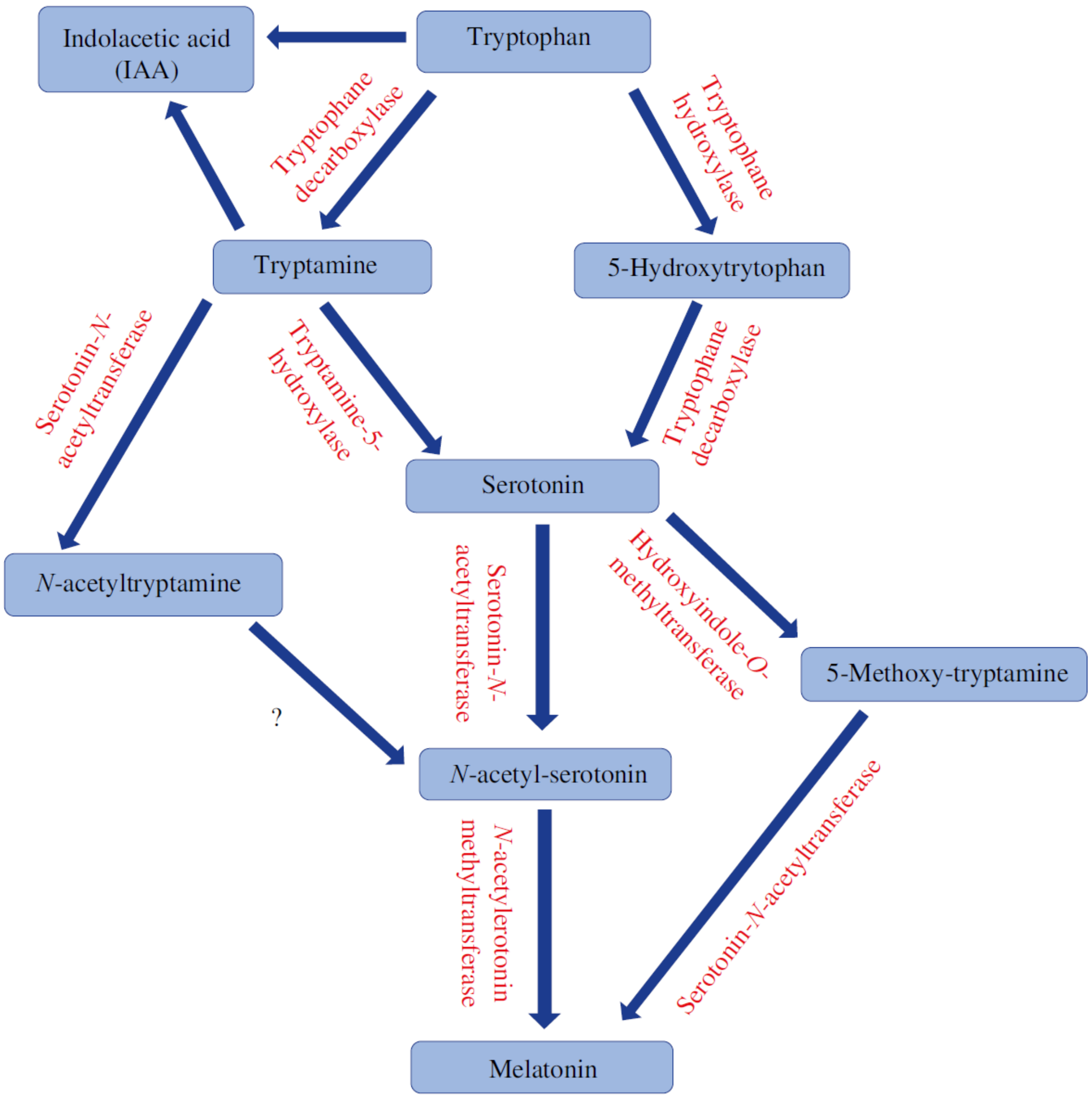
IN THE NAME OF GOD



Indolacetic acid (IAA)

Tryptophan

Tryptophane decarboxylase

Tryptophane hydroxylase

Tryptamine

5-Hydroxytrytophan

Serotonin-*N*-acetyltransferase

Tryptamine-5-hydroxylase

Tryptophane decarboxylase

Serotonin

N-acetyltryptamine

Serotonin-*N*-acetyltransferase

Hydroxyindole-*O*-methyltransferase

5-Methoxy-tryptamine

?

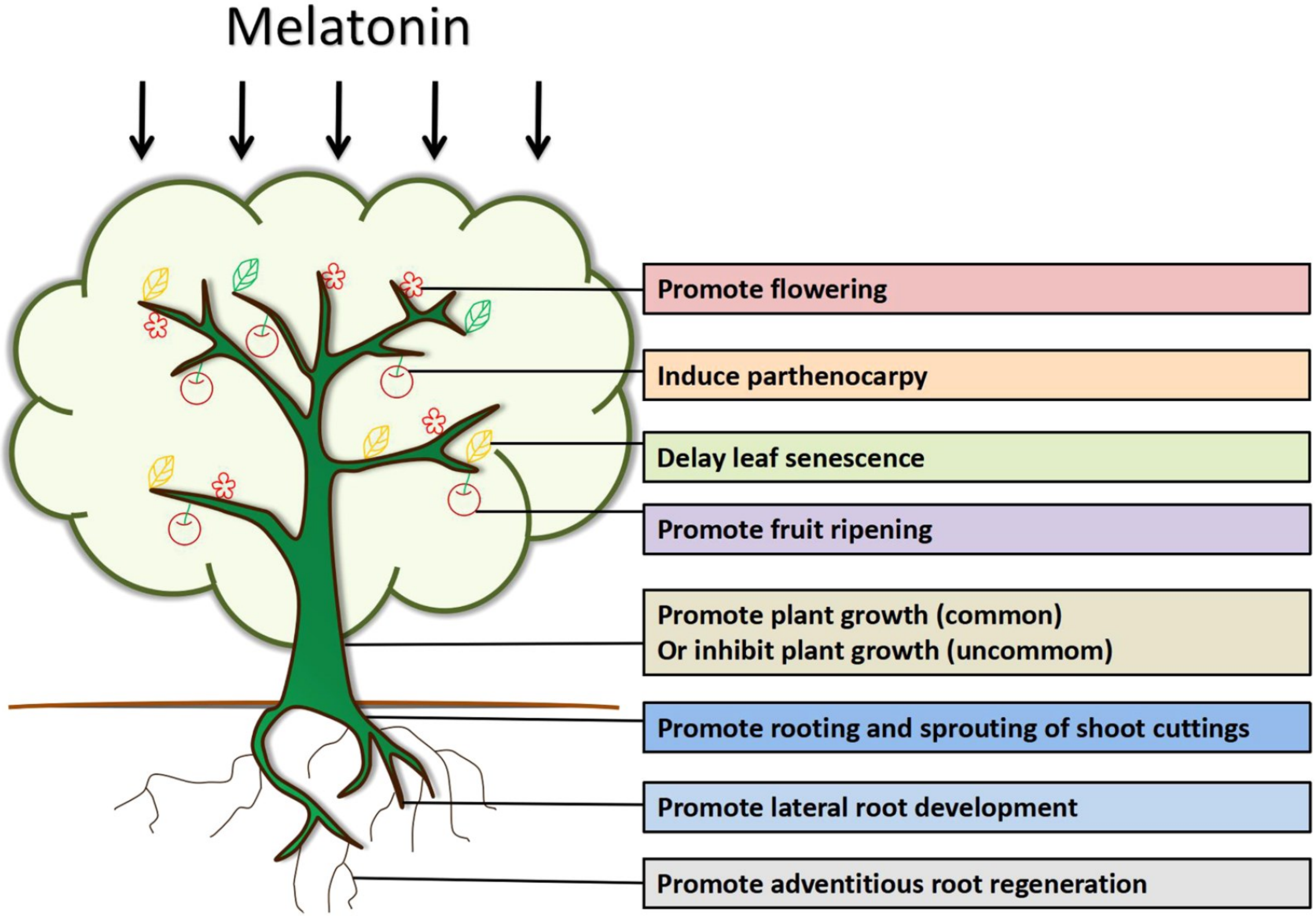
N-acetyl-serotonin

N-acetylerotonin methyltransferase

Serotonin-*N*-acetyltransferase

Melatonin

Fig. 1 A modified pathways of melatonin biosynthesis.



Melatonin

Promote flowering

Induce parthenocarpy

Delay leaf senescence

Promote fruit ripening

Promote plant growth (common)
Or inhibit plant growth (uncommom)

Promote rooting and sprouting of shoot cuttings

Promote lateral root development

Promote adventitious root regeneration

Fig. 3. Effect of melatonin on the growth and development of horticultural plants.

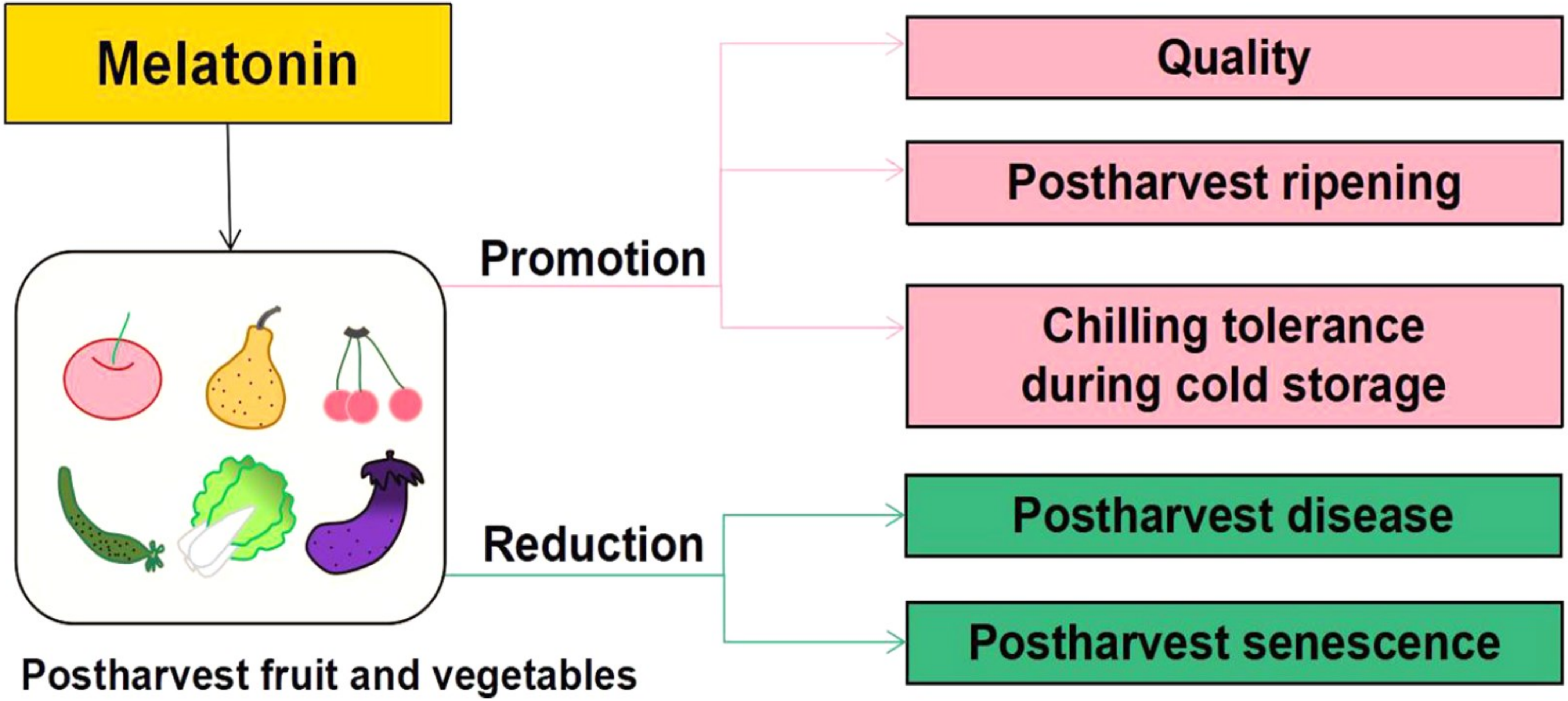


Fig. 4. Effect of melatonin on the postharvest quality of horticultural plants.

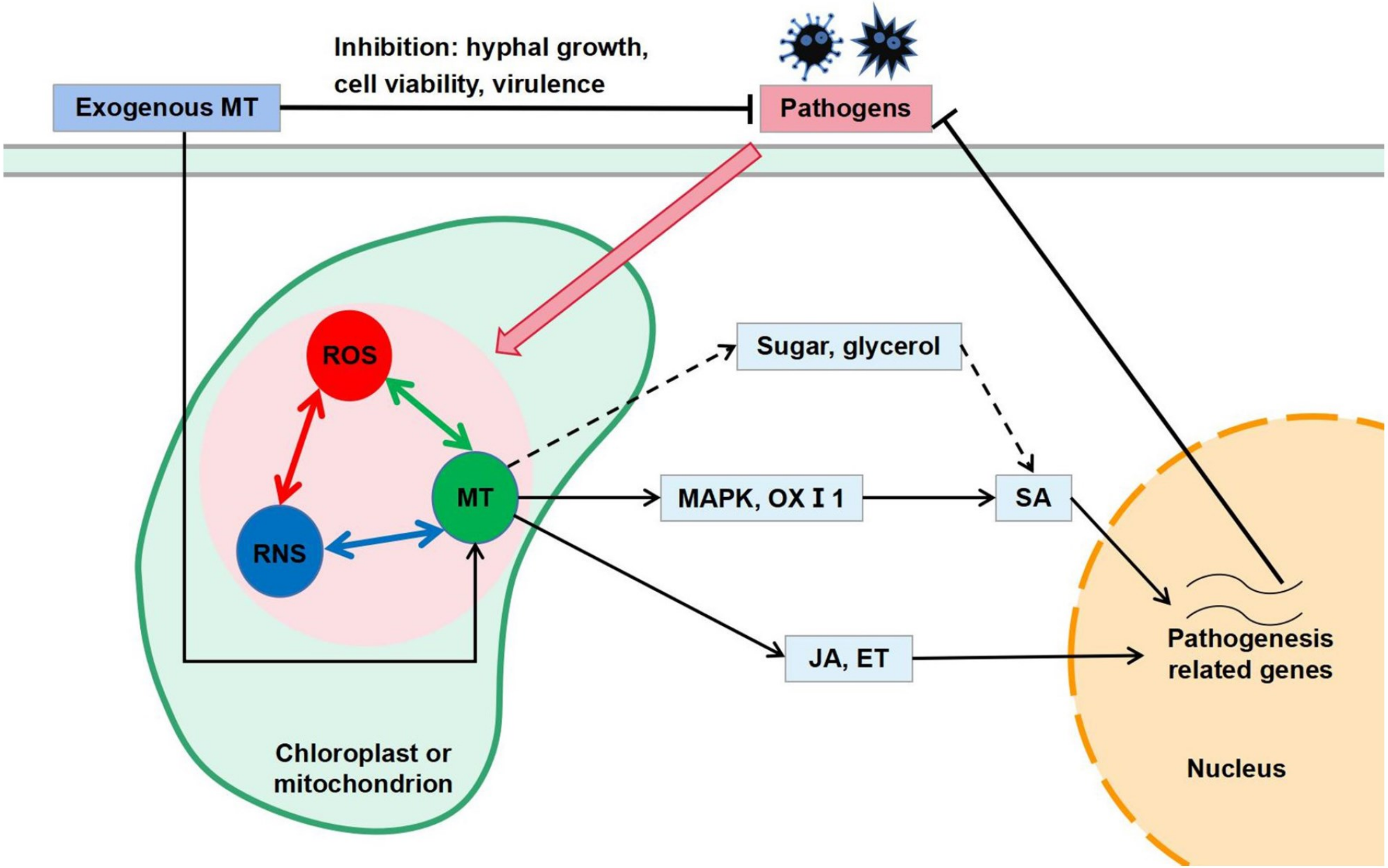


Fig. 5. Mechanism of melatonin against biotic stresses in horticultural plants. Melatonin can induce the pathogenesis related genes expression through SA, JA and ET signalling pathway. Solid lines represent the pathways identified in horticultural plants, while, dashed lines represent this pathway has not been reported in horticultural plants, but it revealed in other plants. Exogenous melatonin can also inhibit the growth and pathogenicity of pathogens directly. MAPK: mitogen-activated protein kinase; OXI1: oxidative signal-inducible 1; ROS: reactive oxygen species; RNS: reactive nitrogen species; MT: melatonin; SA, salicylic acid; JA: jasmonic acid; ET: ethylene.

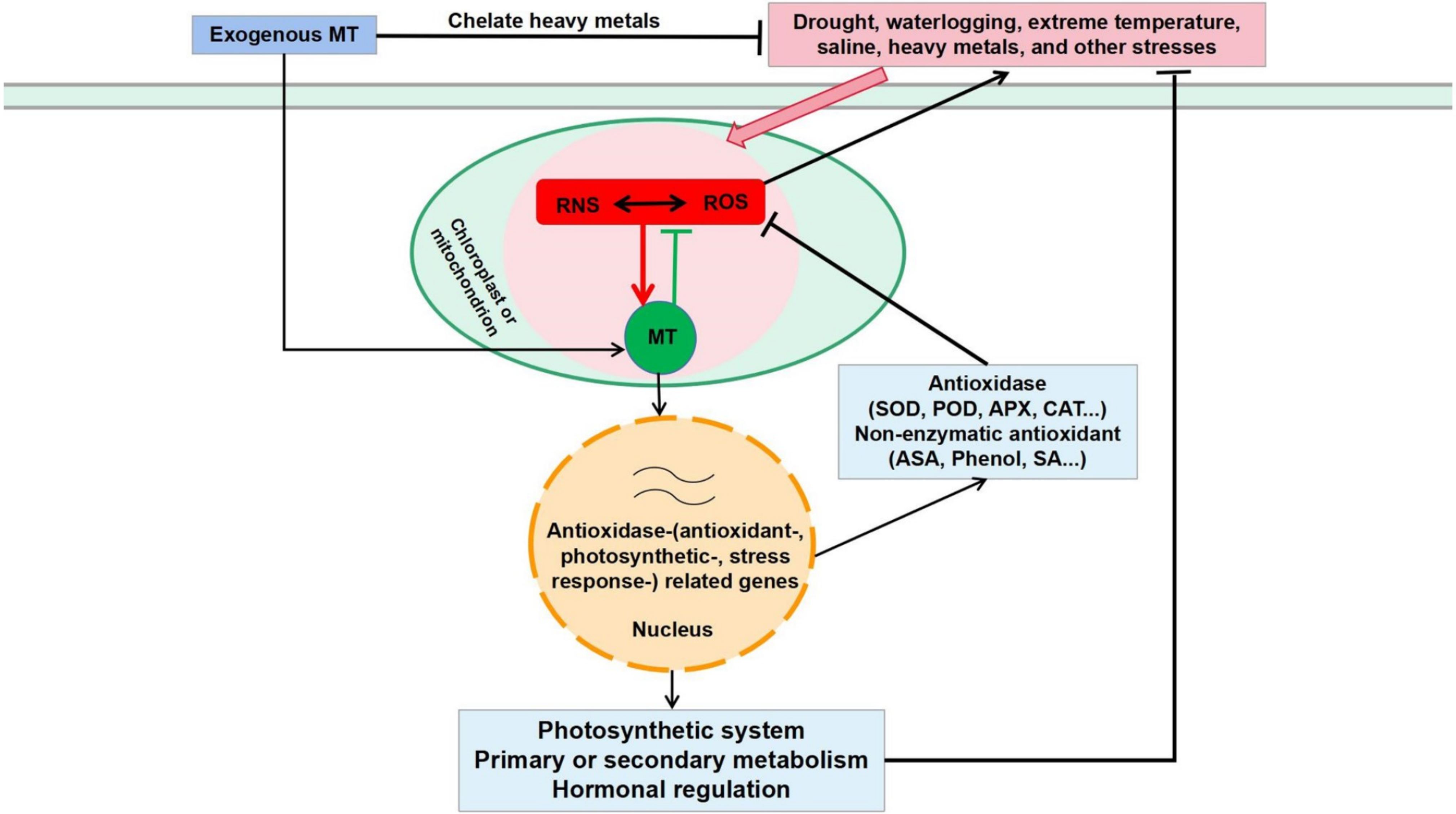
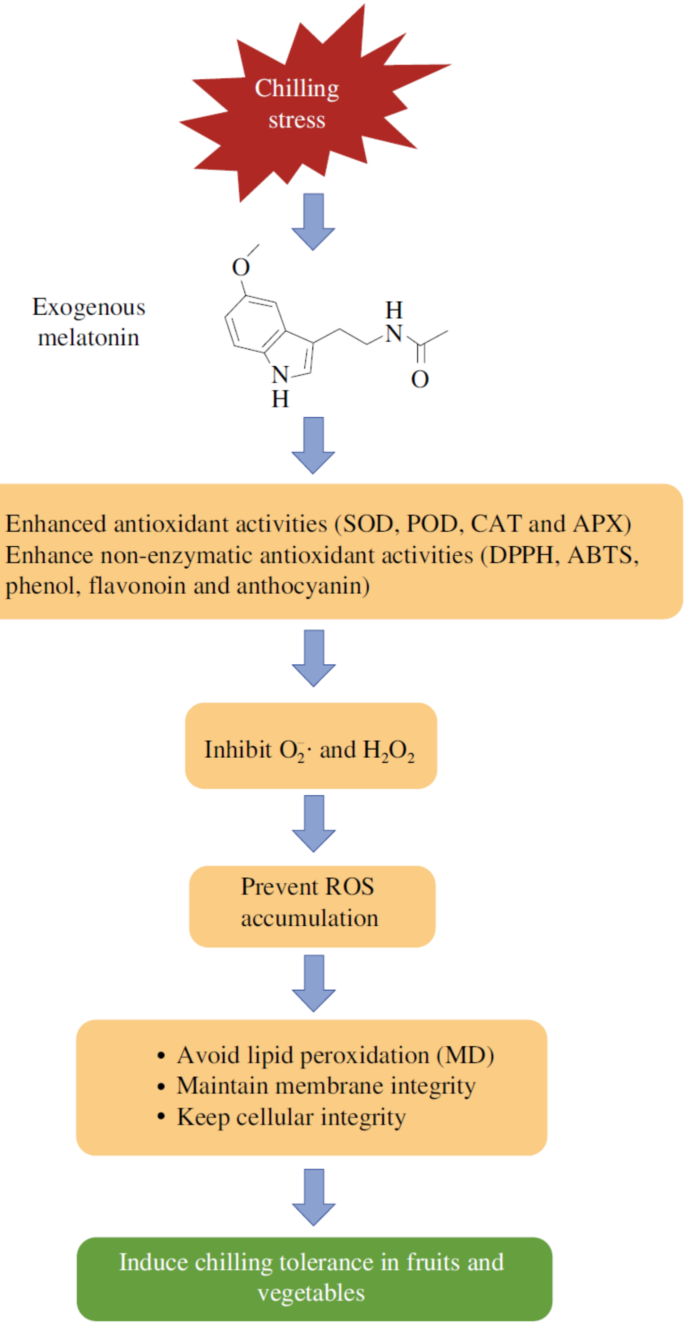


