSTITUTIVE PHOTOMORPHOGENESIS AND DWARFISM (CPD), cytochrome P450 CYP85A, respectively. Kour et al. (2021) mentioned that the biosynthetic pathway of BR is limited at various steps through regulatory feedback mechanisms, which permits maintaining the levels of BR in plant cell by the expression of genes for BR degradation. In particular, expression of the *CPD*, *DET2*, and *DWARF4* genes is modulated as a part of the feedback mechanism (Kour et al., 2021).

The signaling and mechanisms of action of BR begin when they are perceived by the receptor BRASSINOSTEROIDE INSENSITIVE 1 (BRI1) and the kinase associated with BRI1 (BAK1), which will activate the accumulation of the transcription factors BRASSINAZOLE-RESISTANT 1 – 2 (BZR1, BZR2) and initiate the regulation of the expression of BR-associated genes (Zhu et al., 2013).

BR can regulate the ripening and senescence of climacteric and non-climacteric fruits, such as apple (Liu et al., 2022), tomato (Meng et al., 2023), strawberry (Chai et al., 2013), grape (Symons et al., 2006) and others. These studies show that BR can inhibit or promote ethylene production during fruit ripening, and it has been proven that this effect is a function of the applied concentration of BR, which influences the activity of the transcription factor BZR1 and represses genes associated with ethylene biosynthesis (Ji et al., 2021). On the other hand, exogenous application of BR confers tolerance to chilling injury and prevalence of biotic diseases during refrigerated storage in several commercial species (Furio et al., 2019; Islam et al., 2022).

The transcriptional and post-transcriptional signaling by BR affects various physiologically important processes (Wang et al., 2017). An example of the BR effect on post-translational control of enzymes includes altering cell wall properties to control cell elongation (Wolf, 2020). BR signaling alters cell wall properties through the expression of the BR target genes and the post-translational control of enzymes controlling extracellular pH and cell wall synthesis (Wolf, 2020). Additionally, BR signaling controls the cell wall properties through regulation of microtubule alignment as a factor of cellulose arrangement and cell wall architecture (Wolf, 2020). In hormone metabolism, BRs promote the expression of the enzymes ACO and ACS to synthesize ethylene, where BRs control the transcriptional and post-transcriptional regulation of ethylene production by lengthening the half-life of the ACS protein (Khan et al., 2023). BRs accelerate the expression of genes associated with ACS, stabilize ACS proteins by breaking down 26 S proteasomes, and promote the post-transcriptional synthesis of ACS (Khan et al., 2023).

Although there is a review on the biological functionality of BR on postharvest physiology (Ali et al., 2019), an update is required on the biochemical and molecular advances that illustrate the mechanisms of BR on growth, maturation, senescence, and tolerance of biotic and abiotic stresses of horticultural products, and the factors that affect it, such as fruit metabolism, doses, application methods and analogues. Therefore, the objective of this review is to present the current status of the effect of exogenous BR on the growth, maturation, postharvest physiology and biotic or abiotic stress of horticultural products, and its relationship with the molecular response. This review has been divided into four different sections: (1) The role of BR in fruit growth and quality (pre-harvest treatments); (2) BR application and physicochemical changes during ripening; (3) tolerance mechanisms to chilling injury (abiotic stress) and disease prevalence (biotic stress) under the application of BR in the postharvest; and (4) conclusions and future perspectives.

2. Brassinosteroids in pre-harvest: growth and fruit quality

Although it is true that one of the functions of brassinosteroids (BR) is to regulate cell division and expansion (Oh et al., 2020), and the reproductive stage from ramification, flowering and sterility of some plants (Li and He, 2020), there is little evidence that BR can regulate the growth of most fruits. In this regard, Balaguera-López et al. (2020) indicate that BR and other hormones produced in seeds enhance the growth and quality of fruits. Likewise, some research carried out has confirmed the role of BR during this process; however, a specific effect has been seen for each species (Table 1).

The pre-harvest application of BR promoted growth and increased fruit quality (Table 1). These results were evident in the increase in the length, width, volume and weight of the fruit, a higher concentration of sugars, antioxidants and phenols, and lower organic acids (Serna et al., 2012; Thapliyal et al., 2016; Khatoon et al., 2021). There are some studies that explain the mechanisms through which BR promote fruit growth. In tomato, the expression of the *Dwarf* gene (involved in the biosynthesis of castasterone [CS], the immediate precursor of brassinolide [BL]) has been detected during all stages of fruit development, especially during seed development, and has correlated with a high endogenous concentration of BL at all stages of development (Montoya et al., 2005). This increase in BR concentration in fruits has been directly associated with the expression of genes involved in cell division. Fu et al. (2008) found that the application of epibrassinolide (EBR) to the ovary of the cucumber flower increased the expression of cyclin (*CDK*) genes, related to cell division (*CycA, CycB, CycD3;1, CycD3;2* and *CDKB*), which induced parthenocarpic growth of the fruit. Furthermore, these authors reported consistent results when brassinazole (BR inhibitor) was applied. In sugar apple, the induction of parthenocarpy in fruits was also found when applying BL (Mostafa and Kotb, 2018).

It has been demonstrated that BRs are essential for cell division, expansion, and differentiation, and their regulation depends on the BR levels and signaling (Zhiponova et al., 2013; Oh et al., 2020). Additionally, the BR-insensitive tomato mutant *abs1* exhibited a dwarf phenotype and smaller fruits, which was associated with a reduced number and size of cells, altered hormone content, and suppressed expression of cell development genes (Mumtaz et al., 2022). In strawberry, a high BR content was found in early stages of fruit development, and silencing of the transcription factor BZR1 affected normal growth and coloring (Chai et al., 2013). About, Yang et al. (2024) demonstrated

