



Review

Physiology and Application of Gibberellins in Postharvest Horticultural Crops

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Abstract: Gibberellins (GAs) are plant hormones indispensable in regulating the growth and development of fruits. Recent studies have shown that GAs play important roles in delaying horticultural crop ripening and senescence, enhancing the internal and external quality of horticultural crops and resistance to stress and disease. We reviewed the role of GAs in the postharvest physiology of fruits in recent years. GAs are closely related to their ability to retard fruit senescence. GAs could effectively improve fruit storage quality and significantly increase flesh hardness, reduce respiration intensity, inhibit the release of endogenous ethylene, and effectively inhibit fruit softening and ripening. It can also improve the intrinsic and extrinsic quality of fruit storage by improving fruit shape, regulating color, delaying the reduction of soluble solids, promoting sugar accumulation, and delaying vitamin loss. GAs also play a role in postharvest biotic and abiotic stress resistance. The GA treatment effectively reduces the cold damage index, reduces the production and accumulation of superoxide anion (O_2^-), improves the antioxidant capacity of fruits, and maintains the integrity of cell membranes during low-temperature storage. Moreover, GAs could effectively control some postharvest fruit diseases. In conclusion, GAs play an important role in the physiological regulation of postharvest fruits and have important application prospects in postharvest fruits.

Keywords: gibberellins; postharvest; physiology; ripening



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1. Introduction

Bioactive gibberellin (GA) is one kind of phytohormone that regulates plant growth and development. GAs are involved in plant reproductive development, promoting organ growth (enhancing cell elongation and cell division), and activating developmental processes such as seed germination, maturation, and induction of flowering [1]. In recent years, the regulation mechanism of GAs and the application of exogenous plant hormones in the postharvest storage quality of horticultural crops has been studied. GAs were first found in the metabolites of the fungus *Gibberella fujikuroi* and later reclassified as *Fusarium fujikuroi*. GA was discovered as a natural plant hormone in the late 1950s that promoted growth in higherplants [2]. GAs are in a class of phytohormones with kaurene as their backbone. GAs contain a large group of diterpenoid carboxylic acids, which are classified based on their structure.

The biologically active GAs mainly include GA₁, GA₃, GA₄, and GA₇, which play direct or relative roles in plants. Among them, GA₁ is the most widespread and is present in most plants [3], while GA₄ is mainly found in *Arabidopsis thaliana* and some cucurbits. As for the relative roles of GA₁ and GA₄ or GA₃ and GA₇, further studies are needed to

clarify them. At the same time, other types of GAs that are not biologically active in plants can often be converted into biologically active GAs by certain means. For example, GA₁₂ is converted to GA₄ by GA 20-oxidase (GA20ox) and GA3ox, and it can also be converted to intermediate GA₅₃ by GA13ox and then to biologically active GA₁, GA₃, and GA₆ by different pathways in the presence of GA20ox and GA3ox [4].

The current understanding of the physiological roles of gibberellins in postharvest horticulture crops was outlined and discussed. The main content is as follows: (1) GAs are closely related to their ability to retard fruit senescence. GA treatment could improve fruit storage quality and significantly increase flesh hardness, reduce respiration intensity, inhibit the release of endogenous ethylene, and effectively inhibit fruit softening and ripening. (2) They can also improve the intrinsic and extrinsic quality of fruit storage by improving fruit shape, regulating color, delaying the reduction of soluble solids, promoting sugar accumulation, and delaying vitamin C loss. (3) GAs improve fruit chilling resistance through effective control of postharvest chilling damage. The treatment of GA₅ effectively reduces the cold damage index, reducing the production and accumulation of superoxide anion (O₂[−]), improving the antioxidant capacity of fruits, and maintaining the integrity of cell membranes during low-temperature storage. (4) GAs also play a role in postharvest disease control. Overall, GAs, as an important class of plant hormone, play an essential role in the postharvest physiological regulation of fruits. Their application in postharvest could provide valid biotechnology for extending the storage period of fruits.

2. Gibberellins for Regulating the Ripening and Senescence Process

Gibberellins could influence the ripening of fruit by affecting their size, color, flavor, and nutritional value (Table 1). Ripening is generally accomplished when fruits' internal and external components reach optimal states. It has been found that GA₃ affected the size, metabolic contents, and color of fruits during tomato softening [5,6]. Meanwhile, exogenous GA treatment could improve the nutritional traits of bulbs in most garlic cultivars, and it regulates starch synthesis and degradation by affecting related enzyme activities, promoting sucrose accumulation and inhibiting starch regeneration to accumulate soluble sugars in potato tubers [7,8]. Moreover, it has been found that applying exogenous GA₃ and paclobutrazol (PAC, an inhibitor of gibberellin biosynthesis) could prolong and shorten fruit ripening time, respectively [9]. Those results suggested that GAs may exert a delayed influence on fruit ripening.