Fig. 6. Mechanism of melatonin against abiotic stresses in horticultural plants. Melatonin can scavenge ROS and RNS directly and also through the melatonin-mediated induction of antioxidases (SOD, POD, APX, CAT, etc.) and representative non-enzymatic antioxidants (ASA, Phenol, SA, etc.). Melatonin also regulates the abiotic stresses tolerance of plants through regulation of photosynthetic system, primary or secondary metabolism, stress response genes, etc. ROS: reactive oxygen species; RNS: reactive nitrogen species; SOD: superoxide dismutase; POD: peroxidase; APX, ascorbate peroxidase; CAT: catalase; ASA: ascorbic acid; SA: salicylic acid.



Chilling stress

Exogenous melatonin

- Enhanced antioxidant activities (SOD, POD, CAT and APX)
- Enhance non-enzymatic antioxidant activities (DPPH, ABTS, phenol, flavonoin and anthocyanin)

Inhibit $O_2\cdot$ and H_2O_2

Prevent ROS accumulation

- Avoid lipid peroxidation (MD)
- Maintain membrane integrity
- Keep cellular integrity

Induce chilling tolerance in fruits and vegetables

Fig. 2 The melatonin induced cold tolerance by enzymatic and non-enzymatic antioxidants.

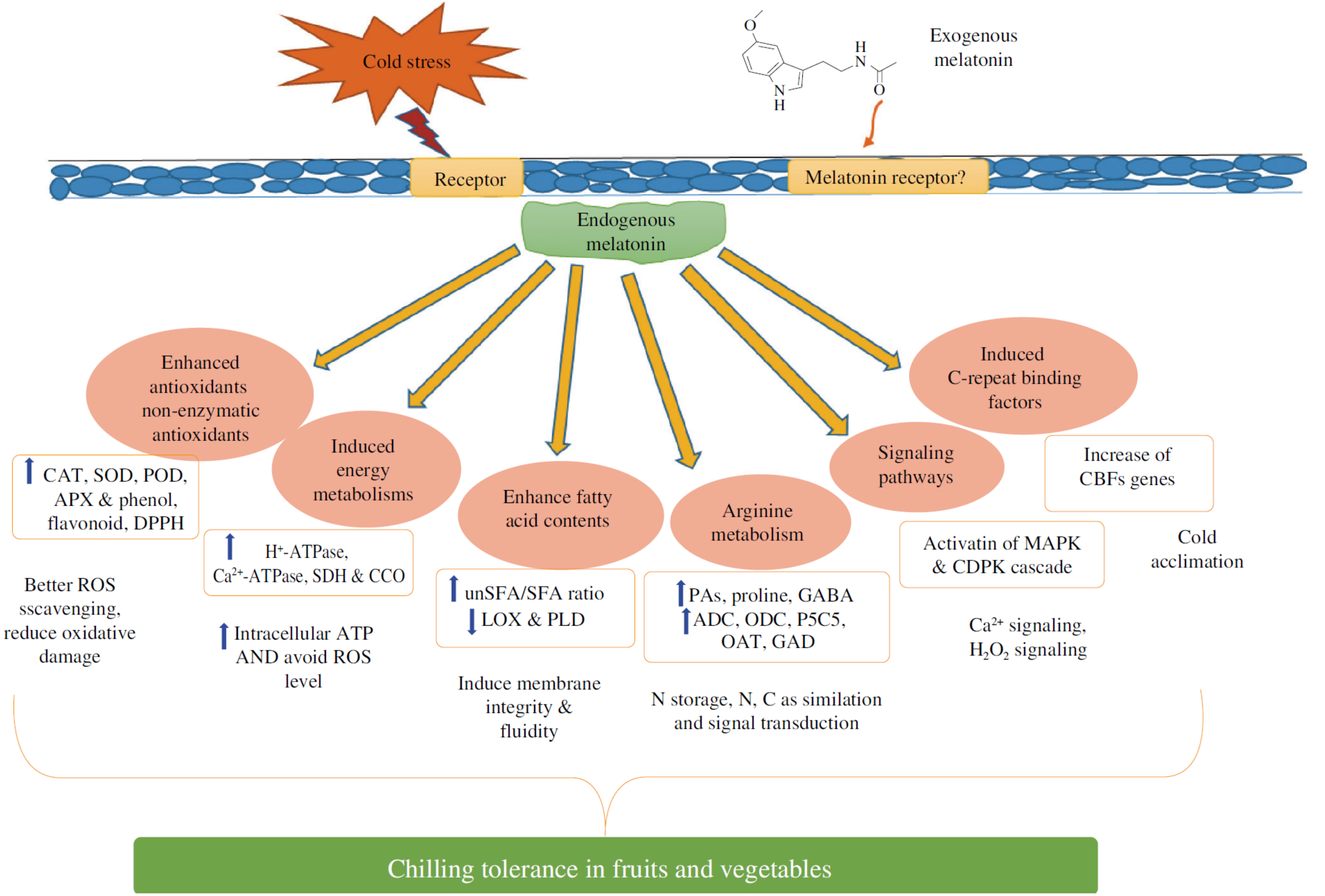


Fig. 4 An overall schematic representation of melatonin mediated mechanism of chilling tolerance in fruits and vegetables cold storage. The arrow represents hypothetical pathways. Upward arrow indicates an increase. ? represent unknown pathway and receptors.

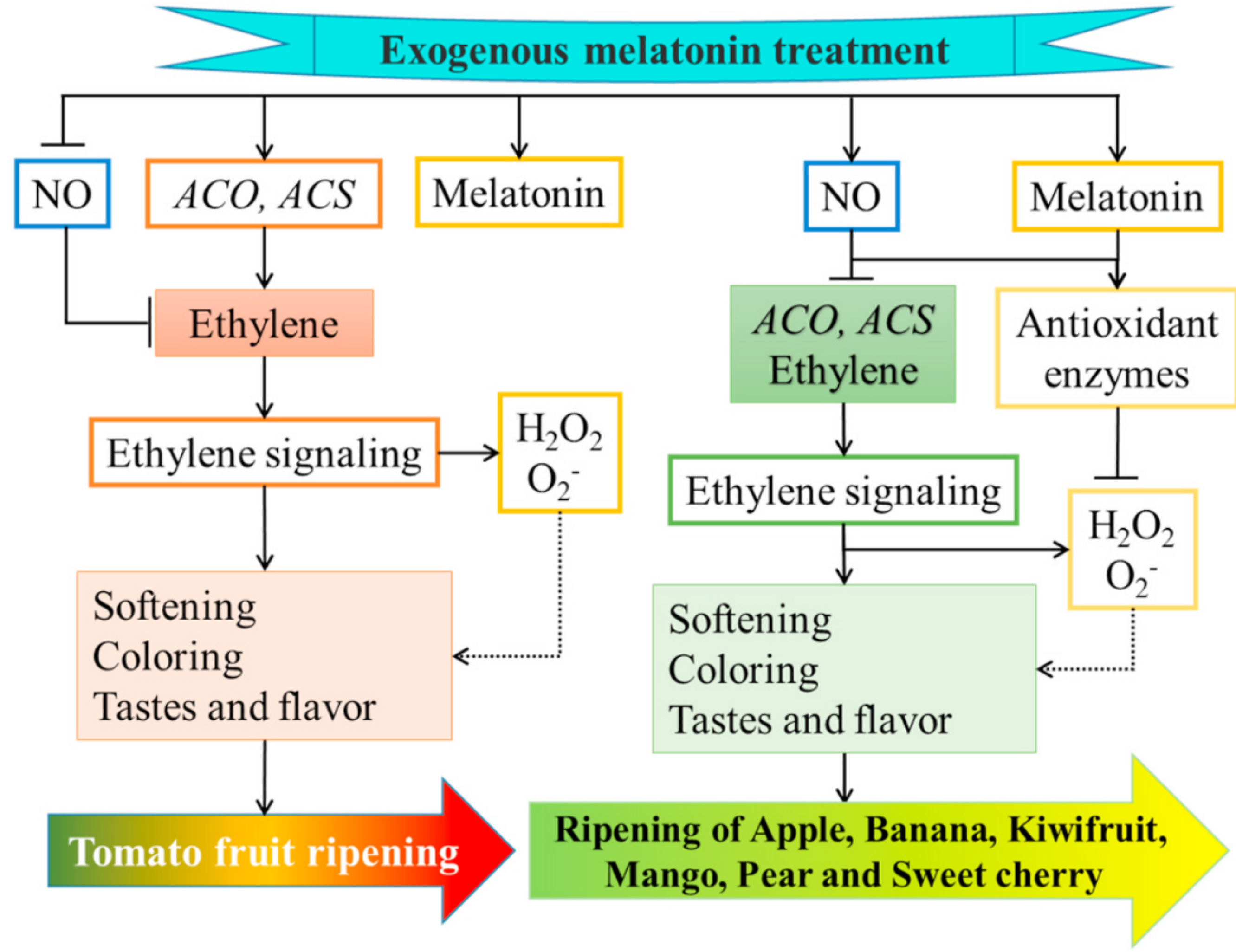


Fig. 1. Proposed roles of exogenous melatonin treatment in promoting or delaying the ripening of postharvest fruit. Melatonin treatment significantly promoted the ripening of tomato fruit, while melatonin treatment significantly delayed the ripening of some other fruits. ACS, 1-aminocyclopropanecarboxylic acid (ACC) synthase; ACO, ACC oxidase, H_2O_2, hydrogen peroxide; NO, nitric oxide; O_2^-, superoxide anion.

Melatonin (MLT) was discovered in the family of monocotyledonous and dicotyledonous edible plants in 1995. In 1995, two papers almost simultaneously reported the presence of MLT in plants .

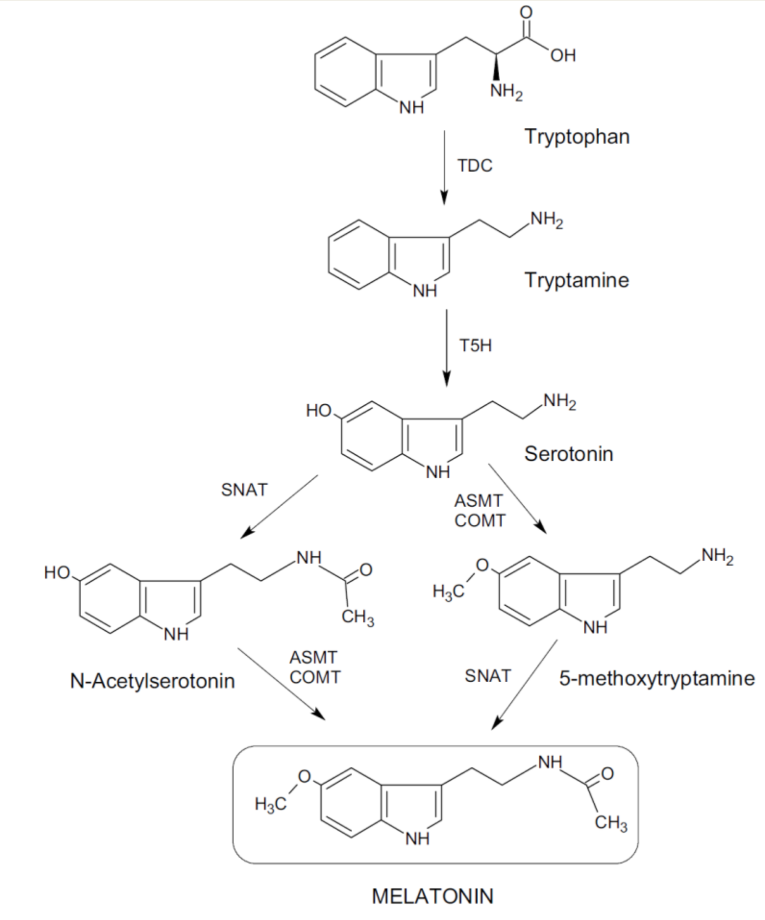
Successive studies have described the availability of MLT in more than 50 plant species in seed, root, shoot, leaf, flower, bulb, coleoptile and fruit.

Since 2006, the number of publications explaining the biological roles of endogenous MLT as well as the metabolic alterations produced by exogenous MLT in plants has shown an exponential increase, reaching a maximum in 2018, with 129 articles

It is probably synthesized in the mitochondria and chloroplasts of leaves and/or roots and then transferred to flowers, fruits, and meristems in plants

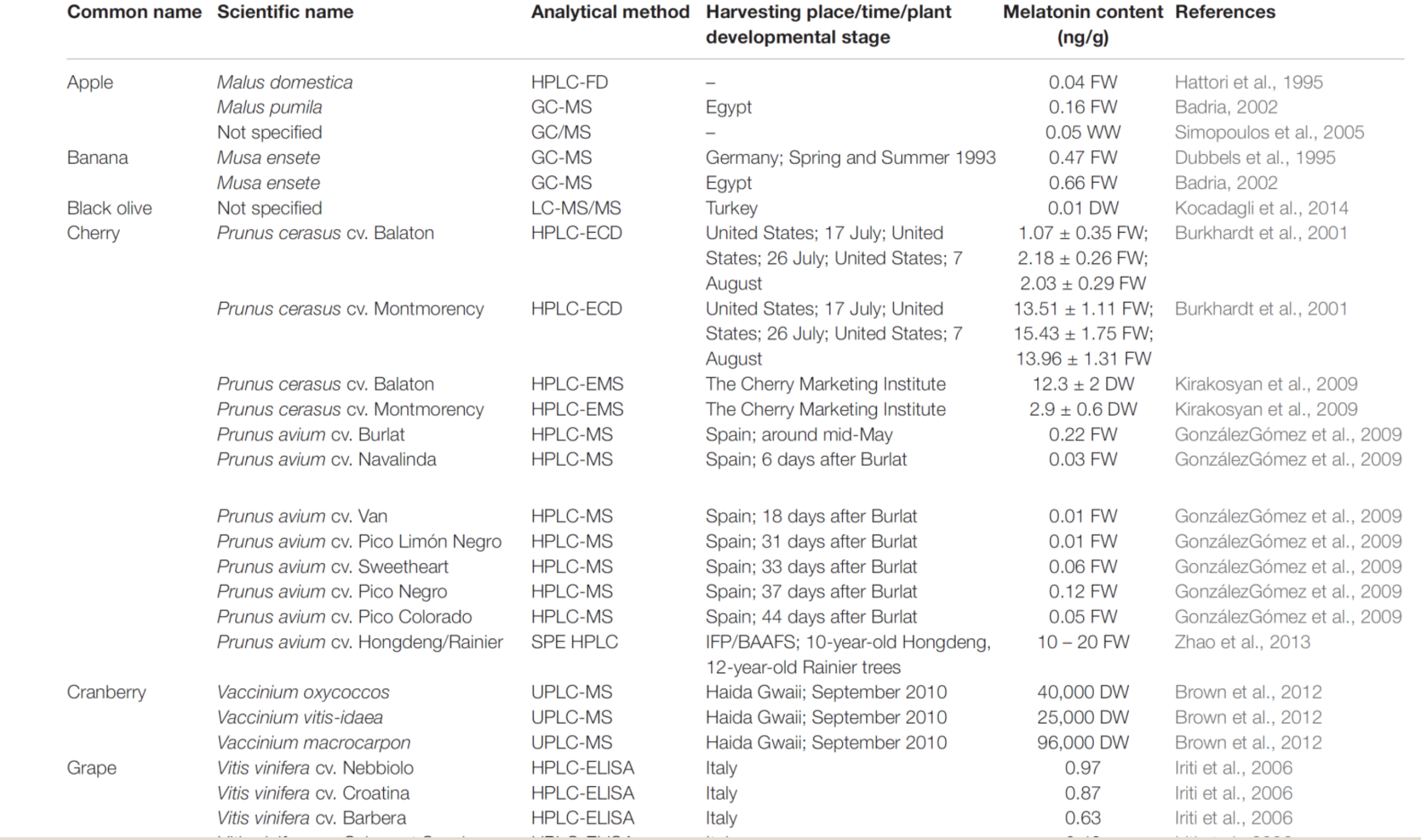
Melatonin is involved in various biological processes in plants, including circadian rhythm and photo-response regulation, leaf senescence, seed germination, and root growth .

Melatonin is synthesized from tryptophan through the catalysis of tryptophan decarboxylase, ryptamine-5 hydroxylase, 5-hydroxytryptamine-N-acetyltransferase, and N-acetyl-5 hydroxytryptamine-methyl transferase in plants, which are then catabolized to 2-hydroxymelatonin by the action of melatonin 2-hydroxylase.

