



Review

Ensuring sufficient intracellular ATP supplying and friendly extracellular ATP signaling attenuates stresses, delays senescence and maintains quality in horticultural crops during postharvest life



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ABSTRACT

Background: As universal energy currency, intracellular ATP (iATP) shortages in horticultural crops during postharvest stresses and senescence. In addition to function as intracellular energy currency, ATP serves as friendly extracellular signaling molecule (eATP).

Scope and approach: Postharvest treatments attenuate stresses, delay senescence and maintain quality in horticultural crops by ensuring sufficient iATP supplying, which was accompanied with lower phospholipase D (PLD) and lipoxygenase (LOX) enzymes activity concomitant with higher antioxidant system activity which along with higher heat shock proteins (HSPs) accumulation resulting in lower reactive oxygen species (ROS) accumulation leading to higher membrane unsaturated/saturated fatty acids (unSFA/SFA), higher shikimate and phenylpropanoid pathways activity revealing by higher phenylalanine ammonia lyase (PAL) enzyme activity leading to higher phenols accumulation, higher endogenous proline and glycine betaine accumulation, higher endogenous polyamines accumulation, and higher pathogenesis (PRs) proteins accumulation, which are crucial for membrane fluidity and integrity maintaining and cell wall fortification. In addition to intracellular energy currency, friendly eATP signaling is crucial for promoting iATP biosynthesis machinery activity and reinforcing defense response by triggering jasmonic and salicylic acids signaling pathways. Also, friendly eATP signaling not only is crucial for regulating stomatal closure which is pivotal for attenuating stresses and delaying senescence in horticultural crops but also is crucial for postharvest biofactories representing high phenols accumulating fresh horticultural crops in response to abiotic stresses which are beneficial for human health.

Key findings and conclusions: Ensuring sufficient iATP supplying and friendly eATP signaling would be crucial for attenuating stresses, delaying senescence and maintaining quality in horticultural crops during postharvest life.

1. Introduction

Fresh horticultural crops as perishable commodities are prone to postharvest quality and quantity economic losses due to biotic and abiotic stresses such as chilling injury and fungal decay (Aghdam & Bodbodak, 2013; Aghdam & Fard, 2017; Cao, Cai, Yang, Joyce, & Zheng, 2014a; Cao, Yang, Cai, & Zheng, 2014b; Chen et al., 2014; Lin et al., 2017a; Zhang et al., 2017a). Intracellular ATP (iATP) status representing by adenylate energy charge (AEC; [ATP + 0.5 ADP]/[ATP + ADP + AMP]) shortages in response to postharvest stresses and senescence (Geigenberger, Riewe, & Fernie, 2010; Pan, Yuan, Zhang, & Zhang, 2017). Ensuring sufficient iATP supplying results from

regulating of iATP biosynthesis [respiratory pathways and γ -aminobutyric acid (GABA) shunt], dissipating [alternative oxidase (AOX) and mitochondrial uncoupling proteins (UCPs)], transporting [ADP/ATP carrier (AAC)] and signaling [sucrose nonfermenting (SNF)-related kinase (SnRKs)] (Wang et al., 2013).

The mitochondrial electron transport system (ETS) catalyzes electrons transporting from nicotinamide adenine dinucleotide (NADH) and flavin adenine dinucleotide (FADH) to O₂. NADH dehydrogenase (complex I), succinate dehydrogenase (SDH; complex II), cytochrome b/c₁ oxidoreductases (COD; complex III), cytochrome c oxidase (CCO; complex IV) and F₀F₁ ATP synthase (complex V) are responsible for transferring 4 electrons to O₂ for reducing O₂ to H₂O. Embden-

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Meyerhof-Parnas (EMP) or glycolysis and oxidative pentose phosphate (OPPP) pathways and tricarboxylic acid cycle (TCA) cycle are responsible for NADH and FADH supplying. The electron transporting by complexes I, III and IV is associated with H^+ pumping leading to generating electrochemical proton potential (proton motive force; PMF) which is couple with ATP biosynthesis by F_0F_1 ATP synthase during oxidative phosphorylation. In addition to ATP biosynthesis, complexes I and III are prevailing reactive oxygen species (ROS) production sites due to electron leakage during stresses and senescence (Li, Yin, Song, & Zheng, 2016c; Lin et al., 2016). Also, ensuring sufficient iATP supplying which is crucial for attenuating stresses, delaying senescence and maintaining quality in horticultural crops during postharvest life results from functional H^+ -ATPase, Ca^{2+} -ATPase and Mg^{2+} -ATPase enzymes activity (He et al., 2017; Lin et al., 2017b; Zhang et al., 2017b). H^+ -ATPase is responsible for ATP-hydrolyzing for generation of electrochemical proton potential (PMF) for secondary active transporting, in addition to energy release. Also, H^+ -ATPase is crucial for removing H^+ from the cytosol which is pivotal for preventing cytosol acidification, via cytosolic pH regulation (Wang et al., 2015a, 2015c). Ca^{2+} -ATPase and Mg^{2+} -ATPase are Ca^{2+} and Mg^{2+} transporters, energized by ATP hydrolysis, which is crucial for maintaining cellular Ca^{2+} and Mg^{2+} homeostasis. Ca^{2+} -ATPase and Mg^{2+} -ATPase are responsible for removing Ca^{2+} and Mg^{2+} from the cytoplasm to apoplast or endomembrane organelles such as mitochondria and vacuole. Higher cytoplasmic Ca^{2+} and Mg^{2+} through disruption of ionic homeostasis result in decreasing vacuole and mitochondria integrity, which lead to insufficient iATP supplying (Lin et al., 2017c).

Ensuring sufficient iATP supplying could be a promising strategy for attenuating stresses and delaying senescence in horticultural crops during postharvest life, which may result in extending postharvest storage life with preserved quality (Fig. 1). Also, ensuring sufficient iATP supplying is crucial for postharvest biofactories representing high phenols accumulating fresh fruits and vegetables in response to abiotic stresses which are beneficial for human health (Fig. 2; Han, Jin, Li, Wang, & Zheng, 2017; Jacobo-Velázquez, Martínez-Hernández, Rodríguez, Cao, & Cisneros-Zevallos, 2011). The results reported by researchers regarding the attenuating stresses, delaying senescence and maintaining quality of horticultural crops by ensuring sufficient iATP supplying in response to postharvest treatments during postharvest life have been summarized in Table 1.

In addition to the function as intracellular energy currency, ATP serves as an extracellular signaling molecule (eATP). At cellular level, ATP release from cytoplasm (iATP) to apoplast (eATP) in response to biotic and abiotic stresses (Choi et al., 2014). Since eATP as a strongly charged molecule is unable for diffusing independently across the plasma membrane for entering to the cytoplasm, having an eATP receptor at cell membrane is indispensable. Chivasa, Tomé, Hamilton, and Slabas (2010) suggested that the unfriendly eATP results in disrupting intracellular mitochondrial and chloroplastic ATP biosynthesis machinery activity and eATP exert as a molecular switch for controlling iATP biosynthesis machinery activity and stresses response pathways operation (Chivasa & Slabas, 2012). According to Chivasa and Slabas (2012), perception of friendly eATP at plasma membrane by DORN1 receptor (L-type lectin receptor kinases, LecRK) via extracellular lectin domain activates intracellular serine threonine kinase domain leading to higher intracellular mitochondrial and chloroplastic ATP biosynthesis activity, but under unfriendly eATP, lower intracellular mitochondrial and chloroplastic ATP biosynthesis machinery activity was concurrent with higher stress response genes expression and PCD (Chivasa & Slabas, 2012). Chivasa et al. (2010) reported that the promoting hypersensitive cell death in Arabidopsis was accompanied with unfriendly eATP which by decreasing mitochondrial ATP biosynthesis protein accumulation resulting in lower iATP production leading to lower ATP releasing from cytoplasm to apoplast, decreasing eATP. Unfriendly eATP is responsible for decreasing iATP biosynthesis machinery activity concurrent with increasing stress response machinery

activity. In addition to lower iATP biosynthesis machinery activity, unfriendly eATP in Arabidopsis under hypersensitive cell death was accompanied with lower antioxidant system proteins accumulation resulting in higher ROS accumulation, lower molecular chaperoning HSPs accumulation, and lower EMP pathway glyceraldehyde-3-phosphate dehydrogenase (GA3PDH) and phosphoglycerate kinase (PGK) proteins accumulation, demonstrating that iATP biosynthesis machinery, antioxidant system activity, HSPs accumulation and EMP pathway activity is under regulation by friendly eATP signaling which is crucial for maintaining plants healthy status (Chivasa et al., 2010). Also, eATP signaling is crucial for regulating stomatal closure in horticultural crops pivotal for photosynthesis, water homeostasis, and pathogen resistance. According to Chen et al. (2018), eATP is crucial for stomatal closure in response to biotic and abiotic stresses. Under biotic and abiotic stresses, the perception of friendly eATP at the plasma membrane by DORN1 receptor leading to phosphorylation of NADPH oxidase which is responsible for H_2O_2 accumulation. H_2O_2 accumulation is crucial for attenuating stresses, delaying senescence and maintaining quality of horticultural crops by triggering stomatal closure (Chen et al., 2018). During postharvest life, functional stomata are crucial for attenuating stresses, delaying senescence and maintaining quality of horticultural crops. Stomata are crucial for uptake of CO_2 , which is pivotal for photosynthesis. Also, stomata are crucial for releasing water vapor which is crucial for water homeostasis. In addition to optimizing photosynthesis along with preventing water loss, stomata serve as entry point for pathogens (Fig. 3; Chen et al., 2018). Activation of friendly eATP signaling in horticultural crops during postharvest life by exogenous ATP treatment is beneficial for attenuating stresses, delaying senescence and maintaining quality. Beneficial impacts of exogenous ATP treatment in horticultural crops may result from friendly eATP signaling via perception at the plasma membrane by LecRKs (Table 2).

2. Ensuring sufficient iATP supplying and friendly eATP signaling attenuates postharvest chilling stress

Chilling stress directly promotes membrane phase transition from a fluid liquid-crystalline to a rigid solid-gel representing higher electrolyte leakage which interrupts iATP supplying enzymes activity resulting in iATP shortages. Insufficient iATP supplying is accompanied by higher phospholipase D (PLD) and lipoxygenase (LOX) enzymes activity along with higher ROS accumulation. Higher PLD and LOX enzymes activity result from higher cytosolic Ca^{2+} due to disrupting Ca^{2+} -ATPase activity. Also, higher ROS accumulation result from interrupting NADH dehydrogenase (complex I) and cytochrome b/c₁ oxidoreductases (complex III) activity. Higher PLD and LOX enzymes activity concomitant with higher ROS accumulation leading to membrane integrity losing representing by higher malondialdehyde (MDA) accumulation due to triggering membrane unsaturated fatty acids (unSFA) peroxidation (Aghdam & Bodbodak, 2013; Pan et al., 2017; Yi et al., 2010; Zhou et al., 2014a, 2014b). Electrolyte leakage and MDA accumulation have been considered as reliable markers of membrane semi-permeability losses and membrane unSFA peroxidation, respectively, which are widely employed for evaluation of membrane integrity (Aghdam & Bodbodak, 2013). Enhancing of postharvest chilling tolerance in cucumber fruit treated with 6-benzyl aminopurine (6-BA; Chen & Yang, 2013), peach fruit treated with methyl jasmonate (MeJA; Jin et al., 2013), glycine betaine (GB; Shan et al., 2016), hypobaric (Wang et al., 2015a), oxalic acid (OA; Jin, Zhu, Wang, Shan, & Zheng, 2014) and GABA (Yang, Cao, Yang, Cai, & Zheng, 2011), pear fruit treated with 1-methylcyclopropan (1-MCP; Cheng, Wei, Zhou, Tan, & Ji, 2015), low temperature conditioning (Wang et al., 2017) and intermittent warming (Wang et al., 2018b), banana fruit treated with nitric oxide (NO; Wang, Luo, Khan, Mao, & Ying, 2015a) and hydrogen sulfide (H_2S ; Li, Limwachiranon, Li, Du, & Luo, 2016a), loquat fruit treated with low temperature conditioning (Jin et al., 2015) and phytosulfokine peptide