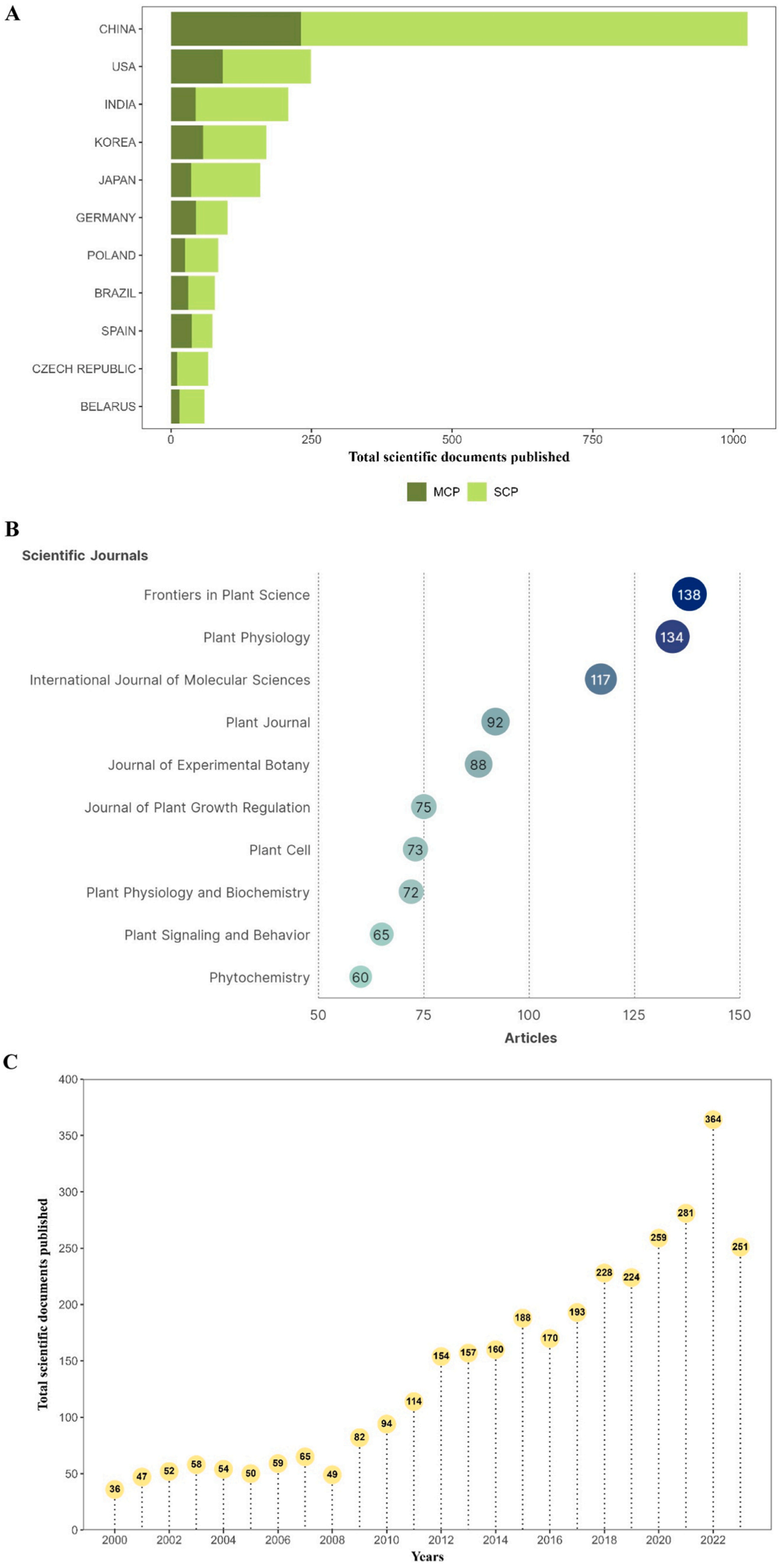

Fig. 1. (A) Main countries leading scientific production on brassinosteroids (BR) between 2000 and 2023. Collaboration within (SCP) and between countries (MCP). (B) Scientific journals that have published the most reports on BR up to 2023 are listed. (C) Global scientific production of BR over the years is presented. The data were extracted from Scopus and analyzed using the R bibliometrix library (v. 2023.06.2.561).

Table 1
Effect of postharvest application of BR on fruit growth and development. BL: brassinolide. EBR: 24-epibrassinolide. HBR: 28-homobrassinolide. BB-16, DI-31 and DI-100: spirostanic analogs (3β-5α-25(R)-dihydroxy-spirostan-6-one). * The original units were retained.

Horticultural species	BR analogue and dose	Application method	Phenological stage of application	Effect on fruit growth	References
Sugar apple (*Annona squamosa*)	2.1 μmol L^{-1} BL	Foliar spraying for five times	During anthesis	Generated parthenocarpic fruit growth. Maintained fruit size	Mostafa and Kotb (2018)
Cherry (*Prunus avium*)	2 μmol L^{-1} HBR	Foliar spraying	During fruit growth	Did not affect berry size. Accelerated color change	Mandava and Wang (2016)
Strawberry (*Fragaria* × *ananassa*)	*0.1 – 0.3 mg L^{-1} BR unspecified	Foliar spraying for three times	Vegetative growth, flowering, and fruit set	Increased fruit volume, sugars, and phenols	Khatoon et al. (2021)
Yellow passion fruit (*Passiflora edulis* f. *flavicarpa*)	0.24 μmol L^{-1} BB-16	Foliar spraying for five times	Third week after the first flower appearance	Didn't show changes in the diameter, length, and thickness of the fruit epidermis. Increased total soluble solids	Gomes et al. (2006)
Cantaloupe (*Cucumis melo* var. *cantalupensis*)	0.21 μmol L^{-1} EBR	Foliar spraying	Vegetative growth and flowering	Increased fruit weight and volume, and postharvest quality	Amarasinghe et al. (2023)
Cucumber (*Cucumis sativus*)	0.2 μmol L^{-1} EBR	Foliar spraying for two times	From ovarian initiation to 4 d after anthesis	Induced parthenocarpic fruit growth. Increased fruit length and expression of genes related to cell division	Fu et al. (2008)
Pear (*Pyrus pyrifolia*)	*0.5 – 1 mg L^{-1} BR unspecified	Foliar spraying for three times	During fruit growth	Increased fruit length, width, volume, and weight. Lower acidity and more sugars	Thapliyal et al. (2016)
Pepper (*Capsicum annuum*)	18.1 – 27.1 μmol L^{-1} DI-31 and DI-100	Foliar spraying for ten times	Vegetative growth, flowering, and fruit set	Increased fruit fresh weight and yield. Lower content of organic acids, sugars and antioxidant capacity	Serna et al. (2012)
Table grape (*Vitis vinífera*)	*1 mg L^{-1} BR unspecified	Cluster spraying for two times	During fruit growth	Increased berry length, width, firmness, soluble solids, antioxidant, and phenols. Reduced acidity	Champa et al. (2015)
	4.2 μmol L^{-1} BL	Cluster spraying for three times	Before fruit set and during fruit growth	Increased berry and bunch weight, volume, and diameter. Increased postharvest and nutritional quality	Belal et al. (2022)

that eggplant plants deficient in endogenous BR levels (due to the overexpression of the *GhPAG1* gene, an enzymatic inhibitor of BR) exhibited reduced pericarp cell size, diminished anthocyanin accumulation, and decreased concentration and expression of auxin (indole-3-acetic acid, IAA) and jasmonic acid (JA) biosynthetic genes in the fruits.

On the other hand, the effects of BR on fruit growth could be due to increased pollen fertility. For example, application of BR to mango trees increased the fruit set by increasing the pollen fertility; 24-epibrassinolide applied as a spray at 0.1 μmol L^{-1} during pre-flowering increased inflorescence length, the number of flowers per inflorescence, and the fruit set (Tepkaew et al., 2022). Additionally, BR modulate stomatal closure in plants, interacting with signaling molecules such as hydrogen sulfide H$_2$S and nitrogen oxide-NO (Hu et al., 2021), indicating that BR have direct influence on fruit growth, affecting transpiration and photosynthesis in unripe fleshy fruits.

The above-mentioned results suggest that BR have a potential signaling function in the regulation of fruit development, by inducing the expression of genes involved in cell division, and interaction with other growth plant hormones (Fig. 2). Given that BR and auxin can have a positive effect on the expression of the same genes, the positive effects of BR on fruit growth can be attributed to a synergistic action of BR and auxin (Fenn and Giovannoni, 2021). It should be noted that the induction of parthenocarpy in fruits is regulated by a complex hormonal interaction that mainly involves auxins, gibberellins, and cytokines (Sharif et al., 2022), and the role of BR in causing parthenocarpy may be related to the synergism and antagonism between these hormones.

In some research, a positive effect has not been found with pre-harvest applications of BR on fruit growth, as was the case for passion fruit (Gomes et al., 2006; Mandava and Wang, 2016). In these cases, several aspects can influence the results, such as the dose, the time of application, the analogue, and the sensitivity of the horticultural species. Given this, Su et al. (2021) showed that loquat hybrids that produced larger fruits (in terms of length, diameter, and number of cells) were characterized by higher concentrations of BR but lower expression of the transcription factor *BZR1* (*EjBZR1*). By overexpressing *EjBZR1* in this variety, loquat fruits decreased the size and number of fruit cells, which is because *EjBZR1* in abundance binds to the promoter site of the *EjCYP90A* gene (related to BR biosynthesis) and inhibits its expression (Su et al., 2021). Therefore, when BR-mediated transcription (*BZR1*) is excessively increased in fruits, BR biosynthesis could be inhibited through an autocatalytic route, which would occur when very high concentrations of BR are applied pre-harvest. In tomato fruits, overexpression of the BR membrane receptor (*SlBRI1*) did not increase fruit weight (Nie et al., 2017). It is recommended to carry out trials where a wide range of minimum and maximum doses reported in the literature are evaluated according to the BR analogue to avoid negative effects on fruit growth.