Table 1. Effect of GAs for regulating the ripening and senescence of horticultural crops.

Horticultural Varieties	Main Points	Concentration	References
Cabbage (<i>Brassica rapa</i> var. <i>glabra</i> Regel)	GA ₃ spraying retarded fruit senescence.	100 µM GA ₃	Fan et al., 2021 [10]
Garlic (<i>Allium sativum</i> L.)	GA ₃ injection improves the nutritional traits of fruits.	1 mM GA ₃	Liu et al., 2019 [7]
Potato (<i>Solanum tuberosum</i> L.)	GA spraying accumulates tuber sugar nutrients.	0.015 g L ^{−1} GA	Xie et al., 2018 [8]
Tomato (<i>Solanum lycopersicum</i> L.)	GA ₃ spraying affects the size of fruits.	50 µM GA ₃	Zhu et al., 2019 [5]
Tomato (<i>Solanum lycopersicum</i> L.)	GA ₃ injection delays color change in fruit at ripening stage.	0.1 mM GA ₃	Li et al., 2019 [7]
Toona (<i>Toona sinensis</i> (A. Juss.) Roem.)	GA ₃ soaking retards fruit senescence.	100 mg L ^{−1} GA ₃	Zhao et al., 2018 [11]

Regarding the molecular mechanisms of exogenous gibberellins in fruit ripening, studies have identified the effects of GAs on ripening characteristics and the expression of ethylene biosynthesis and signaling genes in tomato fruit (Figure 1). It was found that the exogenous GA treatment could effectively increase the expression level of gibberellin-stimulated transcript 1 (*GAST1*), slow down (or inhibit) the decrease of endogenous GA

concentration, inhibit the expression of fruit ripening regulators *RIPENING INHIBITOR* (*RIN*), *NON-RIPENING* (*NOR*), and *COLORLESS NON-RIPENING* (*CNR*), attenuate the expression levels of crucial genes in ethylene synthesis (*ACS2*, *ACS4*, and *ACO1*), and also reduce the expression of key ethylene receptor genes *EYR3* (*NR*) and *ETR4*. The altered expression of these maturation regulators also suppressed the expression of the major ethylene signaling gene *EIN2* to a certain extent [6]. GAs were demonstrated to play a negative role in tomato fruit ripening by regulating the ethylene-related pathways.