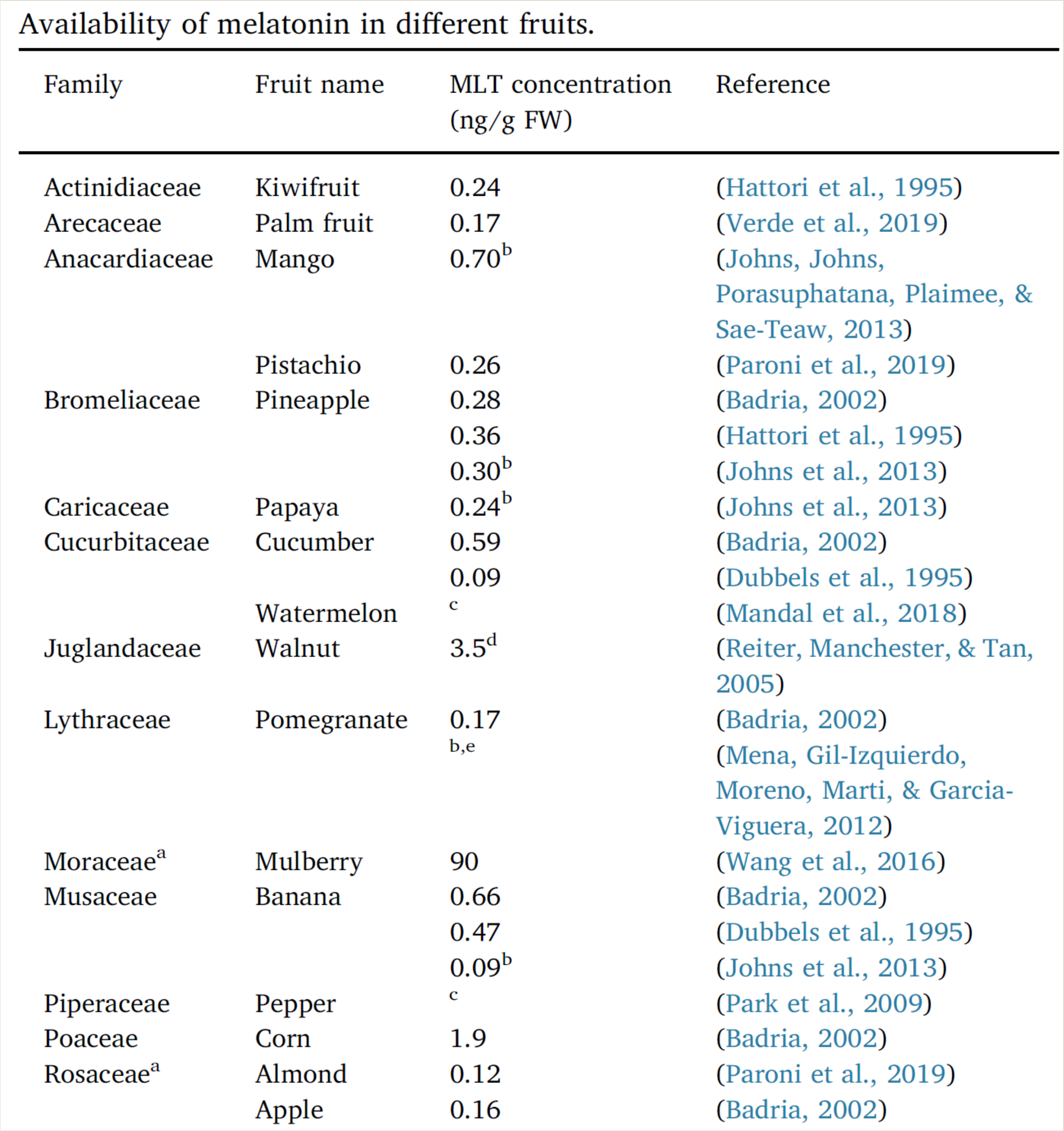


Contents of endogenous melatonin in different post-harvest fruits

The highest melatonin concentrations were detected in Moraceae, Rosaceae and Solanaceae fruits.

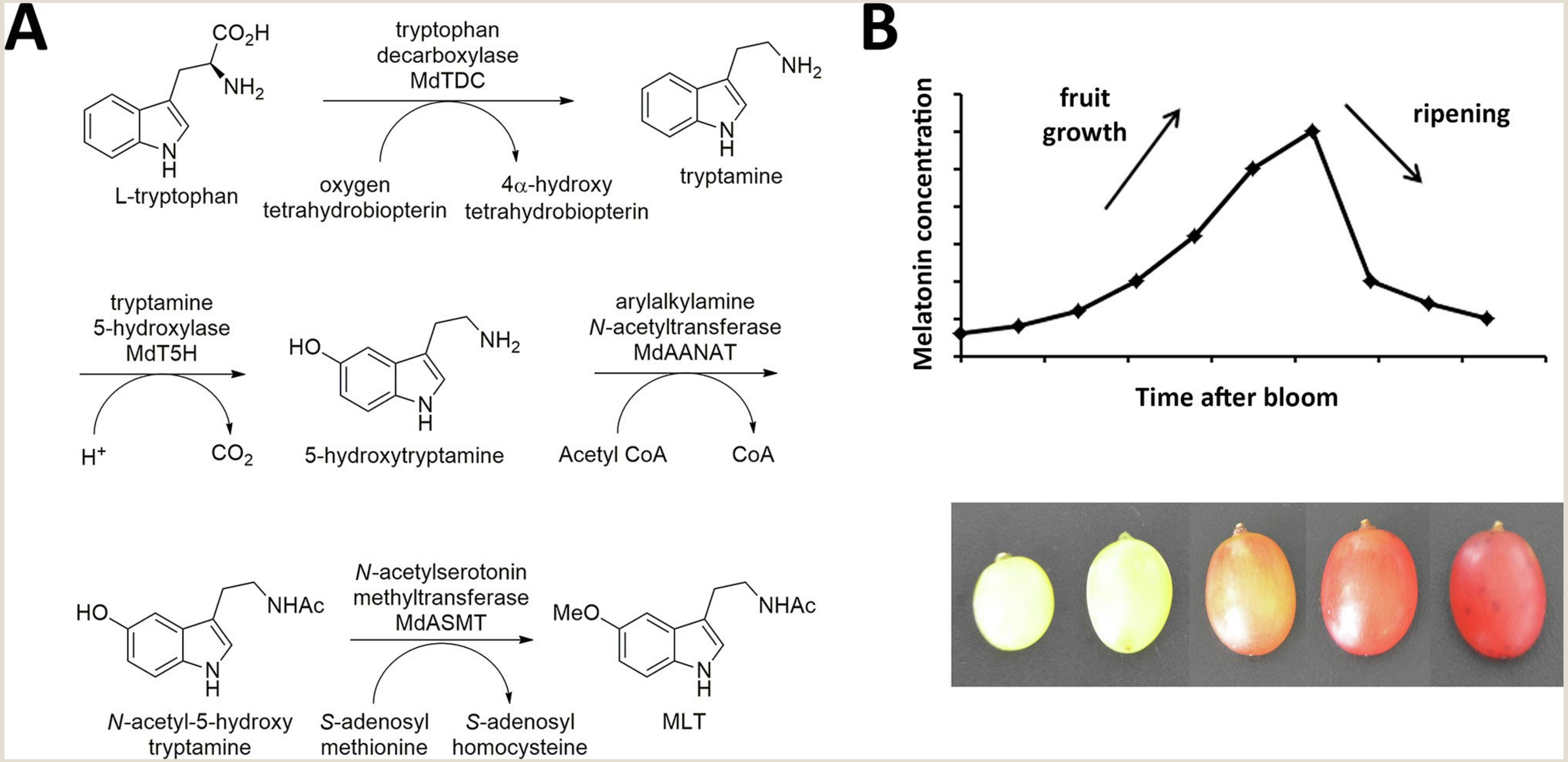


Common name	Scientific name	Analytical method	Harvesting place/time/plant developmental stage	Melatonin content (ng/g)	References
Apple	*Malus domestica*	HPLC-FD	–	0.04 FW	Hattori et al., 1995
	Malus pumila	GC-MS	Egypt	0.16 FW	Badria, 2002
	Not specified	GC/MS	–	0.05 WW	Simopoulos et al., 2005
Banana	*Musa ensete*	GC-MS	Germany; Spring and Summer 1993	0.47 FW	Dubbels et al., 1995
	Musa ensete	GC-MS	Egypt	0.66 FW	Badria, 2002
Black olive	Not specified	LC-MS/MS	Turkey	0.01 DW	Kocadagli et al., 2014
Cherry	*Prunus cerasus* cv. Balaton	HPLC-ECD	United States; 17 July; United States; 26 July; United States; 7 August	1.07 ± 0.35 FW; 2.18 ± 0.26 FW; 2.03 ± 0.29 FW	Burkhardt et al., 2001
	Prunus cerasus cv. Montmorency	HPLC-ECD	United States; 17 July; United States; 26 July; United States; 7 August	13.51 ± 1.11 FW; 15.43 ± 1.75 FW; 13.96 ± 1.31 FW	Burkhardt et al., 2001
	Prunus cerasus cv. Balaton	HPLC-EMS	The Cherry Marketing Institute	12.3 ± 2 DW	Kirakosyan et al., 2009
	Prunus cerasus cv. Montmorency	HPLC-EMS	The Cherry Marketing Institute	2.9 ± 0.6 DW	Kirakosyan et al., 2009
	Prunus avium cv. Burlat	HPLC-MS	Spain; around mid-May	0.22 FW	GonzálezGómez et al., 2009
	Prunus avium cv. Navalinda	HPLC-MS	Spain; 6 days after Burlat	0.03 FW	GonzálezGómez et al., 2009
	Prunus avium cv. Van	HPLC-MS	Spain; 18 days after Burlat	0.01 FW	GonzálezGómez et al., 2009
	Prunus avium cv. Pico Limón Negro	HPLC-MS	Spain; 31 days after Burlat	0.01 FW	GonzálezGómez et al., 2009
	Prunus avium cv. Sweetheart	HPLC-MS	Spain; 33 days after Burlat	0.06 FW	GonzálezGómez et al., 2009
	Prunus avium cv. Pico Negro	HPLC-MS	Spain; 37 days after Burlat	0.12 FW	GonzálezGómez et al., 2009
	Prunus avium cv. Pico Colorado	HPLC-MS	Spain; 44 days after Burlat	0.05 FW	GonzálezGómez et al., 2009
	Prunus avium cv. Hongdeng/Rainier	SPE HPLC	IFP/BAAFS; 10-year-old Hongdeng, 12-year-old Rainier trees	10 – 20 FW	Zhao et al., 2013
Cranberry	*Vaccinium oxycoccos*	UPLC-MS	Haida Gwaii; September 2010	40,000 DW	Brown et al., 2012
	Vaccinium vitis-idaea	UPLC-MS	Haida Gwaii; September 2010	25,000 DW	Brown et al., 2012
	Vaccinium macrocarpon	UPLC-MS	Haida Gwaii; September 2010	96,000 DW	Brown et al., 2012
Grape	*Vitis vinifera* cv. Nebbiolo	HPLC-ELISA	Italy	0.97	Iriti et al., 2006
	Vitis vinifera cv. Croatina	HPLC-ELISA	Italy	0.87	Iriti et al., 2006
	Vitis vinifera cv. Barbera	HPLC-ELISA	Italy	0.63	Iriti et al., 2006



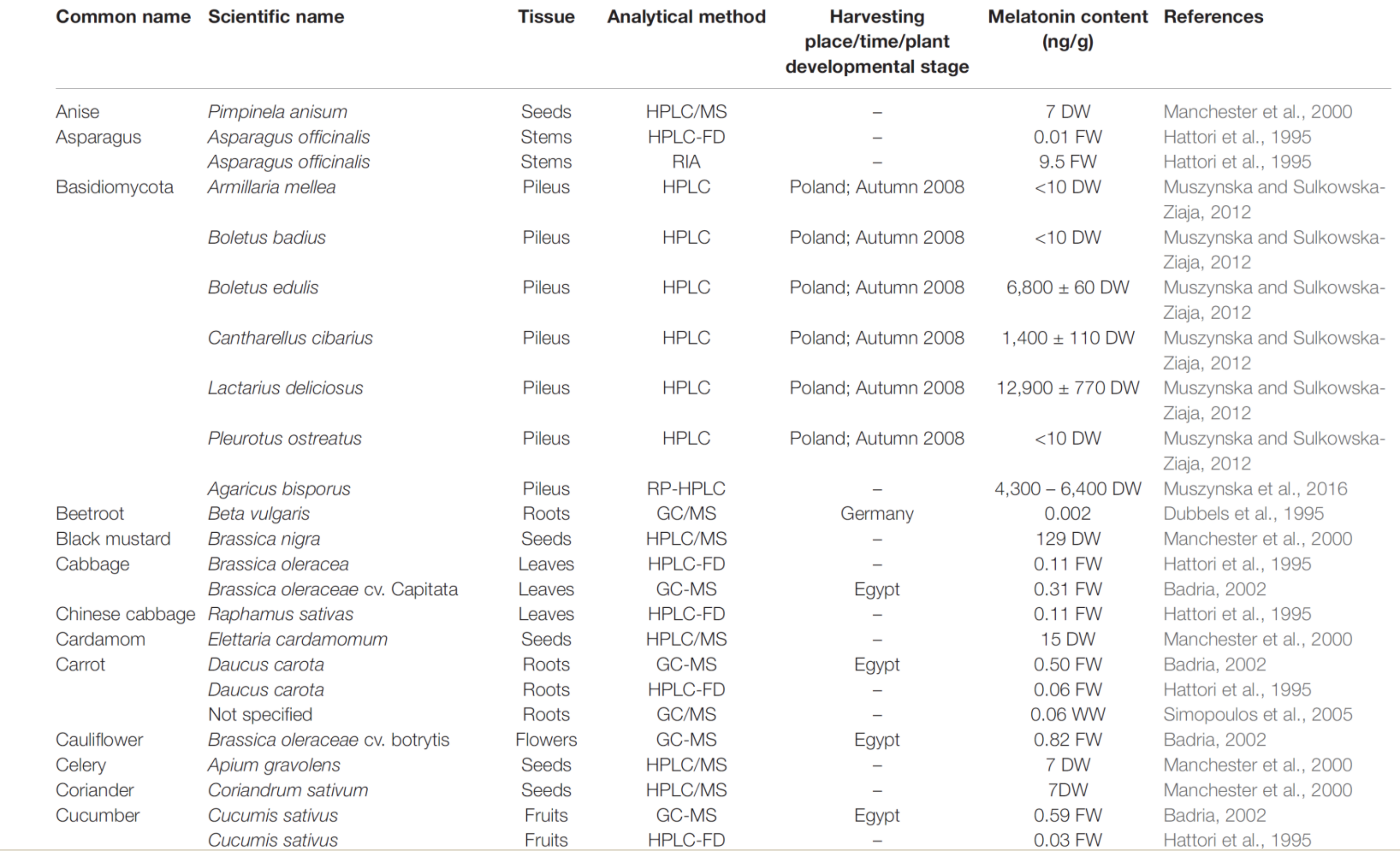
Availability of melatonin in different fruits.

Family	Fruit name	MLT concentration (ng/g FW)	Reference
Actinidiaceae	Kiwifruit	0.24	(Hattori et al., 1995)
Arecaceae	Palm fruit	0.17	(Verde et al., 2019)
Anacardiaceae	Mango	0.70[b]	(Johns, Johns, Porasuphatana, Plaimee, & Sae-Teaw, 2013)
	Pistachio	0.26	(Paroni et al., 2019)
Bromeliaceae	Pineapple	0.28	(Badria, 2002)
		0.36	(Hattori et al., 1995)
		0.30[b]	(Johns et al., 2013)
Caricaceae	Papaya	0.24[b]	(Johns et al., 2013)
Cucurbitaceae	Cucumber	0.59	(Badria, 2002)
		0.09	(Dubbels et al., 1995)
	Watermelon	[c]	(Mandal et al., 2018)
Juglandaceae	Walnut	3.5[d]	(Reiter, Manchester, & Tan, 2005)
Lythraceae	Pomegranate	0.17	(Badria, 2002)
		[b,e]	(Mena, Gil-Izquierdo, Moreno, Marti, & Garcia-Viguera, 2012)
Moraceae[a]	Mulberry	90	(Wang et al., 2016)
Musaceae	Banana	0.66	(Badria, 2002)
		0.47	(Dubbels et al., 1995)
		0.09[b]	(Johns et al., 2013)
Piperaceae	Pepper	[c]	(Park et al., 2009)
Poaceae	Corn	1.9	(Badria, 2002)
Rosaceae[a]	Almond	0.12	(Paroni et al., 2019)
	Apple	0.16	(Badria, 2002)



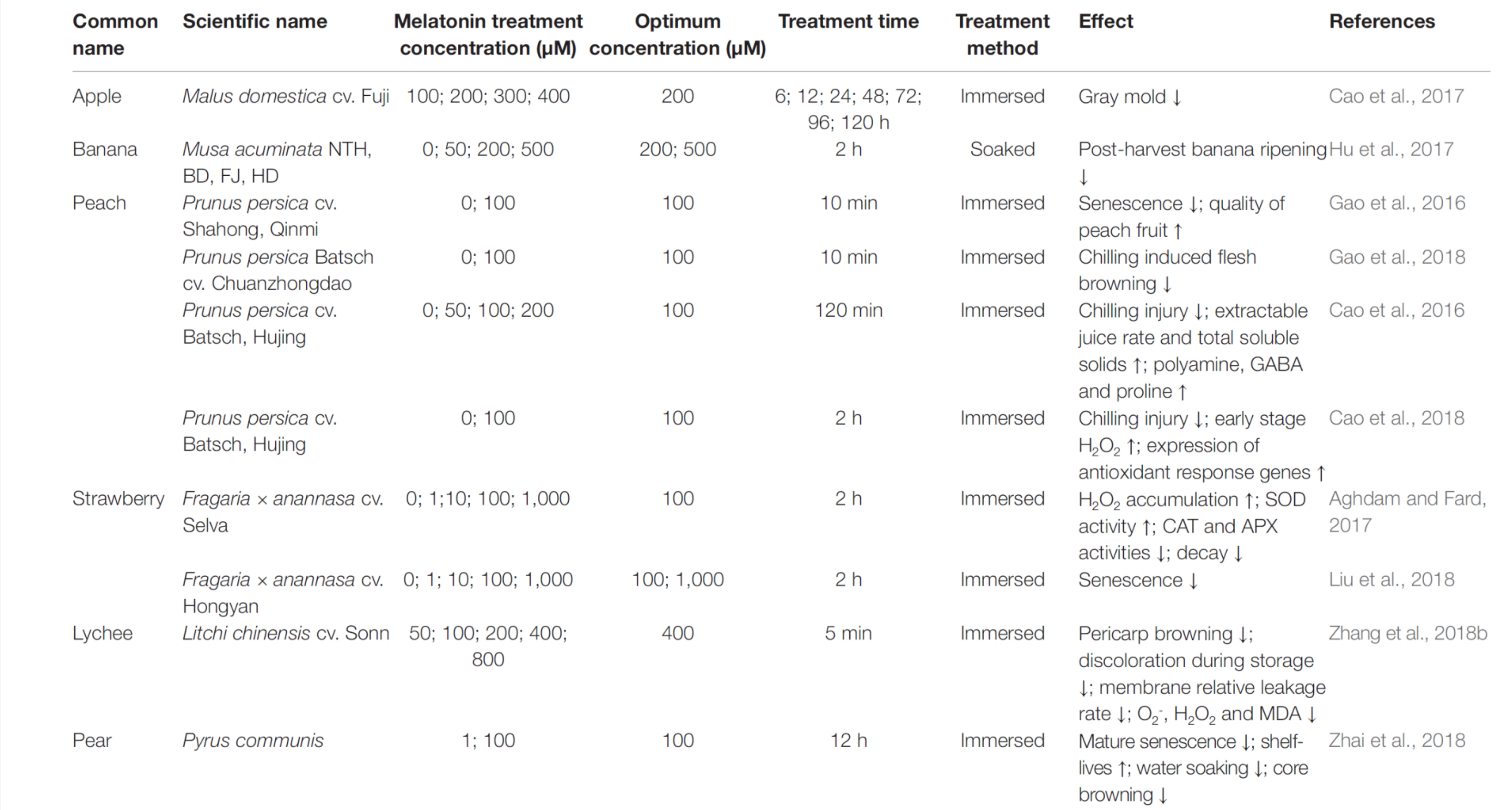
A Biosynthesis of melatonin in Red Fuji apple (Malus domestica Borkh. cv. Red Fuji) reported by Lei et al. (2013) The melatonin biosynthetic pathway genes, including tryptophan decarboxylase (MdTDC), tryptamine 5-hydroxylase (MdT5H), arylalkylamine N-acetyltransferase (MdAANAT) and N-acetylserotonin methyltransferase (MdASMT), were identified. Some fruit varieties contain caffeic acid O-methyltransferase (COMT1), which is able to catalyze the methylation of 5-hydroxy-N-acetyltryptamine to provide melatonin. B Variations in the melatonin content during fruit development. Melatonin concentration increases at preveraison, and decreases during fruit ripening.

Contents of endogenous melatonin in different post-harvest vegetables.