On the other hand, the times of BR application are most frequent during the anthesis stage and fruit growth, with different concentrations depending on the analogue and the species (Table 1). However, this is not the case in all species. In strawberry and paprika, the frequency of BR applications during vegetative, flowering and growth stages increased fruit size (Serna et al., 2012; Khatoon et al., 2021). The opposite was reported in melon, where applying BR during fruit growth decreased its volume, an effect that is not evident if BR applications are only carried out during vegetative growth and flowering (Amarasinghe et al., 2023). These results could be related to what was explained in the previous paragraph, whereby the sensitivity of the species to BR during fruit development can bring negative or positive effects due to the mechanism of action of BZR1. Therefore, more studies are needed for each species at different application times and with different doses to characterize the sensitivity of BR on fruit development.

3. Influence of exogenous brassinosteroids on the control of ripening and senescence of horticultural products

BR can influence the regulation of ripening and senescence of horticultural products by affecting physicochemical characteristics such as color, flavor, and nutritional content during postharvest (Table 2). In this section, a physiological, biochemical, and molecular contextualization will be given of how BR can influence ripening and interact with ethylene.

Various studies have shown that the postharvest application of BR increases the production of ethylene and respiration of horticultural products and, therefore, accelerates ripening (Zaharah et al., 2012; Mazorra et al., 2013; Zhu et al., 2015a; He et al., 2018; Fang et al., 2021). The opposite effect has also been evidenced in other species,

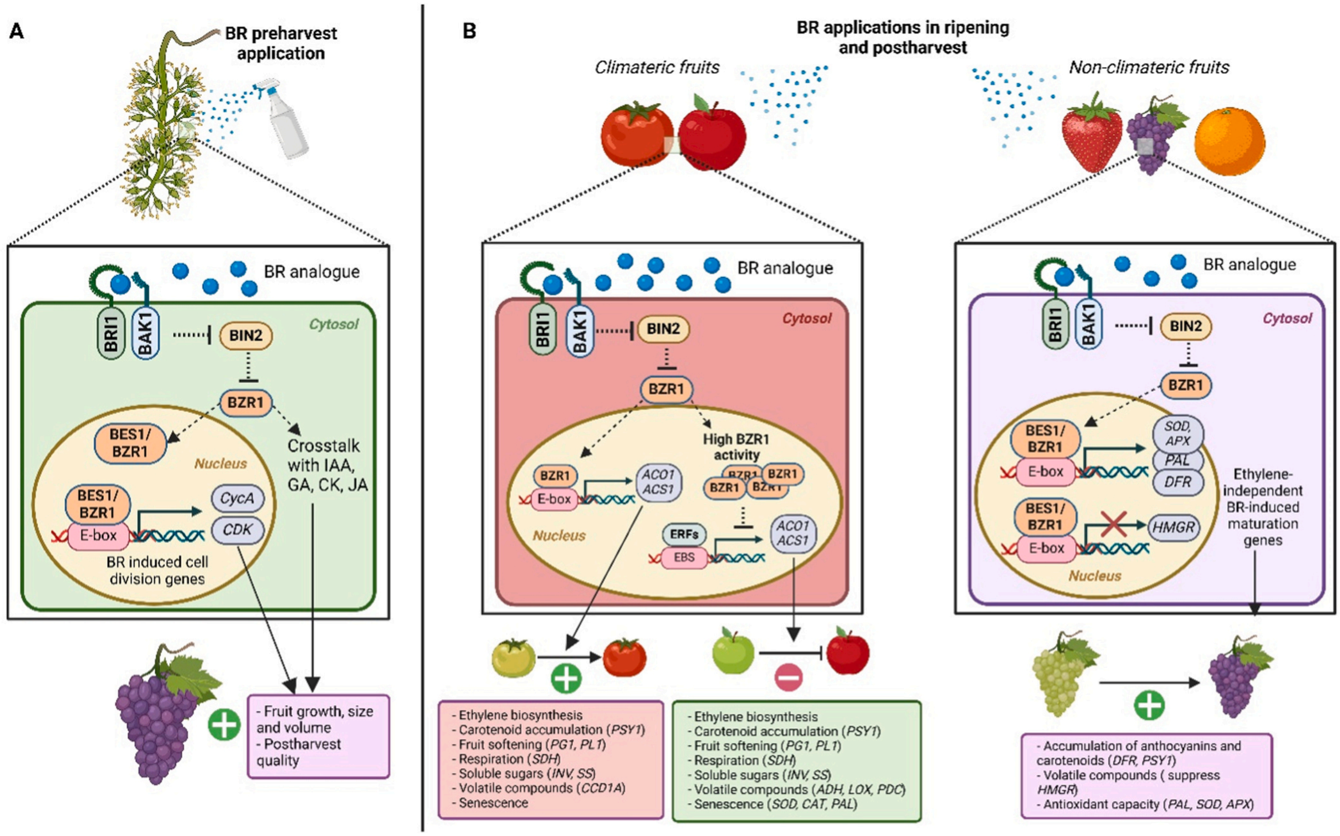

Fig. 2. Model of the molecular mechanism of action of BR on **(A)** fruit development. The BR analogue binds to the BRI1 receptor and its co-receptor kinase BAK1, which inhibits BIN2. BIN2 is responsible for phosphorylating and inactivating BZR1. Once BZR1 is activated, it is targeted to the nucleus to work with other transcription factors (TFs) and cofactors to promote BR-induced gene expression. It also expresses genes involved in cell division such as CDK and CycA. Additionally, BZR1 can collaborate with other TFs to signal the function of other hormones such as IAA, GA, CK and JA, which regulate fruit growth. **(B)** Molecular mechanism of action of BR on ripening of horticultural products in climacteric fruits (left), where BZR1 may regulate ethylene-dependent physicochemical changes in ripening by expressing ethylene biosynthesis genes such as *ACO1* and *ACS1* (Meng et al., 2023). However, in some species, BZR1 accumulation can interfere with ERF transcription, leading to slower changes during ripening by inhibiting the expression of *ACO1* and *ACS1* (Ji et al., 2021). In non-climacteric fruits (on the right), BZR1 can signal physicochemical changes related to ripening, such as in color, aroma, and nutritional quality, in an ethylene-independent manner. Dotted lines indicate other metabolic processes in the pathway. Produced using BioRender with permission to publish.

where BR delay ripening by decreasing said physiological processes (Zhu et al., 2010; Wu and Yang., 2016; Wang et al., 2020; Ji et al., 2021; Zhu et al., 2021; Liu et al., 2022). In tomato and persimmon fruits, the postharvest application of BR increased the expression of genes involved in ethylene biosynthesis (*ACS2, ACS4, ACO1, ACO4*), which increased the respiratory rate of the fruits and accelerated the physicochemical changes associated with maturation and senescence (Zhu et al., 2015a; He et al., 2018). Furthermore, in this same fruit, overexpression of the *SlCYP90B3* gene (involved in BR biosynthesis) (Hu et al., 2020) and of the *SlBZR1* gene (Meng et al., 2023) increases ethylene production, advancing the climacteric peak of tomato fruits, and therefore ripening. The opposite behavior has been observed in apple and pear fruits, where the application of BR reduced the expression of the genes *ACO1, ACS1,* and the ethylene transcription factor *ERF1* (Ji et al., 2021).