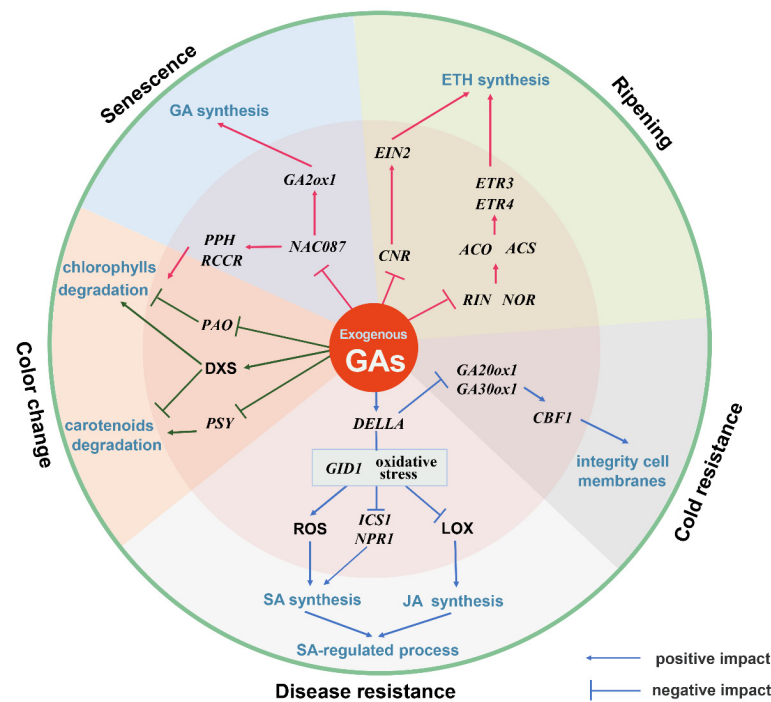


Figure 1. Molecular mechanisms of gibberellins related to regulating postharvest physiology. (1) GAs regulated the ripening process (modeling based on tomato): GAs affect the expression of *EYR3*, *ETR4*, and *EIN2* by regulating *RIN*, *NOR*, and *CNR*. (2) GAs regulated the senescence process (modeling based on cabbage): GAs affect the expression levels of *PPH*, *RCCR*, and *GA2ox1* by regulating the expression of *BrNAC087*. (3) GAs regulated the color change of fruit (modeling based on citrus): the use of GAs can regulate *DXS* activity and gene expression of *PAO* and *PSY*. (4) GAs regulated the cold resistance of fruit (modeling based on tomato): GAs regulate *GA20ox1* and *GA3ox1* expression by affecting the *DELLA* gene expression, which in turn incrementally affects *CBF1* expression. (5) GAs regulated the disease resistance of fruit (modeling based on tomato): GAs affect *DELLA* gene expression through both binding to *GID1* and induced oxidative stress, which in turn regulates the levels of *ROS*, *LOX*, and *ICS1*, *NPR1* to affect *SA* and *JA* biosynthesis and thus the SAR process. Abbreviations: *ACO* (1-aminocyclopropane-1-carboxylic acid oxidase), *ACS* (1-aminocyclopropane-1-carboxylic acid synthase), *CBF1* (C-repeat binding transcription factor 1), *CNR* (*COLORLESS NON-RIPENING*), *DXS* (1-deoxy-D-xylulose 5-phosphate synthase), *EIN2* (*ETHYLENE INSENSITIVE 2*), *ETH* (ethylene content), *ETR* (*ETHYLENE RESPONSE*), *GA* (gibberellin), *GID1* (*GIBBERELLIN INSENSITIVE DWARF 1*), *ICS1* (isochorismate synthase 1), *JA* (jasmonate), *LOX* (lysyl oxidase), *NOR* (*NON-RIPENING*), *NPR1* (nonexpressor of pathogenesis-related genes 1), *PAO* (*pheophorbide a oxygenase*), *PPH* (*pheophytinase*), *PSY* (*phytoene synthase*), *RIN* (*RIPENING INHIBITOR*), *SA* (salicylic acid), *RCCR* (*red chlorophyll catabolite reductase*), *ROS* (reactive oxygen species).

Gibberellins had important roles in regulating fruit senescence. Aging fruit refers to the gradual loss of water, flavor, and nutrition; it also reduces enzyme activity, causes cell aging, and occurs with decay and spoilage. The physiological indicators of fruit aging include enzyme activities of superoxide dismutase (SOD), the function of scavenging reactive oxygen species and is a protective enzyme for plant cells [12], peroxidase (POD), and

catalase (CAT), the function of decomposing H_2O_2 [13], polyphenol oxidase (PPO), trigger fruit browning phenolic substances [14], and malonaldehyde (MDA), and are considered to measure the rate of lipid peroxidation in the cell membrane and be an indicator of the amount of senescence and stress [15]. It was found that GA_3 treatment could significantly reduce the accumulation of MDA and H_2O_2 , enhance the activity of CAT and SOD, and reduce the activity of POD and PPO in the shoots of *Toona sinensis*, which showed that GA treatment could effectively delay the aging process of *Toona* [11].

Molecular mechanisms related to gibberellin delaying plant aging have also been reported. A study identified *BrNAC087* (a homolog of *ANAC087*, senescence-associated NAC transcription factor) as an important regulator of postharvest Chinese flowering cabbage leaf senescence (Figure 1). It was demonstrated that *BrNAC087* acted as a direct activator of two chlorophyll catabolic genes (*BrPPH* and *BrRCCR*) and one GAs inactivation gene *BrGA2ox1*, by specifically binding to the promoters of *BrPPH*, *BrRCCR*, and *BrGA2ox1*. Exogenous GA_3 treatment could effectively inhibit the expression of *BrNAC087* and reduce the expression levels of *BrPPH*, *BrRCCR*, and *BrGA2ox1*, thus reducing chlorophyll degradation and GAs catabolism and achieving the purpose of delaying leaf senescence [10].

