



Preharvest Elicitors Spray Improves Antioxidant Activity, Alleviates Chilling Injury, and Maintains Quality in Harvested Fruit

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Abstract: Antioxidant activity is an important feature for evaluating fruit quality and tolerance to biotic or abiotic stresses. Moreover, antioxidant activity is involved in chilling injury (CI) response and postharvest quality in fruit. Chemical elicitors can induce systemic acquired resistance in fruit against pathogens, which could partially replace synthetic fungicides. Recently, researchers have found that preharvest sprays with chemical elicitors can improve antioxidant activity, reduce CI, and maintain quality in harvested fruit. In this review, we summarize that preharvest elicitors spray improve antioxidant activity in harvested fruit by promoting antioxidant components biosynthesis as well as antioxidant ability in vitro. Moreover, preharvest elicitors spray alleviates CI in fruit by regulation of membrane lipid metabolism and reactive oxygen species metabolism. In addition, preharvest elicitors spray maintains fruit quality by modulation of respiration and ethylene release. Finally, this review points out the issues existing and proposes an outlook on preharvest elicitors spray to maintain postharvest fruit quality.

Keywords: fruit; preharvest elicitor spray; antioxidant activity; chilling injury; postharvest quality

1. Introduction

Fresh fruits have aesthetic appearance and unique flavor as well as nutrition. However, postharvest loss in fruit is huge. The global average of postharvest loss in fresh fruit is estimated to be 40% [1]. Fungal infection is the main reason for postharvest loss of fruit, but over-ripening and senescence, and chilling injury (CI) caused by inappropriate low temperature are also considered to be important causes of the loss [2,3]. Various measures can effectively control quality deterioration and CI in fruit. However, most of them focus on postharvest treatments, which are inconvenient and inevitably increase postharvest procedures and costs [2,4,5].

Chemical elicitors are synthetic chemicals, mainly including salicylic acid (SA), jasmonic acid (JA) and chitosan and their analogs or derivatives. These elicitors can induce fruit resistance against pathogens by eliciting systemic acquired resistance (SAR), which could partially replace synthetic fungicides [6]. Recently, in addition to inhibiting fruit diseases by inducing resistance, chemical elicitor shave been found to contribute to enhancing antioxidant activity, reducing CI, and maintaining postharvest quality in fruit [7–9].

The periods of fruit development are critical for the formation of postharvest resistance and quality in fruit. During the development, continuous cell division and expansion lead to fruit enlargement and the formation of barriers that can contribute to fruit resistant, including epidermal wax, cut in, cell wall, and cell membrane [10]. Meanwhile, products such as sugars, organic acids, aromas, ascorbic acid, carotenoids, and phenolic compounds



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Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). are continuously accumulated in cells, which can affect fruit quality and tolerance biotic or abiotic stresses [11,12]. This review focuses on the effect of preharvest elicitors spray on improving antioxidant activity, alleviating CI, and maintaining quality in harvested fruit, and analyzes the possible reasons.

2. Improvement of Antioxidant Capacity

Phenolics, ascorbic acid, and carotenoids are important antioxidant compounds in fruit, which are known to be beneficial to human health [13].

2.1. Enhancing Phenolics, Ascorbic Acid and Carotenoids Contents

Preharvest elicitors spray effectively enhances the accumulation of phenolic compounds in fruit. Similarly, 0.1 mM methyl jasmonate (MeJA) or 0.5 mM SA that was sprayed 4 times on 'Fino' lemon before harvest increased the contents of total phenolics and two main flavonoids (hesperidin and eriocitrin) [14]. 'Xiaobai' Apricot was sprayed twice with 0.05% chitosan oligochitosan or 1 mmol L^{-1} SA at 7 and 2 days before harvest, resulting in higher contents of total phenolics, total flavonoids and three main phenolic compounds (5-O-caffeoylquinic acid, 3-O-caffeoylquinic acid, quercetin-3-rutinoside) at harvest and during cold storage [7]. Preharvest with phenylalanine increased the total flavonoids and anthocyanins in 'Kent' and 'Shelly' mango fruits and 'Pink Lady' apples [15]. Spraying twice with 0.1%, 0.2%, or 0.4% prohydrojasmon on 4 and 2 weeks before harvest increased the contents of total anthocyanin and total flavonoid and the accumulation of anthocyanin monomers and flavonoids in 'Kent' mango fruit during cold storage, of which 0.4% treatment showed the best effect. On the 21st day of cold storage, the contents of total anthocyanin and total flavonoid in 0.4%-sprayed fruit showed 4 folds and 67% higher than those of the control. Moreover, the contents of anthocyanin monomers, including cyanidin, methyl-cyanidin, cyanidin-3-galactoside, 7-O-methylcyanidin-3-O-β-D-galactopyranoside, as well as quercetin and kaempferol content, were significantly higher than those of the control [16]. In addition, at harvest and during cold storage, contents of total phenolics, total anthocyanins, and anthocyanin monomers enhanced in 'Mollar de Elche' pomegranate sprayed by 1, 5, or 10 mmol L^{-1} MeJA at 94, 64, 34, and 4 days before harvest, of which 5 mmol L^{-1} MeJA spay showed the best effect [17].

Preharvest elicitors spray can significantly enhance the accumulation of ascorbic acid and carotenoids in fruit. At harvest, a higher content of ascorbic acid was observed in 'El-Bayadi' table grapefruit sprayed with 4.0 mM SA 4 times from the pea stage to the version stage [18]. A higher total carotenoid content was shown in 'Black Splendor' plum fruit that was sprayed 3 times with 0.5 mmol L^{-1} SA, 1 mmol L^{-1} acetyl salicylic acid (ASA), or 0.5 mmol L^{-1} Methyl salicylate (MeSA) at 61, 76, and 94 days after flowering. At harvest, the total carotenoid content in the three treated plum fruit increased by 17%, 25%, and 25% compared with the control, which was 18%, 55%, and 36% higher on the 40th day of cold storage, respectively [19]. Similarly, three sprays of 1 mM oxalic acid at 63, 77 and 98 after flowering increased total carotenoid content in 'Black Splendor' plum fruit, which increased by 20% compared with the control on the 35th of cold storage [20]. In addition, the total carotenoid content in 'Neelum', 'Bangalore', 'Banganapalli', and 'Alphonso' mango fruit sprayed twice with 2% hexanal at 30 and 15 days before harvest was 6.7%, 61%, 27%, and 32% higher than that of the control on the 9th day of cold storage [21]. Three sprays of 250 mmol L^{-1} MeJA at flowering, 24 days of turning green, and 7 days of turning red enhanced ascorbic acid content in 'Camarosa' strawberry, which increased by 20% and 63% compared with the control at harvest and 2 days of storage [22]. Further, two sprays of 1.2 mM hexanal4 and 2 weeks before harvest increased ascorbic acid content in 'Allahabad Safeda' guava fruit at harvest and during cold storage [23]. Preharvest elicitors spray on improving phenolics, ascorbic acid and carotenoids accumulation in harvested fruit are shown in Table 1.

