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REVIEW



Phytohormones in postharvest storage of fruit and vegetables: mechanisms and applications

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ABSTRACT

As a ubiquitous and essential part of phytophysiology, phytohormones have attracted tremendous attention for effective regulation of development and senescence of agricultural products. However, the postharvest mechanisms of phytohormones have not been thoroughly understood. This review provides an overview of common phytohormones for extending the shelf life of fruit and vegetables. The modulation principles are discussed in detail based on defence gene expression activation, sensitivity of senescence-related phytohormones inhibition, antioxidant enzymes activity stimulation, and cell membrane integrity maintenance. The applications of jasmonates, salicylic acids, cytokinins, gibberellins, polyamines, and brassinosteroids in preserving fruit and vegetables based on defence signaling network stimulation, senescence-related phytohormones expression or sensitivity repression, as well as antioxidant system enhancement and cell membrane integrity sustentation are introduced. The challenges and problems to be solved are discussed, and new trends of expanding lifespan by combining phytohormones with other treatments are also suggested. Although phytohormones have been demonstrated to have promising efforts in maintaining agricultural products, more novel and effective combination treatments should be developed to complement each other.

KEYWORDS

Fruit and vegetables; phytohormones; postharvest storage; preservation

1. Introduction

Containing a variety of vitamins, dietary fibers, carbohydrates and minerals, fruit and vegetables are essential nutrient sources for the human diet (Li, Zhu, and Sun 2018; Zhan, Zhu, and Sun 2019d). According to the UN Food and Agriculture Organization (FAO), the gap between supply and demand is broadening with increasing population and food loss and waste (Lipinski et al. 2013; Searchinger et al. 2018). The scientific community has also paid attention to this grim situation and warned that bridging the gap is extremely urgent and significant (Alabi, Zhu, and Sun 2020; Tian, Zhu, and Sun 2020d; Willett et al. 2019).

Up to now, various preservation methods have been exploited to maintain the quality of fruit and vegetables, such as rapid precooling to remove the field heat using vacuum cooling (Sun and Hu 2003; Wang and Sun 2002; Zheng and Sun 2004), low-temperature control and monitoring during the cold chain (Luo et al. 2018; Tian et al. 2020a; Zhang, Ma, and Sun 2020), using controlled or modified atmosphere in packaging and storage (Reed 2017; Severino et al. 2015; Sun and Zheng 2006). Generally, these preservation methods can be divided into physical, chemical

and biotechnological treatments, all of which have prominent effects on prolonging the shelf life of the fresh commodity (Table 1).

Physical methods such as cooling are convenient and effective. As fruit and vegetables are complex and various, their effectiveness and limitations vary with products, while chemical methods can be effective but possible chemical residues make them unacceptable by consumers. On the other hand, biotechnological methods, such as enzymic technique and phytohormones, are nontoxic and safe for the industry. In particular, researchers have found that phytohormones are excellent maintainer in extending the shelf life of fresh products. Phytohormones can be produced by plants or artificially synthesized, and both of these phytohormones can participate in biochemical and phytophysiological reactions. Therefore, different from normal chemical methods, phytohormones treatments can provide a prominent technique to modulate the physiological degradation of fresh fruit and vegetables.

Some relevant reviews have been published in the past. Mahajan et al. (2014) summarized the characteristics of diverse postharvest methods of fresh produce according to

Table 1. Comparison of common preservation treatments.