3. Gibberellins for Exterior Quality Control of Horticultural Crops

Gibberellins could influence fruit appearance by regulating cell expansion and enlargement, enhancing fruit stalk length, controlling fruit shape, adjusting pigment content, and modulating fruit color (Table 2). It has been shown that the fruit shape index (the ratio of the longitudinal diameter to the transverse diameter of the fruit and a quality indicator for commercial fruits) was influenced by GAs [16]. Cruz-Castillo et al. showed that GA_3 supplied to the pedicel of ‘Hayward’ kiwifruit increased the length of the terminal pedicel and affected the fruit shape index [17]. Liu et al. found that GA_3 treatment could significantly increase apple fruit stalk length and improve fruit shape [18]. Another study on ‘Chandler’ strawberry showed similar experimental results, which found that GA_3 and cytokinin (substances with cell division activity) could promote cell elongation and thus achieve an elongation of fruit stalk length to improve the fruit shape index [19]. It has been found that GA_3 treatment in tomato fruit can promote cell expansion and enlargement, thus improving the shape index [9]. GA_3 spraying on self-pollinated apple plants increased fruit weight, reduced the proportion of asymmetric fruits, and restored the shape and quality of external fruits to the level of cross-pollinated fruits [18]. It is worth noting that, at the molecular level, GA-related genes could regulate fruit exterior shape during fruit development. It was claimed that, in cucumber, the expression pattern of the GA receptor gene *CsGID1a* was closely related to the formation of fruit form. Silencing the *CsGID1a* gene resulted in fruits exhibiting an abnormal carpel and ovary phenotype, while overexpression of *CsGID1a* in the Arabidopsis double mutant (*gid1a* and *gid1c*) exhibited ‘cucumber ovary-like’ fruits [20].

Table 2. Effect of GAs on regulating the exterior quality of horticultural crops.

Horticultural Varieties	Main Points	Concentration of GAs	References
Apple (<i>Malus pumila</i> Mill.)	GA_3 spraying increases fruit stem length and improves fruit shape index.	100 mg L ⁻¹ GA_3	Liu et al., 2022 [18]
Apple (<i>Malus pumila</i> Mill.)	GA_3 spraying increases fruit weight and improves fruit shape index.	100 mg L ⁻¹ GA_3	Liu et al., 2022 [18]
Broccoli (<i>Brassica capitata</i> var. <i>italica</i>)	GA_3 soaking retards the degradation of chlorophyll in fruit peel and slows down the color change of fruit skin.	10 mg L ⁻¹ GA_3	Wang et al., 2023 [21]
Citrus (<i>Citrus reticulata</i> Blanco)	ProCa spraying reduces chlorophyll and increases carotenoid concentrations in fruits.	400 mg·L ⁻¹ ProCa	Barry et al., 2010 [22]
Citrus (<i>Citrus reticulata</i> Blanco)	PBZ spraying affects fruit color.	1500 mg L ⁻¹ PBZ	Rehman et al., 2018 [23]

Table 2. Cont.

Horticultural Varieties	Main Points	Concentration of GAs	References
Citrus (<i>Citrus reticulata</i> Blanco)	GA ₃ spraying affects fruit color by influencing enzyme activity.	60 mg L ⁻¹ GA ₃	Alos et al., 2006 [24]
Cucumber (<i>Cucumis sativus</i> Linn.)	GA ₃ spraying regulates fruit shape.	50 µM GA ₃	Liu et al., 2016 [20]
Grape (<i>Vitis vinifera</i> L.)	GA ₃ spraying reduces flavanol and anthocyanin content and slows down the color change of fruit skin.	20 ppm GA ₃	Tyagi et al., 2022 [25]
‘Hayward’ kiwifruit (<i>Actinidia chinensis</i> Planch.)	GA ₃ soaking increases fruit stem length and improves fruit shape index.	100 mg L ⁻¹ GA ₃	Cruz-Castillo et al., 2006 [17]
Lychee (<i>Litchi chinensis</i> Sonn.)	GA ₃ soaking retards the degradation of anthocyanins in fruit peel and slows down the color change of fruit skin.	0.05 g L ⁻¹ GA ₃	Qu et al., 2021 [26]
‘Valencia’ orange (<i>Citrus sinensis</i> (Linn.) Osbeck)	GA ₃ spraying retards the degradation of chlorophyll in fruit peel and reduces carotenoid content.	500 µM GA ₃	Keawmanee et al., 2022 [27]
‘Chandler’ strawberry (<i>Fragaria chiloensis</i> (L.) Duchesne)	GA ₃ spraying increases fruit stem length and improves fruit shape index.	75 ppm GA ₃	Sharma et al., 2009 [19]
Tomato (<i>Solanum lycopersicum</i> L.)	GA ₃ spraying improves fruit shape index.	0.1 mM GA ₃	Chen et al., 2020 [9]