Phenolics and flavonoids in fruit are mainly synthesized from phenylpropanoid metabolism pathway. L-phenylalanine is the substrate of phenylpropanoids metabolism

and it can generate phenolics and flavonoids under the continuous activity of phenylalanine ammonialyase (PAL), cinnamate 4-hydroxylase (C4H), and 4-coumarate: coenzyme A ligase (4CL), and cinnamyl alcohol dehydrogenase (CAD) [24,25]. Preharvest phenylalanine spray improved the contents of total flavonoids and total anthocyanins in mango fruit [15]. Similarly, preharvest phenylalanine spray triggered PAL, C4H, 4CL, and CAD activity, increasing the accumulation of total phenolic and flavonoids in muskmelon fruit [26]. Preharvest melatonin up-regulated the levels of SIPAL, SIC4H, and SI4CL expression in cherry tomato fruit during storage [27]. Moreover, preharvest prohydrojasmon spray upregulated the expression of a key transcription factor (MYB114) that regulated key genes for anthocyanin biosynthesis (PAL, CHS, CHI, F3H, ANS, UFGT, FLS, and LAR) in pear fruit at harvest [28]. In addition, preharvest MeJA improved PAL activity, increasing flavonoid accumulation in raspberries at harvest [29]. Preharvest harpin spray increased PAL activity in muskmelon fruit during storage, improving total phenolics and flavonoid content [30]. Preharvest chitosan spray enhanced the activity of PAL, 4CL, CAD, and C4H, promoting the biosynthesis of phenolics and flavonoids in muskmelon fruit during storage [31,32]. Although the effects of preharvest elicitors spray on the biosynthesis of phenolics in harvested fruit have been studied at the biochemical level, the relevant molecular mechanisms remain to be further unlocked.

Ascorbic acid is mainly synthesized through the L-galactose pathway in fruit [33]. However, there is no report on the regulation of the L-galactose pathway in fruit by preharvest elicitors spray. Carotenoids are mainly synthesized through 2-c-methyl-d-erythritol 4-phosphate and/or mevalonate pathway in fruit [34]. The transcriptome results showed that preharvest of benzothiadiazole (BTH) and chitosan spray up-regulated the expression of important transcription factors as WRKYs and NACs, involved in regulating the metabolism of carotenoid compounds in fruit, thereby promoting the synthesis of carotenoids in harvested 'Alba' strawberry fruit [35]. There are few reports on the effect of preharvest elicitors spray on carotenoid biosynthesis in harvested fruit, and the related mechanism needs to be further studied.

Elicitor	Manufacturer	Fruit	Cultivar	Spraying Concentra-	Spraying Times	Spraying Stage		Antiox	idant Compound	ls	Free Radical Scavenging Activit				Refer-
				tion	Times		Phenols	Flavonoids	Anthocyanins	VC	Carotenoids	DPPH ABTS		FRAP	ences
SA	Sigma- Aldrich	Plum	Black Splendor	$0.5 \text{ mmol } \mathrm{L}^{-1}$	3	61, 76 and 94 days after full blossom	\sqrt{a}	b	\checkmark	_	\checkmark	_	_	_	[19,36]
	Oxford Laboratory Reagents	Apricot	Canino	2 or 4 mM	2	30 and 15 days before harvest	_	—	_	—	\checkmark	—	—	—	[37]
	_		Xiaobai	$1 \text{ mmol } \mathrm{L}^{-1}$	2	7 and 2 days before harvest 5 and 15 weeks	\checkmark	\checkmark	—	\checkmark	_	\checkmark	\checkmark	\checkmark	[7]
	—	Palm	Khesab	3%	3	from pollination, and two weeks before harvest	\checkmark	\checkmark	_	—	_	—	—	—	[38]
ASA	Sigma- Aldrich	Plum	Black Splendor	$1 \text{ mmol } \mathrm{L}^{-1}$	3	61,76 and 94days after full blossom	\checkmark	_	\checkmark	_	\checkmark	_	_	—	[19,36]
MeSA	Sigma- Aldrich	Plum	Black Splendor	$0.5 \text{ mmol } \mathrm{L}^{-1}$	3	61,76 and 94days after full blossom flowering and 14,	\checkmark	—	\checkmark	_	\checkmark	_	_	—	[19,36]
BTH	Novartis Crop Protection	Muskmelon	Yindi	$100 \mathrm{~mg~L}^{-1}$	3	28, 42 days after flowering	\checkmark	\checkmark	—	—	—	_	—	—	[39]
Prohydr- ojasmon	—	Pear	Nanhong	$50 \text{ or } 100 \text{ mg}$ L^{-1}	2	100 and 103 days after blooming	\checkmark	\checkmark	\checkmark	—	—	_	—	—	[28]
	_	Mango	Kent, Shelly and Maya	0.1, 0.2 or 0.4%	2	4 and 2 weeks before harvest	_	\checkmark	\checkmark	—	—	_	_	_	[16]
Chitosan	_	Strawberry	Seascape	2, 4, or 6 g L^{-1}	1	just turning red	_	_	\checkmark	_	_	_	_	_	[40]
	—	Grape	Jingxiu	$1~{ m g~L^{-1}}$	1	10 days before harvest	\checkmark	_	_	_	_	—	_	—	[40]
	—		Yaghouti	2% or 3%	3	fruit set, 25 and 50 days after fruit set	_	_	\checkmark	\checkmark	_	\checkmark	_	—	[41]
	WN Group of Publishers	Muskmelon	Manao	0.001	4	14, 21, 28, 40 days after flowering	\checkmark	\checkmark	—	—		—	—	—	[31]
	Cornell Lab	Apricot	Canino	1.5% or 2.5%	2	30 and 15 days before harvest 5 and 15 weeks	_	—	—	—	\checkmark	—	_	—	[37]
	_	Palm	Khesab	1%	3	from pollination and two weeks before harvest	\checkmark	\checkmark	_	—	_	—	_	_	[38]
	Huarun Bio- engineering	Kiwifruit	guichang	28.6%	3	budding phase, fruit setting phase and expanding final phase	\checkmark	\checkmark	_	\checkmark	_	_	_	_	[42]

Table 1. Preharvest elicitors spray improves antioxidant compounds and freeradicalscavengingactivity in fruit.

Table 1. Cont.