These results show that there is a positive and negative effect of BR on the ripening of horticultural products through biochemical processes that are ethylene-dependent. To propose an explanation for these counterproductive phenomena, studies by Ji et al. (2021) in climacteric fruits as apple and pear propose a theory of regulation and signaling of the BR in ripening. These researchers showed that endogenous BR levels play a fundamental role in stimulating or inhibiting fruit ripening. When endogenous levels of BR are high in the fruits, there is an increase in the expression of the *BZR1* gene and a greater accumulation of the BZR1 protein in the nucleus. This nuclear accumulation results in the suppression of the transcription of ethylene biosynthetic genes, such as *ACO1* and *ACS1*, either by direct union to the promoter or through interaction with ERF. The BZR1 that remains in the cytoplasm inhibits the activity of the enzyme ACO1 by direct interactions with protein, resulting in the inhibition of ethylene biosynthesis and, as a consequence, the delay of fruit ripening (Ji et al., 2021). In contrast, when the endogenous levels of BR decrease, a reduction in the expression of *BZR1* is observed. This decrease weakens the suppression of BZR1 in the activity of the enzyme ACO1 and the transcription of ACO1 and ACS1. This leads to an increase in ethylene production, thus triggering the fruit ripening process (Ji et al., 2021).

Although these results were obtained in specific species and environmental conditions, they illustrate an interesting theory whereby ripening regulated in climacteric fruits by BR is linked to the sensitivity of the fruits to the BZR1 transcription factor (Fig. 2). This could explain the different positive and negative ethylene-dependent changes during ripening of climacteric fruits, making the BR dose applied at postharvest one of the main factors to be evaluated in future studies, since this would determine the accumulation of BZR1. However, these results do not explain why the application of BR would increase the synthesis of ethylene if there is an antagonism and/or competition between BR and ethylene. In addition, the overexpression of the *BZR1* gene in tomato fruits accelerated and increased the production of ethylene and the ripening process (Meng et al., 2023), so the accumulation of intracellular BZR1 would not inhibit the biosynthesis of ethylene in these fruits. It could be the case that there is a specific factor in the sensitivity of the

Table 2
Effect of BR application on physicochemical changes during postharvest of horticultural products. B-2000: spirostanic analogs, 3β-5α-25(R)-dihydroxy-spirostan-6-one. EBR: 24-epibrassinolide- BL: brassinolide. TSS: total soluble solids. TTA: total titratable acidity. AOX: alternative oxidase. * The original units were retained.

Horticultural species	BR analogue and dose	Application method	Effect of BR on postharvest	References
Daylily flower (*Hemerocallis citrina*)	1 μmol L^{-1} EBR	Spraying to flower buds	Decreased lipid peroxidation, H_2O_2 content, chlorophyll degradation, and weight loss. Increased antioxidant enzyme activity and maintained sensory quality. Delayed senescence	Yao et al. (2017)
Jujube (*Zizyphus jujuba*)	5 μmol L^{-1} EBR	Immersed for 5 min	Decreased ethylene production, respiratory rate, and firmness loss	Zhu et al. (2010)
Broccoli (*Brassica oleracea* var. *italica*)	2 μmol L^{-1} EBR	Spraying the head surface	Inhibited broccoli yellowing and chlorophyll degradation. Increased antioxidant enzymes and decreased ROS concentration	Fang et al. (2021)
Persimmon (*Diospyros kaki*)	10 μmol L^{-1} EBR	Immersed for 30 min	Increased cell wall degradation, fruit softening, ethylene biosynthesis, and respiration. Accelerated ripening	He et al. (2018)
Carambola (*Averrhoa carambola*)	2.8 μmol L^{-1} EBR	Immersed for 10 min	Delayed firmness loss, color change, senescence, and respiratory rate. Increased the antioxidant system	Zhu et al. (2021)
Asparagus (*Asparagus officinalis*)	10 μmol L^{-1} BL	Immersed for 2 min	Reduced respiratory rate, chlorophyll degradation, and lipid peroxidation. Increased enzymatic and non-enzymatic antioxidant activity	Wu and Yang (2016)
Strawberry (*Fragaria* × *ananassa*)	4×10^{5} μmol L^{-1} BL	Injection into the fruit receptacle	Temporary decrease in ripening and color change	Chai et al. (2013)
Kiwifruit (*Actinidia chinesis*)	5 μmol L^{-1} EBR	Immersed for 10 min	Delayed fruit softening, weight loss, starch degradation, and lipid peroxidation	Lu et al. (2019)
	5 μmol L^{-1} EBR	Immersed for 10 min	Decreased respiratory enzyme metabolism, ROS production, color change, and senescence. Increased enzymatic antioxidant system	Wang et al. (2020)
Corn (*Zea mays*)	2 μmol L^{-1} EBR	Ear spraying	Reduced lipid peroxidation, weight loss, and soluble sugars. Increased expression of antioxidant enzymes, and sucrose transport	Fang et al. (2023)
Mandarin (*Citrus unshiu*)	10.4 μmol L^{-1} EBR	Immersed for 2 min	Rapid weight loss, and increased antioxidant activity	Zhu et al. (2015b)
Mango (*Mangifera indica*)	83 – 125 μmol L^{-1} EBR	Applied to the epidermis of the fruit	Advanced climacteric peaks in ethylene production and respiration rate, color development, and fruit softening	Zaharah et al. (2012)
Apple (*Malus* × *domestica* Borkh.)	10 μmol L^{-1} EBR	-	Activated the expression of *MdBRZ1*.	Liu et al. (2022)
			Delayed the ripening process: decreased ethylene concentration, volatile compounds, TSS, and loss of firmness; increased TTA	
	10 μmol L^{-1} EBR	Immersed for 2 h	Increased MdBZR1 activity.	Ji et al. (2021)
			Suppressed ethylene synthesis and fruit ripening	
Papaya (*Carica papaya*)	1 μmol L^{-1} EBR	Immersed and vacuum infiltrated for 5 min	Increased AOX capacity, ethylene production and respiratory activity	Mazorra et al. (2013)
Pear (*Pyrus ussuriensis*)	3 μmol L^{-1} EBR	Immersed for 2 h	Inhibited ethylene production and biosynthesis, and fruit softening	Ji et al. (2021)
Rose (*Rosa hybrida*)	1 μmol L^{-1} BR unspecified	Immersed the flower stems in the solution.	Increased vase life, antioxidant activity, and relative water content	Naeemi et al. (2022)
Black bean sprouts (*Phaseolus vulgaris*)	3.1 μmol L^{-1} BL	Seeds soaking for 24 h	Promoted antioxidant and PAL activity, phenol content, and shelf life. Reduced lipid peroxidation	Xue et al. (2021)
Tomato (*Solanum lycopersicum*)	3 μmol L^{-1} EBR	Immersed discs	Increased carotenoid content in the peel	Liu et al. (2014)
	5 μmol L^{-1} BL	Immersed for 12 h	Induced fruit ripening, increasing soluble sugars, ascorbic acid, lycopene content, respiration rate, and ethylene production	Zhu et al. (2015a)
	3 μmol L^{-1} EBR	Lanolin-coated fruits	Increased production of volatile compounds and carotenoids	Liu et al. (2023)
Table grape (*Vitis vinifera*)	*0.4 mg L^{-1} BR unspecified	Cluster spray	Increased anthocyanin biosynthesis transcription, and total anthocyanin content	Luan et al. (2016)
	0.14 μmol L^{-1} B-2000 and 0.8 μmol L^{-1} EBR	Cluster spray	Improved berry color, increased TSS and anthocyanin levels	Vergara et al. (2018)
	100 μmol L^{-1} BR unspecified	-	Increased sugar accumulation, coloring, anthocyanin content, and volatile emission in berries. Reduced organic acid content	Zheng et al. (2020)
	3 – 6 μmol L^{-1} EBR	Cluster spray	Increased TSS content, TTA, antioxidants, phenols, and ascorbic acid levels in berries	Asghari and Rezaei-Rad (2018)