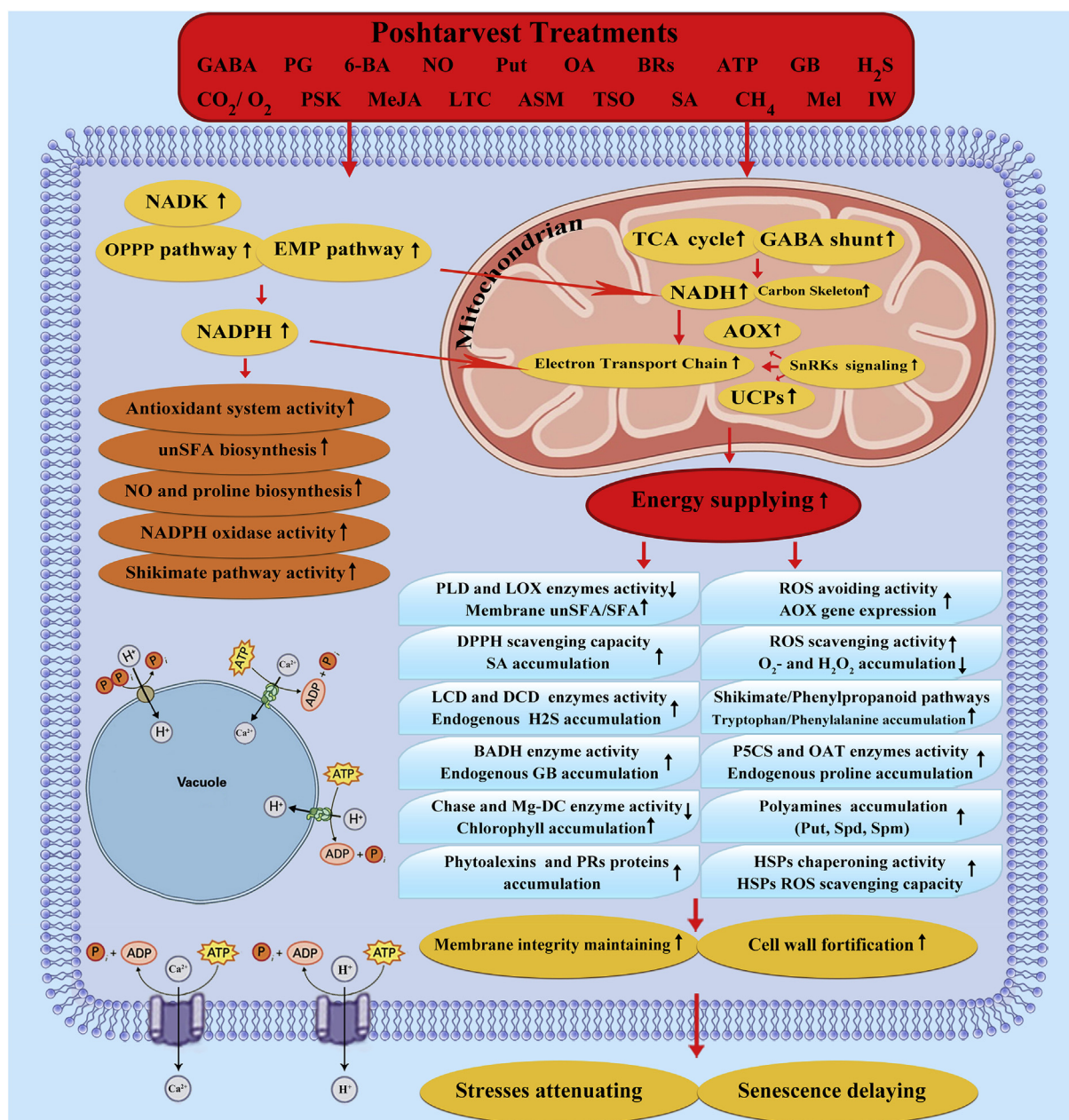


Fig. 1. Schematic overview of biochemical and molecular mechanisms by which postharvest treatments attenuates postharvest stresses and delays senescence by ensuring sufficient iATP supplying leading to cell membrane integrity maintaining and cell wall fortification.

(Song et al., 2017), mango fruits treated with OA (Li, Zheng, Liu, & Zhu, 2014), bamboo shoot treated with brassinosteroids (BRs; Liu et al., 2016) and tomato fruit treated with OA (Li et al., 2016c) resulted from sufficient iATP supplying which is crucial for maintaining membrane integrity representing by lower electrolyte leakage and MDA accumulation.

Zhou et al. (2014b) reported that the blueberry fruits chilling injury manifested by external pitting and internal flesh browning during shelf life (20 °C for 8 days) after cold storage (0 °C for 60 days) was accompanied by iATP shortage, lower ATP and ADP and higher AMP leading to lower AEC, results from lower H^+ -ATPase, Ca^{2+} -ATPase, CCO and SDH enzymes activity. Accompanying with chilling symptoms development in blueberry fruit, insufficient iATP supplying was concurrent with higher O_2^- and H_2O_2 accumulation, resulting from higher LOX enzyme activity along with lower superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX) enzymes activity leading to lower membrane integrity, revealed by higher electrolyte leakage and

MDA accumulation (Zhou et al., 2014a). He et al. (2017) reported that the chilling injury in banana fruit during storage at 7 °C for 30 days was associated with an iATP shortage, lower ATP and ADP and higher AMP leading to lower AEC, concurrent with higher membrane deterioration enzymes PLD and LOX activity, promoting fruit senescence. Pan et al. (2017) reported that the lower chilling injury in papaya fruit manifested by skin pitting, scald and flesh water soaking during storage at 1 °C, in comparison to 6 and 11 °C, for 54 days was accompanied with higher iATP supplying, higher ATP and ADP and lower AMP leading to higher AEC, which resulted from higher H^+ -ATPase, Ca^{2+} -ATPase, CCO and SDH enzymes activity. Supplying sufficient iATP is crucial for membrane fatty acids biosynthesis by acetyl CoA carboxylase (ACCase) which is responsible for biosynthesis of malonyl CoA from acetyl CoA and fatty acids acyl chains desaturation, which are crucial for enhancing membrane fluidity and restoration of the membrane under chilling stress (Yi et al., 2010). Wang et al. (2015a) reported that the NO treatment (0.05 mM) attenuated chilling injury manifested by peel

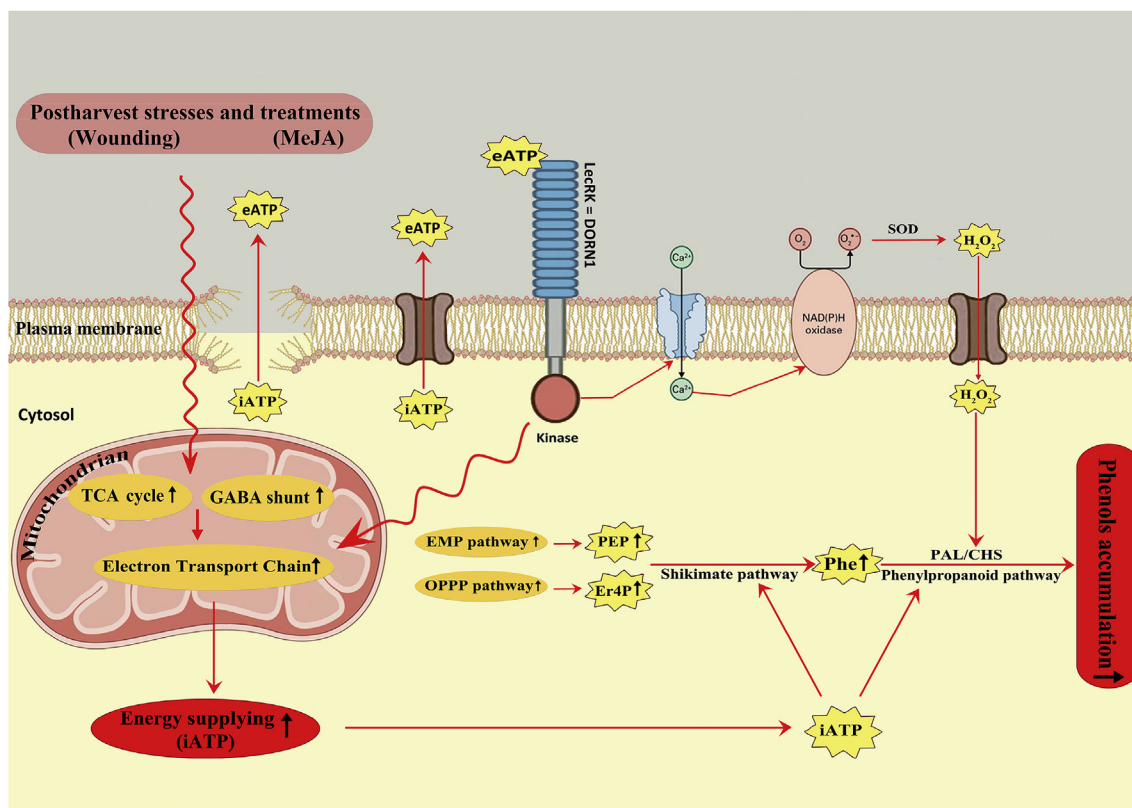


Fig. 2. Schematic overview of biochemical mechanisms by which postharvest stresses and treatments trigger higher phenols accumulation in fruits and vegetables generating postharvest biofactories by ensuring sufficient $iATP$ supplying or triggering $eATP$ signaling.