Elicitor	Manufacturer	Fruit	Cultivar	Spraying Concentra-	Spraying Times	Spraying Stage		Antiox	idant Compound	ls			ree Radic enging Ac		Refer-
				tion	Times		Phenols	Flavonoids	Anthocyanins	VC	Carotenoid	s DPPH	ABTS ⁺	FRAP	ences
Chitosan oligosac- charide	Dalian GlycoBio	strawberry	qingxiang	$50 \text{ mg} \cdot \text{L}^{-1}$	4	seedling stage, before flowering, fruit coloring and full bloom	\checkmark	\checkmark	\checkmark	\checkmark	_	\checkmark	_	_	[43]
Chitosan oligochi- tosan	_	Apricot	Xiaobai	0.05%	2	7 and 2 days before harvest	\checkmark	\checkmark	_	\checkmark	_	\checkmark	\checkmark	\checkmark	[7]
Oligoch- itosan	Jinan Haidebei Marine Bio- engineering	Navel orange	Osbeck	$15 {\rm g} {\rm L}^{-1}$	4	30, 60, and 90days after physiological fruit drop and 10 days before harvest	\checkmark	_	_	_	_	—	_	_	[44]
β-aminob- utyric acid	Sigma- Aldrich	Blueberry	Bluecrop	20 mM	1	7 days before harvest	_	_	\checkmark	_	_	_	_	_	[45]
Oxalic acid	_	Peach	Anjirymaleki	1, 3 or 5 mmol L^{-1}	1	15 days before harvest 130days after full	\checkmark	\checkmark	_	_	—	\checkmark	_	\checkmark	[46]
	_	Kiwifruit	Bruno	5 mM	3	blossom and 2 times at 7 days intervals	\checkmark	\checkmark	—	\checkmark	_	_	_	—	[47]
	Sigma- Aldrich	Sweet cherry	Sweet Heart and Sweet Late	0.5, 1.0 or 2.0 mM	3	98, 112, and 126 days after full blossom	\checkmark	_	\checkmark	_	_	_	_	_	[48]
	—	Plum	Black Splendor	1 mM	3	63,77 and 98 days after fullblossom 130, 137 and 144	\checkmark	—	—	—	\checkmark	—	\checkmark	—	[20]
	—	Kiwifruit	Bruno	$5 \text{ mmol } \mathrm{L}^{-1}$	3	days after the flowering	_	—	—	\checkmark	—	—	—	—	[49]
	Sigma- Aldrich	Pomegranate	Mollar deElche	1, 5 or 10 mM	3	80, 110, 140, and 170 days after full blossom	\checkmark	—	\checkmark	—	—	—	—	—	[50]
	—	Apricot	Red Flesh	0.5, 1 or 2 mM	1	fruit set stage	\checkmark	—	—	\checkmark	—	—	_	_	[51]
	Sigma- Aldrich	Lemon	Fino	0.1, 0.5 or 1.0 mM	5	from physiological fruit dropto 3 days before harvest	\checkmark	_	_	_	—	_	_	—	[52]
Harpin	Eden Bioscience	Muskmelon	Huanghemi	50 mg L $^{-1}$	3	flowering and 14, 28, 42 days after flowering	\checkmark	_	_	\checkmark	_	_	_	_	[53]

Table 1. Cont.

Elicitor	Manufacturer	Fruit	Cultivar	Spraying Concentra-	Spraying Times	Spraying Stage		Antiox	idant Compound	ls			ree Radica nging Ac		Refer-
				tion	Times		Phenols	Flavonoids	Anthocyanins	VC	Carotenoids	5 DPPH	ABTS ⁺	FRAP	ences
Hexanal	Sigma- Aldrich	Mango	Neelum, Banga- lora, Bangana- palli and Alphonso	0.02%	1; 1; 2	15 days before harvest; 30 days before harvest; 15 and 30 days before harvest	_	_	_	\checkmark	\checkmark	_	_	_	[21]
	_	Strawberry	Jewel, Kent, Mira and St. Pierre	0.01	3	once per week before harvest	\checkmark	\checkmark	\checkmark	_	—	—	—	—	[54]
	_	Guava	Allahabad Safeda	0.8, 1.2 or 1.6 mM	2	4 and 2 weeks before harvest	\checkmark	_	_	\checkmark	_	_	_	_	[23]
SNP	Sigma- Aldrich	Muskmelon	Manao	0.5 mM	4	14, 21, 28, 40 days after flowering young fruit stage,	\checkmark	\checkmark	—	—	—	—	—	—	[55]
	Sigma- Aldrich		Manao	0.5 mM	4	early stage of en largement, late stage of enlargement and	\checkmark	\checkmark	_	_	—	—	—	—	[56]
	Sigma- Aldrich	Peach	G.H. Hill	0, 25, 50 or 100 mol L^{-1}	1	mature stage 14 days before harvest	_	_	_	\checkmark	_	_	_	_	[57]
Putrescine and sper- midine	—	Grape	Olhoghi and Rishbaba	1 or 2 mM/1 or 2 mM	2	40 and 20 days before harvest	\checkmark	—	\checkmark	_	_	—	—	—	[58]
Arginine	_	Pomegranate	MalaseSaveh	0, 0.5, 1 or 2 mM	3	20 days interval before commercial harvest young fruit stage,	\checkmark	\checkmark	_	\checkmark	—	\checkmark	_	—	[59]
L-pheny- lalanine	Hunan- Shaofeng	Muskmelon	Manao	8 mM	4	early expansion stage, late expansion stage and one week before harvest	\checkmark	\checkmark	_	—	_	_	_	_	[26]
Melatonin	_	Apricot	Colorado and Mikado	0.1 mM	3	pit hardening, final fruit growth, and 4 days before harvest	\checkmark	_	_	_	_	_	_	—	[60]
	Sigma- Aldrich	Sweet cherry	Ferrovia	0.5 mM	2	2 and 1 weeks prior to harvest	\checkmark	_	—	_	_	_	_	_	[61]
	—	Pear	Nanhong	50 or 200 μmol L ⁻¹	2	dripping and 3 days after	\checkmark	\checkmark	_	_	—	_	_	—	[62]

 $a \sqrt{\text{indicates detected.}} b$ — indicates no assessment.

2.2. Promoting the Antioxidant Activity

Preharvest elicitors spray also improves in vitro antioxidant ability in fruit (Table 1). For example, spraying 5 mmol L^{-1} oxalic acids 15 days before harvest had no significant effect on the values of DPPH and FRAP in 'Anjiry Maleki' peach fruit at harvest. However, the spray increased the values of DPPH and FRAP in the fruit by 25% and 20% compared with the control on the 4th of storage [46]. Another example is that four sprays of 4.0 mM SA at the 'pea stage' to the version stage increased the values of DPPH and ABTS⁺ in 'El-Bayadi' table grapes, which was 63% and 25% higher than that of the control at harvest [18].

DPPH, ABTS⁺, and FRAP are important indicators to evaluate antioxidant ability. DPPH mainly reflects the antioxidant ability of phenols, flavonoids, and terpenoids in fruits [63]. ABTS⁺ and FRAP reflect the antioxidant ability of ascorbic acid and carotenoids in fruit, respectively [64]. Due to the increase of the biosynthesis of phenolics and flavonoids as well as ascorbic acid and carotenoids, preharvest elicitors spray improves antioxidant ability in fruit. The current studies are mainly focus on the antioxidant ability in vitro of harvested fruit, while further research is needed on the antioxidant ability of human cells or in vivo.

3. Preharvest Elicitors Spray Alleviates CI in Fruit

3.1. Reducing the Occurrence of CI

Many fruits are sensitive to low temperatures, which makes them prone to CI during storage at suboptimal temperatures, resulting in surface pitting, water-soaked spots, epidermal or internal browning, abnormal ripening, and other CI symptoms. Cold-sensitive fruits mainly grow in tropical or subtropical regions, including citrus, bananas, avocados, mangos, pineapples, peaches, apricots, plums, papayas, pomegranates, melons, etc. [65]. Preharvest elicitors spray can effectively alleviate CI in fruit. For example, 'Lane Late' sweet orange fruit sprayed with 2, 4, 6, or 8 mM SA 10 days before harvest reduced CI index of fruit stored for 93 days at 5 °C. Compared with the control, the CI index decreased by 76.15% in the fruit sprayed with 8 mM SA on the 93rd day of cold storage, before harvest [8]. Another example is that preharvest spray at 7 and 2 days with 0.05% chitosan, oligochitosan, or 1 mmol L⁻¹ SA reduce CI in 'Xiaobai' apricot that was stored for 14 days at 2 °C [7]. In addition, 0.02% hexanal spray at 15 and 10 days before harvest decreased the CI index in 'Fantasia' nectarine fruit by 55% compared to the control on the 45th day of storage at 2 °C [66]. Preharvest elicitors spray on CI alleviation in fruit during cold storage are shown in Table 2.