Treatments		Advantages	Disadvantages	Reference
Physical method	Irradiation treatment	Sterilization, no residue and heat loss, stimulating secondary metabolisms	Narrow usage, low speed, unacceptable in some countries	Arvanitoyannis, Stratakos and Tsarouhas (2009)
	Heat treatment	Delaying Senescence, sterilization and decay control	Non-enzymatic browning, high energy and labor costs	Mahajan et al. (2014)
	Edible coating	Less water loss, better color and texture, higher quality and natural aroma contents	Expensive, lack of materials with desired properties, regulatory changes	Mahajan et al. (2014) Dhall (2013)
	Controlled atmosphere storage (CA)	Retarding physiologic metabolic activities, reducing spoilage	Expensive	Both et al. (2017)
	Modified atmosphere packaging (MAP)	Senescence delaying, respiration and spoilage reduction	Condensation inside package leading to safety risk and degradation	Jayas and Jeyamkondan (2002)
	Microwave and ultrasonic wave treatment	Sterilization, efficient	Heat loss, quality deterioration	Guo et al. (2017) Tian et al. (2020b) Tian et al. (2020c) Tian et al. (2021) Zhang, Zhu, and Sun (2018)
	Electric and magnetic treatment	Rapidity, quality maintenance	Small scale, expensive	Bobinaite et al. (2015) Mahato, Zhu, and Sun (2019) Zhan et al. (2018) Zhan, Zhu, and Sun (2019a)
	Ultra-high-pressure treatment	Sterilization, rapidity, quality maintenance	Expensive, inactivation of enzymes	Volkert et al. (2012)
Chemical method	Synthetic chemical treatment	Rapidity, inexpensive, efficiency	Chemical residue	Mahajan et al. (2014)
Biotechnological method	Enzymatic treatment Phytohormones	Nontoxicity, specificity Secondary metabolite, effective and harmless	Narrow range Many specific reactions remain to be confirmed	Hanušová et al. (2013) Shi et al. (2019) Song et al. (2018)

physical, chemical, gaseous, and emerging treatments. Voß et al. (2014) described modeling ways to understand transport and signaling pathways of phytohormones. Wani et al. (2016) reviewed various roles, engineering techniques, and crosstalk of phytohormones under cold, drought, and high-temperature conditions in crop plants. However, no review is available on the mechanisms and effects of phytohormones on extending the postharvest shelf life of fruit and vegetables. Therefore, the current review focus on the effect of phytohormones on physiological change during the postharvest stage. The mechanisms of these phytohormones based on activating defensive genes expression, repressing sensitivity of senescence-related phytohormones, stimulating antioxidant enzymes activities, and maintaining cell membrane integrity are presented, applications of six common phytohormones in extending the shelf life of fruit and vegetables are discussed, future challenges on developing phytohormones as an effective postharvest technology are highlighted. It is hoped that the current review should provide a further understanding of phytohormones regulation pathways for their better utilization in preserving agricultural products.

2. Mechanisms of phytohormones modulation

Phytohormones are a group of signal molecules produced in plants. They have significant effects on regulating metabolism even with an extremely low concentration (Wani et al. 2016). Although different definition and criterion may affect the classification of phytohormones (Mander and Liu 2010), jasmonates (JAs), salicylic acid (SA), cytokinins (CTK), gibberellins (GAs), polyamines (PAs), brassinosteroids (BRs), abscisic acid (ABA), and ethylene (ETH) are recognized as the common phytohormones (Arif et al. 2020; Wani et al. 2016; Yang and Li 2017).

JAs are originated from fatty acids in membrane metabolism composing with methyl jasmonate (MeJA) and free acid jasmonic acid (JA). JAs play multiple roles in plant growth, development, and reproduction. It also shows various defence responses from pathogen to environment stresses (Wani et al. 2016). Thereby, the JA pathway is an important part of the defence system (Gapper, McQuinn, and Giovannoni 2013).

SA is a natural phenolic, which is another inevitable member of the defence system. As an omnipresent phytohormone, SA also shows vital effects on growth, development, ripening, and reactions to environmental stresses (Yang and Li 2017; Glowacz et al. 2017; Abdelrahman et al. 2017). Moreover, different concentrations of SA play converse roles in plants. Low SA concentration can enhance environmental resistance while high concentrations of SA may induce cell degradation (Wani et al. 2016).

CTKs are a range of process regulators in the plant. Previous researches indicated that CTK can stimulate cell division, bud differentiation, seed germination, chloroplast formation and particularly delay of senescence (Wani et al. 2016). It has been demonstrated by the USA Environment Protection Agency (EPA) that CTK, like kinetin and 6-benzylaminopurine (6-BA), are nontoxic plant growth regulators in agriculture (Xu et al. 2012). Therefore, CTK has become a widely used compound in prolonging the shelf life of fruit and vegetables.