Gibberellins could modulate fruit color changes by influencing the content of pigments such as chlorophylls, carotenoids, and anthocyanins. It was also found that GA₃ treatment on broccoli could control chlorophyll metabolism and delay yellowing [21]. GA₃ treatment on ‘Valencia’ orange induced chlorophyll accumulation and reduced carotenoid contents (β-astaxanthin, all-trans-violaxanthin, and 9-cis-violaxanthin) [27]. It has also been shown that GA₃ treatment could inhibit the degradation of anthocyanins to suppress lychee browning [26]. The treatment of GA₃ on grapes reduced the flavonol and anthocyanin content and also slowed down the color change of the skin [25]. In addition, Prohexadion-calcium (ProCa, an inhibitor of GA biosynthesis with growth retarding activity) was shown to reduce chlorophyll and increase carotenoid concentrations in the yellow matter of citrus fruits [22]. Similarly, GA biosynthesis inhibitor polycarbazole (PBZ) was found to exert a similar effect in citrus fruit color conversion [23].

It was further suggested that gibberellins successfully affect the accumulation of various pigments in the fruit by regulating the activities of various enzymes in the fruit. Exogenous GA₃ delayed strawberry fruit color change by inhibiting the increase in phenylalanine ammonia-lyase (PAL) activity and delaying the decrease in chlorophyllase and peroxidase (enzymes that may be involved in chlorophyll metabolism) activity (Figure 1). Similar results have been found in studies on the mechanism of color break regulation in citrus fruits, where the use of exogenous GAs delayed the reduction of 1-deoxy-D-xylulose 5-phosphate synthase (DXS) activity, while the increasing gene expression of *pheophorbide oxygenase* (PAO) and *phytoene synthase* (PSY) increased the content of their corresponding transcripts, and delayed the consumption of pericarp chlorophyll and the accumulation of total carotenoids and retarded fruit color change [24].

4. Gibberellins for Improving the Internal Quality of Horticultural Crops

Gibberellins could influence taste and texture quality, such as fruit hardness, water loss, soluble solids, acids, and nutrient contents (Table 3). It was demonstrated that the GA₃ treatment of kiwifruit could effectively delay the decrease of fruit hardness, maintain the total acid content, and accumulation of soluble solids [28]. Moreover, several studies have also shown that GA₃ treatment effectively delays postharvest fruit weight loss and decay of the ‘Angelino’ plum [29] and Japanese plum varieties of ‘Obilnaja’ and ‘BlackStar’ [30]. Meanwhile, Ozturk et al. also found that the application of GA₃ with CaCl₂ significantly

delayed the weight loss of sweet cherry [31]. These findings further support the fact that GAs are effective in delaying the aging of fruits. GA₃ treatment of plum fruit increased the soluble solids content and reduced the titratable acidity at harvest, which could effectively maintain the fruit quality during storage [32]. Zang et al. found that the soluble solids content increased in GA₃-treated ‘rabbit eye’ blueberry, thus improving the fresh eating quality of ‘rabbit eye’ blueberry [33]. A similar phenomenon in sweet cherry cultivars was that GA₃ treatment significantly increased acidity levels [34]. Meanwhile, it was also found that treating the Japanese plum with GA₃ effectively controlled the degradation of soluble solids and titratable acids [35]. Similar results have been found in apples and mangoes [16]. In addition, the water content in fruits treated with GAs has been varied, and Forchlorfenuron (CPPU) and GA₃ have been reported to significantly reduce water loss in banana and broccoli [36].

Gibberellins could also influence the nutrient contents of vitamins, phenols, and soluble proteins. ‘Barhee’ dates were sprayed with different rates of GAs which effectively controlled the degradation of the vitamin C (Vc) content in the fruit [37]. Li et al. dipped the fruits of plum varieties into GA₃ solution after harvest and found that the application of GA₃ to plums significantly delayed the decrease in ascorbic acid concentration and the increase in total phenolic content [38]. Meanwhile, studies on fruits such as ‘rabbiteye’ blueberry, Japanese plum, and ‘nanguo’ pear fruit have shown that GA₃ treatment can delay the reduction of ascorbic acid concentration and total phenolic content in the fruits, maintaining the postharvest fruit quality [33,35,39]. Besides, the results of some studies showed that the spraying of different concentrations of GA₃ significantly improved the quality of garlic and Welsh onion; their soluble protein content was significantly higher [7,40]. It was also found that the phenolic content of fruit was significantly higher after GA₃ spraying on ‘Cabernet Sauvignon’ grapes [41].