Elicitor	Manufacturer	Fruit	Cultivar	Spraying Concentration	Spraying Times	Spraying Stage	Storage Temperature (°C)/Days	References
SA		Navel orange	Lane Late	2, 4, 6 or 8 mM	1	10 days before harvest	3/93	[67]
	—	Sweet orange	Lane Late and Valencia Late	2, 3, 4, 6, 8 or 9 mM	1	10 days before harvest	3/93	[8]
	Sigma-Aldrich	Grapefruit	Ray Ruby	6, 8 or 12 mM	— a	20 days intervals before harvest	8/90	[68]
	—	Peach	Flordaking	1, 2 or 3 mM	3	the cell division, cell enlargement and pit-hardening stages	1/42	[69]
	_	Apricots	Xiaobai	$1 \text{ mmol } L^{-1}$	2	7 and 2 days before harvest	2/70	[7]
	_	Pineapple	Comte de Paris	2.0 mM	4	15-day intervals before harvest	10/20	[70]
	_	Jujube	Peyuan	$150 { m mg} { m L}^{-1}$	1	3 weeks before harvest	—/35	[71]
MeSA	Aladdin	Apricots	Kate	0.05, 0.1 or 0.2 mmol L^{-1}	2	72 d and 74 d after full blossom	2/32	[72]
MeJA	Sigma-Aldrich	Grapefruit	Ray Ruby	3, 4 or 5 mM		20 days intervals before harvest	8/90	[68]
	Sigma-Aldrich	Pomegranates	Malas	1 or 2 mM	1	15 days before harvest	4/28	[73]
	Sigma-Aldrich	Pomegranate	Mollar de Elche	5 mM	5	80, 110, 140 and 170 days after full blossom, and 4 d before harvest	2/90	[74]
Chitosan oligochitosan	—	Apricots	Xiaobai	0.05%	2	7 and 2 days before harvest	2/70	[7]
β-aminobutyric acid	—	Apple	Honeycrisp	40 mM	2	2 and 4 weeks before harvest; 1 and 2 weeks before harvest	0.5 or 3/4 months; 0.5/5 months	[75]
Arginine	—	Pomegranate	MalaseSaveh	0, 0.5, 1 or 2 mM	3	20 days interval before commercial harvest	4/120	[59]
SNP	Sigma-Aldrich	Peach	G.H. Hill	0, 25, 50 or 100 mol L^{-1}	1	14 days before harvest	4/28	[57]
Melatonin	_	Apricot	Colorado and Mikado	0.1 mM	3	pit hardening, final fruit growth, and 4 days before harvest	1 and 8 /21 and 28	[60]
Hexanal	_	Nectarine	Fantasia	0.02%	2	15 and 10days before harvest	2/45	[66]
Putrescine	_	Pear	Spadona	0.5, 1 or 2 mM	3		0/21	[76]

Table 2. Preharvest elicitors spray alleviates chilling injury in fruit.

 \overline{a} — indicates unspecified.

3.2. Improving ROS Scavenging Ability

Oxygen burst caused by CI leads to excessive H_2O_2 accumulation that accelerates peroxidation of the cell membrane, leading to the production of malondialdehyde (MDA), which also destroys membrane integrity [5]. Preharvest elicitors sprayed as SA can increase the activity of antioxidant enzymes as well as the concentration of antioxidant compounds, which contribute to reducing H_2O_2 damage in fruit and vegetables [14]. Preharvest MeIA and SA spray improved the activities of catalase (CAT), ascorbate peroxidase (APX), and peroxidase (POD) as well as the biosynthesis of phenols and flavonoids in 'Fino' and 'Verna' lemon fruit during cold storage [14]. Moreover, during cold storage, higher activities of superoxide dismutase (SOD), CAT, APX, and POD and accumulations of total phenols, total anthocyanins, total carotenoids, and total flavonoids were found in 'Black Splendor' and 'Royal Rosa' plum fruit that was preharvest sprayed with SA, acetylsalicylic acid (ASA), or MeSA [19,36]. Preharvest MeJA spray increased total phenols, total anthocyanins, total flavonoids, and vitamin C contents, thereby improving ROS scavenging and antioxidant activity in fruit [17]. Moreover, preharvest spray with SA or chitosan oligochitosan in the 'Xiaobai' apricot orchard decreased MDA content and increased contents of total phenols, total flavonoids, and vitamin C. Additionally, preharvest chitosan oligochitosan and SA spray enhanced free radical-scavenging capacity, including DPPH free radical scavenging capacity, ABTS free radical scavenging capacity, cupric ion reducing antioxidant activity, and ferric reducing antioxidant activity, elevating scavenging ability of free radicals in fruit [7]. Although the effects of preharvest elicitors spray on activity of antioxidant enzymes and biosynthesis of antioxidants in harvested fruit have been studied at the biochemical level, the relevant molecular mechanisms remain to be further revealed.

3.3. Decreasing Membrane Lipid Metabolism

Destruction of the cell membrane is considered to bean important characteristic of CI. The content of unsaturated fatty acids (USFAs) in the cell membrane is closely related to CI in fruit [52]. A high content of USFAs contributes to the fluidity of cell membrane and membrane integrity and increases the cold tolerance of fruit [65,77]. Preharvest MeJA spray maintained USFAs content in 'Mollar de Elche' pomegranate fruit during cold storage and reduced the ratio of unsaturated/saturated fatty acids, contributing to maintaining the integrity of cell membrane and alleviating CI in fruit [78]. Low temperature leads to degradation and peroxidation of membrane lipids that cause the loss of membrane integrity and functionality, resulting in the appearance of CI symptoms in fruit [79,80]. Phospholipase D (PLD) is a key enzyme in membrane phospholipid metabolism, which can directly hydrolyze ester bonds of phosphoglyceride and catalyze the decomposition of phospholipid into phospholipid acid (PA) and diacylglycerol [81]. The occurrence of CI increases PLD activity in fruit that induces PA accumulation, while excessive production of PAleads to H_2O_2 accumulation, which destroys the integrity of the cell membrane [82]. Preharvest hexanal spray inhibited membrane phospholipid metabolism in 'Fantasia' nectarine fruit by down-regulating PLD expression, thereby maintaining the integrity of the cell membrane [66]. Although the effects of preharvest elicitors spray on membrane lipid metabolism in harvested fruit have been studied at the biochemical level, the relevant molecular mechanisms remain to be further proclaimed.