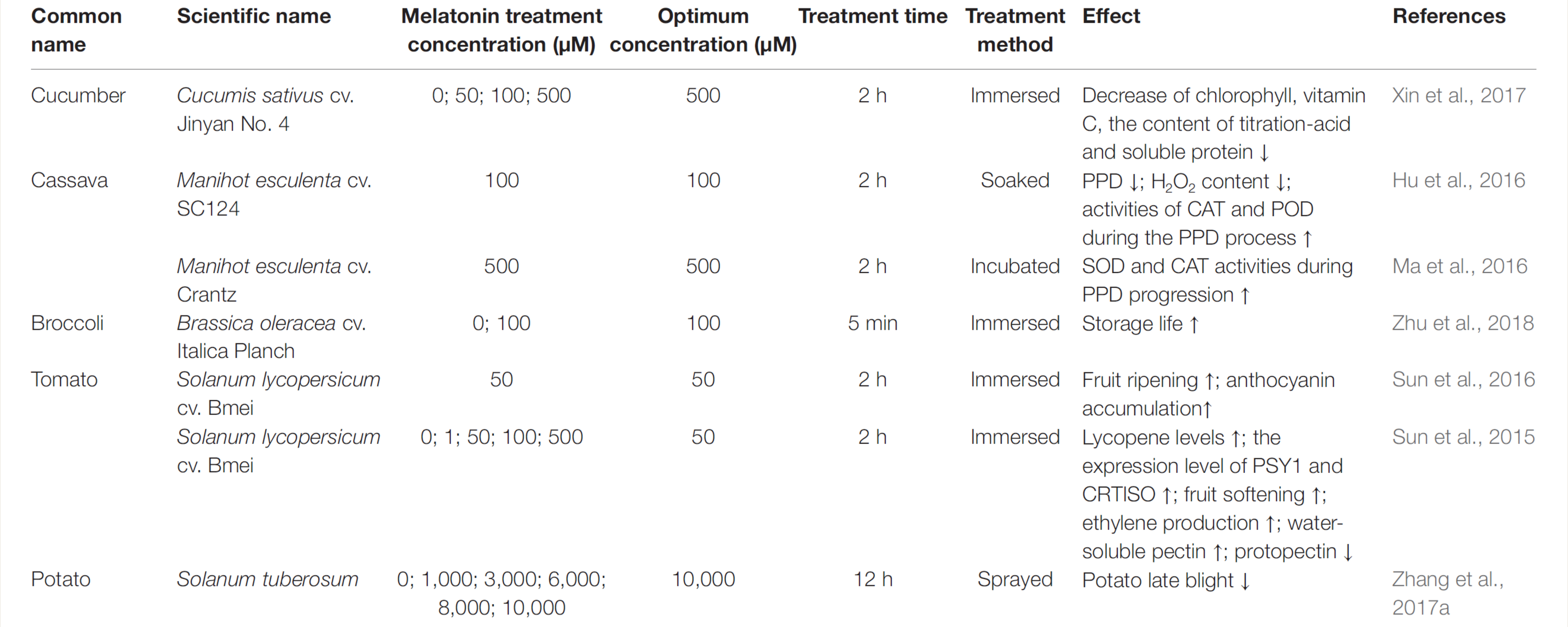
Common name	Scientific name	Tissue	Analytical method	Harvesting place/time/plant developmental stage	Melatonin content (ng/g)	References
Anise	*Pimpinela anisum*	Seeds	HPLC/MS	–	7 DW	Manchester et al., 2000
Asparagus	*Asparagus officinalis*	Stems	HPLC-FD	–	0.01 FW	Hattori et al., 1995
	Asparagus officinalis	Stems	RIA	–	9.5 FW	Hattori et al., 1995
Basidiomycota	*Armillaria mellea*	Pileus	HPLC	Poland; Autumn 2008	<10 DW	Muszynska and Sulkowska-Ziaja, 2012
	Boletus badius	Pileus	HPLC	Poland; Autumn 2008	<10 DW	Muszynska and Sulkowska-Ziaja, 2012
	Boletus edulis	Pileus	HPLC	Poland; Autumn 2008	6,800 ± 60 DW	Muszynska and Sulkowska-Ziaja, 2012
	Cantharellus cibarius	Pileus	HPLC	Poland; Autumn 2008	1,400 ± 110 DW	Muszynska and Sulkowska-Ziaja, 2012
	Lactarius deliciosus	Pileus	HPLC	Poland; Autumn 2008	12,900 ± 770 DW	Muszynska and Sulkowska-Ziaja, 2012
	Pleurotus ostreatus	Pileus	HPLC	Poland; Autumn 2008	<10 DW	Muszynska and Sulkowska-Ziaja, 2012
	Agaricus bisporus	Pileus	RP-HPLC	–	4,300 – 6,400 DW	Muszynska et al., 2016
Beetroot	*Beta vulgaris*	Roots	GC/MS	Germany	0.002	Dubbels et al., 1995
Black mustard	*Brassica nigra*	Seeds	HPLC/MS	–	129 DW	Manchester et al., 2000
Cabbage	*Brassica oleracea*	Leaves	HPLC-FD	–	0.11 FW	Hattori et al., 1995
	Brassica oleraceae cv. Capitata	Leaves	GC-MS	Egypt	0.31 FW	Badria, 2002
Chinese cabbage	*Raphamus sativas*	Leaves	HPLC-FD	–	0.11 FW	Hattori et al., 1995
Cardamom	*Elettaria cardamomum*	Seeds	HPLC/MS	–	15 DW	Manchester et al., 2000
Carrot	*Daucus carota*	Roots	GC-MS	Egypt	0.50 FW	Badria, 2002
	Daucus carota	Roots	HPLC-FD	–	0.06 FW	Hattori et al., 1995
	Not specified	Roots	GC/MS	–	0.06 WW	Simopoulos et al., 2005
Cauliflower	*Brassica oleraceae* cv. botrytis	Flowers	GC-MS	Egypt	0.82 FW	Badria, 2002
Celery	*Apium gravolens*	Seeds	HPLC/MS	–	7 DW	Manchester et al., 2000
Coriander	*Coriandrum sativum*	Seeds	HPLC/MS	–	7DW	Manchester et al., 2000
Cucumber	*Cucumis sativus*	Fruits	GC-MS	Egypt	0.59 FW	Badria, 2002
	Cucumis sativus	Fruits	HPLC-FD	–	0.03 FW	Hattori et al., 1995

Effects of exogenous melatonin on the preservation and quality of post-harvest fruits

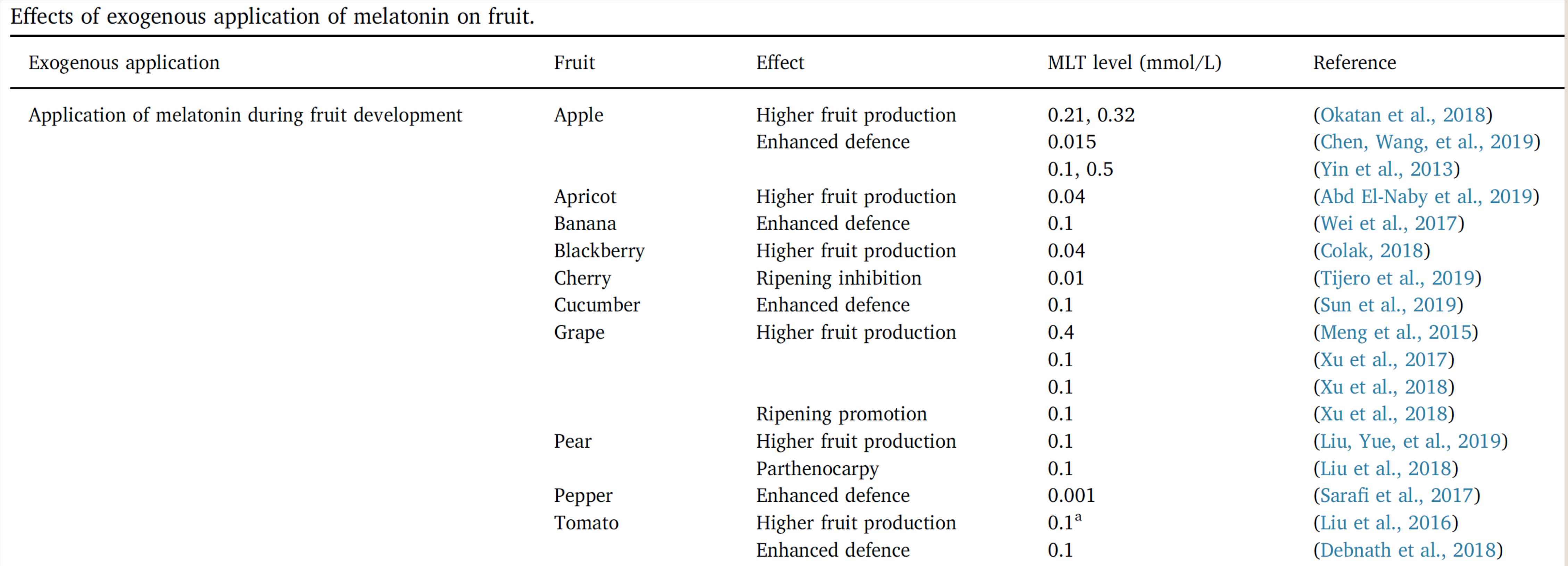


Common name	Scientific name	Melatonin treatment concentration (μM)	Optimum concentration (μM)	Treatment time	Treatment method	Effect	References
Apple	*Malus domestica* cv. Fuji	100; 200; 300; 400	200	6; 12; 24; 48; 72; 96; 120 h	Immersed	Gray mold ↓	Cao et al., 2017
Banana	*Musa acuminata* NTH, BD, FJ, HD	0; 50; 200; 500	200; 500	2 h	Soaked	Post-harvest banana ripening ↓	Hu et al., 2017
Peach	*Prunus persica* cv. Shahong, Qinmi	0; 100	100	10 min	Immersed	Senescence ↓; quality of peach fruit ↑	Gao et al., 2016
	Prunus persica Batsch cv. Chuanzhongdao	0; 100	100	10 min	Immersed	Chilling induced flesh browning ↓	Gao et al., 2018
	Prunus persica cv. Batsch, Hujing	0; 50; 100; 200	100	120 min	Immersed	Chilling injury ↓; extractable juice rate and total soluble solids ↑; polyamine, GABA and proline ↑	Cao et al., 2016
	Prunus persica cv. Batsch, Hujing	0; 100	100	2 h	Immersed	Chilling injury ↓; early stage H_2O_2 ↑; expression of antioxidant response genes ↑	Cao et al., 2018
Strawberry	*Fragaria* × *anannasa* cv. Selva	0; 1;10; 100; 1,000	100	2 h	Immersed	H_2O_2 accumulation ↑; SOD activity ↑; CAT and APX activities ↓; decay ↓	Aghdam and Fard, 2017
	Fragaria × *anannasa* cv. Hongyan	0; 1; 10; 100; 1,000	100; 1,000	2 h	Immersed	Senescence ↓	Liu et al., 2018
Lychee	*Litchi chinensis* cv. Sonn	50; 100; 200; 400; 800	400	5 min	Immersed	Pericarp browning ↓; discoloration during storage ↓; membrane relative leakage rate ↓; O_2^-, H_2O_2 and MDA ↓	Zhang et al., 2018b
Pear	*Pyrus communis*	1; 100	100	12 h	Immersed	Mature senescence ↓; shelf-lives ↑; water soaking ↓; core browning ↓	Zhai et al., 2018

Effects of exogenous melatonin on the preservation and quality of post-harvest vegetables

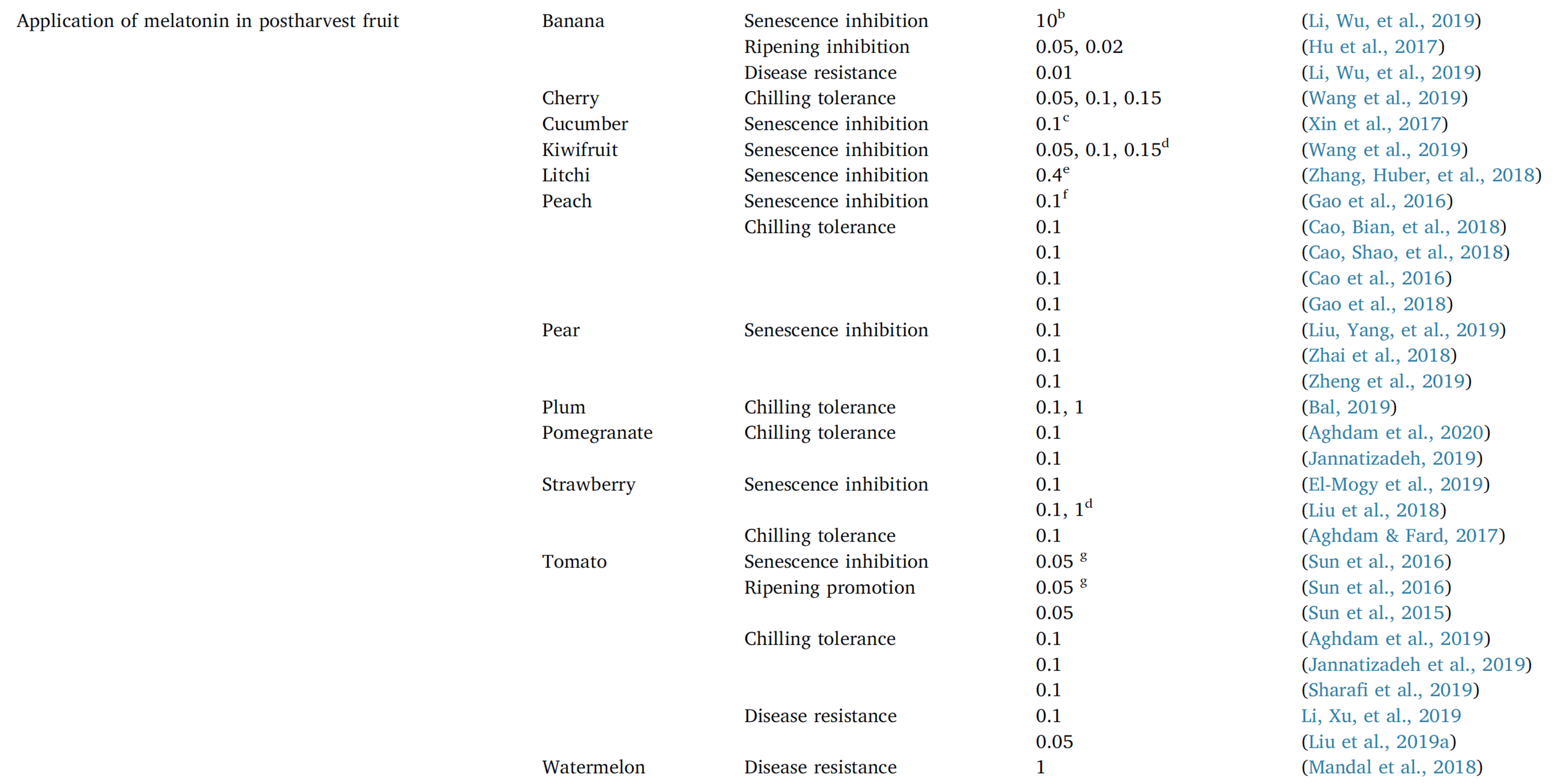


Common name	Scientific name	Melatonin treatment concentration (μM)	Optimum concentration (μM)	Treatment time	Treatment method	Effect	References
Cucumber	*Cucumis sativus* cv. Jinyan No. 4	0; 50; 100; 500	500	2 h	Immersed	Decrease of chlorophyll, vitamin C, the content of titration-acid and soluble protein ↓	Xin et al., 2017
Cassava	*Manihot esculenta* cv. SC124	100	100	2 h	Soaked	PPD ↓; H_2O_2 content ↓; activities of CAT and POD during the PPD process ↑	Hu et al., 2016
	Manihot esculenta cv. Crantz	500	500	2 h	Incubated	SOD and CAT activities during PPD progression ↑	Ma et al., 2016
Broccoli	*Brassica oleracea* cv. Italica Planch	0; 100	100	5 min	Immersed	Storage life ↑	Zhu et al., 2018
Tomato	*Solanum lycopersicum* cv. Bmei	50	50	2 h	Immersed	Fruit ripening ↑; anthocyanin accumulation↑	Sun et al., 2016
	Solanum lycopersicum cv. Bmei	0; 1; 50; 100; 500	50	2 h	Immersed	Lycopene levels ↑; the expression level of PSY1 and CRTISO ↑; fruit softening ↑; ethylene production ↑; water-soluble pectin ↑; protopectin ↓	Sun et al., 2015
Potato	*Solanum tuberosum*	0; 1,000; 3,000; 6,000; 8,000; 10,000	10,000	12 h	Sprayed	Potato late blight ↓	Zhang et al., 2017a



Effects of exogenous application of melatonin on fruit.

Exogenous application	Fruit	Effect	MLT level (mmol/L)	Reference
Application of melatonin during fruit development	Apple	Higher fruit production	0.21, 0.32	(Okatan et al., 2018)
		Enhanced defence	0.015	(Chen, Wang, et al., 2019)
			0.1, 0.5	(Yin et al., 2013)
	Apricot	Higher fruit production	0.04	(Abd El-Naby et al., 2019)
	Banana	Enhanced defence	0.1	(Wei et al., 2017)
	Blackberry	Higher fruit production	0.04	(Colak, 2018)
	Cherry	Ripening inhibition	0.01	(Tijero et al., 2019)
	Cucumber	Enhanced defence	0.1	(Sun et al., 2019)
	Grape	Higher fruit production	0.4	(Meng et al., 2015)
			0.1	(Xu et al., 2017)
			0.1	(Xu et al., 2018)
		Ripening promotion	0.1	(Xu et al., 2018)
	Pear	Higher fruit production	0.1	(Liu, Yue, et al., 2019)
		Parthenocarpy	0.1	(Liu et al., 2018)
	Pepper	Enhanced defence	0.001	(Sarafi et al., 2017)
	Tomato	Higher fruit production	0.1[a]	(Liu et al., 2016)
		Enhanced defence	0.1	(Debnath et al., 2018)



Application of melatonin in postharvest fruit	Banana	Senescence inhibition	10[b]	(Li, Wu, et al., 2019)
		Ripening inhibition	0.05, 0.02	(Hu et al., 2017)
		Disease resistance	0.01	(Li, Wu, et al., 2019)
	Cherry	Chilling tolerance	0.05, 0.1, 0.15	(Wang et al., 2019)
	Cucumber	Senescence inhibition	0.1[c]	(Xin et al., 2017)
	Kiwifruit	Senescence inhibition	0.05, 0.1, 0.15[d]	(Wang et al., 2019)
	Litchi	Senescence inhibition	0.4[e]	(Zhang, Huber, et al., 2018)
	Peach	Senescence inhibition	0.1[f]	(Gao et al., 2016)
		Chilling tolerance	0.1	(Cao, Bian, et al., 2018)
			0.1	(Cao, Shao, et al., 2018)
			0.1	(Cao et al., 2016)
			0.1	(Gao et al., 2018)
	Pear	Senescence inhibition	0.1	(Liu, Yang, et al., 2019)
			0.1	(Zhai et al., 2018)
			0.1	(Zheng et al., 2019)
	Plum	Chilling tolerance	0.1, 1	(Bal, 2019)
	Pomegranate	Chilling tolerance	0.1	(Aghdam et al., 2020)
			0.1	(Jannatizadeh, 2019)
	Strawberry	Senescence inhibition	0.1	(El-Mogy et al., 2019)
			0.1, 1[d]	(Liu et al., 2018)
		Chilling tolerance	0.1	(Aghdam & Fard, 2017)
	Tomato	Senescence inhibition	0.05 [g]	(Sun et al., 2016)
		Ripening promotion	0.05 [g]	(Sun et al., 2016)
			0.05	(Sun et al., 2015)
		Chilling tolerance	0.1	(Aghdam et al., 2019)
			0.1	(Jannatizadeh et al., 2019)
			0.1	(Sharafi et al., 2019)
		Disease resistance	0.1	Li, Xu, et al., 2019
			0.05	(Liu et al., 2019a)
	Watermelon	Disease resistance	1	(Mandal et al., 2018)

In summary, exogenous melatonin can be used to improve the post-harvest preservation of fruits and vegetables. However, melatonin concentration and treatment method and time should be carefully considered when exogenous melatonin is used to improve post-harvest preservation. The most important factor is the melatonin concentration, which should be optimized to obtain the best effect.

exogenous applications of MLT to pear trees increased the size of pear fruit by improving the net photosynthetic rate and maximal quantum efficiency of photosystem II photochemistry during the late stage of pear fruit development. In that work, MLT increased fruit weight by 47.8% compared to the control pears as well as the content of soluble sugars, particularly sucrose and sorbitol. Exogenous MLT in Starkrimson pear trees induced the expansion and division of mesocarp cells, promoting the production of seedless fruit without fertilization (Liu et al., 2018). This effect was attributed to the MLT-induced high contents of gibberellins GA3 and GA4 in the pear fruit, which in turn induced the biosynthesis of sucrose as well as the activation of the chlorophyll-related genes

It has been indicated that this effect is produced due to MLT triggers the activation of the shikimic acid pathway, which results in the accumulation of aromatic AA and, subsequently, in the upregulation of MLT biosynthesis. However, the MLT receptors in fruit as well as the permeability and diffusion of exogenous MLT in fruit skin have never been described.