species to the mechanism of BR action, or that these molecular pathways between BR and ethylene are not interconnected in all fruits. Although significant progress has been made understanding the molecular mechanisms of ripening mediated by BR, more studies are needed to explain this synergism-antagonism between these two hormones. In addition, in future research with exogenous BR applications at postharvest, it is recommended to test a broader dose range of the BR supplied to horticultural products to corroborate the model proposed by Ji et al. (2021).

Unlike climacteric fruits, where ethylene is fundamental, hormonal control of ripening in non-climacteric fruits is not well understood. In non-climacteric fruits, such as grape and strawberry, it has been shown that concentration, biosynthesis and mechanism of action of the BR are indispensable for the ripening fruit (Table 2). The exogenous application of BR influences the production of ethylene and respiration of non-climacteric fruits, although BR applications regulate other physicochemical changes during ripening that will be discussed later. In grape fruits, the postharvest application of BR controlled 2406 differentially expressed genes (DEG), in which about 50% were upregulated and the other 50% suppressed, and caused changes in color, sugars, acids and volatility in the berries (Pei et al., 2023). Therefore, BR can regulate ripening and independent changes in ethylene in non-climacteric fruits (Fig. 2).

Additionally, BR could positively regulate the ripening of fleshy fruits through downregulation of sphingolipid-related genes, such those involved in synthesis of serine palmitoyltransferase I (*OeSPT*) or sphingosine kinase (*OeSPHK*) (Hu et al., 2021). In this way, the action of BR on fruit ripening would be mediated by sphingolipids involved in fruit ripening and abscission (Hu et al., 2021).

Fruit color is one of the key quality characteristics for consumers and determines the acceptability of a horticultural product (Reyes et al., 2023). Regarding the discussion about the promotion and/or inhibition of the ripening process mediated by BR mentioned above, some authors reported a delay in color change, especially when associated with reduced degradation of chlorophyll in vegetables (Wu and Yang., 2016; Fang et al., 2021) and fruits (Zhu et al., 2021). Meanwhile, the regulation of pigment synthesis in the fruit epidermis involved in the change of color has been studied in depth in tomato fruits, elucidating the mechanism of the BR action. Liu et al. (2014) showed that exogenous EBR applications increased the accumulation of carotenoids such as lycopene and β-carotene in tomato epidermis, and that overexpressing *BZR1* in transgenic tomato lines increases the accumulation of these pigments. Accumulation of these pigments in tomato fruits occurs because *BZR1* directly activates the phytoene synthase 1 (*PSY1*) gene, inducing the production of phytoene, thus initiating the differentiation of chromoplasts and accumulation of carotenoids, and also binds directly to promoters of several genes of transcription factors related to the fruit ripening (Meng et al., 2023).

In table grape, the application of BR increased the pinkish-red hue and accumulation of anthocyanins in the berries (Vergara et al., 2018). These changes have been linked to an increase in the gene expression for enzymes involved in the biosynthesis of these pigments, such as dihydroflavonol 4-reductase (*DFR*), *CHI*, *CHS*, *LDOX*, *ANS*, *LAR*, *MYBPA1*, and *UFGT* (Luan et al., 2016; Xu et al., 2015; Zhou et al., 2018). These results provide information on the regulatory mechanisms of the signaling of BR during fruit ripening, color change, and pigment metabolism in fruits.

Fruit softening is another quantitative and qualitative characteristic that functions as an indicator of the ripening process. When BR positively regulated the ripening and ethylene-dependent processes, its application also induced loss of firmness in the fruits and has been associated with a lower content of soluble pectin and cellulose, greater activity of enzymes that degrade the cell wall such as polygalacturonase (PG), pectate lyase (PL), endo-1,4-beta-glucanase (EG) and pectinesterase (PE), and the expression of genes that codify for these enzymes (*DkPG1*, *DkPL1*, *DkPE1*, *DkPE2*, and *DkEGasa1*) (He et al., 2018). However, when BR suppress ethylene activity and the changes associated with ripening, the fruit firmness loss is slowed after its application (Zhu et al., 2021; Liu et al., 2022). In any case, the degradation of the cell wall is associated with increased transpiration and, therefore, increased water loss and weight loss of the fruits.

The metabolism of sugars and organic acids has been influenced by the application of BR in fruits and vegetables. Total soluble sugars increase and total acidity decreases when BR application precedes ethylene and respiration peaks; otherwise BR inhibit fruit ripening (Table 2). The increase in soluble sugars during ripening is an indicator of the postharvest quality of the fruits due to the solubilization of polysaccharides such as starch and pectin, since they are used as substrates in respiratory metabolism and can follow four metabolic pathways: the glycolysis pathway, the tricarboxylic acid cycle (TCA), the cytochrome pathway (CCP) and the pentose phosphate pathway (PPP) (Yu et al., 2022). In turn, organic acids can be reduced to soluble sugars through gluconeogenesis, and, therefore, reduce in concentration during ripening. In carambola fruits, the application of BR slowed the accumulation of soluble sugars and organic acids due to decreased fructose-6-biphosphate content (a crucial product of the glycolytic pathway) and the enzymatic activity of the succinate dehydrogenase (a key enzyme of the TCA), and increased glucose-6-phosphate dehydrogenase (G-6-PDH) and 6-phosphate gluconate dehydrogenase (key enzymes for the route of pentose phosphate) (Zhu et al., 2021). In kiwi fruits, a similar behavior was observed via the decrease in the activity of succinate dehydrogenase and cytochrome oxidase (Wang et al., 2020).

In addition, in kiwi fruits, the decrease in the concentration of soluble sugars (glucose, fructose and sucrose) occurred after BR application due to activities of sucrose phosphate synthase, hexokinase and fructokinase (Lu et al., 2019). Therefore, BR could slow fruit ripening by prioritizing soluble sugars to the metabolic route of the pentose phosphate, over the glycolysis and TCA pathway, and delaying enzymatic activity in sugar metabolism, which would decrease senescence of the fruits. On the other hand, in corn, pre-harvest application of BR increased the expression of sucrose transport proteins (*SUT, SWEET*) in the grains before harvest, which increased the postharvest quality of corn (Fang et al., 2023).

In grapes, BR treatment enhanced the accumulation of sugars and increased the fruit aroma, and the mechanism of BR action included the crosstalk between BR and methyl jasmonate (Pei et al., 2023). DWF4, a key enzyme in BR biosynthesis, could negatively interact with TIFY proteins, which determine transcriptional activities of jasmonic acid-responsive genes. Therefore, as a result of BR treatment, methyl jasmonate had minor inhibition action on grape ripening (Pei et al., 2023).