3.4. Reducing Pulp Browning

Epidermal or internal browning is a typical symptom of fruit CI. Preharvest SA and chitosan oligochitosan spray decreased polyphenol oxidase (PPO) activity in 'Xiaobai' apricot fruit, alleviating pulp browning in fruit during cold storage [7]. Preharvest sodium nitroprusside (SNP) spray alleviated CI-induced browning of pulp tissue of 'G.H. Hill' peach fruit by decreasing PPO activity [57]. Cell membrane degradation caused by CI increases the possibility of interaction between polyphenols and PPO, which oxidizes polyphenols to quinones, and further polymerizes and forms dark brown products [70].

However, the specific regulation of enzymatic browning in fruit by preharvest elicitors spray remains to be further explained.

4. Preharvest Elicitors Spray Delays Ripening and Maintains Postharvest Quality of Fruit

Fruit ripening caused by ethylene is an important cause of quality deterioration in harvested fruit. Many reports have elucidated that preharvest elicitors spray can effectively retard fruit ripening by inhibiting ethylene production, thereby maintaining postharvest quality and prolonging shelf life of fruit [83].

4.1. Retarding Ripening

Ethylene release and increased respiration are typical physical features of climacteric fruit, which play a critical role in fruit maturation and ripening [84]. The peak of ethylene in 'Black Splendor' plum fruit retarded after spraying with 0.5 mmol L^{-1} SA, 1 mmol L^{-1} ASA, or $0.5 \text{ mmol } L^{-1}$ MeSA 3 times at 61, 76, and 94 days after full blossom, respectively [36]. Moreover, the respiration rate in 'Dashehari' mango fruit retarded by 7 days during cool storage after spraying with 1200, 1600, or 2000 µM hexanal before harvest [85]. Preharvest elicitors spray can retard the peak of ethylene and respiration in climacteric fruit as well as decrease ethylene release and respiratory rate. In 'Zill' mango fruit, sprayed with 150 µM SA before harvest delayed the peak of ethylene by 2 days and decreased the ethylene accumulation by 82% compared with the control during cool storage [83]. These elicitors spray also can inhibit ethylene release and respiratory rate in non-climacteric fruit. 'Fino' lemon fruit that was sprayed with 0.1 mM MeJA or 0.5 mM SA 4 times before harvest had a decrease in ethylene production and respiration rate [14]. Similarly, compared with the control, the respiratory rate in 'Mollar de Elche' pomegranate fruit decreased by 33.33% on the 60th of storage after 5 mmol L^{-1} MeJA sprayed 4 times at 94, 64, 34 and 4 days before harvest [17]. Preharvest elicitors spray on inhibiting ethylene production and respiration rate in fruit after harvest are shown in Table 3. Although the effect of preharvest elicitors spray on respiratory rate in fruit has been studied, how the spray affects respiratory metabolism needs to be further revealed.

Ethylene plays a dual role in fruit as it participates both in the fruit in the ripening and defense response of climacteric fruits [86]. 1-Aminocyclopropane-1-carboxylic acid synthase (ACS) and 1-aminocyclopropane-1-carboxylic acid oxidase (ACO) are two key enzymes involved in ethylene biosynthesis. Preharvest elicitors spray reduces ethylene release in climacteric and non-climacteric fruit during storage. The gene expression of MiACS and MiACO in 'Zill' mango fruit preharvest sprayed with SA was reduced by 90% and 96% on the 9th and 7th day of storage, respectively [83]. Preharvest chitosan spray decreased the gene expression of AdACS2 and AdACO2 by 30% and 50% in 'Garmrok' kiwifruit compared with the control on the 60th day of storage [86]. Similarly, preharvest chitosan oligosaccharides spray reduced FaACS and FaACO gene expression in 'Qingxiang' strawberry fruit by 92% and 66% compared with the control at harvest [43]. Ethylene receptors negatively regulate ethylene signal transduction, while ethylene response factors (ERFs) are positively regulated by ethylene [87]. Transcriptome analysis showed that preharvest BTH and chitosan spray decreased ERF expression in 'Alba' strawberries after harvest, thereby inhibiting ethylene signal transduction [35]. Moreover, at harvest, ETR2 was down-regulated in 'Stark Red Gold' peach fruit that was preharvest sprayed with MeJA [88]. Although the effects of preharvest elicitors spray on biosynthesis and signal transduction of ethylene in harvested fruit have been studied, the relevant regulation mechanisms remain to be further announced.

				Spraying	Spraying Storage				Postharvest Quality			
Elicitor	Manufacturer	Fruit	Cultivar	Concentration	Times	Spraying Stage	Temperature (°C)/Days	TSS	TA	TSS/TA	Firmness	References
SA	_	Navel orange	Lane Late	2, 4, 6 or 8 mM	1	10 days before harvest	5/93	\sqrt{a}	\checkmark	c	\checkmark	[67]
	Sigma-Aldrich	Lemon	Fino	$0.5 \text{ mmol } \mathrm{L}^{-1}$	4	21 days intervals untile 3 days before harvest	8/35			—	\checkmark	[14]
	Sigma-Aldrich	Mango	Zill	150 μM	1	100 days after anthesis	25/11	$\times {}^{b}$	\checkmark		\checkmark	[83]
	Sigma-Aldrich	Peach	Cresthaven	1 or 2 mM	2	23 and 15 days before harvest cell division, pit hardening or	20/2	×	\checkmark	—	\checkmark	[89]
	—		Flordaking	1, 2 or 3 mM	3	lag phase and cell enlargement stage	1/42	×	\checkmark	×	\checkmark	[69]
	_	Apricot	Xiaobai	$1 \text{ mmol } L^{-1}$	2	7 and 2 days before harvest	2/70	\checkmark	\checkmark		\checkmark	[7]
	Cornell Lab	1	Canino	2 or 4 mM	2	30 and 15 days before harvest	0/28	×	v	×	v	[37]
	—	Grape	Thompson Seedless	100 mg L^{-1}	2	pea and veraison stage	20/7	—	—	—		[90]
	Sigma-Aldrich		Flame Seedless	1.0, 1.5 or 2.0 mM	2	pea and veraision stage	3-4/75	\checkmark	\checkmark	\checkmark	\checkmark	[91]
	Sigma-Aldrich		Magenta and Crimson	1 mM	3	40% berries, veraison stage and 3 days before harvest	2/45	\checkmark	×		_	[50]
	_		Superior Seedless	1, 2, or 4 mM	3	fruit set, berry variation and 14 days before harvest	28/44	\checkmark	\checkmark	\checkmark	\checkmark	[92]
	Sigma-Aldrich	Plum	Black Splendor	$0.5 \mathrm{~mmol~L^{-1}}$	3	61,76 and 94 days after full blossom	2/50	\checkmark	×	\checkmark	\checkmark	[19]
	—	Strawberry	Festival	2 or 4 mmol	3	full flowering, green fruits and pink stage	4/12	\checkmark	—	—	\checkmark	[93]
	_	Sweet cherry	Sweet Heart, Sweet Late and Lapins	$0.5 \mathrm{~mmol~L}^{-1}$	3	98, 112 and 126 days after full blossom (SE/SL)/66, 75 and 81 days after full blossom (L)	2/28	\checkmark	\checkmark	_	\checkmark	[94]
	Sigma-Aldrich	Jujube	Dongzao	2 mM	4	30, 60, 90, and 110 days after full blossom	0/60	_	—		_	[95]
	_	Wax apple	Taaptipjaan	0.5 or 1.0 mM	1	24 h before harvest	13/9	_	_		\checkmark	[96]
	—	Palm	Khesab	3%	3	5 and 15 weeks from pollination, and two weeks before harvest	2/60	×	—			[38]
ASA	Sigma-Aldrich	Grape	Magenta and Crimson	1 mM	3	40% berries, veraison stage and 3 days before harvest	2/45	\checkmark	×		_	[17]
	_	Strawberry	Festival	0.25 or 0.50 mmoL	3	full flowering, green fruits and pink stage	4/12	\checkmark	—		\checkmark	[93]
	—	Sweet cherry	Sweet Heart, Sweet Late and Lapins	$1.0 \mathrm{~mmol~L}^{-1}$	3	98, 112 and 126 days after full blossom	2/28	\checkmark	\checkmark	_	\checkmark	[94]