Melatonin in fruit set and development: parthenocarpy

During the development of cherry fruits (*Prunus avium*), the highest levels of melatonin were reached in stage II, embryo development and endocarp lignification, which has also been related to ROS accumulation in “watery” seeds, indicating that oxidative stress induced rapid melatonin biosynthesis

Melatonin in fruit ripening and senescence

In peach fruits, melatonin treatment effectively slowed senescence in the two peach cultivars assayed, as indicated by reduced weight loss, the incidence of decay and the respiration rate, while firmness and the total soluble solids and ascorbic acid contents were maintained. Similarly, the postharvest application of melatonin delayed senescence and maintained the quality of peach fruit, which may be attributed to its capacity to mediate antioxidative actions, suggesting that melatonin treatment could be considered as a promising method for delaying senescence and maintaining fruit quality of postharvest peach fruit

exogenous application of melatonin positively regulates fruit ripening, while negatively regulating fruit senescence

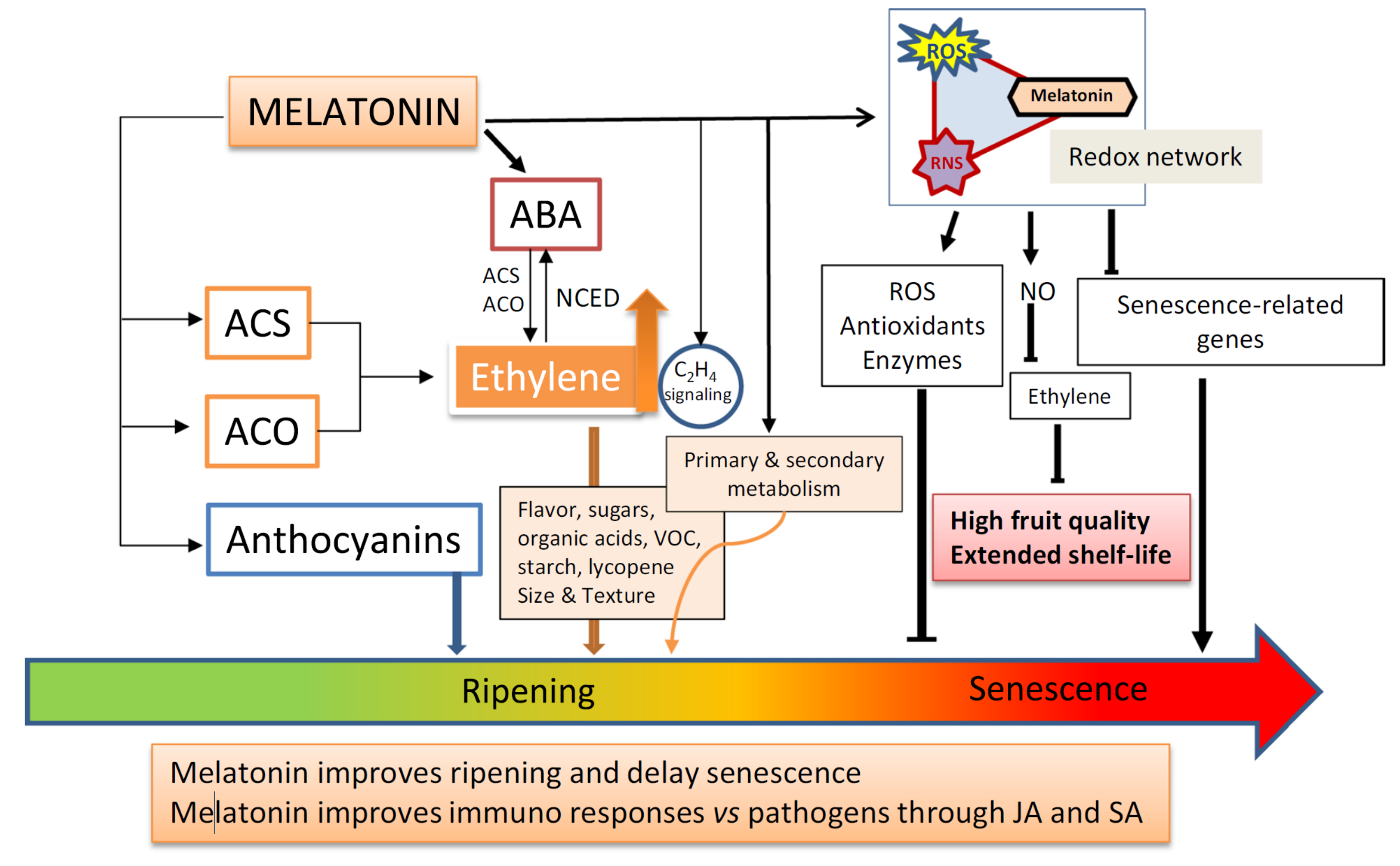
In grape berries, melatonin treatment enhanced ethylene production, which partially contributed to polyphenol accumulation (anthocyanins) and an increase in antioxidant activities. In *Moldova* grape berries, melatonin accumulated rapidly from the onset of véraison, reached a maximum 94 days after bloom and then exhibited low levels in the late stages of berry ripening. Treatment with between 10 and 100 μM melatonin increased the levels of ABA, hydrogen peroxide and ethylene production and promoted berry ripening compared with a control treatment. The suppression of ethylene biosynthesis had the greatest inhibitory effects on melatonin-induced berry ripening compared with the effects of ABA and hydrogen peroxide. Melatonin also promoted ethylene production via ABA. The authors pointed out that the use of melatonin during berry ripening probably accelerates berry ripening .

In melatonin-treated strawberry, improvements in postharvest decay indicators and high ATP content, antioxidant activity and polyphenol levels have been described.

Melatonin treatment delayed fruit deterioration and also significantly reduced CO2 production compared to control fruits.

During the cold storage of pears, melatonin has the potential to retain the commercial value of postharvest pear fruits and delay senescence by limiting ethylene production and the reactive oxygen burst. In pear fruits, too, melatonin and also nitric oxide decreased the rate of polygalacturonase and cellulase upregulation, inhibited the expression of ethylene biosynthesis genes (ACS and ACO) and reduced respiration and ethylene production rates, delaying fruit senescence

Immediately after harvest, plum fruits (*Prunus domestica*) were immersed in several melatonin solutions at 1 °C for 40 days. It was found that the 0.1 and 1 mM melatonin solutions were the most effective treatments for reducing weight loss and maintaining greater firmness. The ascorbic acid content, total phenolic content and antioxidant activity were greater in melatonin-treated plums than the control. The authors suggested that melatonin treatment may be a useful technique to extend the postharvest life of plum while maintaining an acceptable fruit quality



Proposed role(s) of melatonin in fruit ripening and senescence. Melatonin acts by upregulating both ethylene biosynthesis and anthocyanin biosynthesis enzymes, accelerating fruit ripening and also promotes ABA biosynthesis on diverse elements of ethylene signaling and the enhancement of diverse steps of primary and secondary metabolism. The effect of melatonin in senescence is the contrary, delaying it. Melatonin, through the redox network involving ROS and RNS (mainly NO), decreases the ROS level, upregulating diverse antioxidative enzymes and metabolites, which delay senescence. Also, several senescence-related genes are downregulated by melatonin. All this improves fruit quality and extends fruit shelf life

Mechanisms of exogenous melatonin functions in post-harvest fruits and vegetables

Exogenous Melatonin Increases Antioxidant Enzymes For Scavenging ROS

Exogenous Melatonin Induces Non- Enzymatic Antioxidants

Relationship Between Exogenous Melatonin and Hormones in Post-Harvest Stage

Exogenous Melatonin Increases Oxidative Protein Repair-Related Enzymes

Exogenous Melatonin Activates the γ-Aminobutyric Acid (GABA) Shunt Pathway

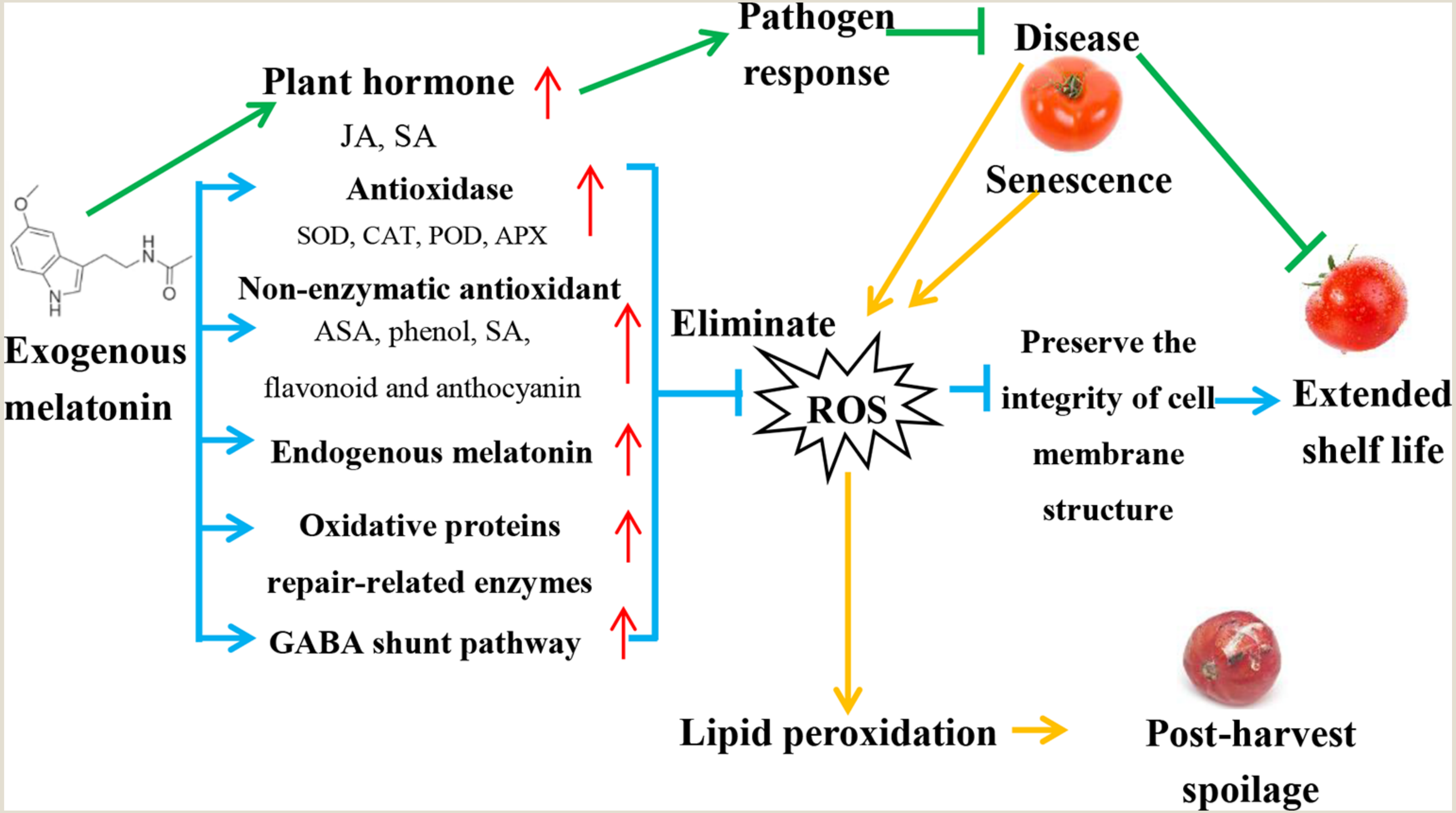
- The senescence of fruits and vegetables is accompanied by the loss of cell membrane integrity and function, which is manifested by an increase in membrane leakage .
- This structural/functional membrane dysfunction is caused by the excessive production of reactive oxygen species (ROS), including O2-, H2O2, hydroxyl radical (OH-), and singlet oxygen (1O2), which are potent compounds destroying biological macromolecules and affecting the metabolism of post-harvest fruits and vegetables.
- During storage, the ROS in fruits increases continuously and induces lipid peroxidation. Lipid peroxidation can catalyze the oxygenation of unsaturated fatty acids through ROS and lipid oxidases (such as LOX) to form volatile substances such as hydrogen peroxide derivatives Subsequently, these substances are decomposed to produce oxidative free radicals, triggering a chain reaction of lipid peroxidation and eventually causing the deterioration of fruits and vegetables.

Exogenous Melatonin Increases Antioxidant Enzymes For Scavenging ROS

Melatonin upregulates the antioxidant enzyme activity of peach fruits and reduces the levels of O2- and H2O2 in different peach varieties, thereby maintaining the metabolic balance of ROS, reducing lipid peroxidation, and delaying senescence.

Moreover, evaluation of oxidase activity, together with antioxidant enzyme activity, after melatonin treatment would provide further insights into the mechanistic role of melatonin as an antioxidant.

Model of exogenous melatonin-mediated post-harvest preservation mechanism in fruits and vegetables.



Exogenous Melatonin Induces Non- Enzymatic Antioxidants

- Melatonin can act as a signaling molecule that upregulates downstream defense genes encoding many non-enzymatic antioxidants.
- Ascorbic acid (ASA) is a typical non-enzymatic antioxidant that can directly scavenge ROS. Exogenous melatonin triggers the ASA-glutathione cycle in post-harvest peaches by upregulating the transcriptional expression of antioxidant-related enzymes, which results in increased ASA level and prolonged shelf-life of post-harvest fruits and vegetables.

Melatonin can increase the activity of glucose-6-phosphate dehydrogenase, shikimate dehydrogenase, and phenylalanine ammonia-lyase that promote the accumulation of total phenols and endogenous SA, which is beneficial to inhibit fungal decay and to prolong the shelf-life of post-harvest peach. Phenolic compounds can protect membrane lipids from peroxidation by preventing the occurrence and propagation of oxidative chain reactions

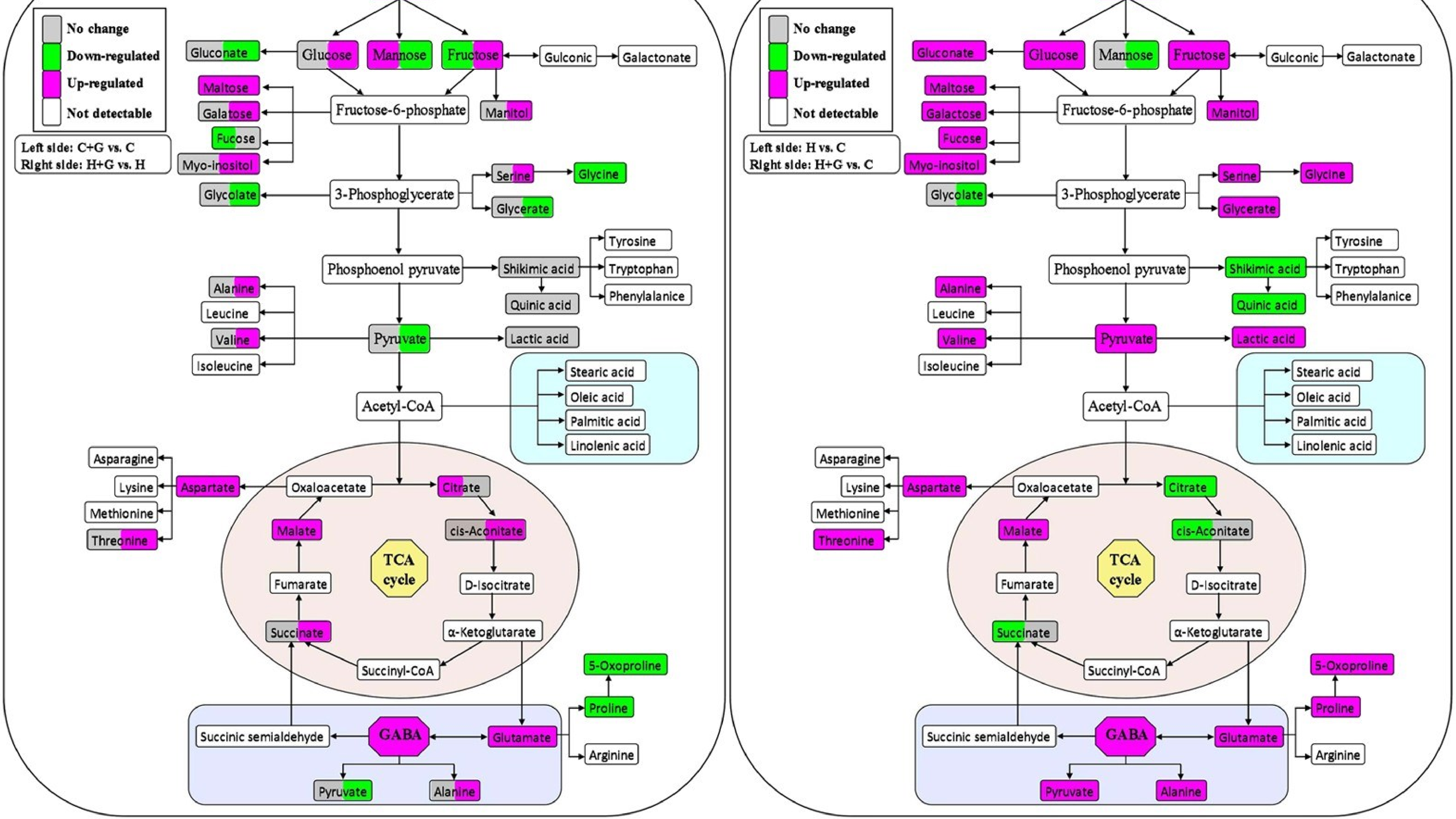
Exogenous Melatonin Increases Oxidative Protein Repair-Related Enzymes

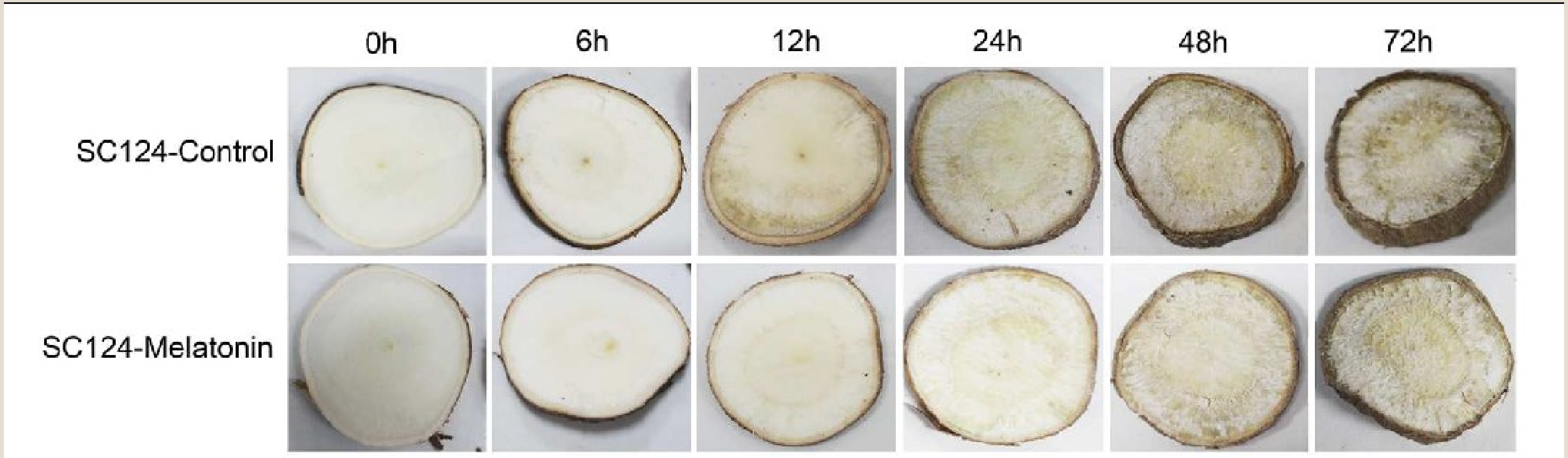
Under environmental stress and senescing process, ROS damages the conformations and functions of proteins through the oxidative modification of amino acid side chains. Methionine and cysteine are sulfur-containing amino acids that are highly susceptible to damage caused by ROS.

Zhang et al. (2018b) found that treatment of 400 μM melatonin markedly enhances the expression of *LcMsrA1*, *LcMsrA2*, *LcMsrB1*, and *LcMsrB2* in lychee fruits during storage and significantly extends the duration of viable protein repair mechanisms and protection from ROS.