browning in banana fruit during storage at 7 °C for 20 days which was accompanied with higher $iATP$ supplying, higher ATP and ADP and lower AMP leading to higher AEC, results from higher H^+ -ATPase, Ca^{2+} -ATPase, CCO and SDH enzymes activity, concurrent with higher EMP pathway activity revealed by higher fructokinase and glucokinase enzymes activity and higher OPPP pathway activity revealed by higher glucose-6-phosphate dehydrogenase (G6PDH) and 6-phosphogluconate dehydrogenase (6PGDH) enzymes activity, resulting higher membrane integrity revealed by lower electrolyte leakage. Wang et al. (2018a) reported that the chilling injury manifested by peel browning in pear fruit during shelf life (20 °C for 15 days) after cold storage (0 °C for 180 days) was accompanied with lower $iATP$ supplying, lower ATP and ADP and higher AMP leading to lower AEC, results from lower NADH dehydrogenase, ATP synthase and V-PPase enzymes activity and genes expression, concurrent with higher PLD enzyme activity and gene expression resulting lower membrane integrity revealed by higher electrolyte leakage and MDA accumulation. Wang et al. (2017; 2018b) reported that the low temperature conditioning (10 °C for 25 days) and intermittent warming (20 °C for 1 day every 20 days during storage at 0 °C for 120 days) treatments attenuated chilling injury manifested by peel browning in pear fruit during shelf life (20 °C for 15 days) after cold storage (0 °C for 120 days) which was accompanied with higher $iATP$ supplying, higher ATP and ADP and lower AMP leading to higher AEC, results from higher NADH dehydrogenase, ATP synthase and V-PPase enzymes activity and genes expression, concurrent with lower PLD enzyme activity and gene expression resulting higher membrane integrity revealed by lower electrolyte leakage and MDA accumulation. Attenuating chilling injury in peach fruit treated with GABA (5 mM; Yang et al., 2011), MeJA (1 μ M; Jin et al., 2013), OA (5 mM; Jin et al., 2014), hypobaric (10–20 kPa; Wang et al., 2015a) and GB (10 mM; Shan et al., 2016), cucumber fruit treated with 6-BA (50 mM; Chen & Yang, 2013), mango fruit treated with OA (5 mM; Li et al., 2014), tomato fruit treated with OA (5 mM; Li et al., 2016c), pear fruit treated

with 1-MCP (0.5 μ LL⁻¹; Cheng et al., 2015), low temperature conditioning (10 °C for 25 days; Wang et al., 2017) and intermittent warming (20 °C for 1 day every 20 days during storage at 0 °C for 120 days; Wang et al., 2018b), bamboo shoot treated with BRs (0.5 μ M; Liu et al., 2016), banana fruit treated with H_2S (0.5 mM; Li et al., 2016a), and loquat fruit treated with LTC (14 days at 10 °C; Jin et al., 2015) and phytosulfokine peptide (250 nM; Song et al., 2017) have been attributed to higher $iATP$ supplying, higher ATP and ADP and lower AMP leading to higher AEC, resulting from higher H^+ -ATPase, Ca^{2+} -ATPase, CCO and SDH enzymes activity, which were accompanied with higher antioxidant system activity along with lower LOX enzyme activity leading to lower O_2^- and H_2O_2 accumulation, higher membrane unsFA/SFA ratio owing to higher linoleic and linolenic acids accumulation along with lower palmitic, stearic and oleic acids accumulation, higher phenols accumulation leading to higher DPPH/ABTS/FRAP scavenging capacity, higher endogenous proline accumulation results from higher pyrroline-5-carboxylate synthetase (P5CS) and ornithine aminotransferase (OAT) enzymes activity along with lower proline dehydrogenase (PDH) enzyme activity, higher lycopene accumulation with singlet oxygen scavenging capacity assayed by SOAC results from higher phytoene synthase 1 (PSY1) and ζ -carotene desaturase (ZDS) genes expression, higher endogenous GB accumulation results from higher betaine aldehyde dehydrogenase (BADH) enzyme activity, higher endogenous GABA accumulation results from higher GAD enzyme activity, higher fruit firmness results from lower cell wall degrading enzymes polygalacturonase (PG) and endo-1,4-b-glucanase (EGase) activity and lower lignin accumulation results from lower MYB1 and 4-coumarate:CoA ligase (4CL) genes expression, all of them leading to higher membrane integrity revealed by lower electrolyte leakage and MDA accumulation.

Also, ensuring sufficient $iATP$ supplying is crucial for heat shock proteins (HSPs) biological functions which are pivotal for attenuating postharvest chilling injury and fungal decay in horticultural crops

Table 1

Ensuring sufficient iATP supplying in response to postharvest treatments during postharvest life attenuating stresses and delaying senescence of horticultural crops.

Commodity	Treatments	Biochemical effects	References
Chilling injury attenuating			
Peach	GABA (5 mM)	Chilling injury ↓; ATP and ADP ↑ AMP ↓ AEC ↑; SOD and CAT activity ↑; AA/GSH cycle activity ↑	Yang et al. (2011)
Peach	MeJA (1 μM)	Chilling injury ↓; ATP and ADP ↑ AMP ↓ AEC ↑; H ⁺ -ATPase, Ca ²⁺ -ATPase, CCO and SDH activity ↑; O ₂ ⁻ and H ₂ O ₂ accumulation ↓; Electrolyte leakage and MDA accumulation ↓	Jin et al. (2013)
Cucumber	6-BA (1 mM)	Chilling injury ↓; ATP and ADP ↑ AMP ↓ AEC ↑; SOD, APX, CAT and GR activity ↑; O ₂ ⁻ and H ₂ O ₂ accumulation ↓; Phenols accumulation ↑; ABTS scavenging capacity ↑; Electrolyte leakage and MDA accumulation ↓	Chen and Yang (2013)
Mango	OA (5 mM)	Chilling injury ↓; ATP and ADP ↑ AMP ↓ AEC ↑; H ⁺ -ATPase, Ca ²⁺ -ATPase, CCO and SDH activity ↑; O ₂ ⁻ and H ₂ O ₂ accumulation ↓; SOD, CAT, APX and GR activity ↑; Proline accumulation ↑; P5CS activity ↑ and PDH activity ↓; Electrolyte leakage and MDA accumulation ↓	Li et al. (2014)
Peach	OA (5 mM)	Chilling injury ↓; ATP and ADP ↑ AMP ↓ AEC ↑; H ⁺ -ATPase, Ca ²⁺ -ATPase, CCO and SDH activity ↑; Linoleic and linolenic acids ↑; Palmitic, stearic and oleic acids ↓; Membrane unSFA/SFA ↑; Electrolyte leakage and MDA accumulation ↓	Jin et al. (2014)
Pear	1-MCP (0.5 μL L ⁻¹)	Chilling injury ↓; ATP and ADP ↑ AMP ↓ AEC ↑; H ⁺ -ATPase, Ca ²⁺ -ATPase, CCO and SDH activity ↑; Linoleic and linolenic acids ↑; Palmitic, stearic and oleic acids ↓; Membrane unSFA/SFA ↑; Electrolyte leakage and MDA accumulation ↓	Cheng et al. (2015)
Banana	NO (0.05 mM)	Chilling injury ↓; ATP and ADP ↑ AMP ↓ AEC ↑; H ⁺ -ATPase, Ca ²⁺ -ATPase, CCO and SDH activity ↑; FK, GK, G6PDH and 6PGDH activity ↑; Electrolyte leakage ↓	Wang et al. (2015b)
Tomato	OA (5 mM)	Chilling injury ↓; ATP and ADP ↑ AMP ↓ AEC ↑; H ⁺ -ATPase, Ca ²⁺ -ATPase, CCO and SDH activity ↑; Lycopene accumulation ↑; PSY1 and ZDS genes expression ↑; Electrolyte leakage and MDA accumulation ↓	Li et al. (2016c)
Pear	Low temperature conditioning (LTC; 10 °C for 25 days) Intermittent warming (IW; 20 °C for 1 day every 20 days)	Chilling injury ↓; ATP and ADP ↑ AMP ↓ AEC ↑; NADH dehydrogenase, ATP synthase and V-PPase enzymes activity and genes expression ↑; PLD enzyme activity and gene expression ↓; Electrolyte leakage and MDA accumulation ↓	Wang et al. (2017, 2018a, 2018b)
Bamboo	BRs (0.5 μM)	Chilling injury ↓; ATP and ADP ↑ AMP ↓ AEC ↑; H ⁺ -ATPase, Ca ²⁺ -ATPase, CCO and SDH activity ↑; Proline accumulation ↑; P5CS and OAT activity ↑; PDH enzyme activity ↓; Electrolyte leakage and MDA accumulation ↓	Liu et al. (2016)
Peach	Hypobaric (20 kPa)	Chilling injury ↓; ATP and ADP ↑ AMP ↓ AEC ↑; O ₂ ⁻ and H ₂ O ₂ accumulation ↓; SOD and CAT activity ↑; LOX activity ↓; Electrolyte leakage and MDA accumulation ↓	Wang et al. (2015a)
Banana	H ₂ S (0.5 mM NaHS)	Chilling injury ↓; ATP and ADP ↑ AMP ↓ AEC ↑; H ⁺ -ATPase, Ca ²⁺ -ATPase, CCO and SDH activity ↑; Electrolyte leakage and MDA accumulation ↓	Li et al. (2016a)
Loquat	LTC (14 days at 10 °C)	Chilling injury ↓; ATP and ADP ↑ AMP ↓ AEC ↑; H ⁺ -ATPase, Ca ²⁺ -ATPase, CCO and SDH activity ↑; Endogenous GB accumulation ↑; BADH activity ↑; Electrolyte leakage and MDA accumulation ↓	Jin et al. (2015)
Peach	GB (10 mM)	Chilling injury ↓; ATP and ADP ↑ AMP ↓ AEC ↑; Endogenous GB accumulation ↑; BADH activity ↑; GABA accumulation ↑; GAD activity ↑; Proline accumulation ↑; P5CS and OAT activity ↑; Electrolyte leakage and MDA accumulation ↓	Shan et al. (2016)
Loquat	Phytosulfokine (PSK; 250 nM)	Chilling injury ↓; ATP and ADP ↑ AMP ↓ AEC ↑; Fruit firmness ↑; PG and EGase activity ↓; Lignin accumulation ↓; MYB1 and 4CL genes expression ↓	Song et al. (2017)
Zucchini	Putrescine (1 mM)	Chilling injury ↓; GABA-T activity ↑; ATP and AEC ↑; DAO activity ↑; Proline and GB accumulation ↑; FAD2 gene expression ↑; CAT, APX and GR activity ↑; LOX activity ↓; H ₂ O ₂ accumulation ↓; AA accumulation ↑; FRAP scavenging capacity ↑; Glucose, fructose and raffinose accumulation ↑; MDA accumulation ↓	Palma et al. (2015), (2016)
Zucchini	LTC (2 days at 15 °C)	Chilling injury ↓; ATP and ADP ↑ AMP ↓ AEC ↑; GABA shunt pathway activity ↑; DAO activity ↑; AOX genes expression ↑; APX and CAT activity ↑; AA accumulation ↑; H ₂ O ₂ accumulation ↓; Electrolyte leakage and MDA accumulation ↓	Carvajal, Palma, Jamilena, and Garrido (2015)
Anthurium	GABA (1 mM) GABA (5 mM) Salicylic acid (SA; 2 mM)	Chilling injury ↓; GABA shunt pathway activity ↑; GABA-T activity ↑; ATP and ADP ↑ AMP ↓ AEC ↑; Membrane unSFA/SFA ↑; Linoleic and linolenic acid ↑; Palmitic, stearic and oleic acids ↓; PLD and LOX activity ↓; CAT, SOD, APX and GR activity ↑; H ₂ O ₂ accumulation ↓; Proline and GB accumulation ↑; PAL/PPO enzyme activity ↑; Phenols accumulation ↑; DPPH scavenging capacity ↑; Electrolyte leakage and MDA accumulation ↓	Aghdam, Naderi, Sarcheshmeh, and Babalar (2015), Aghdam et al. (2016b, 2016c, 2016d)
Fungal decay attenuating			
Pear	Acibenzolar-S-methyl (ASM; 100 mg L ⁻¹)	Blue mold decay caused by <i>Penicillium expansum</i> ↓; ATP and ADP ↑ AMP ↓ AEC ↑; H ⁺ -ATPase, Ca ²⁺ -ATPase, CCO and SDH activity ↑	Ge et al. (2017)
Strawberry	Melatonin (Mel; 0.1 mM)	Fungal decay ↓; H ₂ O ₂ accumulation ↑; SOD activity ↑; CAT and APX activity ↓; GABA shunt pathway activity ↑; GABA-T activity ↑; ATP and ADP ↑ AMP ↓ AEC ↑; Membrane unSFA/SFA ↑; Linoleic and linolenic acids ↑; Palmitic, stearic and oleic acids ↓; PAL activity ↑	Aghdam and Fard (2017)
Orange	GABA (0.5 mM)	Fungal decay ↓; ATP supplying ↑; Citrate accumulation ↑; GABA-T gene expression ↑; GAD gene expression ↓; CAT and SOD activity ↑	Sheng et al. (2017)
Loquat	MeJA (10 μM)	Anthraxnose decay caused by <i>Colletotrichum acutatum</i> ↓; ATP and ADP ↑ AMP ↓ AEC ↑; Polyamines putrescine, spermidine and spermine accumulation ↑	Cao et al. (2014a)