Table 3. Effect of GAs on regulating the internal quality of horticultural crops.

Horticultural Varieties	Main Points	Concentration of GAs	References
Apple (<i>Malus pumila</i> Mill.)	GA ₃ spraying retards the decrease in soluble solids content in fruits.	100 mg L ⁻¹ GA ₃	Liu et al., 2022 [18]
Banana (<i>Musa nana</i> Lour.)	GA ₃ and CPPU treatments reduce water loss in fruits.	50 mg L ⁻¹ GA ₃ + 10 mg L ⁻¹ CPPU	Huang et al., 2012 [36]
‘rabbit eye’ blueberry (<i>Vaccinium virgatum</i> Ait.)	GA ₃ spraying retards the decrease in soluble solids content of fruits.	500 mg L ⁻¹ GA ₃	Zang et al., 2016 [33]
‘rabbit eye’ blueberry (<i>Vaccinium virgatum</i> Ait.)	GA ₃ spraying retards the decline of ascorbic acid concentration and the increase of total phenolic content of fruits.	500 mg L ⁻¹ GA ₃	Zang et al., 2016 [33]
Broccoli (<i>Brassica capitata</i> var. <i>italica</i>)	GA ₃ and CPPU treatments reduce water loss.	50 mg L ⁻¹ GA ₃ + 10 mg L ⁻¹ CPPU	Huang et al., 2012 [36]
Sweet cherry (<i>Cerasus pseudocerasus</i> (Lindl.) G. Don)	GA ₃ spraying retards fruit weight loss.	30 mg L ⁻¹ GA ₃	Burhan et al., 2022 [31]
Sweet cherry (<i>Cerasus pseudocerasus</i> (Lindl.) G. Don)	GA ₃ spraying raises fruit acidity levels.	60 mg L ⁻¹ GA ₃	Ozkan et al., 2016 [34]
‘Barhee’ date (<i>Ziziphus jujuba</i> Mill.)	GA ₃ spraying retards the decline of Vc content in fruits.	50 ppm GA ₃	Awad et al., 2012 [37]
Garlic (<i>Allium sativum</i> L.)	GA ₃ injection increases soluble protein content of fruits.	1 mM GA ₃	Liu et al., 2019 [7]
‘Cabernet Sauvignon’ grape (<i>Vitis vinifera</i> L.)	GA ₃ spraying increases phenol content of fruits.	15 mg L ⁻¹ GA ₃	Song et al., 2023 [41]
Kiwifruit (<i>Actinidia chinensis</i> Planch.)	GA ₃ spraying retards the decline of fruit hardness and soluble solids content.	0.3 g L ⁻¹ GA ₃	Yang et al., 2023 [28]
Welsh onion (<i>Allium cepa</i> L.)	GA ₃ spraying increases soluble protein content of fruits.	40 ppm GA ₃	Yamazaki et al., 2015 [40]
‘Nanguo’ pear (<i>Pyrus</i> spp)	GA ₃ soaking retards the decline of ascorbic acid concentration and the increase of total phenolic content of fruits.	100 mg L ⁻¹ GA ₃	Martínez-Romero et al., 2000 [39]
Plum (<i>Prunus salicina</i> Lindl.)	GA ₃ spraying retards the decrease in soluble solids content of fruits and reduces titratable acidity at harvest.	200 mg L ⁻¹ GA ₃	Barac et al., 2022 [32]

Table 3. Cont.