Exogenous Melatonin Activates the γ-Aminobutyric Acid (GABA) Shunt Pathway

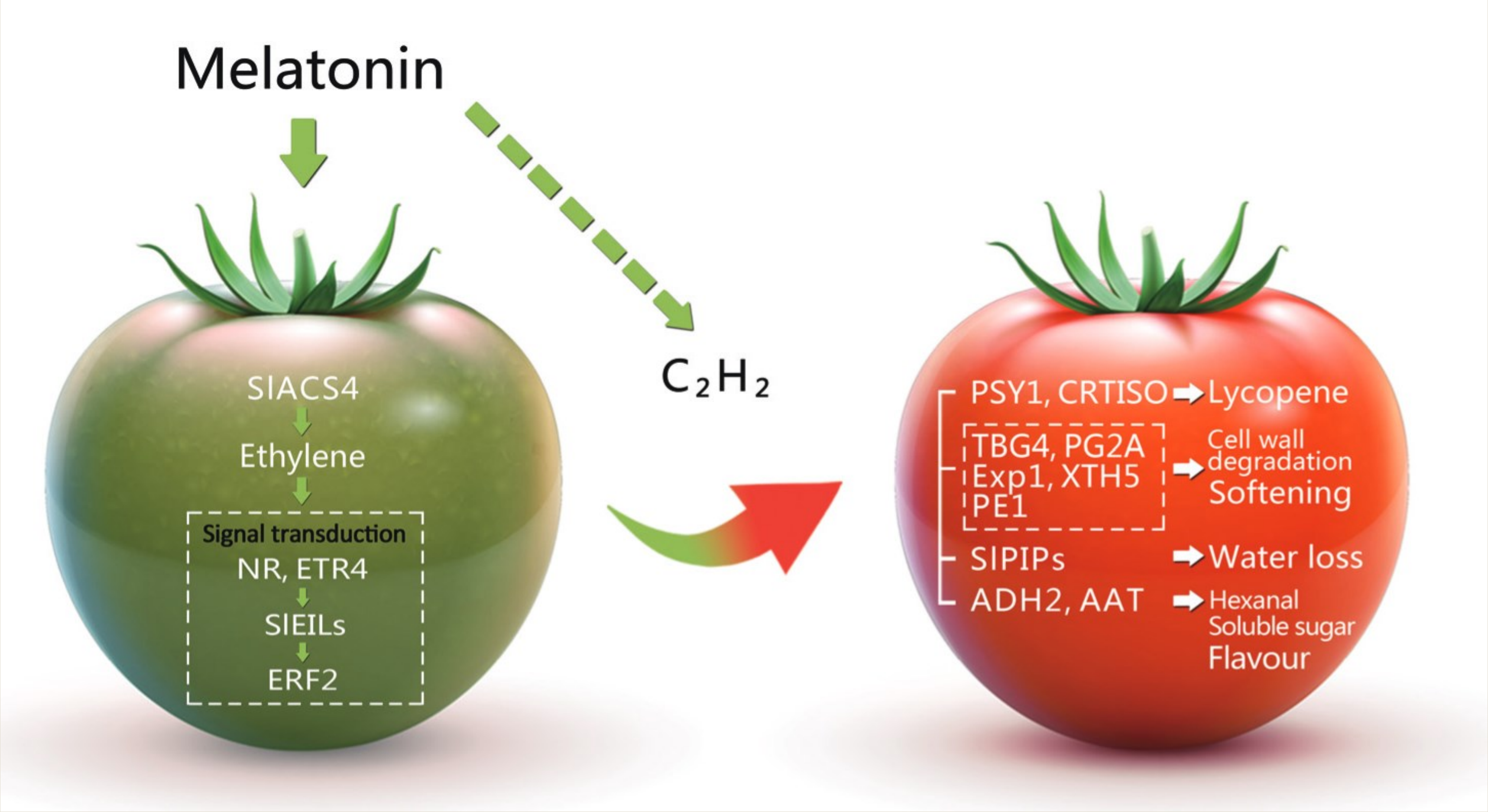
- GABA is a four-carbon non-proteinogenic amino acid widely found in plants and is mainly produced by the GABA shunt of the (TCA) Tricarboxylic Acid cycle. Three enzymes, glutamine decarboxylase, GABA transaminase (GABA-T), and succinic semialdehyde dehydrogenase (SSADH) are involved in this pathway.
- Exogenous melatonin can increase the activity of GABA-T enzyme by providing more NADH and succinic acid for the TCA cycle and mitochondrial electron transport chain. This in turn produces more ATP for fruits and vegetables to remove excess H2O2 and ROS, thus prolonging the shelf-life of post-harvest fruits.
- Aghdam and Fard (2017) has found that exogenous melatonin can improve the GABA shunt pathway, thereby enhancing the inhibition of the post-harvest decay of strawberry fruits.

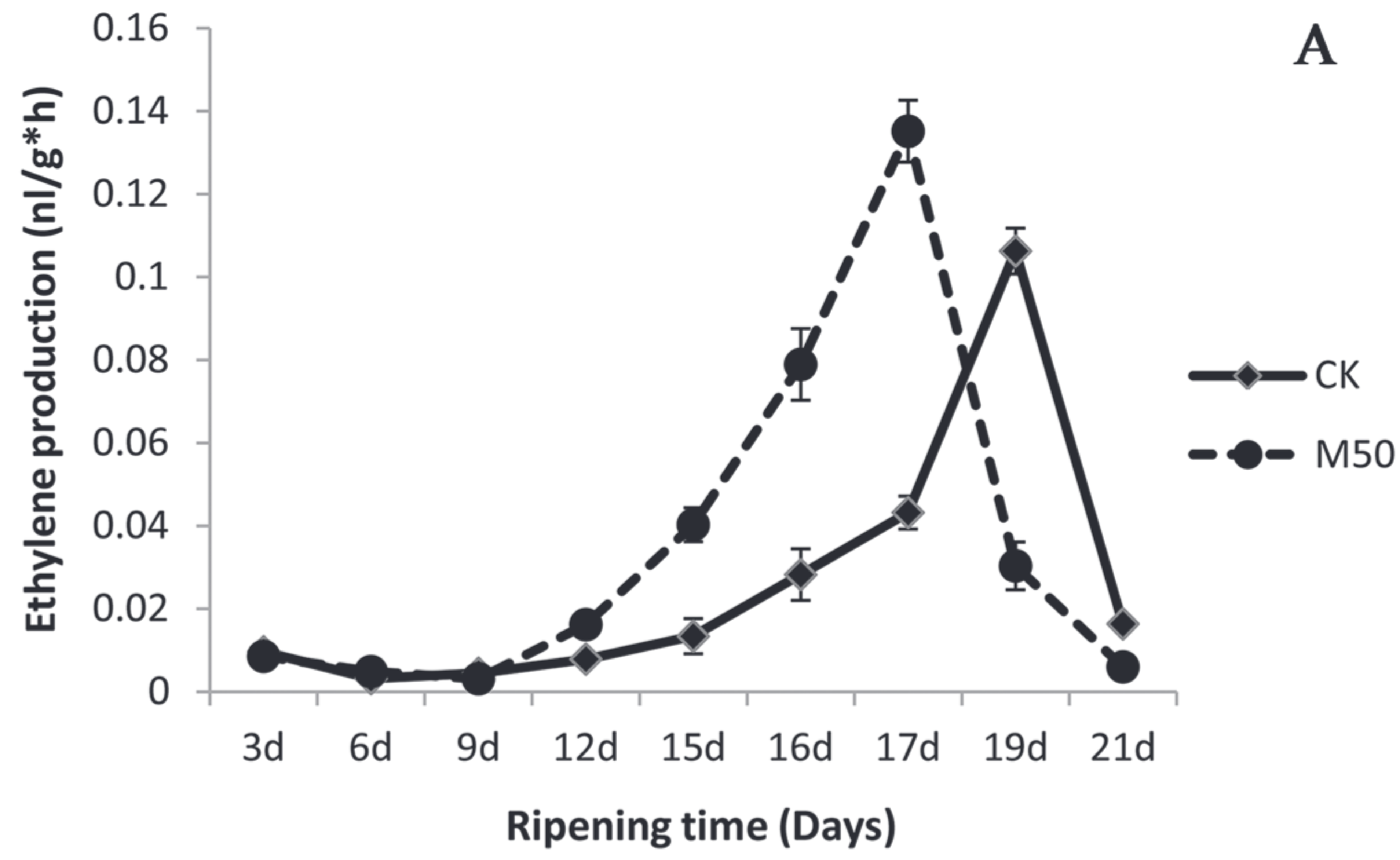

No change
Down-regulated
Up-regulated
Not detectable
Left side: C+G vs. C
Right side: H+G vs. H
Gluconate
Glucose
Mannose
Fructose
Gulconic
Galactonate
Maltose
Galatose
Fucose
Myo-inositol
Fructose-6-phosphate
Manitol
3-Phosphoglycerate
Serine
Glycine
Glycolate
Glycerate
Tyrosine
Tryptophan
Phenylalanice
Phosphoenol pyruvate
Shikimic acid
Quinic acid
Alanine
Leucine
Valine
Isoleucine
Pyruvate
Lactic acid
Acetyl-CoA
Stearic acid
Oleic acid
Palmitic acid
Linolenic acid
Asparagine
Lysine
Methionine
Threonine
Aspartate
Oxaloacetate
Citrate
cis-Aconitate
Malate
TCA cycle
Fumarate
D-Isocitrate
Succinate
α-Ketoglutarate
Succinyl-CoA
5-Oxoproline
Proline
Succinic semialdehyde
GABA
Glutamate
Arginine
Pyruvate
Alanine
No change
Down-regulated
Up-regulated
Not detectable
Left side: H vs. C
Right side: H+G vs. C
Gluconate
Glucose
Mannose
Fructose
Gulconic
Galactonate
Maltose
Galactose
Fucose
Myo-inositol
Fructose-6-phosphate
Manitol
3-Phosphoglycerate
Serine
Glycine
Glycolate
Glycerate
Tyrosine
Tryptophan
Phenylalanice
Phosphoenol pyruvate
Shikimic acid
Quinic acid
Alanine
Leucine
Valine
Isoleucine
Pyruvate
Lactic acid
Acetyl-CoA
Stearic acid
Oleic acid
Palmitic acid
Linolenic acid
Asparagine
Lysine
Methionine
Threonine
Aspartate
Oxaloacetate
Citrate
cis-Aconitate
Malate
TCA cycle
Fumarate
D-Isocitrate
Succinate
α-Ketoglutarate
Succinyl-CoA
5-Oxoproline
Proline
Succinic semialdehyde
GABA
Glutamate
Arginine
Pyruvate
Alanine



Effect of melatonin on PPD of tuberous roots in SC124 variety. After soaking water (control) or 100 μM melatonin (melatonin treatment) for 2 h, cassava tuberous roots were sliced into 5-mm-thick slices

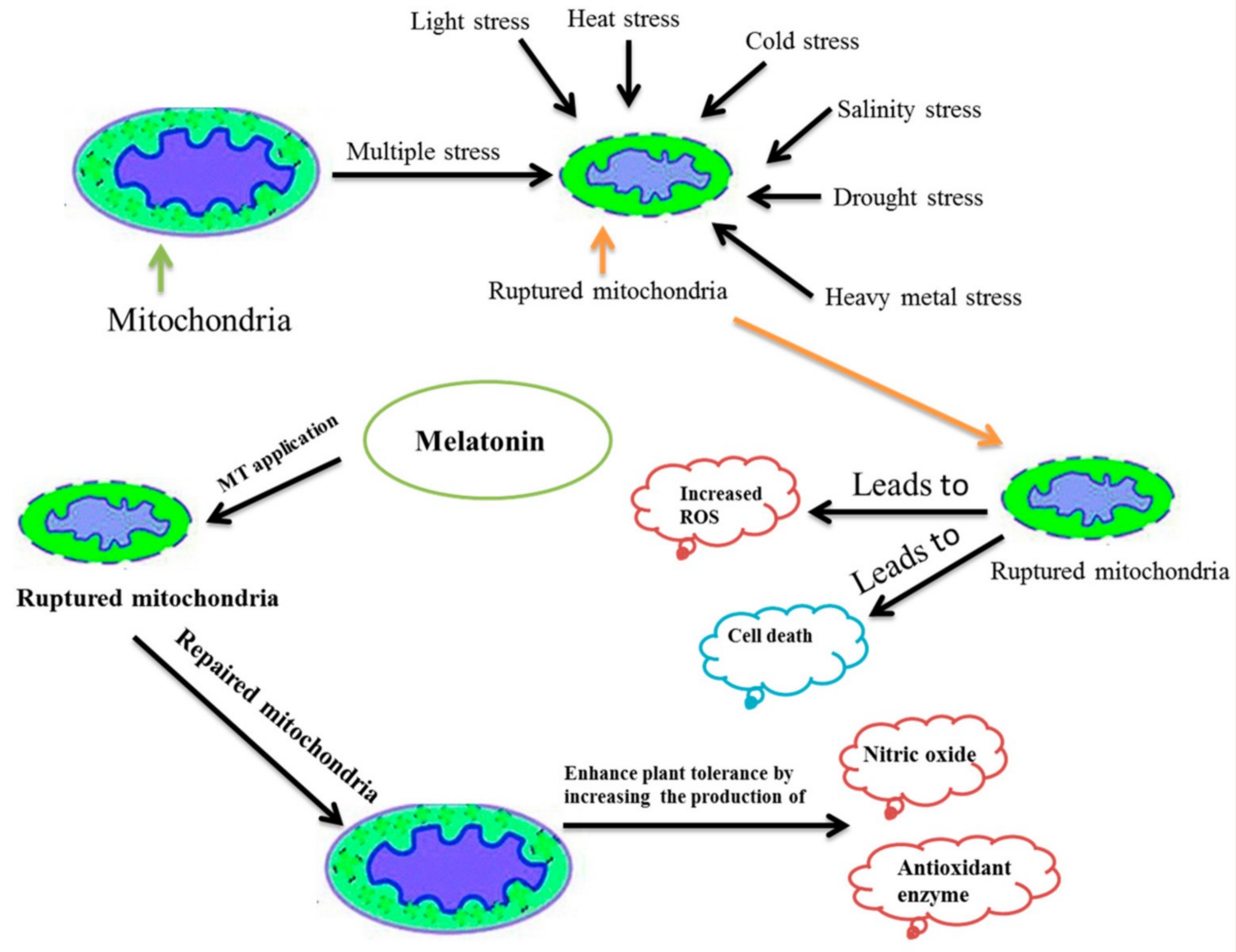
A model of the role of melatonin in postharvest ripening tomato fruits. Melatonin may promote tomato fruit ripening by affecting ethylene production and signalling. Arrows represent positive regulation, the dotted lines represent regulatory steps in which a direct physical link between upstream and downstream components has yet to be demonstrated.

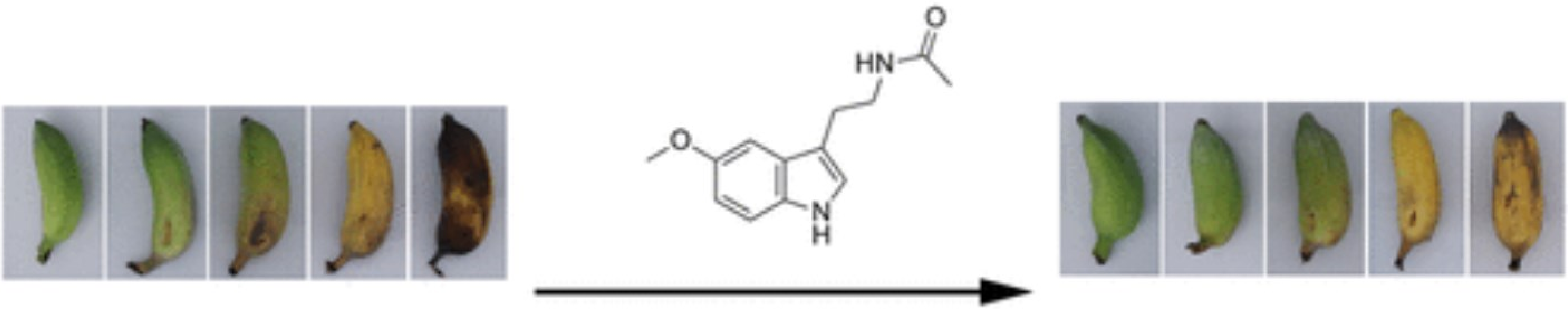



A
Ethylene production (nl/g*h)
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
3d
6d
9d
12d
15d
16d
17d
19d
21d
Ripening time (Days)
CK
M50

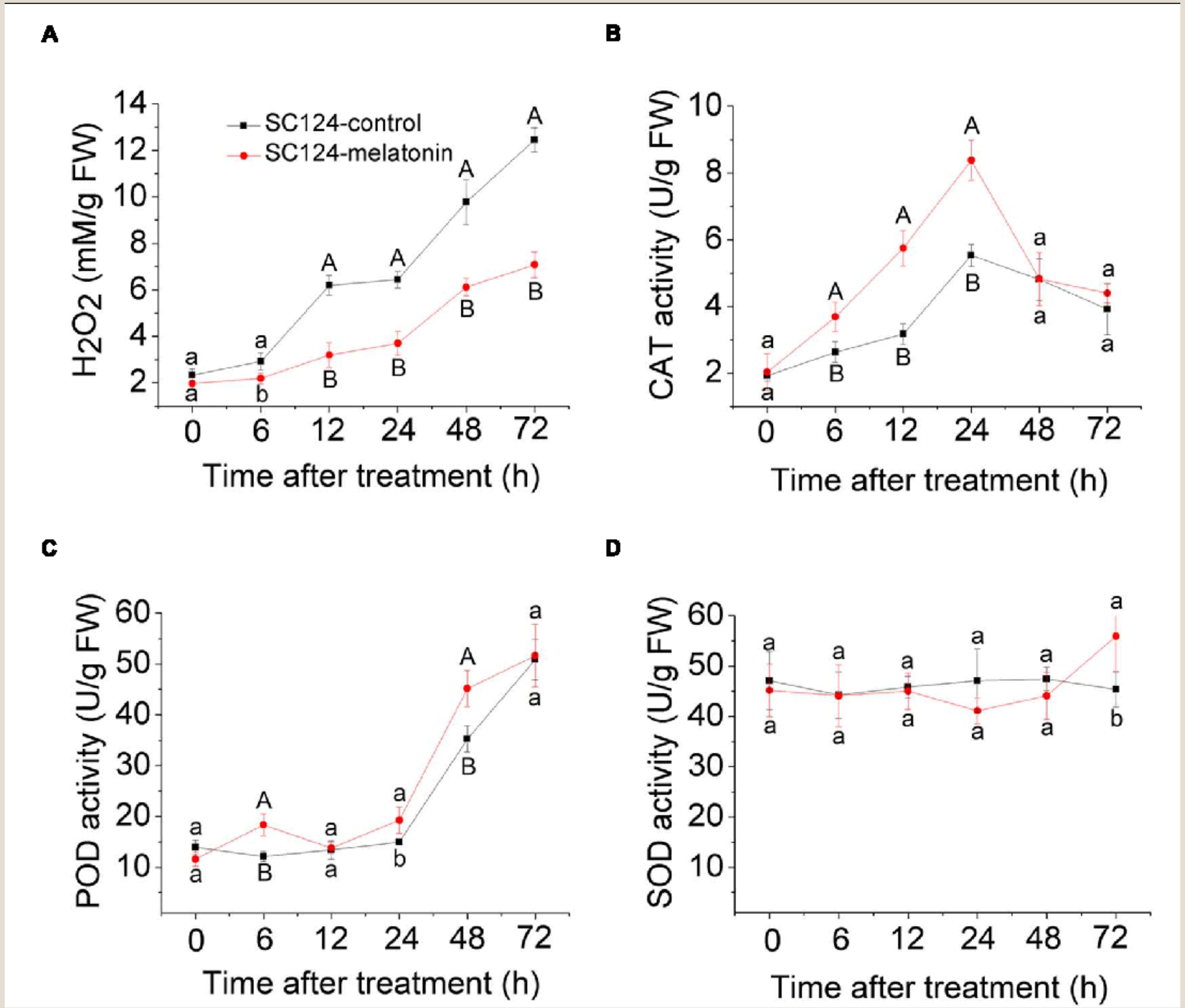
- Melatonin Effect on Postharvest Produce
- The shelf-life and quality of postharvest produce decline due to the deterioration. For this reason, many treatments have been implemented to maintain the quality and shelf life of postharvest fruits and vegetables [69,70,71,72]. Usually, the produce is stored in a cold environment which induces oxidative stress by elevating the production of ROS; this is the main drawback of cold storage [73]. However, treatment with melatonin alleviates the ROS activity and increases the antioxidant enzymes production [70]. In other cases, the application of exogenous melatonin triggered the endogenous melatonin biosynthetic activity via the antagonistic crosstalk with calcium, preventing the product from postharvest deterioration [74]. Additionally, the postharvest quality of horticultural produce is mainly dependent on the preharvest factors as it cannot be increased after harvesting but can only be maintained [75]. In line with that, the tomato seeds fertigated with melatonin had not only increased their yield but also kept the postharvest quality by exhibiting an increase of vitamin C, lycopene and calcium contents. The treated plants also recorded for more soluble solids and P content than that of control [76]. In another study, the exogenous application of melatonin on the clusters of grapes attached to the vine had altered metabolism of polyphenol, carbohydrate biosynthesis and more importantly ethylene signaling in berries of grapes. The restricted ethylene production resulted in better antioxidant activity [74], which is an important factor for maintaining postharvest quality. Moreover, melatonin regulates salicylic acid, jasmonic acid, nitric oxide and ethylene which collectively generate the resistance against diseases in a very familiar action [64]. The cooperative or antagonistic approach of ethylene and jasmonate is mainly dependent on the interaction of their downstream signaling pathway [77]. Jasmonic acid encourages the synthesis of lycopene in tomato independently to ethylene and exogenously applied ethylene is widely used to trigger and initiate ripening in climacteric fruits [78,79]. Correspondingly, ethylene does not only affect the biochemical structure but also increases the respiration rate of fruit and vegetables [80]. Likewise, the exogenously applied melatonin influenced the ethylene biosynthesis pathway and conferred better aroma, color, sugar and overall postharvest quality of tomato [81]. The research provides a good base for utilizing melatonin in keeping the postharvest quality of produces. Both of these hormones regulated by melatonin play an important role in defining the postharvest status of produce by means of their possible involvement in providing resistance against postharvest diseases and deterioration. Still, not a great deal of research material is available on melatonin postharvest application. However, melatonin may be considered as a potential substance to reduce the percentage of postharvest losses and enhance the shelf life of postharvest produce. According to a recent report, the silencing of fruit shelf-life regulator (SIFR) gene has been reported for controlling the postharvest ripeness in tomato and also extended the fruit shelf life by inhibiting the ethylene production [82]. For that reason, it will be interesting to see how exogenous melatonin affects the postharvest maturity by regulating the expression level of SIFR gene. Furthermore, Table 2 represents the reported studies on melatonin application over postharvest products.