(continued on next page)

Table 1 (continued)

Commodity	Treatments	Biochemical effects	References
Senescence delaying			
Kiwifruit	Pure N ₂	ATP, ADP and AMP ↓; SnRK1 signaling pathway ↑; F0F1 ATP synthase, AAC, AOX and UCPs genes expression ↑; ROS accumulation ↓	Huang et al. (2014)
Daylily	Methane (CH ₄ ; 100% methane rich water; MRW)	ATP and ADP ↑ AMP ↓ AEC ↑; Endogenous gaseous antioxidant methane molecule accumulation ↑; Membrane unSFA/SFA ↑; Linoleic and linolenic acids ↑; Palmitic, stearic and oleic acids ↓; O ₂ ⁻ and H ₂ O ₂ accumulation ↓; Electrolyte leakage and MDA accumulation ↓	Hu et al. (2018)
Spinach	H ₂ S (2.4 mM NaHS)	Leaf yellowing ↓; Endogenous H ₂ S accumulation ↑; LCD and DCD activity ↑; ATP and ADP ↑ AMP ↓ AEC ↑; Chlorophyll degradation ↓; Chlorophyllase and Mg-dechelate activity ↓; SOD and CAT activity ↑; DPPH and O ₂ ⁻ scavenging capacity ↑; Electrolyte leakage and MDA accumulation ↓	Hu et al. (2015)
Broccoli	50% O ₂ /50% CO ₂	Floret yellowing ↓; ATP and ADP ↑ AMP ↓ AEC ↑; EMP pathway activity ↓; TCA, OPPP and cytochrome pathways activity ↑; PGI activity ↓; SDH, G6PDH, 6PGDH and CCO activity ↑	Li et al. (2016b)
Broccoli	H ₂ S (0.8 mM NaHS)	Floret yellowing ↓; LCD and DCD activity ↑; Endogenous H ₂ S accumulation ↑; ATP and ADP ↑ AMP ↓ AEC ↑; TCA cycle activity ↑; EMP, OPPP and cytochrome pathways activity ↑; GK, FK, SDH, G6PDH, 6PGDH and CCO activity ↑; H ⁺ -ATPase and Ca ²⁺ -ATPase activity ↑; Chlorophyll accumulation ↑	Li et al. (2017a)
Tulip	Sucrose (10 mM)	Flower PCD ↓; ATP and ADP ↑ AMP ↓ AEC ↑; DNase activity ↓, DNA fragmentation or degradation ↓; Cytochrome c releasing from mitochondria to cytoplasm ↓; ROS accumulation ↓	Azad et al. (2008)
Daylily	H ₂ S (4 mM NaHS)	Flower PCD ↓; DNA laddering ↓; Endogenous H ₂ S accumulation ↑; LCD and DCD activity ↑; ATP and ADP ↑ AMP ↓ AEC ↑; SOD, CAT and APX activity ↑; O ₂ ⁻ and H ₂ O ₂ accumulation ↓; MDA accumulation ↓; Chlorophyll degradation ↓; Respiration intensity ↓	Liu et al. (2017)
Browning attenuating			
Longan	Propyl gallate (PG; 0.5 mM)	Pericarp browning ↓; ATP and ADP ↑ AMP ↓ AEC ↑; H ⁺ -ATPase, Ca ²⁺ -ATPase and Mg ²⁺ -ATPase activity ↑; NADK activity ↑; NADPH accumulation ↑; O ₂ ⁻ accumulation ↓; SOD, CAT and APX activity ↑; AA and GSH accumulation ↑; AAO activity ↓; PLD and LOX activity ↓; Membrane unSFA/SFA ↑; PPO activity ↓; Phenols and flavonoids accumulation ↑; NADPH accumulation ↑; MDA accumulation ↓	Lin et al. (2013, 2015, 2017b, 2017c, 2018)
Litchi	Tea seed oil (TSO; 0.1%)	Pericarp browning ↓; ATP and ADP ↑ AMP ↓ AEC ↑; H ⁺ -ATPase, Ca ²⁺ -ATPase, CCO and SDH activity ↑; SnRK2 signaling pathway ↑; AAC gene expression ↑; Electrolyte leakage and MDA accumulation ↓	Zhang et al. (2017b)
Litchi	O ₂ (100%)	Pericarp browning ↓; ATP and ADP ↑ AMP ↓ AEC ↑; Electrolyte leakage ↓	Duan et al. (2004)
Longan	O ₂ (100%)	Pericarp browning ↓; ATP and ADP ↑ AMP ↓ AEC ↑; Electrolyte leakage and MDA accumulation ↓	Su et al. (2005)
Mushroom	O ₂ (100%)	Cap browning ↓; ATP and ADP ↑ AMP ↓ AEC ↑; PPO gene expression and enzyme activity ↓; Electrolyte leakage ↓	Li et al. (2017c)
Longan	Chlorine dioxide (ClO ₂ ; 25 mg L ⁻¹)	Pericarp browning ↓; ATP and ADP ↑ AMP ↓ AEC ↑; SDH and CCO activity ↑; NAD and NADH accumulation ↑	Chumyarn et al. (2016)
Mushroom	80% O ₂ /20% CO ₂	Cap browning ↓; ATP and ADP ↑ AMP ↓ AEC ↑; EMP pathway activity ↓; PGI activity ↓; TCA cycle activity ↑; SDH activity ↑; Cytochrome pathway activity ↑; CCO activity ↑; OPPP pathway activity ↑; G6PDH and 6PGDH activity ↑; H ⁺ -ATPase and Ca ²⁺ -ATPase activity ↑; AOX gene expression and enzyme activity ↑; O ₂ ⁻ , H ₂ O ₂ and NO accumulation ↓; NADH dehydrogenase, SDH, cytochrome b/c ₁ oxidoreductases, cytochrome c oxidase and F ₀ F ₁ ATP synthase genes expression ↑	Li et al. (2017b)

(Aghdam, Sevillano, Flores, & Bodbodak, 2013a). HSPs have N-terminal ATP binding domain with ATPase activity which is crucial for HSPs biological function (Xu et al., 2012). Attenuating postharvest chilling injury and fungal decay by HSPs accumulation in horticultural crops in response to postharvest treatments have been attributing to HSPs molecular chaperoning activity which is crucial for maintaining protein function such as mitochondrial ETS portions (Aghdam, Sevillano, Flores, & Bodbodak, 2013b). In addition to molecular chaperoning function, HSPs are crucial for enhancing antioxidant system activity by triggering antioxidant enzymes activity and boosting AA/DHA and GSH/GSSG ratio which are pivotal not only for attenuating postharvest chilling injury and fungal decay but also are crucial for horticultural crops nutritional quality (Aghdam et al., 2013b). Also, in addition to synergist action with the antioxidant system, HSPs not only have direct ROS scavenging capacity due to its free amino acids residues but also exhibit membrane phospholipids binding capacity preventing phospholipases enzymes activity (Zhang et al., 2018a). Higher HSPs accumulation in horticultural crops attenuates chilling injury and fungal decay by maintaining membrane fluidity and integrity due to lower

membrane unSFA peroxidation by lowering ROS accumulation concomitant with lowering membrane degrading PLD enzyme activity (Aghdam et al., 2013a, 2013b; Zhang et al., 2018a).

Apyrase as Ca²⁺ and Mg²⁺ dependent membrane ATPase, is responsible for maintaining eATP homeostasis creating friendly eATP, which is crucial for response to biotic and abiotic stresses (Choi et al., 2014). Deng et al. (2015) reported that the chilling stress by disrupting membrane integrity leading to releasing ATP from cytoplasm to apoplast of *Populus euphratica* leads to generating unfriendly eATP which by inhibition of vesicular trafficking results in disrupting membrane repairing leading to lower membrane integrity, revealed by higher electrolyte leakage. Also, Deng et al. (2015) reported that the *Arabidopsis* plant overexpressing apyrase 2 gene (*PeAPY2*), which as ecto ATPase is responsible for eATP hydrolyzing, exhibited higher chilling tolerance representing with lower electrolyte leakage, which by generating friendly eATP promoted vesicular trafficking results in membrane repairing leading to higher membrane integrity. Friendly eATP in *Arabidopsis* overexpressing *PeAPY2* gene was accompanied with higher membrane integrity, demonstrated that friendly eATP is crucial for

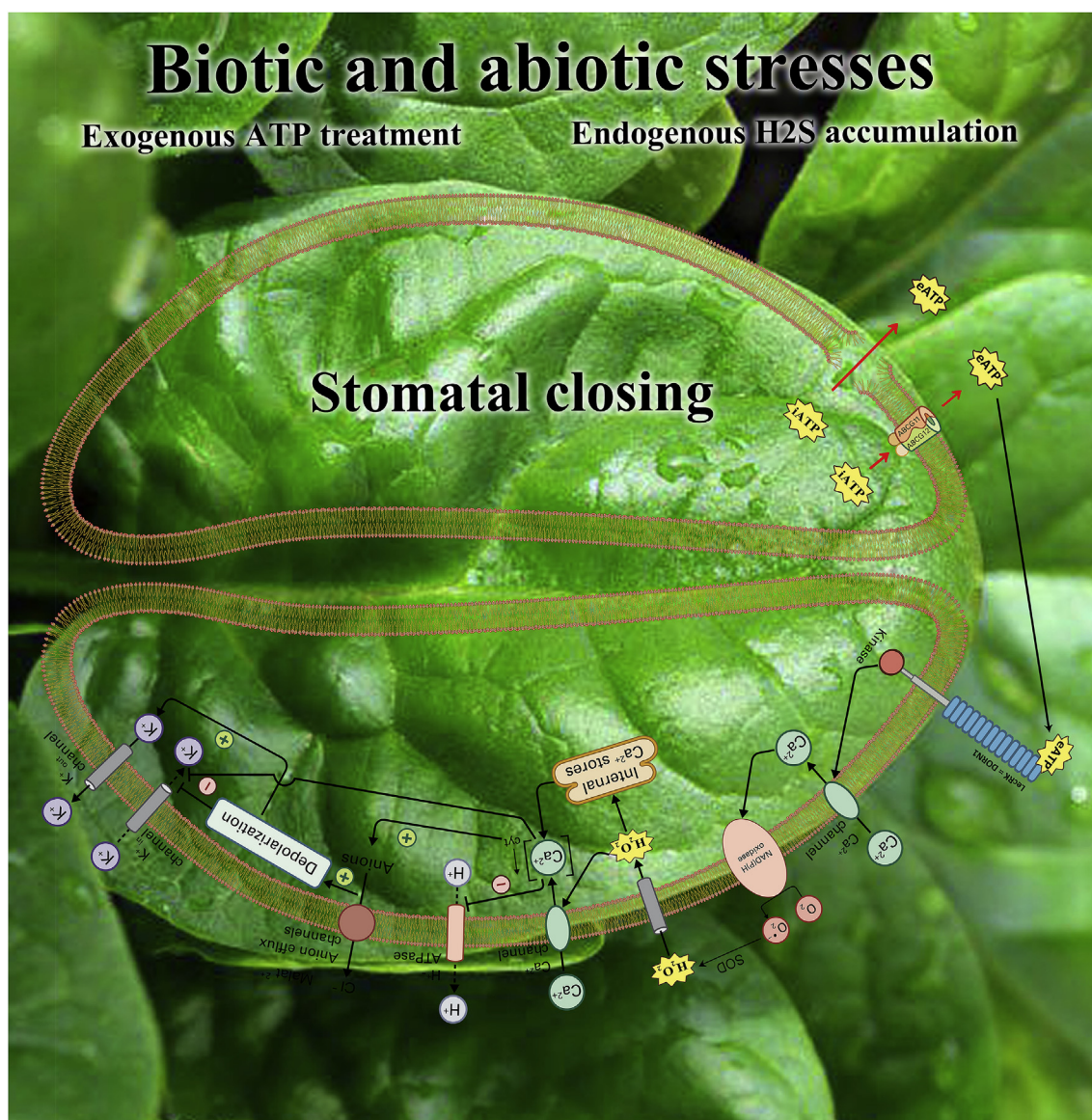


Fig. 3. Extracellular ATP signaling triggers stomatal closing by enhancing H₂O₂ accumulation via activating NADPH oxidase.

maintaining membrane integrity.