The emission of volatile compounds during the postharvest is a process that responded positively and negatively to BR applications. In climacteric fruits such as tomato, the EBR application promoted the formation of volatile compounds by increasing carotenoid content, which correlated with the synthesis of the 6-methyl-5-hepten-2-one (MHO) volatile, which is synthesized by the carotenoid pathway through the *CCD1A* gene (Liu et al., 2023), thereby promoting the accumulation of carotenoids in tomato and thus enhancing the flavor of the fruit. This finding was also reported in apple, where the enzymatic activity, the production of volatile compounds and the genes involved in volatile biosynthesis (ADH, LOX, PDC) were suppressed by the postharvest application of EBR (Liu et al., 2022). Overexpressing BZR1 decreased the production of volatile compounds in apple fruits, mainly alcohols such as hexanol, octanol, 2-hexanol and heptanol, and this effect was increased when the BZR1 was silenced (Liu et al., 2022).

On the other hand, in non-climacteric fruits such as grapes, BR accelerated the biosynthesis of terpenoid aromatic compounds, such as α-pinene, D-limonene and γ-terpinene, which influence the aromatic composition of grapes, and this correlated with the reduction of the activity of 3-hydroxy-3-methylglutaril CoA reductase (HMGR, key enzyme in the mevalonic acid pathway) (Zheng et al., 2020), indicating that there is a signaling network complex between the BR action and *HMGR* expression. In grapes, BR and jasmonates interacted at the cellular level by increasing the synthesis of terpenoids, alcohols, and aldehyde volatile compounds (Li et al., 2023a).

Finally, the senescence of horticultural products is an inevitable and irreversible process, during which the biochemistry and physiology of the plants are altered, influencing the physicochemical characteristics mentioned above such as color, texture, sugar and acid content, aroma and taste. These processes related to senescence are characterized by the oxidative stress that is generated naturally within the cells, controlled by complex signaling networks, with ethylene leading many of these processes (Tang et al., 2020). BR application during ripening accelerates or delays senescence in some species, depending on its interaction with ethylene-dependent processes (Table 2). At the endogenic level, it was found by transcriptomic analysis that BR were involved in the postharvest senescence processes in *Brassica* spp., specifically in the pathways and mechanisms involved in oxidative stress of senescence (Ahlawat et al., 2022). The majority of studies in which BR have prolonged the postharvest life of fruits have been characterized by the increase in the enzymatic antioxidant system in fruits, such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX) and other enzymes such as phenylalanine ammonium lyase (PAL); and the decrease in lipid peroxidation and concentration of reactive oxygen species (ROS) (Zhu et al., 2010; Wang et al., 2020; Zhu et al., 2021; Fang et al., 2021). Therefore, the senescence process is delayed and the postharvest life of the organs is extended, as is the case for flowers such as rose and Azucena, where vase life is increased (Yao et al., 2017; Naeemi et al., 2022). The regulation of the enzymatic and non-enzymatic antioxidant activity of the BR during fruit ripening will be explained in the next section, discussing the tolerance conferred by BR under biotic and abiotic stresses in horticultural products.

4. Mechanisms of tolerance of BR against biotic and abiotic stress during postharvest

4.1. Chilling injury

BR participate in signaling of responses to abiotic and biotic stress in plants (Bajguz et al., 2020). BR postharvest application in horticultural products susceptible to low temperatures confers tolerance to chilling injury (CI), due to the increase in signaling, synthesis, and accumulation of antioxidant substances that reduce oxidative stress (Table 3). The increase in the antioxidant system is the main mechanism whereby fruits tolerate CI. BR application increases antioxidant enzymatic activity, since the activity of SOD, CAT, POD, and APX enzymes increases, thereby reducing the concentration of ROS, such as superoxide anion ($O_2^{\cdot -}$) and hydrogen peroxide (H_2O_2), and the damage caused by them, resulting in lower rates of lipid peroxidation and malondialdehyde (MDA) production (Massolo et al., 2022).

The non-enzymatic antioxidant system and the synthesis of osmoprotectants also confer a tolerance response mediated by BR. The increase in carotenoid concentration after BR application was related to cold stress tolerance in mandarin fruits (Gutiérrez-Villamil et al., 2023). High concentration of phenols during cold storage with BR application increased the membrane protection due to an increase in PAL activity and reduced activity of the polyphenol oxidase (PPO) (Islam et al., 2022). Likewise, the activity of the enzymes involved in proline biosynthesis (PDH, P5CS) positively correlated with the exogenous application of BR, and a low incidence of CI and maintenance of postharvest quality were evidenced.

To elucidate the molecular mechanism of BR action on tolerance to CI, Hu et al. (2022) overexpressed the key gene involved in the biosynthesis of BR (*CYP90B3*) in tomato fruits and found that the tolerance of these fruits to CI was enhanced through increased antioxidant enzymatic activity (SOD, CAT, POD, APX), reduced activity of lipolytic enzymes of the membrane (LOX, PLD), and increased expression of the transcription factor *C-repeat binding factors* (*CBF1*) involved in the components of the cold response system in plants and fruits. In addition, a multi-omic analysis showed that BR applications in tomato and banana fruits decreased CI and regulated differentially expressed genes (DEG) involved in the response to cold stress in plants (*HSFA3, SHSP*, and *TPR*), the redox process of the fruit (*GPX*, *CAT*, *POD, PAL,* and *LOX*), fruit texture (*CESA*, *β-Gal, PE, PL,* and *PAE*), transduction of hormonal signals (*ACS3, BSK1, JAR1, ARF,* and *ERF*), and transcription factors (*WRKY* and *MYB*) (Li et al., 2018; Bai et al., 2021). This exogenous BR application reduces the expression of biosynthetic genes of BR (*DWF4*) but promotes the expression of the *BZR1* transcription factor during cold storage of fruits, and, in turn, can regulate the expression of zinc finger protein (*HDT1*) involved in CI tolerance (Hu et al., 2023). Therefore, the exogenous application of BR activates BZR1-type molecular and transcriptional action mechanisms to signals and induces the expression of genes that help the fruits to tolerate CI through heat shock proteins, cold response proteins, zinc finger protein, enzymes that scavenge ROS, and signal transduction with other hormones (Fig. 3).

Table 3
Effect of postharvest application of BR on tolerance of chilling injury during cold storage of horticultural products. DI.31: spirostanic analogs. EBR: 24-epibrassinolide- BL: brassinolide. CI: chilling injury. * The original units were retained.