Schematic representation of melatonin defense mechanism pathway.





Exogenous melatonin extends shelf life of banana



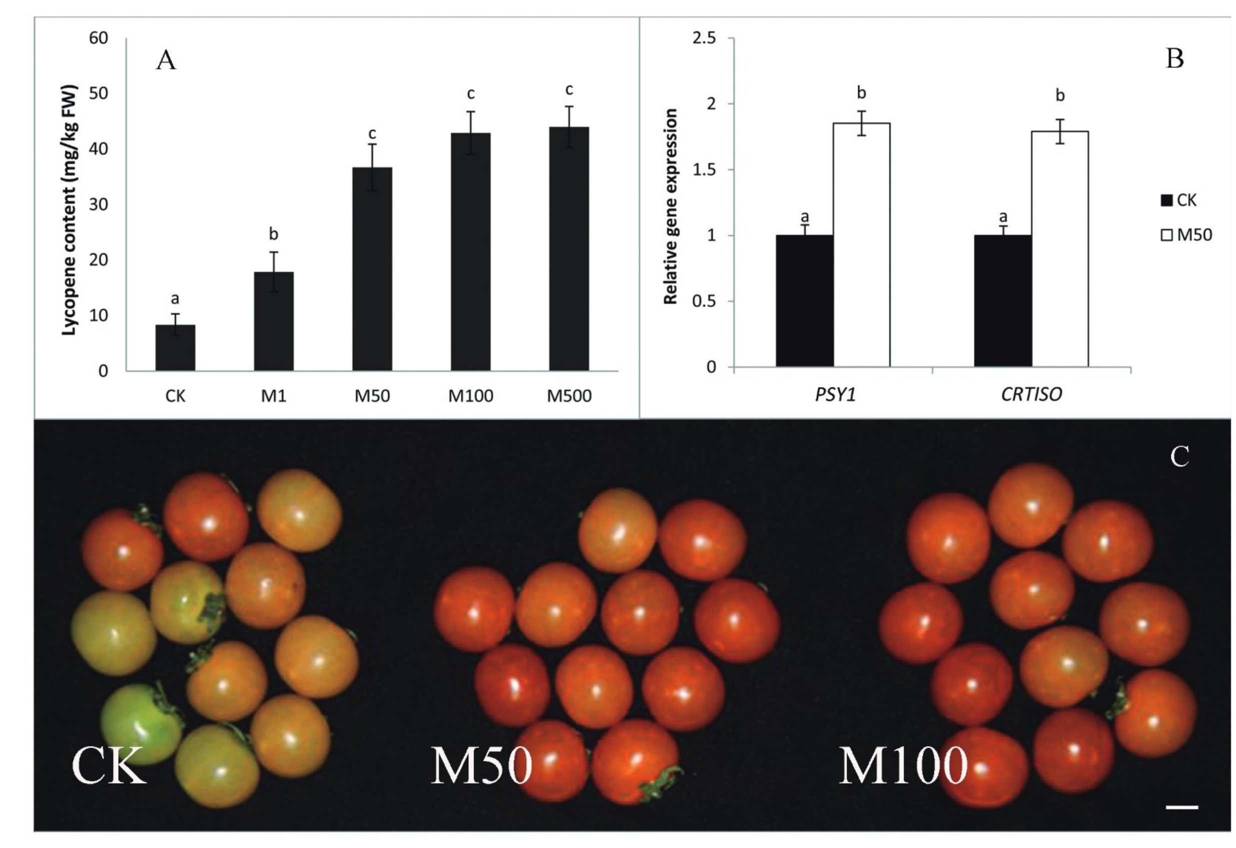
Effect of melatonin on H2O2 accumulation (A) and activities of CAT (B), POD (C), and SOD (D) during the PPD process in SC124 variety. Data are means ± SE calculated from four biological replicates

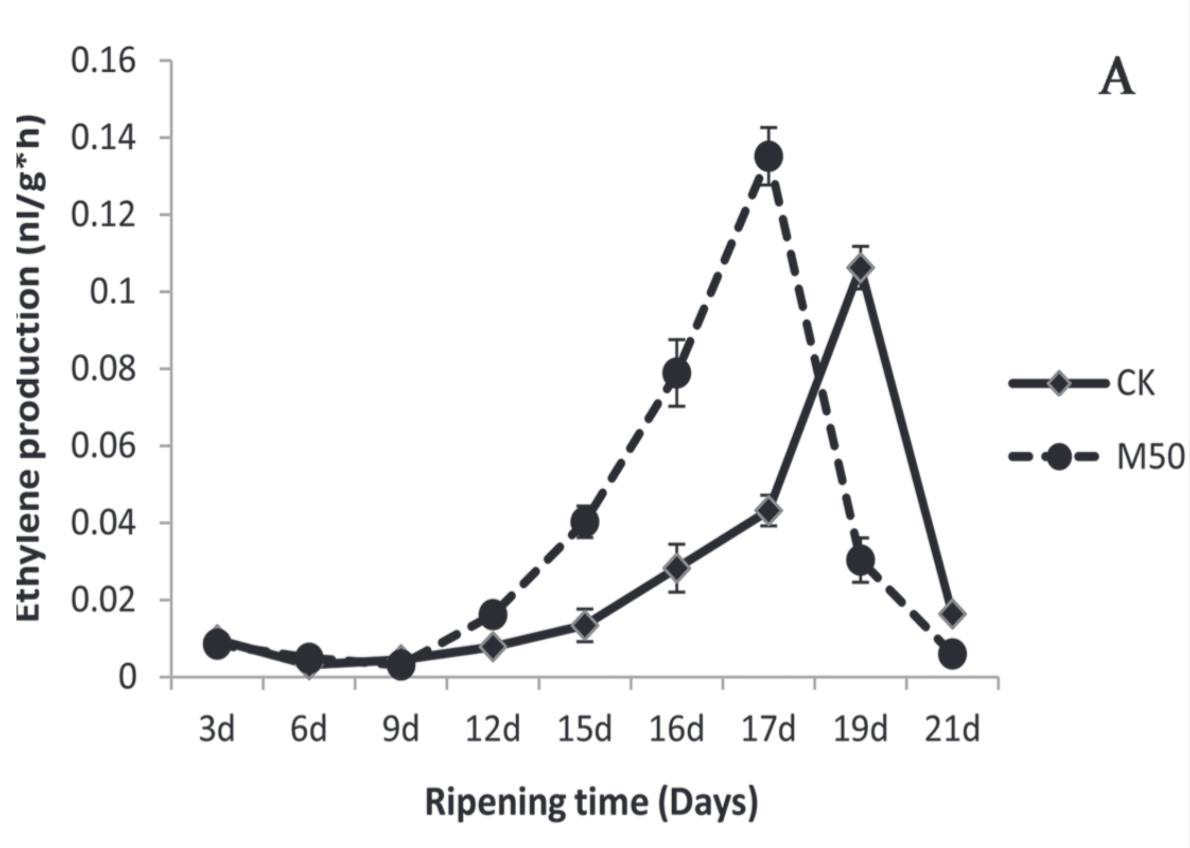
Relationship Between Exogenous Melatonin and Hormones in Post-Harvest Stage

- Exogenous melatonin could reduce the production of ethylene in four varieties of bananas during post-harvest ripening (Hu et al., 2017). Melatonin can effectively inhibit the expression of genes related to ethylene biosynthesis such as *Musa* 1-aminocyclopropane-1-carboxylate oxidase 1 and *Musa* 1-aminocyclopropane-1-carboxylate synthase 1, which results in delayed fruit senescence.

- By contrast, melatonin promotes the formation of ethylene by up-regulating the expression of 1-aminocyclopropane-1- carboxylic acid synthase, thereby accelerating the ripening of tomatoes. Exogenous melatonin treatment slightly promotes ethylene synthesis and the subsequent timing of the climacteric peak

Notably, melatonin is positively correlated with fruit ripening but is negatively correlated with climacteric fruit senescence. These findings suggest that melatonin plays a unique role in maturation and senescence and balances the production of ethylene. Moreover, the effects of melatonin on the ripening and preservation of post-harvest fruits and vegetables also depend on their maturity and starch content.





Melatonin has antioxidant, immune modulatory, and anti-inflammatory effects, suggesting that it has an ability for inhibiting bacterial, viral, and parasitic infections.

Melatonin increases the expression of pathogenesis-, nitric oxide (NO)-, and salicylic acid (SA)-related genes, and leads to an increased resistance to the pathogen, indicating that melatonin may be a signaling molecule in pathogen response (Arnao and Hernández-Ruiz, 2018).

MLT can alter the content of NO in fruit by modulating the expression of NO synthase Melatonin synthesis gene.

Melatonin acts upstream of the pathogen resistance signaling pathway, induces the biosynthesis of NO, ethylene, JA, and SA, then elicits disease resistance .

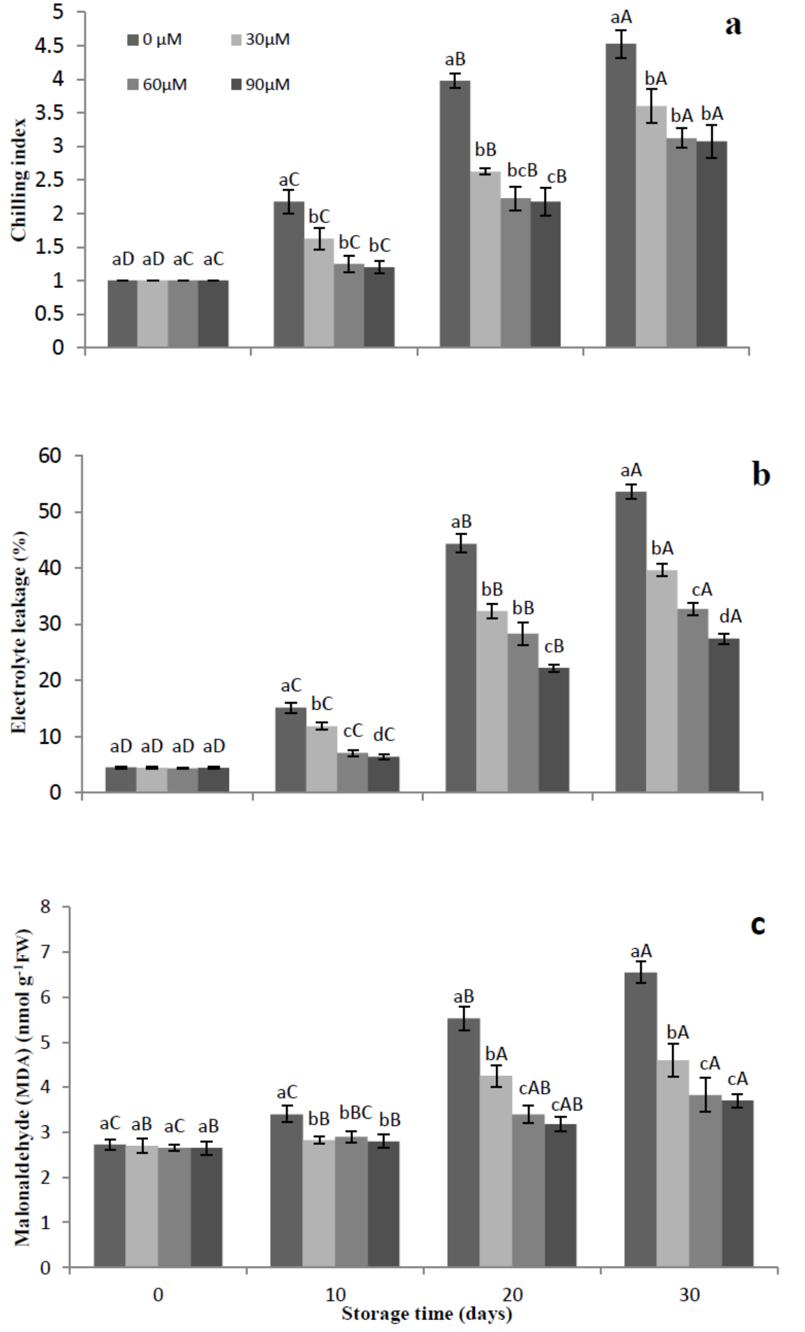
It appears that melatonin is involved in innate plant immunity against fungal and bacterial pathogens via an SA/JA/ethylene and NO-dependent pathway.

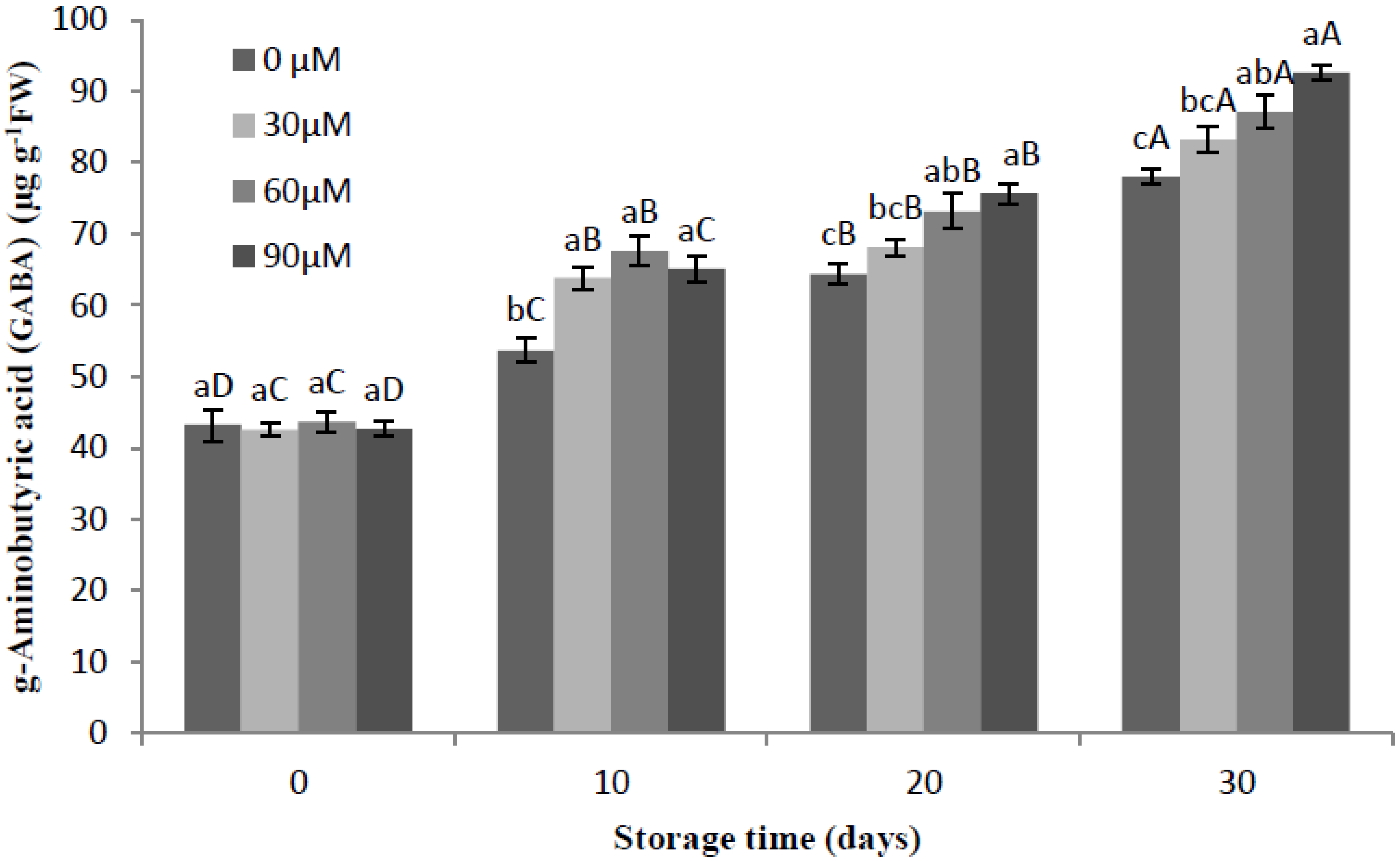
Although most of these findings in plants are not directly related to post-harvest fruits and vegetables, they suggest that crosstalk between melatonin, JA, SA, and NO is deeply related to pathogen responses during the post-harvest fruits and vegetables deterioration.