3. Ensuring sufficient iATP supplying and friendly eATP signaling attenuates postharvest decay

In addition to chilling injury, postharvest fungal decay also associates with iATP shortages (Aghdam & Bodbodak, 2013; Cao et al., 2014a; Chen et al., 2014; Ge et al., 2017; Lin et al., 2017a; Yi et al., 2008, 2010; Zhang et al., 2017a). Attenuating postharvest decay in litchi fruit treated with exogenous ATP (Yi et al., 2008, 2009, 2010), longan fruit treated with ATP (Lin et al., 2017a; Zhang et al., 2017a), loquat fruit treated with MeJA (Cao et al., 2014a) and pear fruit treated with acibenzolar-S-methyl (Ge et al., 2017) resulted from sufficient iATP supplying which is crucial for cell wall fortification. Chen et al. (2014) reported that postharvest decay caused by *Phomopsis langanae* in longan fruit during storage at 28 °C for 5 days was accompanied with an iATP shortage, lower ATP and ADP and higher AMP leading to lower AEC, resulting in lower membrane integrity revealed by higher electrolyte leakage. Also, fungal decay in longan fruit caused by *Lasiodiplodia theobromae* manifested with pericarp browning was concomitant with lower membrane integrity revealed by higher electrolyte leakage

and MDA accumulation. Lower membrane integrity was consequent from lower membrane unSFA/SFA ratio resulting from lower oleic, linoleic, linolenic and gondoic acids accumulation along with higher palmitic and stearic acids accumulation. Higher lipase, PLD and LOX enzymes activity leading to lower phosphatidylcholine and phosphatidylinositol accumulation along with higher phosphatidic acid accumulation concomitant with lower antioxidant enzymes CAT, SOD and APX activity along with lower antioxidant molecules AA and GSH accumulation leading to higher O₂^{•−} accumulation and lower DPPH scavenging capacity contributes to lower longan fruits membrane unSFA/SFA ratio (Sun et al., 2018; Zhang et al., 2018b).

In addition to maintaining membrane integrity, resulting from higher membrane unSFA/SFA ratio due to contribution of ATP in membranes fatty acids biosynthesis and acyl chains desaturation, attenuating postharvest decay by sufficient iATP supplying in litchi fruit may attributed to higher phytoalexins and pathogenesis (PRs) proteins biosynthesis and accumulation with antimicrobial attributes, which are ATP consuming. Cao et al. (2014b) reported that higher postharvest decay resistance of Qingzhong loquat fruit during storage at 20 °C for 10 days attributed to higher linolenic and linoleic accumulation concurrent with lower O₂^{•−} and H₂O₂ accumulation resulting from lower

Table 2

Beneficial impacts of exogenous ATP treatment in attenuating postharvest stresses and delaying postharvest senescence of horticultural crops which may result from friendly eATP signaling.

Commodity	Treatments	Biochemical effects	References
Litchi	ATP (1 mM)	Downy mildew decay caused by <i>Peronophythora litchi</i> ↓; Pericarp browning ↓; ATP and ADP ↑ AMP ↓ AEC ↑; PLD, LAH and LOX activity ↓; Electrolyte leakage and MDA accumulation ↓	Yi et al. (2008)
Litchi	ATP (1 mM)	Downy mildew decay caused by <i>Peronophythora litchi</i> ↓; SOD, CAT and APX activity ↑; Phenols accumulation ↑; DPPH scavenging capacity ↑	Yi et al. (2010)
Longan	ATP (0.8 mM)	Fungal decay caused by <i>Phomopsis langanae</i> ↓; ATP and ADP ↑ AMP ↓ AEC ↑; SOD, CAT and APX activity ↑; AA and GSH accumulation ↑; DPPH scavenging capacity ↑; O ₂ [−] accumulation ↓; MDA accumulation ↓	Lin et al. (2017a)
Longan	ATP (0.8 mM)	Fungal decay caused by <i>Lasiodiplodia theobromae</i> ↓; ATP and ADP ↑ AMP ↓ AEC ↑; EMP-TCA respiratory pathways ↓; NAD and NADH accumulation ↓; OPPP pathway ↑; NADP and NADPH accumulation ↑; NADK activity ↑; CCO, AAO, and PPO enzymes activity ↓	Zhang et al. (2017a)
Carnation	ATP (0.1 mM)	ATP and ADP ↑ AMP ↓ AEC ↑; PLD and LOX activity ↓; SOD, CAT and APX activity ↑; Respiration intensity ↑; Ethylene production ↓; Fresh weight ↑; Electrolyte leakage and MDA accumulation ↓	Song et al. (2014)
Longan	ATP (1 mM)	Pericarp browning ↓; Phenols and flavonoids accumulation ↑; PPO and peroxidase activity ↓; Electrolyte leakage ↓	Yao et al. (2014)
Longan	ATP (0.8 mM)	Pericarp browning ↓; Phenols, flavonoids and anthocyanins accumulation ↑; AA accumulation ↑; PPO activity ↓; Electrolyte leakage ↓	Chen et al. (2015)
Litchi	ATP (1 mM)	Pericarp browning ↓; ATP and ADP ↑ AMP ↓ AEC ↑; ROS accumulation ↓; Electrolyte leakage and MDA accumulation ↓	Yang et al. (2009)
Litchi	ATP (1 mM)	Pericarp browning ↓; Energy supplying ↑; SOD, CAT and APX activity ↑; Phenols accumulation ↑; DPPH scavenging capacity ↑	Yi et al. (2010)
Mung bean sprouts	ATP (1 mM)	Sprouts browning ↓; PPO activity ↓; Phenols accumulation ↑; H ₂ O ₂ accumulation ↓; SOD activity ↑; Ascorbic acid accumulation ↑; Firmness ↑; PG, PME and PL genes expression ↓; Electrolyte leakage ↓	Chen et al. (2018)

LOX enzyme activity along with higher antioxidant enzymes CAT and APX activity. Pathogen infection triggers releasing of free unSFA, C18:1, C18:2 and C18:3, which undergo oxidation at double bond on carbon 9 by ROS leading to azelaic acid (AZA) biosynthesis and accumulation. Higher AZA accumulation triggers glycerol-3-phosphate (G3P) biosynthesis via enhancing G3P dehydrogenase and glycerol kinase genes expression. Then, higher G3P accumulation by triggering salicylic acid biosynthesis and accumulation leading to conferring SAR, which is associated with maintaining the transcriptional stability of lipid transfer proteins DIR1 and AZI1 (Lim, Singhal, Kachroo, & Kachroo, 2017). Also, higher linolenic acid (18:3) may enhance pathogen resistance in *Arabidopsis* by triggering oxidative burst by H₂O₂ accumulation via activating NADPH oxidase (Lim et al., 2017). In addition to higher linolenic acid, lower oleic acid (18:1) enhanced pathogen resistance by triggering higher NO accumulation via stabilizing nitric oxide associated protein 1 (NOA1) which lead to higher NO biosynthesis and accumulation (Lim et al., 2017). Oleic acid (18:1) negatively regulates the stability of NOA1 which is responsible for NO biosynthesis and accumulation, so physically binding of oleic acid (18:1) to NOA1 leading to NOA1 degradation in a protease-dependent manner, which results in lower NO accumulation. Also, oxidation of unSFA by LOX or ROS results to phyto-oxylipins accumulation, which is crucial for the fungal decay resistance by eliciting systemic resistance or directly antifungal activity (Lim et al., 2017).

Attenuating blue mold decay caused by *Penicillium expansum* in pear fruit treated with acibenzolar-S-methyl (100 mg L^{−1}; Ge et al., 2017), downy mildew decay caused by *Peronophythora litchi* in litchi fruits treated with ATP (1 mM; Yi et al., 2010; Yi et al., 2008) and decay caused by *Phomopsis langanae* in longan fruit treated with ATP (0.8 mM; Lin et al., 2017a) have been attributed to higher iATP supplying, higher ATP and ADP and lower AMP leading to higher AEC, resulting from higher H⁺-ATPase, Ca²⁺-ATPase, CCO and SDH enzymes activity, which were accompanied with higher antioxidant system activity resulting in lower O₂[−] and H₂O₂ accumulation, lower PLD and LOX enzymes activity, higher phenols accumulation leading to higher DPPH scavenging capacity, all of them leading to higher membrane integrity revealed by lower electrolyte leakage and MDA accumulation. Higher phenylpropanoid pathway activity revealed by higher PAL enzyme activity in litchi fruit in response to exogenous ATP treatment, resulting from supplying sufficient iATP, not only leads to cell wall fortification by deposition of phenols and lignin to cell wall, but also leads to signaling molecule salicylic acid accumulation, which are crucial for

attenuating fungal decay (Yi et al., 2008, 2009, 2010). Cao et al. (2014a) reported that the MeJA treatment (10 μM) attenuated post-harvest anthracnose decay caused by *Colletotrichum acutatum* in loquat fruit during storage at 20 °C for 6 days was accompanied with higher iATP supplying, higher ATP and ADP and lower AMP leading to higher AEC, concurrent with higher polyamines putrescine, spermidine and spermine accumulation. In response to pathogen infection, endogenous polyamines accumulation is crucial for attenuating fungal decay. Higher endogenous polyamines especially putrescine and spermidine can be used for biosynthesis of hydroxycinnamic acid amides (HCAAs) which have antifungal activity. In addition to HCAAs accumulation, attenuating fungal decay by endogenous polyamines spermidine and spermine accumulation may result from triggering endogenous NO accumulation. Also, polyamines oxidation by diamine oxidase (DAO) and polyamine oxidase (PAO) is accompanying with H₂O₂ and GABA accumulation, which are crucial for attenuating fungal decay (Jiménez-Bremont et al., 2014).