Horticultural species	BR analogue and dose	Application method	Cold storage conditions	Effect of BR on chilling injury (CI) tolerance	References
Banana (*Musa spp.*, AAA group cultivar 'Brazil')	40 µmol L^{-1} EBR	Immersed for 10 min	12 d at 8 °C	Reduced CI and lipid peroxidation. Increased defense proteins, energy status and cold resistance	Li et al. (2018)
	80 µmol L^{-1} BL	Immersed for 2 min	8 d at 2 °C	Lower CI, membrane peroxidation, and ROS. Increased soluble sugars, proline, phenols, flavonoids, and unsaturated fatty acids in the membrane	Zhang et al. (2022)
Eggplant (*Solanum melongena*)	10 µmol L^{-1} EBR	Immersed for 10 min	15 d at 1 °C	Inhibited pulp browning, CI, and reduction of total phenolic content. Preservation of cell membrane integrity	Gao et al. (2015)
Peach (*Prunus persica*)	10 µmol L^{-1} EBR	Immersed for 10 min	28 d at 1 °C	Inhibited lipid peroxidation, ROS production, CI, and fruit softening. Increased total phenols and proline synthesis	Gao et al. (2016)
	15 µmol L^{-1} EBR	Immersed for 10 min	28 d at 5 °C	Decreases CI, BL accumulation, and synthesis. Increases *BZR1* signaling and other cold tolerance genes	Hu et al. (2023)
Lime (*Citrus latifolia*)	10 µmol L^{-1} EBR	Immersed for 2 min	65 d at 4 °C	Delayed chlorophyll degradation, CI, TSS, and color change. Increased ascorbic acid content, total phenols, and antioxidant activity	Tavallali (2018)
	*1 mg L^{-1} BR unspecified	Immersed for 5 min	21 d at 1 °C	Decreased CI, lipid peroxidation, and ROS production. Increased antioxidant enzymes	Mohammadrezakhani, Pakkish (2017)
Mandarin (*Citrus reticulata* Blanco) cv. 'Arrayana'	10.4 µmol L^{-1} EBR and 11.3 µmol L^{-1} DI-31	Immersed for 15 min	40 d at 4°C + 7 d at 19 °C	Reduced CI, electrolyte leakage, weight loss, and respiratory rate. Increased carotenoids, antioxidant activity, and total phenols	Gutiérrez-Villamil et al. (2023)
Mango (*Mangifera indica*)	10 µmol L^{-1} BL	Immersed for 10 min	28 d at 5 °C	Decreased CI, electrolyte leakage. Increased plasma membrane unsaturated fatty acids	Li et al. (2012)
Blood orange (*Citrus sinensis* L. Osbeck cv. Sanguinello)	10 µmol L^{-1} EBR	Immersed for 10 min	45 d at 2 °C	Lower CI, electrolyte leakage, and organic acid. Greater accumulation of soluble sugars, antioxidant activity, phenols, and anthocyanins	Habibi et al. (2021)
Green bell pepper (*Capsicum annuum* L.)	15 µmol L^{-1} EBR	Immersed for 20 min	18 d at 3 °C	Reduced CI, lipid peroxidation, and chlorophyll degradation. Increased antioxidant enzymes	Wang et al. (2012)
Pomegranate (*Punica granatum*)	15 µmol L^{-1} EBR	Immersed for 20 min	84 d at 5 °C + 3 d at 20 °C	Decreased CI, lipid peroxidation, LOX activity, ROS production. Increased antioxidant enzyme activity, PAL, and decreased PPO. Maintained postharvest quality	Islam et al. (2022)
Tomato (*Solanum lycopersicum*)	6 µmol L^{-1} EBR	Immersed for 20 min	21 d at 1 °C	Lower incidence of CI, lipid peroxidation. Increase in PAL activity, phenol, and proline concentration	Aghdam et al. (2012)
Table grape (*Vitis vinifera*)	*1.5 mg L^{-1} BR unspecified	Immersed for 5 min	35 d at −0.5 °C	Reduced CI, lipid peroxidation, and senescence. Increased the enzymatic antioxidant system	Pakkish et al. (2019)
Zucchini squash (*Cucurbita pepo*)	0.1 µmol L^{-1} EBR	Fruit spraying	25 d at 4 °C	Reduced incidence of CI, yellowing, weight loss, and lipid peroxidation. Increased antioxidant capacity and phenols	Massolo et al. (2022)
Kale sprouts (*Brassica oleracea* var. *acephala*)	0.21 µmol L^{-1} BL	Sprouts spraying	7 d at 4 °C	Decreased weight loss, browning index, MDA content, H_2O, and $O_2^{\cdot -}$ production. Increased antioxidant activity, and total phenols through regulation of ascorbate-glutathione cycle	Du et al. (2024)

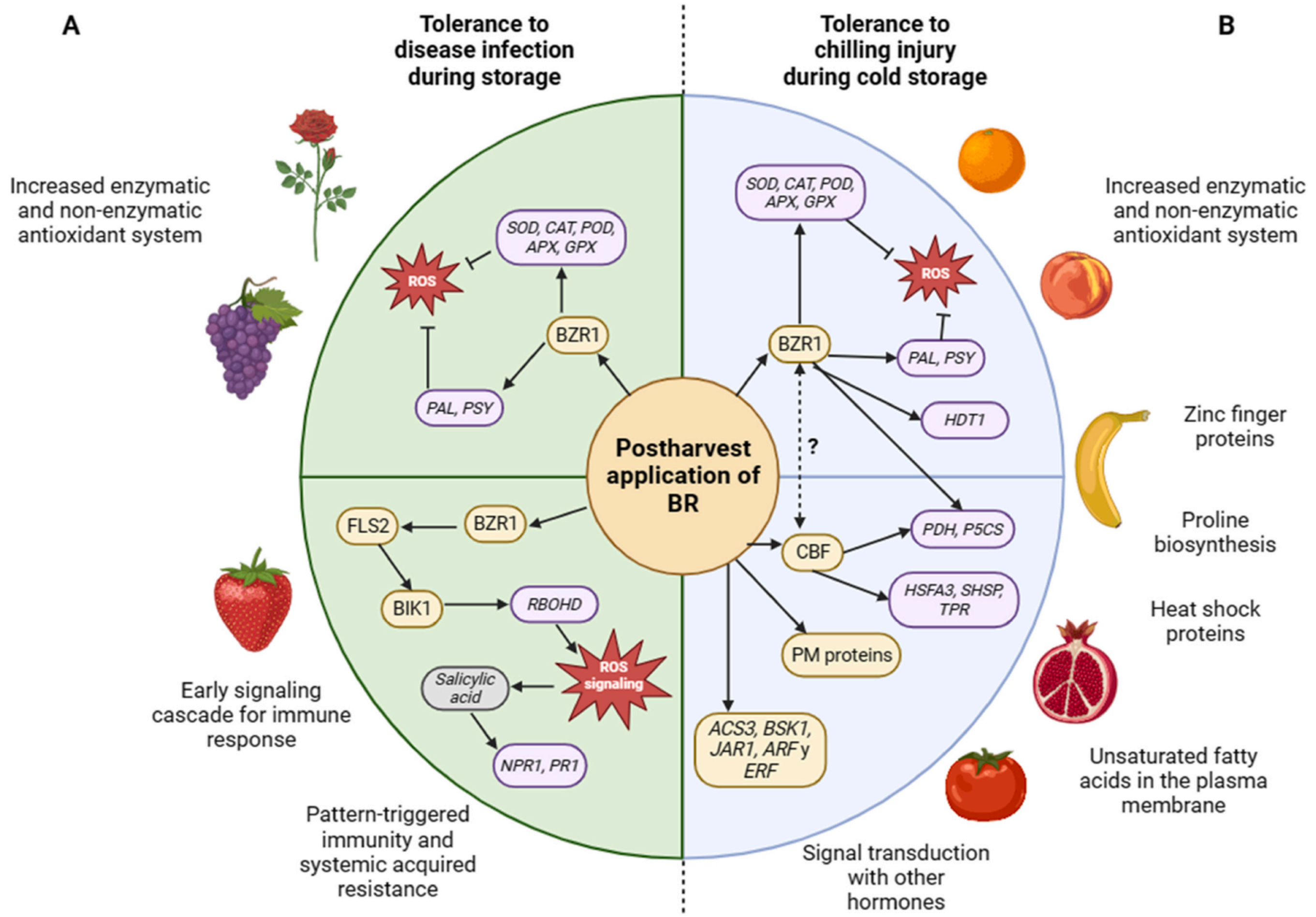

Fig. 3. Mechanisms and functionality of BR in postharvest applications for improving **(A)** tolerance to disease infection and **(B)** chilling injury during the storage of horticultural products. The abbreviation PM refers to the plasma membrane, and the dotted line indicates unknown signaling. Produced using BioRender with permission to publish.