Table 3. Preharvest elicitors spray maintains postharvest quality in fruit.

Table 3. Cont.

				Spraying	Spraying		Storage		Posthar	vest Quality		
Elicitor	Manufacturer	Fruit	Cultivar	Concentration	Times	Spraying Stage	Temperature (°C)/Days	TSS	TA	TSS/TA	Firmness	References
	Sigma-Aldrich	Plum	Black Splendor	$1 \mathrm{mmol}\mathrm{L}^{-1}$	3	61,76 and 94 days after full blossom	2/50	\checkmark	×	\checkmark	\checkmark	[19,36]
MeSA	—	Apricot	Kate	0.05, 0.1 or 0.2 mmol L^{-1}	2	72 d and 74 days after full blossom	2/32	\checkmark	\checkmark	—	\checkmark	[72]
	Sigma-Aldrich	Grape	Magenta and Crimson	1 mM	3	40% berries, veraison stage and 3 days before harvest	2/45	\checkmark	×	_	_	[17]
	Sigma-Aldrich	Plum	Black Splendor	$0.5 \text{ mmol } \mathrm{L}^{-1}$	3	61,76 and 94days after full blossom	2/50	\checkmark	×	\checkmark	\checkmark	[19]
MeJA	Sigma-Aldrich	Lemon	Fino	$0.1 \text{ mmol } \mathrm{L}^{-1}$	4	21 days intervals untile 3 days before harvest	8/35	\checkmark	\checkmark	_	\checkmark	[14]
	Sigma-Aldrich	Mango	Mahachanok	20, 40, 80 or 120 μL mL ⁻¹	1	90 days after anthesis	15/24	_	_	\checkmark	\checkmark	[97]
	_	Plum	Black Splendor and Royal Rosa	0.5 or 1.0 mM	3	-	20/9;2/50	×	\checkmark	_	\checkmark	[98]
	_		Fortune	$1120 ext{ or } 2240 ext{ mg}$ $ ext{L}^{-1}$	1	115 days after full blossom	0/28	×	_	_	\checkmark	[99]
	—	Strawberry	Chilean	0.25 mM	3	80% flowering, turning fruit and full ripe fruit stage 100% red stage; large green andafter 7 days at 100% red	22/3	_	_	\checkmark	\checkmark	[100]
	Sigma-Aldrich		Camarosa	$250 \text{ mmol } \text{L}^{-1}$	1; 2; 3	receptacle stages; flowering, after 24 days at the large green, and after 7 days at 100% red	25/3	—	—	\checkmark	\checkmark	[22]
	Sigma-Aldrich	Pomegranate	Malas	1 or 2 mM	1	receptacle stages 15 days before harvest	4/80			_	\checkmark	[73]
	Sigma-Aldrich	U	Mollar de Elche	1, 5 or 10 mmol L^{-1}	4	94, 64, 34 and 4 days before harvest	10/60			_		[78]
Prohydroja	smon —	Mango	Kent, Shelly and Maya	0.1%, 0.2% or 0.4%	2	4 and 2 weeks before harvest	12/21	\checkmark	×	_	×	[26]
Chitosan	Oxford Laboratory Reagents	Apricot	Canino	1.5% or 2.5%	2	30 and 15 days before harvest	0/28	×	\checkmark	×	\checkmark	[37]
		Grape	Jingxiu	$1\mathrm{g}\mathrm{L}^{-1}$	1	10 days before harvest	20/16;0/42	×	\checkmark	×	_	[40]
	—		Yaghouti	2% or 3%	3	fruit set, 25 and 50 days after fruit set	-/40	\checkmark	\checkmark	\checkmark	\checkmark	[41]
	—	Strawberry	Alba and Romina	0.5% or 1%	5	flowering and followed every 5 days	0.5/7	—	_	_	_	[101]

Table 3. Cont.

				Spraying	Spraying		Storage		Posthary	vest Quality		- 1
Elicitor	Manufacturer	Fruit	Cultivar	Concentration	Times	Spraying Stage	Temperature (°C)/Days	TSS	TA	TSS/TA	Firmness	References
	_		Chilean	1.5%	3	80% flowering, turning fruit stage and full ripe fruit stage	22/3	_	_	\checkmark	\checkmark	[100]
	Nova-Chem		Seascape	2, 4, or 6 g L^{-1}	1	just turning red budding phase, fruit setting	3/28;13/35		×	—	\checkmark	[102]
	Huarun Bioengineering	Kiwifruit	Guichang	28.6%	3	phase and expanding final phase	25/25	×	×	—	\checkmark	[42]
	Sigma-Aldrich		Garmrok	$\begin{array}{c} 100 \text{ or } 500 \\ \text{mg} \cdot \text{L}^{-1} \end{array}$	4	146, 154, 161 and 170 daysafter full blossom	0/90	×	×	—	\checkmark	[103]
	_	Palm	Khesab	1%	3	5 and 15 weeks from pollination and two weeks before harvest	2/60	×	—	_	—	[38]
Chitosan oligochi- tosan	_	Apricot	Xiaobai	0.05%	2	7 and 2 days before harvest	2/70	×	_	_	—	[7]
	Haidebei Marine Bioengineering	Jujube	Dongzao	0.7 g L ⁻¹ 2 kDa, 5 kDa or 10 kDa; 0.3, 0.7 or 1.0 g L ⁻¹ 10 kDa	4	30, 60, 90 and 110 days after full blossom	0/60	_	_	_	\checkmark	[104]
β- aminobuty acid	ric —	Apple	Honeycrisp	40 mM	2	4, 2 and 1 weeks before harvest	0.5 or 3/4 months; 0.5/5 months	_	\checkmark	_	\checkmark	[75]
uciu	Sigma-Aldrich	Blueberry	Bluecrop	20 mM	1	7 days before harvest	2/20	×	\checkmark	_	\checkmark	[45]
Oxalic acid	Sigma-Aldrich	Lemon	Fino	0.1, 0.5 or 1.0 mM	5	from physiological fruit dropto 3 days before harvest	10/35	\checkmark	\checkmark	_	\checkmark	[52]
ucru	—	Apricot	Red Flesh	0.5, 1 or 2 mM	1	fruit set stage	25/5	×	\checkmark	×	\checkmark	[51]
	—	Peach	Anjirymaleki	1, 3 or 5 mmol L^{-1}	1	15 days before harvest	1/28	—	—	—	\checkmark	[46]
	—	Kiwifruit	Bruno	5 mM	3	130 days after full blossom and 2 times at 7 days intervals	20/15	×	×	—	\checkmark	[47]
	—		Bruno	$5 \text{ mmol } \mathrm{L}^{-1}$	3	130, 137 and 144 days after the flowering	20/13	×	×	—	—	[49]
	Sigma-Aldrich	Plum	Black Splendor	1 mM	3	63, 77 and 98 days after full blossom	2/35	×	\checkmark	×	\checkmark	[20]
Hexanal	—	Apple	Honeycrisp	0.02%	2	30 and 15 days before harvest	2.5/120		_	—		[105]
	—		Honeycrisp	0.02%	2	30 and 15 days before harvest	2.5/120	\checkmark	_	—	\checkmark	[106]
	—	Mango	Dashehari	800, 1200, 1600 or 2000 μM	2	15 and 30 days before harvest	12/35	\checkmark	\checkmark	—	—	[85]