Horticultural Varieties	Main Points	Concentration of GAs	References
Plum (<i>Prunus salicina</i> Lindl.)	GA ₃ spraying retards the reduction of soluble solids and titratable acid content in fruits.	50 mg L ⁻¹ GA ₃	Erogul et al., 2015 [35]
Plum (<i>Prunus salicina</i> Lindl.)	GA ₃ soaking retards the decline of ascorbic acid concentration and the increase of total phenolic content of fruits.	200 µL L ⁻¹ GA ₃	Li et al., 2006 [38]
Plum (<i>Prunus salicina</i> Lindl.)	GA ₃ spraying retards the decline of ascorbic acid concentration and the increase of total phenolic content of fruits.	50 mg L ⁻¹ GA ₃	Erogul et al., 2015 [35]
‘Angelino’ plum (<i>Prunus salicina</i> Lindl.)	GA ₃ spraying retards fruit weight loss and decay.	50 mg L ⁻¹ GA ₃	Erogul et al., 2016 [29]
‘BlackStar’ plum (<i>Prunus salicina</i> Lindl.)	GA ₃ spraying retards fruit weight loss and decay.	50 ppm GA ₃	Harman et al., 2016 [30]
‘Obilnaja’ plum (<i>Prunus salicina</i> Lindl.)	GA ₃ spraying retards fruit weight loss and decay.	50 ppm GA ₃	Harman et al., 2016 [30]

5. Gibberellins for Improving Cold Resistance in Horticultural Crops

Gibberellins participate in plant responses to biotic and abiotic stresses. When fruits are subjected to postharvest stress, the exogenous application of GAs can effectively regulate biotic and abiotic stress resistance. Cold damage is one of the more important abiotic stresses in the postharvest aspect of fruits, and it is a major constraint to the low-temperature storage of cold-sensitive fruits, resulting in sunken skins, watery spots, dry scars, flesh flocculation or lignification, reduced flavor, failure to properly ripen, and accelerated decay. It was found that elevated GA₃ levels were accompanied by the down-regulation of DELLA genes (members of the GRAS protein family that repress GA responses, degraded by the 26S-proteasome upon interaction with the GID1-GA complex) and the expression of key GA biosynthetic genes, *GA20ox1* and *GA3ox1*, was down-regulated in the application of exogenous GA₃ (Figure 1). Zhu et al. found that GA₃ treatment reduced the cold damage index, maintained the integrity of cell membranes during low-temperature storage, and activated the feedback mechanism of GA anabolism and the expression of C-repeat binding transcription factor 1 (*CBF1*), an important regulator of cold resistance, thus effectively improving the cold resistance of tomato fruits [42]. Ding et al. showed that, during low-temperature storage of the GA-deficient mutant *gib-3* tomato fruit, the cold damage index was significantly higher than that of normal fruit, and the breakage of microstructures such as cell membranes and cell walls was accelerated and more severe. GA deficiency also led to an up-regulation of *GA3ox1* and a significant down-regulation of *CBF1*, indicating that GA deficiency reduced the cold resistance of the fruit [43]. Ding et al. treated cherry tomato with GA₃ and stored them at low temperatures; the fruit cold damage index decreased significantly, effectively maintaining the stability of the cell membrane during storage, reducing the production and accumulation of O₂⁻ and improving the antioxidant capacity of the fruit. The results indicated that GA treatment effectively controlled postharvest cold damage in the fruit [44] (Table 4).

Table 4. Effect of GAs on regulating cold resistance of horticultural crops.

Horticultural Varieties	Main Points	Concentration of GAs	References
Tomato (<i>Solanum lycopersicum</i> L.)	GA ₃ spraying maintains the integrity of fruit cell membranes during low-temperature storage and activates cold resistance regulation.	0.5 mM GA ₃	Zhu et al., 2016 [42]
Cherry tomato (<i>Solanum lycopersicum</i> L.)	GA ₃ spraying maintains the integrity of fruit cell membranes during low-temperature storage and enhances antioxidant capacity.	0.2 mmol L ⁻¹ GA ₃	Ding et al., 2015 [44]
<i>gib-3</i> tomato (<i>Solanum lycopersicum</i> L.)	GA ₃ deficiency leads to accelerated destruction of fruit cell membranes during low-temperature storage and reduces cold resistance.	GA mutant	Ding et al., 2016 [43]