Lin et al. (2017a) reported that the ATP treatment (0.8 mM) attenuated postharvest decay caused by *Lasiodiplodia theobromae* in longan fruit during storage at 28 °C for 5 days, which was accompanied with higher iATP supplying, higher ATP and ADP and lower AMP leading to higher AEC, concurrent with lower EMP-TCA respiratory system activity leading to lower NADH accumulation, higher NAD kinase (NADK) enzyme activity which is responsible for producing NADP from NAD by ATP consumption, higher OPPP pathway activity leading to higher NADPH accumulation, and lower respiratory terminal oxidase CCO, ascorbic acid oxidase (AAO), and polyphenol oxidase (PPO) enzymes activity. Higher NADPH in longan fruit treated with ATP can use for ATP biosynthesis in ETS by oxidation via external NADPH dehydrogenases (Wang et al., 2015a), unSFA biosynthesis by NADPH-dependent 3-ketoacyl-ACP reductase and enoyl-ACP reductase, antioxidant system activity via GR and MDHAR antioxidant enzymes in AA/GSH cycle for ROS scavenging, NO biosynthesis by NADPH dependent nitric oxide synthase (NOS), and proline biosynthesis from glutamate by NADPH dependent P5C reductase, which all are crucial for attenuating chilling injury and fungal decay (Corpas & Barroso, 2014; Wang et al., 2015c). Also, NADPH can use by NADPH oxidase for generating oxidative burst, which is crucial for attenuating fungal decay (Corpas & Barroso, 2014). NADPH can use by shikimate dehydrogenase (SKDH) in shikimate pathway, which is crucial for supplying aromatic amino acids tryptophan and phenylalanine. Tryptophan can be used for melatonin biosynthesis pathway which acts as universal

biostimulator and signaling biomolecule with superior antioxidant cascade activity and phenylalanine can be used for phenylpropanoid pathway which is crucial for phenols accumulation. Sufficient iATP supplying (ATP for shikimate kinase) and reducing power (NADPH for shikimate dehydrogenase) are crucial for shikimate pathway activity (Buchanan, Grisse, & Jones, 2015). Sufficient iATP supplying in longan fruit treated with exogenous ATP may result from eATP signaling which not only is crucial for iATP biosynthesis machinery activity but also is crucial for secondary messengers, Ca^{2+} , ROS, and NO accumulation, which are crucial for reinforcement of plants defense response. Recently, Tripathi, Zhang, Koo, Stacey, and Tanaka (2018) reported that the attenuating necrotrophic fungus, *Botrytis cinerea*, infection in Arabidopsis by exogenous ATP treatment result from eATP signaling by DORN1 receptor which activate jasmonic acid (JA) signaling via reducing JAZ1 protein stability by triggering SCF^{COI1} proteasome pathway through secondary messengers, Ca^{2+} , ROS, and NO. In addition to jasmonic acid, Tripathi et al. (2018) suggested that the activating salicylic acid (SA) signaling pathway in response to eATP signaling is crucial for attenuating *Botrytis cinerea* infection. According to Tripathi et al. (2018), friendly eATP signaling may be crucial of attenuating postharvest decay caused by *Botrytis cinerea* in horticultural crops via triggering JA/SA signaling pathways.

Also, attenuating postharvest fungal decay in horticultural crops with higher HSPs accumulation results from its chaperoning function which is crucial for biogenesis, maturation, and stabilization of membrane pattern recognition receptors (PRRs) and cytosolic resistance (R) proteins which are crucial for response to fungal infection (Park & Seo, 2015). Also, HSPs by reprogramming of auxin, salicylic acid, jasmonic acid and ethylene as defense hormones attenuates fungal pathogen infection (Wei et al., 2017).

4. Ensuring sufficient iATP supplying and friendly eATP signaling delays postharvest senescence

During postharvest life, horticultural crops senescence encompassing fruit external browning due to phenols oxidation, vegetable leaf yellowing due to chlorophyll degradation and flower petal and sepal wilting due to triggering DNA laddering during programmed cell death (PCD) were associated with insufficient iATP supplying (Chumyam, Shank, Uthaibutra, & Saengnil, 2016; Lin et al., 2016, 2018; Liu et al., 2011; Wang et al., 2013; Yi et al., 2010; Zhang et al., 2017a). Attenuating postharvest senescence in broccoli treated with H_2S (Li et al., 2017a) and 50% CO_2 /50% O_2 (Li, Lv, Guo, & Wang, 2016b), spinach treated with H_2S (Hu, Liu, Li, & Shen, 2015), daylily flower treated with H_2S (Liu et al., 2017) and methane rich water (Hu, Liu, & Li, 2018), tulip flower treated with sucrose (Azad, Ishikawa, Ishikawa, Sawa, & Shibata, 2008), carnation flower treated with ATP (Song et al., 2014), and mung bean sprout treated with ATP (Chen et al., 2018) resulted from sufficient iATP supplying, leading to higher membrane integrity revealed by lower electrolyte leakage and MDA accumulation (Fig. 1). Delaying postharvest senescence in spinach leaf (Hu et al., 2015), broccoli floret (Li et al., 2017a) and daylily flower (Liu et al., 2017) treated with H_2S have been attributed to higher endogenous H_2S accumulation by enhancing L-cysteine desulfhydrase (LCD) and D-cysteine desulfhydrase (DCD) enzymes activity leading to higher iATP supplying. Higher TCA cycle activity revealed by higher SDH enzyme activity, higher EMP pathway activity revealed by higher fructokinase and glucokinase enzymes activity, higher OPPP pathway activity revealed by higher G6PDH and 6PGDH enzymes activity and higher cytochrome pathway activity revealed by higher CCO and SDH enzymes activity concurrent with higher H^+ -ATPase and Ca^{2+} -ATPase enzymes activity are responsible for higher iATP supplying in spinach leaf, broccoli floret and daylily flower treated with H_2S . Also, under higher endogenous H_2S accumulation in spinach leaf, broccoli floret and daylily flower treated with H_2S , transferring an electron from sulfide to oxygen via CCO may contribute in higher ATP biosynthesis by coupling

with oxidative phosphorylation (Vökel & Grieshaber, 1997). Sufficient iATP supplying in spinach leaf, broccoli floret and daylily flower treated with H_2S was accompanied with lower chlorophyll degradation result from lower chlorophyllase and Mg-dechelate enzymes activity, higher antioxidant system activity leading to lower O_2^- and H_2O_2 accumulation, and delaying PCD by attenuating DNA laddering, which all of them resulting higher membrane integrity revealed by lower electrolyte leakage and MDA accumulation. Also, delaying senescence in spinach leaf, broccoli floret and daylily flower by higher endogenous H_2S accumulation may result from preventing water loss by triggering stomatal closure (Wang et al., 2015b). Higher endogenous H_2S accumulation triggers eATP signaling by enhancing ABC transporters expression which are responsible for releasing of ATP from cytoplasm to apoplast. Perception of eATP at the plasma membrane by LecRKs resulting in H_2O_2 accumulation by activating of NADPH oxidase. Higher H_2O_2 accumulation by increasing K^+ efflux in guard cells leads to stomatal closure and maintains water homeostasis which is crucial for delaying postharvest senescence (Wang et al., 2015b).

Also, delaying postharvest senescence in broccoli in response to 50% O_2 /50% CO_2 treatment (Li et al., 2016b) and mushroom in response to 80% O_2 /20% CO_2 treatment (Li, Kitazawa, Wang, & Sun, 2017b) have been attributed to higher iATP supplying, higher ATP and ADP and lower AMP leading to higher AEC, results from lower EMP pathway activity revealed by lower phosphoglucose isomerase enzyme activity concurrent with higher TCA cycle activity revealed by higher SDH enzyme activity, higher OPPP pathway activity revealed by higher G6PDH and 6PGDH enzymes activity, higher cytochrome pathway activity revealed by higher CCO enzyme activity, and higher H^+ -ATPase and Ca^{2+} -ATPase enzymes activity, concurrent with higher AOX, NADH dehydrogenase, SDH, cytochrome b/c1 oxidoreductases, CCO and F_0F_1 ATP synthase genes expression, which were accompanied with lower O_2^- and H_2O_2 accumulation. Also, synergist function of AOX pathway with OPPP pathway is crucial for attenuating stresses and delaying senescence. Hu et al. (2018) reported that during senescence of daylily buds, exhibiting higher biomedical capacity, during storage at 2 °C for 12 days, lower iATP supplying, lower ATP and ADP along with higher AMP leading to lower AEC, was concomitant with lower endogenous gaseous antioxidant methane (CH_4) molecule accumulation along with higher PPO enzyme activity. Also, Hu et al. (2018) reported that the delaying daylily buds senescence manifested with browning in response to postharvest methane treatment as methane rich water (100%) results from higher iATP supplying, higher ATP and ADP along with lower AMP leading to higher AEC, which was concomitant with higher endogenous gaseous antioxidant methane molecule accumulation, lower PPO enzyme activity, higher unSFA/SFA ratio owing to lower palmitic and stearic acids accumulation along with higher oleic, linoleic and linolenic acids accumulation, and lower O_2^- and H_2O_2 accumulation, leading to higher membrane integrity revealed by lower electrolyte leakage and MDA accumulation.

In plants, mitochondrial energy dissipation pathways, a redox potential dissipating system represented by AOX and a proton electrochemical potential dissipating system represented by UCPs, are crucial for iATP supplying during senescence and stresses (Pu et al., 2015; Vercesi et al., 2006). By mitochondrial energy dissipation pathways, ATP biosynthesis via F_0F_1 ATP synthase uncouples from electrochemical proton potential resulting from ETS leading to lower ATP biosynthesis (Vercesi et al., 2006). In response to stress, AOX activity by maintaining electrons flow results in TCA cycle activity continuation due to supplying NAD^+ , which may not only result in sufficient iATP and carbon skeletons supplying but also is crucial for avoiding ROS accumulation (Vanlerberghe, 2013). Jiang et al. (2017) reported that during postharvest senescence in litchi fruit, higher *NAC1* gene expression may result from higher endogenous ABA and H_2O_2 accumulation. *NAC1* act as a negative regulator of litchi fruit senescence by triggering AOX1 gene expression which is crucial for avoiding ROS production and maintaining sufficient iATP supplying, both are crucial

for delaying fruit senescence. UCPs are responsible for dissipating the electrochemical proton potential generated by ETS. UCPs are not only crucial for avoiding mitochondrial ROS accumulation but also are crucial for maintaining TCA cycle flux (Vercesi et al., 2006). Lowering mitochondrial electrochemical proton potential via UCPs increase complex I and II activity in ETS lead to NADH reoxidation which connects TCA cycle flux to ETS and, consequently to iATP supplying (Vercesi et al., 2006).

Azad et al. (2008) reported that the iATP shortage, lower ATP and ADP and higher AMP leading to lower AEC, triggered PCD during tulip petal senescence by promoting DNase activity, DNA fragmentation or degradation and cytochrome c releasing from mitochondria to cytoplasm which may result in higher ROS accumulation. Also, Azad et al. (2008) reported that the exogenous sucrose treatment delayed PCD during tulip petal senescence by supplying higher iATP, higher ATP, and ADP and lower AMP leading to higher AEC, resulting in lower DNase activity, DNA fragmentation or degradation and cytochrome c releasing from mitochondria to cytoplasm which may result in lower ROS accumulation. Song et al. (2014) reported that the exogenous ATP treatment (0.1 mM) delayed postharvest senescence of cut carnation flowers during storage at 25 °C for 10 days which was accompanied with higher iATP supplying, higher ATP and ADP and lower AMP leading to higher AEC, concurrent with lower PLD and LOX enzymes activity and higher antioxidant enzymes SOD, CAT and APX activity, resulting in higher membrane integrity revealed by lower electrolyte leakage and MDA accumulation. Chen et al. (2015) reported that the delaying postharvest senescence manifested with pericarp browning of longan fruit during storage at 28 °C for 5 days by exogenous ATP treatment (0.8 mM) was accompanied with higher phenols, flavonoids, anthocyanins and ascorbic acid accumulation along with lower PPO enzyme activity resulting higher membrane integrity revealed by lower electrolyte leakage. Beneficial impacts of exogenous ATP treatment on delaying senescence in cut carnation cut flower and longan fruit may result from friendly eATP signaling leading to extending postharvest life of carnation cut flower and longan fruit.