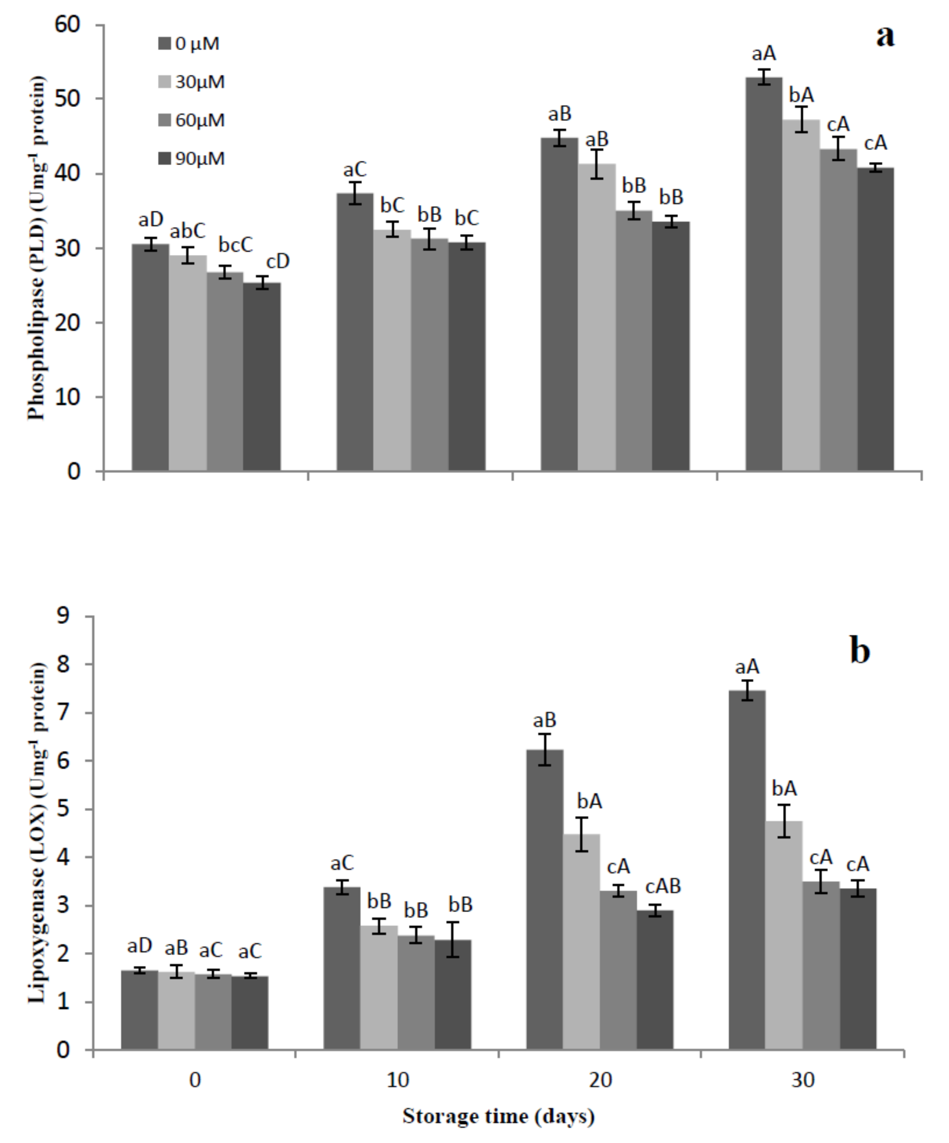
Indole acetic acid (IAA) is a plant growth hormone that can promote the expansion and vacuolation of plant cells. Biosynthesis of melatonin and IAA starts from tryptophan, indicating that melatonin and IAA compete for the same starting precursor.

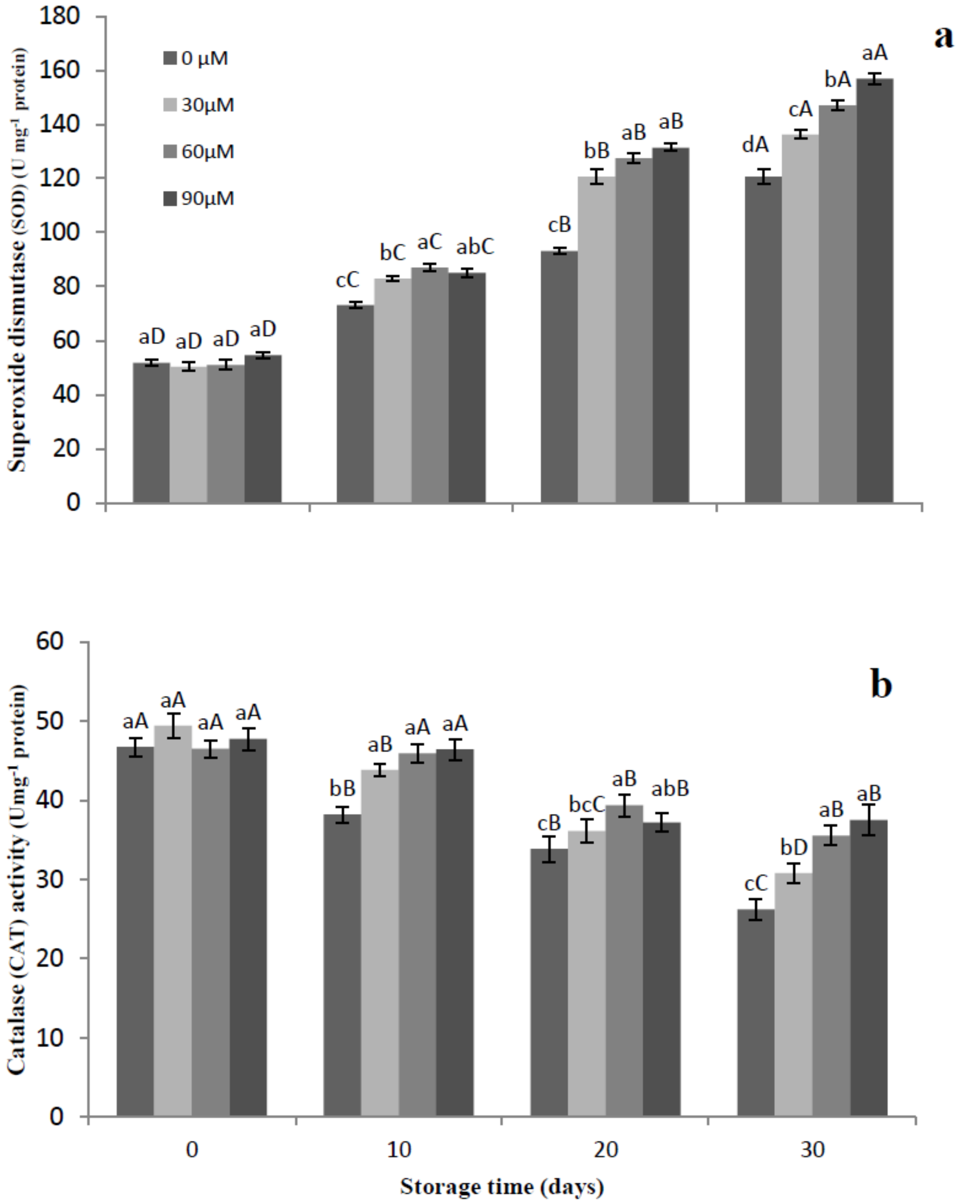
Experiments have shown that IAA accumulates at the third growth stage in cherries (35 days after flowering), whereas melatonin level declines at the same growth stage.

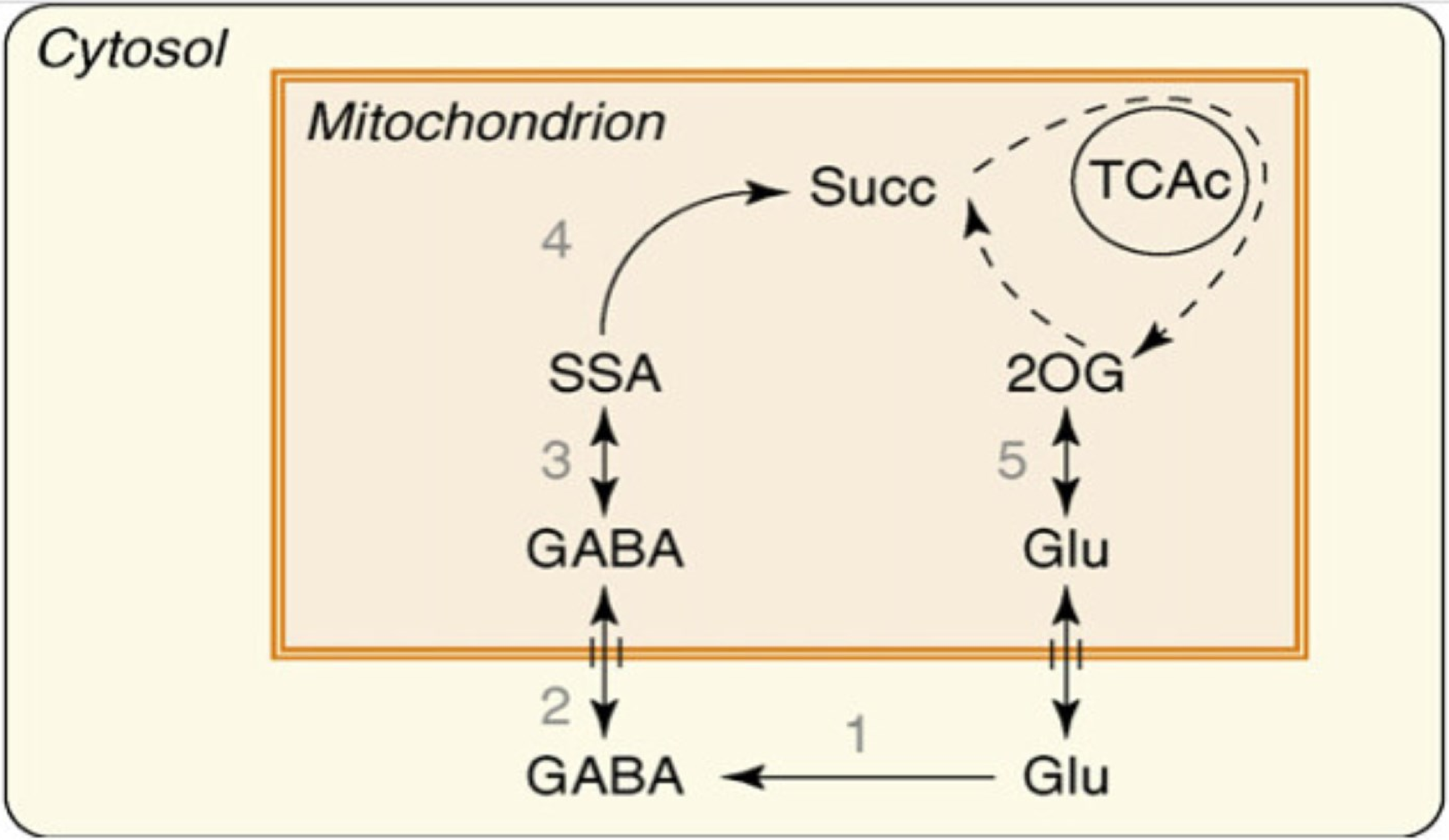
Chen found that exogenous melatonin treatment increases the level of endogenous free IAA and effectively promotes the development of seedling roots, indicating that melatonin and IAA have synergistic effects.

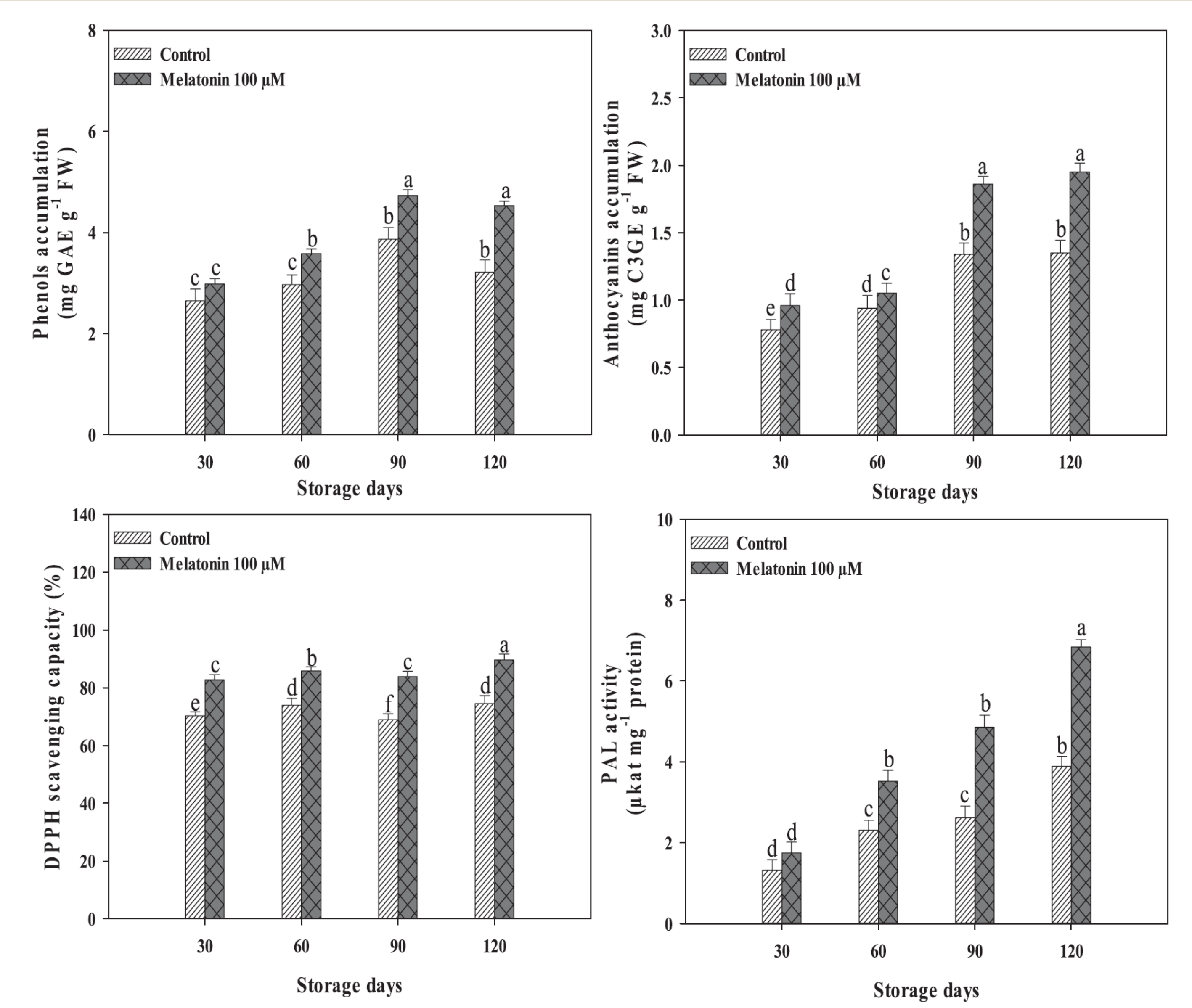

a
0 µM
30µM
60µM
90µM
Chilling index
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5
aD aD aC aC
aC bC bC bC
aB bB bcB cB
aA bA bA bA
b
Electrolyte leakage (%)
0
10
20
30
40
50
60
aD aD aD aD
aC bC cC dC
aB bB bB cB
aA bA cA dA
c
Malonaldehyde (MDA) (nmol g-1FW)
0
1
2
3
4
5
6
7
8
aC aB aC aB
aC bB bBC bB
aB bA cAB cAB
aA bA cA cA
0
10
20
30
Storage time (days)

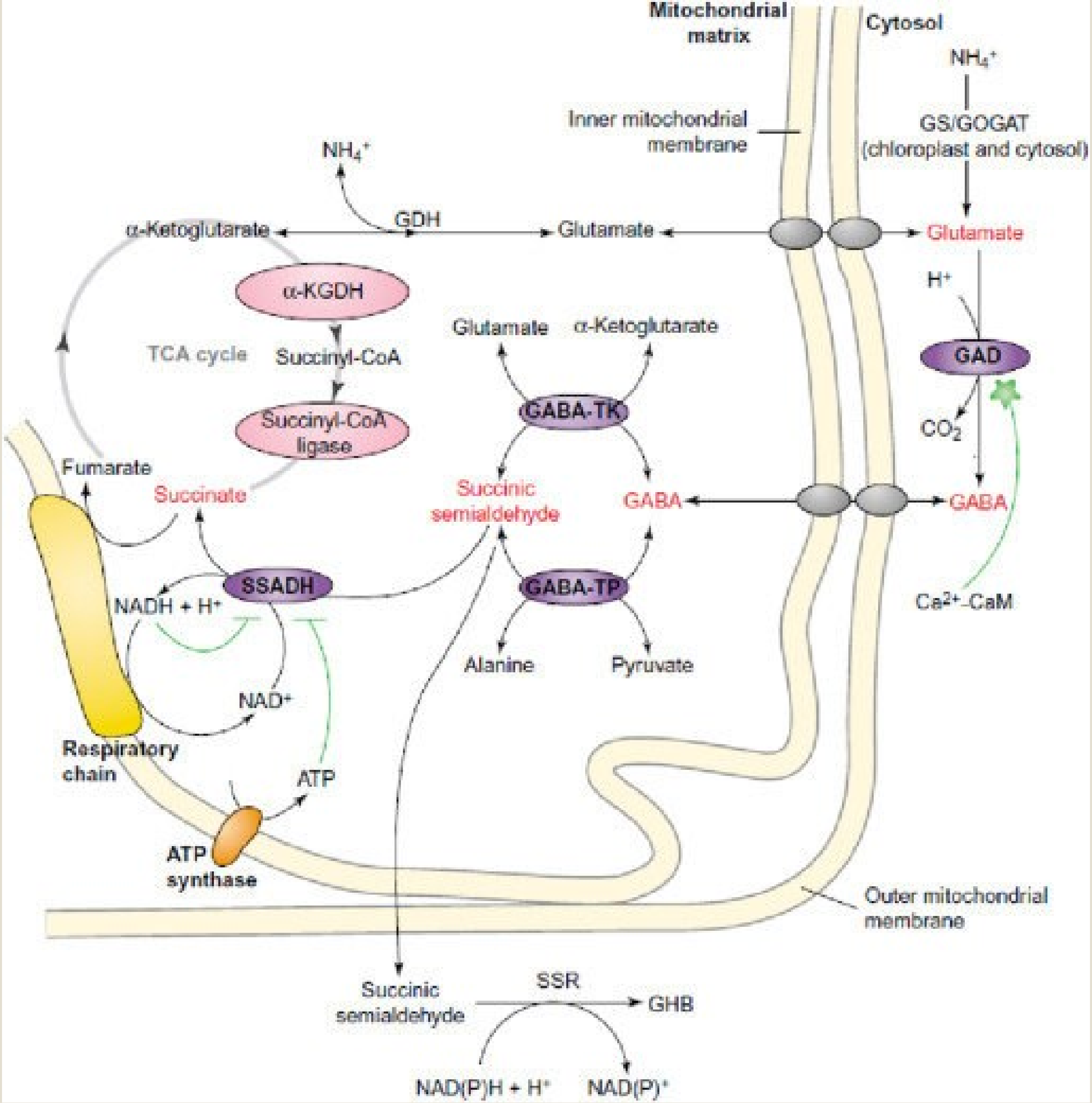

g-Aminobutyric acid (GABA) (μg g-1FW)
100
90
80
70
60
50
40
30
20
10
0
0 μM
30μM
60μM
90μM
aD
aC
aC
aD
bC
aB
aB
aC
cB
bcB
abB
aB
cA
bcA
abA
aA
0
10
20
30
Storage time (days)


a
0 µM
30µM
60µM
90µM
Phospholipase (PLD) (Umg-1 protein)
60
50
40
30
20
10
0
aD
abC
bcC
cD
aC
bC
bB
bC
aB
aB
bB
bB
aA
bA
cA
cA
b
Lipoxygenase (LOX) (Umg-1 protein)
9
8
7
6
5
4
3
2
1
0
aD
aB
aC
aC
aC
bB
bB
bB
aB
bA
cA
cAB
aA
bA
cA
cA
0
10
20
30
Storage time (days)


a
Superoxide dismutase (SOD) (U mg^{-1} protein)
180
160
140
120
100
80
60
40
20
0
0 µM
30µM
60µM
90µM
aD aD aD aD
cC bC aC abC
cB bB aB aB
dA cA bA aA
b
Catalase (CAT) activity (Umg^{-1} protein)
60
50
40
30
20
10
0
aA aA aA aA
bB aB aA aA
cB bcC aB abB
cC bD aB aB
0
10
20
30
Storage time (days)


Cytosol
Mitochondrion
Succ
TCAc
4
SSA
2OG
3
5
GABA
Glu
2
1
GABA
Glu


Control
Melatonin 100 µM
Phenols accumulation (mg GAE g^{-1} FW)
0
2
4
6
8
c
c
c
b
b
a
b
a
30
60
90
120
Storage days
Anthocyanins accumulation (mg C3GE g^{-1} FW)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
e
d
d
c
b
a
b
a
30
60
90
120
Storage days
DPPH scavenging capacity (%)
0
20
40
60
80
100
120
140
e
c
d
b
f
c
d
a
30
60
90
120
Storage days
PAL activity (µkat mg^{-1} protein)
0
2
4
6
8
10
d
d
c
b
c
b
b
a
30
60
90
120
Storage days


Mitochondrial matrix
Cytosol
NH4+
GS/GOGAT (chloroplast and cytosol)
Inner mitochondrial membrane
NH4+
GDH
α-Ketoglutarate
Glutamate
Glutamate
α-KGDH
H+
Glutamate
α-Ketoglutarate
TCA cycle
Succinyl-CoA
GAD
GABA-TK
Succinyl-CoA ligase
CO2
Fumarate
Succinate
Succinic semialdehyde
GABA
GABA
SSADH
GABA-TP
Ca2+-CaM
NADH + H+
NAD+
Alanine
Pyruvate
Respiratory chain
ATP
ATP synthase
Outer mitochondrial membrane
Succinic semialdehyde
SSR
GHB
NAD(P)H + H+
NAD(P)+

THE END