Another cold stress tolerant mechanism during the cold storage of horticultural products is the increase in unsaturated fatty acid contents in plasma membranes, since it is beneficial to reduce the phase transition temperature and maintain the plasma membrane fluidity (He and Ding, 2020). BR application during cold storage increased the contents of unsaturated fatty acids, mainly long chain fatty acids such as palmitic methyl acid, methyl stearate, oleic acid, linoleic acid, linolenic acid and methyl lignocerate, which facilitated the maintenance of the normal membrane fluidity (Li et al., 2012; Zhang et al., 2022). This parameter has been little studied during postharvest after BR applications under cold storage. Although there are two reports on the effect of the BR on unsaturated fatty acids biosynthesis, it is recommended that this variable be included in future studies to elucidate the interaction of BR and CI at the molecular level.

It is important to mention that, according to the studies reported in Tables 2 and 3, BR analog most used in research is the 24-epibrassinolide (EBR, active byproduct of the biosynthesis of brassinolides). The doses evaluated of EBR vary widely and can range between 0.1 and 15 μmol L^{-1}.

4.2. *Postharvest diseases*

The appearance and development of diseases during postharvest of fruits and vegetables are processes interacting with the biochemistry of senescence, so they can happen naturally as a consequence of the deterioration of horticultural products (Yahia et al., 2019b). Various studies have shown that BR can reduce the incidence and severity of diseases during the postharvest of horticultural products, which gives them greater quality and longer shelf life (Table 4). As well as for CI tolerance, the functionality of BR to confer immunity to diseases in horticultural products is associated with an effective antioxidant response (SOD, CAT, POD, APX, PAL) that limit pathogen development and colonization of the fruits (Zhu et al., 2015b; Naeemi et al., 2022).

Recently, Li et al. (2023b) reported the possible molecular mechanism of immunity to *Botrytis cinerea* produced by BR postharvest application in strawberry fruits. These authors showed that after applying the BR in strawberries, the signal transduction by the BAK1 kinase (kinase associated with the BR receptor) interact with the FLS2 kinase (molecular receptor of pathogenic immunity and defense) to signal to the BIK1 kinase (kinase 1 botrytis-induced). Consequently, BIK1 interacts directly with RBOHD, contributing to the outbreak of ROS and improving the genetic expression of salicylic acid (SA) synthesis related to the plant defense leading to fungal resistance (Li et al., 2023b). Therefore, the application of BR to horticultural products during postharvest could increase the expression of BAK1 and this would increase the accumulation of ROS, which would generate the early signaling of defense and immunity genes against pathogens (Fig. 3). These results illustrate the molecular mechanism of the BR action during pathogen resistance in strawberry fruits during postharvest. It is recommended that these signaling pathway in climacteric species be investigated and the response evaluated.

Table 4
Effect of postharvest application of BR on tolerance to disease incidence during storage of horticultural products. EBR: 24-epibrassinolide. DI-31: spirostanic analogs.

Horticultural species	BR analogue, dose, and application	Application method	Pathogen inoculation	Effect of BR on postharvest disease tolerance	**References**
Jujube (*Zizyphus jujuba*)	5 μmol L^{-1} EBR	Immersed for 5 min	Blue mold rot (*Penicillium expansum*), 5 $\times 10^3$ spores mL^{-1}	Reduced pathogen incidence and injury. Colonization and spore germination were not inhibited. Increased enzymatic antioxidant activity	Zhu et al. (2010)
Strawberry (*Fragaria* x *ananassa*)	0.23 μmol L^{-1} DI-31 and 2.1 μmol L^{-1} EBR	Foliar spraying every 30 days	Grey mold (*Botrytis cinerea*), 5 $\times 10^4$ spores mL^{-1}	Reduced pathogen incidence	Furio et al. (2019)
Mandarin (*Citrus unshiu*)	10.4 μmol L^{-1} EBR	Immersed for 2 min	-	Reduced incidence of fruit diseases and ROS production. Increased antioxidant enzyme activity	Zhu et al. (2015b)
Rose (*Rosa hybrida*)	1 μmol L^{-1} BR unspecified	Soak the flower stems in the solution	Grey mold (*B. cinerea*), 2 $\times 10^5$ spores mL^{-1}	Inhibited the development of the disease. Increased antioxidant enzyme activity	Naeemi et al. (2022)
Table grape (*Vitis vinifera*)	0.8 – 1.7 μmol L^{-1} EBR	Cluster spraying	Grey mold (*B. cinerea*), 1 $\times 10^6$ spores mL^{-1}	Decreased disease severity, ROS production, and lipid peroxidation. Increased antioxidant enzymes	Liu et al. (2016)

5. Conclusions and future perspectives

Currently, the exogenous application of BR, as an important growth regulator in plants, has a considerable effect on the development of fruits, physicochemical changes during ripening, senescence (Fig. 2), and tolerance to biotic and abiotic stress during postharvest of different horticultural products (Fig. 3). Therefore, the exogenous application of BR can be used to control fruit growth, delay the senescence of horticultural products, and confer tolerance to CI and pathogen infection during the postharvest period. Within this review, it was found that the BR analog most implemented in research is EBR, with doses between 0.1 and 15 μM, due to its great biological affinity within the action mechanisms. However, there are other spirostanic analogues that show promising results in the growth and postharvest physiology of fruits. Within the reviewed functionalities, it was found that BR:

- Have a signaling function in the regulation of fruit development, by inducing the expression of genes involved in cell division, and in the interaction with other growth hormones, which could induce parthenocarpy in some species. It is important to consider the sensitivity of species to BR during the fruit development, since it can generate negative or positive effects due to the mechanism of action of BZR1. It is recommended to carry out more studies for each species at different times of application and with different doses to characterize the sensitivity of BR on the development of the fruits;
- Can positively or negatively control (depending on the application dose) the ripening of climacteric fruits, possibly due to the negative interaction between the BZR1 transcription factor and the ethylene biosynthesis, according to the model proposed by Ji et al. (2021), which would explain why BR application promotes or delays color changes, fruit softening, metabolism of sugars, organic acids, and volatile compounds of climacteric fruits (Fig. 2). However, this effect is not seen in all species, for example, with tomato, the overexpression of BZR1 did not delay ripening (Meng et al., 2023). More studies are needed to help understand this synergism-antagonism between ethylene and BR during ripening, with exogenous applications of BR in postharvest testing and a broader dose range supplied to horticultural products;
- Can accelerate or delay the senescence of horticultural products by controlling the expression of genes involved in enzymatic and non -enzymatic antioxidant responses;
- Confer tolerance to CI during postharvest storage of horticultural products, by activating the molecular and transcriptional action mechanisms by BZR1 to signal and induce gene expression such as heat shock proteins (HSP), cold response proteins (CBF), zinc fingers (HDT1), ROS scavenger enzymes (SOD, CAT, PAL), synthesis of unsaturated fatty acids and signal transduction with other hormones (Fig. 3);
- Cause fungal immunity in fruits during postharvest period by an early signaling mediated by BAK1-FLS2-BIK, which induces the expression of defense and immunity genes against pathogens associated with salicylic acid (Fig. 3).

Finally, this review proposes a basis to carry out research on the physiological aspects of the regulation of BR in fruits and vegetables during the development and postharvest period, and also points to the need for in-depth research of molecular mechanisms.

CRediT authorship contribution statement

Diego Alejandro Gutierrez Villamil: Writing – review & editing, Writing – original draft, Visualization, Conceptualization. **Stanislav Magnitskiy:** Writing – review & editing, Writing – original draft, Conceptualization. **Helber Enrique Balaguera Lopez:** Writing – review & editing, Writing – original draft, Supervision, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

While preparing this work, the authors did not use AI and AI-assisted technologies in the writing process.

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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