In plants, SnRKs play crucial roles in iATP signaling during senescence and stresses (Pu et al., 2015). The lower iATP supplying during senescence and stresses resulting in low energy syndrome (LES) which by triggering SnRKs signaling pathway resulting in attenuating senescence and stresses. SnRK1, as iATP sensor by sensing iATP status via measuring cytosolic ATP/AMP ratios, is responsible for plant response to lower iATP supplying which by metabolic reprogramming decodes lower iATP supplying signals leading to maintaining iATP homeostasis (Tomé et al., 2014; Wang et al., 2013). Also, ROS accumulation results from lower iATP supplying may activate SnRK1 signaling pathway (Hulsmans, Rodriguez, De Coninck, & Rolland, 2016). Huang et al. (2014) reported that the delaying postharvest senescence in kiwifruit treated with N₂ during storage at 15 °C results from lowering iATP adenylate pool, lower ATP, ADP, and AMP. Efficiently economize iATP lead to activation SnRK1 signaling pathway for supplying sufficient iATP by triggering higher energy producing genes expression and enzymes phosphorylation such as F₀F₁ ATP synthase, AAC, AOX and UCPs which result in higher iATP supplying concurrent with lower ROS accumulation. Mitochondrial AAC is responsible for importing ADP into mitochondria which are necessary for ATP biosynthesis by F₀F₁ ATP synthase, and exporting ATP towards cytosol for consuming by metabolic pathways which are crucial for delaying senescence and attenuating stresses (Huang et al., 2014). Also, SnRK1 by anti-senescence function can be beneficial for delaying leafy vegetable senescence. Kim, Cho, and Yoo (2017) reported that the SnRK1 delayed *Arabidopsis* leaf senescence by ethylene signaling EIN3 repression leading to down-regulation senescence genes expression. Since preserving green is crucial for leafy vegetables, SnRK1 can govern degreening progression of leafy vegetables during postharvest life. In addition to sensing lower iATP supplying by SnRK1, SnRK2s are crucial for ABA signaling during senescence and stresses. Wang et al. (2013) reported that the perception

of lower iATP supplying owing to higher respiration intensity during litchi fruit senescence (25 °C for 6 days) by activating SnRK2 signaling pathway leads to higher iATP producing genes expression and enzymes phosphorylation such as F₀F₁ ATP synthase, AAC, AOX and UCPs resulting slowing down fruit deterioration by higher iATP supplying concurrent with lower ROS accumulation, but at progressive fruit senescence disruption of SnRK2 signaling pathway leads to fast fruit deterioration due to lower iATP supplying concurrent with higher ROS accumulation. Also, Wang et al. (2013) reported that the exogenous ATP treatment (1 mM) delayed litchi fruit senescence during storage at 25 °C for 6 days, which was accompanied with higher iATP supplying owing to lower respiration intensity. The higher iATP supplying may result from activating SnRK2 signaling pathway leading to higher F₀F₁ ATP synthase, AOX, and UCPs genes expression. Zhang et al. (2017b) reported that the tea seed oil treatment (0.1%) attenuated litchi fruit pericarp browning during storage at 25 °C for 8 days which was accompanied with higher iATP supplying due to higher H⁺-ATPase and Ca²⁺-ATPase enzyme activity. Zhang et al. (2017a, 2017b) suggested that the tea seed oil treatment ensured iATP supplying in litchi fruit by enhancing SnRK2 signaling pathway leading to higher AAC gene expression. Lower pericarp browning in litchi fruit treated with tea seed oil was associated with higher membrane integrity revealed by lower electrolyte leakage. Liu et al. (2015) reported that litchi fruit senescence during shelf life (25 °C for 48 h) after cold storage (1 °C for 21 days) manifested by pericarp browning was accompanied with lower iATP supplying, lower ATP and ADP and higher AMP leading to lower AEC, which by activating SnRK2 signaling pathway leading to higher F₀F₁ ATP synthase gene expression. SnRKs manipulation may allow postharvest industry to achieve a potential strategy for postharvest management to enhance commodities values via extending shelf life by ensuring sufficient iATP supplying.

5. Ensuring sufficient iATP supplying and friendly eATP signaling attenuates postharvest browning

Postharvest browning of horticultural crops has been attributed to senescence and stresses, which were associated with iATP shortages, leading to lower membrane integrity resulting from higher ROS accumulation by lower antioxidant system activity concurrent with higher PLD and LOX enzymes activity, which in turn by disrupting cellular compartmentalization, resulting in PPO coming into contacting with phenols result in browning (Chumyam et al., 2016; Lin et al., 2016, 2017c, 2018; Liu et al., 2011). Attenuating postharvest browning in mushroom treated with high O₂/CO₂ (Li et al., 2017b) and high O₂ (Li, Sun, Kitazawa, & Wang, 2017c), litchi fruit treated with tea seed oil (Zhang et al., 2017b), pure oxygen (Duan et al., 2004) and ATP (Yi et al., 2010), longan fruit treated with propyl gallate (Lin et al., 2013, 2015, 2018), chlorine dioxide fumigation (Chumyam, Shank, Faiyue, Uthabutra, & Saengnil, 2017; Chumyam et al., 2016) and ATP (Chen et al., 2015) resulted from sufficient iATP supplying, leading to higher membrane integrity revealed by lower electrolyte leakage and MDA accumulation (Fig. 1). Liu et al. (2011) reported that the pericarp browning in litchi fruit during shelf life (25 °C for 12 h) after cold storage (5 °C for 30 days) was accompanied by iATP shortages, lower ATP and ADP and higher AMP leading to lower AEC, concurrent with higher PLD and LOX enzymes activity. Li, Zhang, and Ge (2017d) reported that higher browning in fresh-cut pear fruit was concurrent with lower unSFA/SFA ratio resulting from higher LOX enzyme activity. This indicated that higher membrane fluidity and integrity is pivotal for attenuating browning. Lin et al. (2017c) reported that the higher pericarp browning in longan fruit in response to exogenous H₂O₂ treatment during storage at 25 °C for 10 days was accompanied by iATP shortage, lower ATP and ADP and higher AMP leading to lower AEC, which results from lower H⁺-ATPase, Ca²⁺-ATPase and Mg²⁺-ATPase enzymes activity in plasma, vacuole and mitochondria membranes resulting to breaking ion homeostasis and decreasing plasma, vacuole and

mitochondria membranes integrity. Also, Lin et al. (2016) reported that the higher pericarp browning in longan fruit in response to exogenous H_2O_2 treatment during storage at 25°C for 10 days was accompanied with lower iATP supplying resulting from higher EMP-TCA respiratory system activity along with higher NAD and NADH accumulation, lower OPPP pathway activity along with lower NADP and NADPH accumulation and higher respiratory terminal oxidase CCO and AAO enzymes activity. Higher NAD and NADH accumulation in longan fruit in response to exogenous H_2O_2 treatment leading to lower NADP and NADPH accumulation result from lower NADK enzyme activity. Attenuating postharvest browning in litchi fruit treated with pure oxygen (Duan et al., 2004) and ATP (1 mM; Yi et al., 2010), longan fruit treated with propyl gallate (0.5 mM; Lin et al., 2013, 2015, 2017c; 2018) and chlorine dioxide fumigation (10 mg L^{-1} ; Chumyarn et al., 2016, 2017) and mushroom treated with higher O_2 (Li et al., 2017c) have been attributed to higher iATP supplying, higher ATP and ADP and lower AMP leading to higher AEC, results from higher H^+ -ATPase, Ca^{2+} -ATPase and Mg^{2+} -ATPase enzymes activity, which were accompanied with higher antioxidant system activity, lower PLD and LOX enzymes activity leading to higher membrane unSFA/SFA ratio concurrent with higher PAL/PPO genes expression and enzymes activity leading to higher phenols and flavonoids accumulation resulting higher DPPH scavenging capacity. Also, higher NADK enzyme activity leads to higher NADP^+ accumulation which can be used for higher NADPH accumulation via higher OPPP pathway activity by increasing G6PDH and 6PGDH enzymes activity. Higher NADPH accumulation resulting in higher antioxidant enzymes MDHAR and GR activity leading to higher AA/DHA and GSH/GSSG ratio which resulting in lower O_2^- and H_2O_2 accumulation. Lower O_2^- accumulation in longan fruit treated with propyl gallate results from higher antioxidant enzymes SOD, CAT and APX activity along with higher antioxidant molecules AA and GSH accumulation, but also may result from lower AAO enzyme activity which is crucial for maintaining AA accumulation along with lower CCO enzyme activity which by decreasing electron leakage leads to lower O_2^- accumulation. Also, higher NADPH accumulation may be responsible for higher GSH accumulation concurrent with higher membrane unSFA/SFA ratio in longan fruit treated with propyl gallate which are crucial for maintaining membrane integrity revealed by lower electrolyte leakage and MDA accumulation (Lin et al., 2013, 2015, 2017c, 2018).

Recently, Chen et al. (2018) reported that the attenuating browning and maintaining quality of mung bean sprouts during storage at 25°C for 3 days in response to postharvest ATP treatment (1 mM) was accompanied with lower PPO enzyme activity along with higher phenols accumulation, lower H_2O_2 accumulation resulting from higher SOD enzyme activity leading to higher ascorbic acid accumulation, higher firmness resulting from lower PG, pectin methyltransferase (PME) and pectate lyase (PL) genes expression and lower electrolyte leakage revealing higher membrane integrity. Chen et al. (2018) suggested that the beneficial impacts of exogenous ATP treatment was results from eATP signaling by perception at plasma membrane by LecRKs leading to increasing secondary messengers such as cytosolic Ca^{2+} , H_2O_2 and NO, which are crucial for attenuating postharvest stresses, delaying senescence and maintaining quality of horticultural crops (Aghdam & Bodbodak, 2013; Choi et al., 2014).

6. GABA shunt pathway attenuates postharvest chilling stress by ensuring sufficient iATP supplying

In plants, GABA as four-carbon non-protein amino acid has a signaling and metabolic function in response to biotic and abiotic stresses (Michaeli & Fromm, 2015). GABA shunt pathway is responsible for GABA biosynthesis from glutamate in the cytosol by glutamate decarboxylase (GAD), which is associated with H^+ consumption and CO_2 release. After transporting of GABA from cytosol to mitochondrial by GABA permease (GABP) as a mitochondrial GABA carrier, succinic