				Spraying	Spraying		Storage			Poforoncoc		
Elicitor	Manufacturer	Fruit	Cultivar	Concentration	Times	Spraying Stage	Temperature (°C)/Days	TSS	TA	TSS/TA	Firmness	References
	Sigma-Aldrich		Neelum, Bangalora, Banganapalli and Alphonso	0.02%	1; 1; 2	15 days before harvest; 30 days before harvest; 15 and 30 days before harvest	25/-;13/-	×	_	_	\checkmark	[21]
	_		Alphonso and Banganapalli	2%	2	30 and 15 days before harvest	14/21; 28/21	\checkmark	\checkmark	\checkmark	_	[107]
	_	Nectarines	Fantasia	2%	2	15 and 10 days before harvest	2/45	—	_	—	\checkmark	[66]
	—	Strawberry	Jewel and Wendy	0.01% or 0.02%	2	7 and 3 days before harvest	4/9	—	×	—	\checkmark	[108]
	_	Guava	Allahabad Safeda	0.8, 1.2 or 1.6 mM	2	4 and 2 weeks before harvest	6-8/35	\checkmark	\checkmark	_	\checkmark	[23]
Putrescine and sper- midine	Olhoghi and Rishbaba	Grape	Olhoghi and Rishbaba	1 or 2 mM/1 or 2 mM	2	40 and 20 days before harvest	1.5/55	×	\checkmark	_	_	[58]
Melatonin	_	Apricot	Colorado and Mikado	0.1 mM	3	pit hardening, final fruit growth and 4 days before harvest	1 or 8/28	\checkmark	×	—	\checkmark	[60]

Table 3. Cont.

 $\overline{{}^a} \sqrt{\text{indicates an increase.}} {}^b \times \text{indicates a decrease.} {}^c - \text{indicates no assessment.}$

4.2. Maintaining Sugarand Organic Acid

The ratio of sugars and organic acids is an important characteristic of fruit quality. Generally, total soluble solid (TSS) and titratable acid (TA) content are used to indicate sugars and organic acids in fruit. Preharvest elicitors spray can delay the increase of TSS content and maintain TA content [69].

In climacteric fruit, TSS content increases with ripening and then decreases with senescence, while TA only decreases after harvest [109,110]. On the 6th week of storage, compared with the control, TSS and TSS/TA content were 12.3% and 31.56% lower, while TA content was 23.19% higher in 'Flordaking' peach fruit sprayed with 3 mM SA before harvest [69]. Moreover, 0.5 mmol L^{-1} SA, 1 mmol L^{-1} ASA, or 0.5 mmol L^{-1} MeSA sprayed 'Black Splendor' plum fruit 3 times at 61, 76, and 94 days after anthesis, which increased TA content in fruit by 44.09%, 39.48% and 35.48% on the 50th of storage compared with the control, respectively [19]. In non-climacteric fruit, the concentration of TSS and TA gradually declined after harvest. Higher TSS and TA content were found in 'Magenta' and 'Crimson' seedless grapefruit sprayed with 1 mM ASA before harvest [50]. TSS content in 'Fino' lemon was 11% higher than that of the control on the 35th of storage after spraying with 0.1 mM MeJA 4 times before harvest [14]. Preharvest elicitors spray o maintaining TSS and TA in harvested fruit are shown in Table 3.

In fruits, sugars are stored in the form of starch, but there are few reports on the effect of preharvest elicitors spray on the degradation or accumulation of starch. However, preharvest elicitors spray delays ethylene biosynthesis and fruit ripening. Meanwhile, the TSS accumulation in fruit is delayed, which is associated with the inhibition of sucrose conversion. Higher sucrose content was found in 'Kate' apricot preharvest sprayed with MeSA during 32 days of storage [72]. In addition, a higher accumulation of sucrose, glucose, and fructose was found in 'Fino' lemon fruit preharvest sprayed with SA during 35 days of storage [14]. During 60 days of storage, preharvest MeJA spray kept fructose and glucose content in 'Mollar de Elche' pomegranate [17]. With fruit ripening and, organic acids are consumed as substrates of the tricarboxylic acid cycle (TCA) cycle in fruit. Preharvest elicitors spray delays respiration and fruit ripening [69]. Indeed, during 32 days of storage, the concentration of citric acid, malic acid, and total organic acids was higher in 'Kate' apricot fruit preharvest sprayed with MeSA [72]. Similarly, preharvest MeJA spray maintained the concentration of malic acid, succinic acid, oxalic acid, and ascorbic acid in 'Mollar de Elche' pomegranate [17].

4.3. Maintaing Fruit Firmness

Softening is an important cause of quality deterioration and shortens shelf life in climacteric and non-climacteric fruit. Preharvest elicitors spray can maintain firmness in fruit during storage.1, 2 or 3 mM SA sprayed 'Flordaking' peach fruit 3 times before harvest maintained the firmness during storage. On the 6th week of storage, the firmness in peach fruit sprayed with 3 mM SA was 1.68 fold higher than that of the control [69]. Moreover, 0.05% chitosan oligochitosan or 1 mmol L^{-1} SA sprayed twice on 'Xiaobai' apricot fruit at 7 and 2 days before harvest increased the firmness in fruit by 24% and 35% compared to the control on the 14th day of storage, respectively [7]. Similarly, the firmness in the 'Mahachanok' mango sprayed with 20, 40, 80, or 120 μ L mL⁻¹ MeJA at 90 days after anthesis was higher than that of the control during storage. Among them, 80 μ L mL⁻¹ MeJA spray showed the best effect, which increased the firmness by 20.75% compared with the control on the 24th of storage [97]. Compared with the control, the firmness showed 2 folds higher in 'Flame Seedless' table grapes sprayed with 2.0 mM SA twice at the pea stage and veraison stage on the 75th day of storage [91]. Preharvest elicitors spray on maintaining firmness in harvested fruit is shown in Table 3. This delay in fruit softening that was observed in the preharvest spray of elicitors could be connected to the inhibition in the ethylene released and the respiration rate that delayed the fruit ripening.