6. Gibberellins Regulate Disease Resistance in Horticultural Crops

Research has indicated that gibberellin treatment effectively controlled the incidence of disease during storage. Disease is a series of morphological, physiological, and biochemical pathological changes in fruits under the influence of biotic or abiotic factors. In the horticultural postharvest sector, this mainly manifests as the phenomenon of fruit that are healthy at harvest but infected with disease afterward, and as fruits that are apparently intact but diseased at harvest and only show traces of disease after harvest. *Trichothecium roseum* [45] and *Fusarium* [46] are susceptible to postharvest fruit infestation, causing pink mold and white mold, which cause extensive fruit rot. Ma et al. found that GA₃ did not inhibit the growth of *Trichothecium roseum* and *Fusarium*, but when mixed with azoxystrobin (AZX), the spot area of both diseases was reduced to different degrees compared to the two alone, thus inferring that GA₃ improved fruit resistance by regulating the physiological activity of postharvest fruits [47]. Black skin disease is a major physiological disease that occurs on pear fruit after harvesting, producing irregular black-brown spots of varying sizes on the surface of the fruit skin, which seriously reduces the quality of the appearance of the fruit [48]. Ma et al. treated ‘apple pear’ fruit with GA₃ and found that POD, CAT, APX, and SOD activities increased, while PPO activity decreased and the thickness of surface protective tissue increased; the results indicated that GA treatment effectively controlled ‘apple pear’ black skin disease [49]. In addition, in studies on persimmon’s black spots, GAs were found to reduce rot by inhibiting the extracellular enzyme activity of *Alternaria alternata* (*A. alternata*) to maintain fruit cell wall integrity and limit pathogen expansion and access to host nutrients [50]. Similarly, one study found that GAs use reduced fruit cuticle dehiscence and susceptibility to persimmon fruit black spot disease during late fruit growth and storage. The present results suggest that GAs cause delayed fruit ripening and are a major factor in enhancing resistance to persimmon fruit black spots during harvest and storage [51] (Table 5).

Table 5. Effect of GAs on regulating disease resistance of horticultural crops.

Horticultural Varieties	Main Points	Concentration	References
Melon (<i>Citrus limon</i> (L.) Osbeck)	GA ₃ and AZX spraying inhibits the growth of <i>Trichothecium roseum</i> and <i>Fusarium</i> .	100 mg L ^{−1} GA ₃ + 100 mg L ^{−1} AZX	Ma et al., 2005 [47]
‘apple pear’ pear (<i>Pyrus</i> spp.)	GA ₃ spraying increases the thickness of protective tissue on the fruit surface and controls black skin disease.	50 mg L ^{−1} GA ₃	Ma et al., 2018 [49]
Persimmon (<i>Diospyros kaki</i> Thunb.)	GA ₃ spraying reduces fruit cuticle cracking and controls black spot.	200 µg mL ^{−1} GA ₃	Biton et al., 2014 [51]
<i>gib-3</i> tomato (<i>Solanum lycopersicum</i> L.)	GA regulates early blight resistance by regulating hormone content.	GA mutant	Wu et al., 2018 [52]

The molecular mechanisms of gibberellin to regulate disease resistance in fruits were studied. DELLA regulates the balance of salicylic acid (SA)/jasmonate (JA) signaling during plant immunity [53]. SA and JA play key roles in the induction of the systemic acquired resistance (SAR) process for defense against pathogenic bacteria infestation, while isochorismate synthase 1 (*ICS1*) transcription activates SA biosynthesis; nonexpressor of *pathogenesis-related* genes 1 (*NPR1*) is an important regulator of the SA-regulated SAR process [54] (Figure 1). Early blight caused by *Streptomyces aegypti* infestation is one of the most common postharvest fungal diseases [55]. A study indicated that *ICS1* and *NPR1* were up-regulated, PAL, PPO, CHI, and GLU activities were significantly enhanced, brassinolide (BR) content was increased, fruit incidence was significantly reduced, and spot area was significantly decreased in the GA-deficient mutant strain *gib-3* tomato fruit, indicating that GAs negatively regulated postharvest tomato fruit resistance to early blight [52].

7. Conclusions

In conclusion, as important plant hormones, gibberellins play a significant role in the postharvest physiological regulation of fruits. During the storage of fruits, GAs can effectively delay the respiratory leap in some fruits and can delay the weight loss and decay of fruits by inhibiting ethylene production, reducing respiration intensity, scavenging free radicals in the body to maintain cell membrane integrity, and delaying the senescence of fruit stalks to prevent them from falling off. They can also improve the intrinsic and extrinsic quality of fruit storage by improving fruit shape, regulating color, and delaying the reduction of soluble solids. GAs also play an important role in enhancing postharvest stress resistance in fruits. This review systematically described the role of GAs in the physiological regulation of postharvest fruits and their existing applications, providing a more comprehensive perspective to further enhance the scope of their application in postharvest fruits and to clarify their usage in practice. At the same time, this paper lays a certain foundation for accelerating and improving the research on the physiological aspects of the regulation of GAs in postharvest fruits, and also points to a certain direction for in-depth molecular-level mechanism research.

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