semialdehyde (SSA) generate from GABA by GABA transaminase (GABA-T) and enter into TCA cycle as succinate by NAD^+ dependent succinic semialdehyde dehydrogenase (SSADH), which act as electron donor to the mitochondrial ETS (Michaeli & Fromm, 2015). Insufficient iATP and carbon skeleton supplying in response to stresses and senescence which have oxidative facet may result from the sensitivity of succinyl-CoA synthetase and α -ketoglutarate dehydrogenase to oxidative stress leading to lowering TCA cycle activity (Michaeli & Fromm, 2015). During postharvest senescence and stresses, functional GABA shunt pathway activity could attenuate oxidative stress by providing NADH and succinate for the TCA cycle and ETS which are not only crucial for sufficient iATP and carbon skeleton supplying but also for attenuating H_2O_2 accumulation (Aghdam et al., 2016b; Aghdam, Naderi, Malekzadeh, & Jannatizadeh, 2016d; Michaeli & Fromm, 2015; Palma, Carvajal, Jamilena, & Garrido, 2014; Palma, Carvajal, Ramos, Jamilena, & Garrido, 2015). Palma et al. (2014) reported that higher chilling tolerance in Natura zucchini fruit during storage at 4°C for 14 days attributed to higher GABA shunt pathway activity representing by higher GABA-T enzyme activity resulting in higher iATP supplying. Palma et al. (2015) reported that the putrescine treatment attenuated chilling injury in Sinatra zucchini fruit, resulting from higher GABA shunt pathway activity representing by higher GABA-T enzyme activity resulting in higher iATP supplying. Also, exogenous putrescine treatment uptakes resulting to higher putrescine accumulation in Sinatra zucchini fruit during storage at 4°C for 3 days, but consumption of endogenous putrescine due to higher DAO enzyme activity during storage at 4°C for 14 days' results to GABA biosynthesis, which contribute to higher iATP supplying by GABA-T enzyme activity. Higher iATP supplying in Sinatra zucchini fruit treated with putrescine during storage at 4°C for 14 days was accompanied with higher endogenous proline and GB accumulation concurrent with higher oleate desaturase (FAD2) gene expression leading to higher membrane integrity revealed by lower MDA accumulation (Palma, Carvajal, Jamilena, & Garrido, 2016). Also, Palma et al. (2016) reported that the higher iATP supplying in Sinatra zucchini fruit treated with putrescine resulting by higher GABA shunt pathway activity during storage at 4°C for 14 days was accompanied with higher antioxidant enzymes CAT, APX and GR activity along with lower LOX enzyme activity leading to lower H_2O_2 accumulation. Also, higher AA accumulation in Sinatra zucchini fruit treated with putrescine leading to higher FRAP scavenging capacity, which concurrent with higher glucose, fructose and raffinose accumulation leading to higher membrane integrity revealed by lower MDA accumulation (Palma et al., 2016). Aghdam et al., (2016b, 2016d) reported that the attenuating chilling injury in anthurium cut flower by preharvest spray GABA (1 mM) and postharvest steam end dipping GABA (5 mM) and salicylic acid (2 mM) during storage at 4°C for 21 days attributed to higher GABA shunt pathway activity representing by higher GABA-T enzyme activity resulting in higher iATP supplying, higher ATP and ADP and lower AMP leading to higher AEC, which was accompanied with higher membrane unSFA/SFA ratio owing to lower palmitic, stearic and oleic acids accumulation along with higher linoleic and linolenic acids accumulation, lower PLD and LOX enzymes activity, higher antioxidant enzymes CAT, SOD, APX and GR activity leading to lower H_2O_2 accumulation, higher endogenous proline and GB accumulation and higher PAL/PPO enzyme activity leading to higher phenols accumulation resulting higher DPPH scavenging capacity, all of them resulting higher membrane integrity revealed by lower electrolyte leakage and MDA accumulation (Aghdam, Jannatizadeh, Sheikh-Assadi, & Malekzadeh, 2016a; Aghdam, Naderi, Jannatizadeh, Sarcheshmeh, & Babalar, 2016c). Thus, functional GABA shunt pathway could be a powerful mechanism to overcome chilling stress by ensuring sufficient iATP supplying.

7. GABA shunt attenuates postharvest decay by ensuring sufficient iATP supplying

Aghdam and Fard (2017) reported that the attenuating postharvest decay in strawberry fruit by melatonin treatment (0.1 mM) during storage at 4 °C for 12 days attributed to signaling function of H_2O_2 accumulation resulted from higher SOD enzyme activity concurrent with lower CAT and APX enzymes activity leading to higher GABA shunt pathway activity, higher GABA-T enzyme activity, resulting in higher iATP supplying, higher ATP and ADP and lower AMP leading to higher AEC, which was accompanied with higher unSFA/SFA ratio owing to lower palmitic, stearic and oleic acids accumulation along with higher linoleic and linolenic acids accumulation concurrent with higher phenylpropanoid pathway activity representing by higher PAL enzyme activity. Melatonin not only has ROS avoiding and scavenging cascade capacity, but also by promoting complexes I, III, and V activity accelerate electron flow via ETC leading to higher iATP biosynthesis (Tan et al., 2013). Sheng et al. (2017) reported that the GABA treatment (0.5 mM) attenuated postharvest decay in orange fruit which was accompanied with higher iATP supplying concurrent with higher citrate accumulation resulted from higher GABA-T gene expression and lower GAD gene expression, leading to higher antioxidant enzymes CAT and SOD activity. Since attenuating postharvest decay has higher iATP and carbon skeleton demand, GABA shunt pathway could supply NADH and succinate for TCA cycle and ETS which not only crucial for sufficient iATP and carbon skeleton supplying but also for attenuating H_2O_2 accumulation (Michaeli & Fromm, 2015). TCA cycle not only is crucial for iATP production but also has metabolic function by producing glutamate from 2-oxoglutarate, which may be used for the production of proline, NO, polyamines and GABA, which are beneficial for attenuation postharvest stresses (Aghdam & Bodbodak, 2013; Aghdam & Fard, 2017). Higher iATP and carbon skeleton not only are required for higher phenylpropanoid pathway activity which is crucial for cell wall fortification (Yi et al., 2008), but also are crucial for maintaining higher unSFA/SFA ratio, higher antioxidant system activity and higher phytoalexins and PRs proteins biosynthesis and accumulation with anti-fungal function (Aghdam et al., 2016b, 2016d; Yi et al., 2008). Yang, Sun, Fu, and Yu (2017) reported that the lower postharvest decay caused by *Alternaria alternata* in tomato fruit treated with glutamate ($100 \mu\text{g mL}^{-1}$) results from higher GABA shunt pathway activity by higher GAD, GABA-T and SSADH genes expression, higher EMP pathway activity by higher hexokinase and pyruvate kinase genes expression and higher TCA cycle activity by higher SDH and malate dehydrogenase enzymes activity, attenuating cell death via sufficient iATP supplying, concurrent with triggering salicylic acid signaling by higher PRs genes expression and enzymes activity (Yang et al., 2017).

8. Ensuring sufficient iATP supplying and friendly eATP signaling are crucial for postharvest biofactories

Postharvest biofactories representing high phenols accumulating fresh fruits and vegetables in response to abiotic stresses which are beneficial for human health (Han et al., 2017; Jacobo-Velázquez et al., 2011). Carrot in response to postharvest wounding stress exhibits higher phenols accumulation leading to higher DPPH scavenging capacity (Han et al., 2017). Higher phenols accumulation in carrot in response to postharvest wounding stress have higher iATP and carbon skeleton demand (Han et al., 2017). Carrot in response to postharvest wounding stress exhibited higher iATP supplying, higher ATP and ADP along with lower AMP leading to higher ATP, resulting from higher EMP and OPPP pathways activity, higher TCA cycle activity and higher ETS activity. Lower glucose and fructose accumulation in carrot in response to postharvest wounding stress attributed to higher OPPP and EMP pathways activity which by supplying sufficient carbon skeletons Er4P and PEP leading to higher phenylalanine accumulation by shikimate acid pathway. In addition to higher shikimate acid pathway,

higher phenylalanine accumulation by higher PAL, cinnamate 4-hydroxylase (C4H), and 4CL genes expression representing higher phenylpropanoid pathway activity leading to higher phenols accumulation (Han et al., 2017). Higher iATP supplying is crucial for shikimate and phenylpropanoid pathways activity leading to higher phenols accumulation. Also, Jacobo-Velázquez et al. (2011) reported that wounding stress by disrupting carrot cells membrane integrity results in releasing of ATP from cytoplasm (iATP) to apoplast (eATP). By perception of eATP as signaling molecule at the plasma membrane by DORN1 receptor via extracellular lectin domain activates intracellular serine threonine kinase domain leading to increasing cytosolic Ca^{2+} via Ca^{2+} channels resulting higher NADPH oxidase activity leading to higher O_2^- accumulation (Choi et al., 2014). Higher SOD enzyme activity is responsible for H_2O_2 accumulation in carrot in response to wounding stress which as signaling molecule is crucial for triggering phenylpropanoid pathway activity representing by higher PAL enzyme activity leading to higher phenols accumulation resulting higher oxygen radical absorbance capacity (ORAC; Jacobo-Velázquez et al., 2011). Also, higher H_2O_2 accumulation in carrot in response to wounding stress can results from higher NADH dehydrogenase and cytochrome b/c₁ oxidoreductase activity which results from electron leakage leading to higher O_2^- accumulation which by higher SOD enzyme activity results in higher signaling molecule H_2O_2 accumulation (Han et al., 2017; Jacobo-Velázquez et al., 2011). Also, Li et al. (2018) reported that the pitaya fruits treated with MeJA under wounding stress exhibited higher phenols accumulation, which was coincided with higher iATP supplying, higher ATP and ADP along with lower AMP leading to higher AEC, resulting from higher H^+ -ATPase, SDH, and CCO enzymes activity. Lower sugars accumulation in pitaya fruits treated with MeJA under wounding stress results from triggering sugars consumption by EMP and OPPP pathways for PEP and Er4P supplying which are crucial for shikimate pathway activity leading to phenylalanine supplying for phenylpropanoid pathway. Higher phenols accumulation in pitaya fruits treated with MeJA under wounding stress was concomitant with higher iATP and skeleton carbon supplying (Fig. 2; Li et al., 2018). Accordingly, sufficient iATP supplying and friendly eATP signaling are crucial for higher phenols accumulation in fresh fruits and vegetables in response to abiotic stresses representing postharvest biofactories which are beneficial for human health.

9. Conclusion

Fresh horticultural crops as perishable commodities are prone to postharvest quality and quantity losses due to biotic and abiotic stresses, such as chilling injury and fungal decay, leading to economic losses. Ensuring sufficient iATP supplying results from ATP biosynthesis (respiratory pathways and GABA shunt), dissipating (AOX and UCPs), transporting (ADP/ATP carrier, AAC) and signaling (SnRKs). Intracellular ATP status representing by AEC shortage during postharvest senescence and stresses. Intracellular ATP biosynthesis results from EMP and OPPP pathways activity, TCA cycle activity, ETS activity along with GABA shunt pathway activity. Postharvest treatments attenuate stresses, delay senescence and maintain quality in horticultural crops during postharvest life by ensuring sufficient iATP supplying, probably by activating SnRKs signaling pathway, which associated with higher membrane unSFA/SFA ratio owing to higher linoleic and linolenic acids accumulation along with lower palmitic, stearic and oleic acids accumulation, lower membrane degrading PLD and LOX genes expression and enzymes activity, higher HSPs accumulation, higher antioxidant system activity leading to lower O_2^- and H_2O_2 accumulation, higher endogenous GB accumulation by higher BADH enzyme activity, higher endogenous GABA accumulation by higher GAD enzyme activity, higher endogenous proline accumulation results from higher P5CS and OAT enzymes activity along with lower PDH enzyme activity, higher lycopene accumulation results from higher PSY1 and ZDS genes expression, lower cell wall degrading enzymes PG and EGase

activity, lower lignin accumulation by lower *MYB1* and *4CL* genes expression, higher phytoalexins and PRs proteins biosynthesis and accumulation with antifungal function, higher phenylpropanoid pathway activity representing by higher PAL enzyme activity, higher AOX gene expression, higher polyamines putrescine, spermidine and spermine accumulation, higher OPPP respiratory pathway activity leading to higher NADPH supplying, higher endogenous H₂S accumulation and lower chlorophyll degradation, which are crucial for maintaining membrane integrity and cell wall fortification (Table 1). In addition to the function as intracellular energy currency, ATP serves as a friendly extracellular signaling molecule (eATP) which is crucial for iATP biosynthesis machinery activity and defense hormones jasmonic and salicylic acids signaling pathways. Also, friendly eATP signaling not only is crucial for regulating stomatal closure in horticultural crops pivotal for photosynthesis, water homeostasis, and pathogen resistance but also is crucial for postharvest biofactories representing high phenols accumulating fresh fruits and vegetables in response to abiotic stresses which are beneficial for human health. Beneficial impacts of exogenous ATP treatment in horticultural crops may result from friendly eATP signaling via eATP perception at the plasma membrane by LecRKs. Activation of friendly eATP signaling in horticultural crops during postharvest life by exogenous ATP treatment is beneficial for attenuating stresses, delaying senescence and maintaining quality (Table 2). Therefore, ensuring sufficient iATP supplying and friendly eATP signaling would be crucial for attenuating stresses and delaying senescence in horticultural crops during postharvest life resulting in extending postharvest storage life with preserved nutritional quality.

Conflicts of interest

The authors declare that they have no conflict of interest.

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