Fruit respiration is associated with the degree of water transpiration and weight loss [111]. Preharvest elicitors spray inhibited the water transpiration in fruit after har-

vest [92]. This is correlated to the inhibition of respiration that was observed in fruit preharvest treated with elicitors. On the other hand, preharvest application of elicitors strengthened the structure of the epidermal tissue of fruit and enhanced the thickness of the cuticle and density of wax, thereby further inhibiting water transpiration in harvested fruit [39,112]. Additionally, some elicitors spray, such as chitosan, can form a protective film on the surface of the fruit, which could further hinder water transpiration of the fruit [7].

Fruit softening also relates to the activity of cell wall degradation enzymes (CWDEs) [111]. Pectin, hemicellulose, and cellulose are the main components of the cell wall in fruit, and they can be depolymerized and degraded under the action of CWDEs, which causes the collapse of the cell wall, leading to fruit softening. The CWDEs mainly include polygalacturonases (PG), pectin methyl esterases (PME), and cellulases [44]. Cellulose content increased by 20.08% in 'Qingxiang' strawberry fruit preharvest sprayed with chitosan oligosaccharides compared with the control [43]. On the 7th day of storage, the activities of PME, PG, and cellulose were 26%, 17.43%, and 79.16% lower in 'Agate' muskmelon fruit sprayed with ASA before harvest than that in the control, respectively [113]. On the 9th day of storage, preharvest hexanal spray reduced the activities of PME and PG in 'Neelum' mango fruit, which was 50% and 42% lower than that of control, respectively [21]. Moreover, on the 14th day of storage, the PME activity decreased and protopectin content increased in 'Allahabad Safeda' guava fruit preharvest sprayed with hexanal, which was 33.3% lower and 1.3 folds higher than that of the control, respectively [23]. Compared with the control, the PME activity was 25% lower in 'Flame Seedless' grapefruit preharvest sprayed with SA [91]. In addition, preharvest SA and chitosan spray decreased PG activity in 'Tupi' blackberry fruit during storage. At the 6 days of storage, the PG activity in SA and chitosan-sprayed fruit was 5.5% and 14.4% lower than that of the control, respectively [9]. On the 21stday of storage, higher protopectin content was found in 'Osbeck' navel orange preharvest sprayed with oligochitosan, which was 19.6% higher than that of the control. Moreover, the sprayed fruit showed lower PG and PME activity, which was 58.3% and 30.8% lower than that of the control, respectively [44]. Furthermore, preharvest hexanal spray down-regulated *PME* expression in 'Jewel' and 'Wendy' strawberry fruit during storage [108]. Thus, in all, preharvest treatments with elicitors inhibit the expression of CWDE in harvested fruit during storage, while fruit firmness also involves in water transpiration and epidermal structure. Further studies are required to elucidate the relevant molecular mechanisms modulated by preharvest elicitors spray.

5. Concluding Remarks and Perspectives

In addition to inducing SAR in fruit, preharvest elicitors spray can improve phenylpropanoids metabolism and carotenoids biosynthesis, whichin crease the accumulation of flavonoids, carotenoids, and ascorbic acid, thereby enhancing antioxidant activity in harvested fruit. Antioxidant activity is an important property of fruits, which is correlated to scavenging ability of ROS. The increase in antioxidant activity maintains the integrity of the cell membrane and reduces lipid peroxidation, which is probably related to the reduced ROS in fruits, thereby improving cold tolerance of fruit. Moreover, the spray also inhibits membrane phospholipid metabolism, and maintains the function and fluidity of cell membrane in fruits, which alleviate CI in harvested fruit during cold storage reduces CI, maintaining postharvest quality of fruits. In addition, preharvest elicitors spray retards fruit ripening by inhibiting ethylene production and respiration rate, which maintains the levels of sugars and organic acids as well as firmness in harvested fruit during storage (Figure 1).

A possible mode of action of how preharvest elicitors spray alleviates CI, maintains quality, and improves antioxidant capacity in harvested fruit is shown in Figure 1. Preharvest elicitors spray is a simple and effective strategy in controlling CI and maintaining quality in harvested fruit, which reduces the postharvest process and costs. However, preharvest elicitors spray still has challenges in practical agricultural applications. Firstly, most of the elicitors are registered for disease control, but only a few of them have been registered for improving antioxidant activity, controlling CI, maintaining quality, and in harvested fruit. Therefore, it is necessary to improve the register of the relevance elicitors. Secondly, there are tremendous differences in the effect of different elicitors on different species or cultivars of fruits. Therefore, it is important to screen the appropriate elicitor, concentration and application time according to the different fruits. Thirdly, fertilization, irrigation, pruning and other practices modulate the elicitors' action. Moreover, the spraying method, such as the density and intensity of the spray, and the equipment used also affect the effect of the application of preharvest elicitor. Hence, the time, concentration, and frequency of elicitors spraying need to be screened based on different cultivation techniques. Fourthly, climate factors, such as temperature, light and rainfall, affect preharvest application. Therefore, it is important to investigate the influence of these climatic factors and their changes on the effect of applying these measures. Fifthly, postharvest environmental factors, including temperature, relative humidity, and gas composition, also affect the application effects of the elicitor, the optimum combination of pre-and postharvest environmental factors needs to be screened. Finally, although some researchers have elucidated the effects of preharvest elicitors spray on postharvest properties of fruits and revealed the preliminary mechanisms of action at physiological and cytological levels, the in-depth mechanisms of action are still unclear. Hence, approaches of multi-omic, epigenetic and molecular biology need to be used to further reveal the mechanism of preharvest elicitors spray on controlling CI and maintaining the quality of fruit during storage.

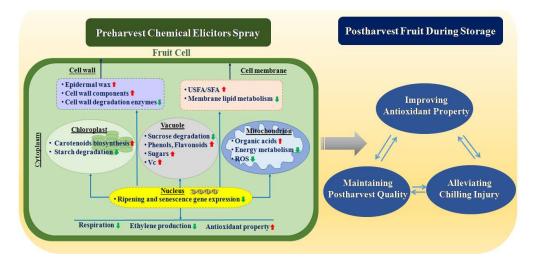


Figure 1. A possible mode of action of preharvest elicitors spray improves antioxidant property, alleviates chilling injury, and maintains quality in harvested fruit. ROS indicates reactive oxygen species; USFS/SFA indicates unsaturated/saturated fatty acids; Vc indicates vitamin C.

Due to the rapid cell division and significant cell expansion in fruit during the growth and development stage, the fruit is more sensitive to the stimuli of external elicitors. Additionally, preharvest fruit has a better active metabolism than the harvested fruit which is usually stored at cold temperatures. Therefore, in a way, the effects of preharvest elicitors spray on delaying ripening and senescence and improving resistance are better than that of postharvest treatment. Moreover, the elicitors are metabolized in the fruit and induce the biosynthesis of various natural metabolites that are safer than chemical fungicides, have a broader spectrum of activity, and will not be easily braked by a resistant isolate. Finally, more attention needs to be paid to strengthening the relationship between pre- and postharvest, expanding the breadth and depth of pre- and postharvest research.

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