GAs regulate growth and development in plants (Wani et al. 2016). With a gibberellane carbon skeleton and

carboxyl in seventh carbon, GAs can activate seed germination as well as cell division. GAs also have antagonistic effects with senescence-related hormones, such as ETH and ABA (Huang et al. 2014). Hence, GAs are widely used in extending the shelf life of horticultural products.

PAs mainly consist of two or more amine groups including spermine, spermidine, or putrescine and can regulate physiological-biological processes from DNA replication to organ development as well as protective responses to environmental stresses. As a result, PAs have been applied in postharvest to integrate disorders caused by abiotic stresses (Koushesh Saba, Arzani, and Barzegar 2012; Song et al. 2018).

BRs are a group of sterolide compounds derived from mevalonic acid. Their biosynthesis is similar to CTK (Bajguz and Hayat 2009), and thus impact on plant production and adaption to environment stresses (Ali et al. 2018). Recent experiments also explored BRs treatments for enhancing fruit tolerance during biotic and abiotic stresses (Aghdam et al. 2012; Li et al. 2012).

Finally, ABA and ETH are usually considered as two senescence and maturity regulation phytohormones. Both are increased in senescent and injured horticultural products after harvest. Therefore, proper control of the level of synthesis and metabolism of these two phytohormones is effective and significant in preserving fruit and vegetables (Kashyap and Banu 2019). Although the phytohormones presented above are mainly involved in growth and development modulation in plants, they can be applied to prevent postharvest disorders and diseases of fruit and vegetables for quality maintenance in a number of ways.

2.1. Activating the expression of defence genes

Pathological decay, physiological disorder, mechanical injury, and senescence are critical reasons for postharvest quality degradation (Luo and Sheng 2010). The defence system is developed to face those abiotic and biotic stresses. These defensive responses comprise insect resistance mainly triggered by JAs (Guo, Major, and Howe 2018; Kazan 2015; Shin et al. 2017) and disease resistance basically induced by SAs (Aghdam and Bodbodak 2013; Shi et al. 2019). JA and SA do not completely work alone. They always have crosstalk with other phytohormones (Arif et al. 2020).

JAs play a prerequisite role in the defence system. These compounds trigger defence responses mainly through relieving suppression of jasmonate ZIM-domain gene (JAZ, a family of proteins acting as repressors of many transcription factors) to JA response genes. Then response genes transcribe to produce phytoalexins and protease inhibitors to survive in unpredictable environments (Howe, Major, and Koo 2018; Taiz and Zeiger 2015). Studies on module plants like Arabidopsis thaliana and Oryza sativa (L.) revealed a specific, tunable and evolvable signaling pathway of JAs (Guo, Major, and Howe 2018; Howe, Major, and Koo 2018; Kazan 2015; Okada, Abe, and Arimura 2015).

Both endogenous and exogenous JAs need to be conjugated with amino acid under the participation of

dihydrodipicolinate synthase, JA conjugation enzyme (JAR1 protein), to generate bioactive jasmonate (Taiz and Zeiger 2015). The best known receptor-active conjugation is jasmonoyl-L-isoleucine (JA-Ile), which exists in higher plants extensively (Howe, Major, and Koo 2018). This bioactive compound combines with coronatine insensitive 1 (COI1, protein binding with Skp1/Cullin counterparts to act as the mediated proteasome, SCFCOII) (Adams and Turner 2010) to localize to protein JAZ, resulting in degradation of JAZ repressors (Howe, Major, and Koo 2018). Once JAZ is inhibited, transcription factor MYC2 (a basic helix-loop-helix transcription factor which functions as a master regulator to many jasmonate-response genes) (Okada, Abe, and Arimura 2015) starts activating jasmonate-response genes transcription

Jasmonate-response genes comprise tremendous hereditary factors including ETH responses gene Ethylene insensitives (EINs), senescence-related gene WRKY and cold acclimation gene ICE (Howe, Major, and Koo 2018; Kazan 2015). These factors govern various physiological output responses from biotic to abiotic outputs (Howe, Major, and Koo 2018; Hu et al. 2013). All of these genes are under the trigger of MYC2. MYC2 is suppressed by JAZ, of which synthesis and degradation ratio are regulated by the concentration of JA-Ile (Taiz and Zeiger 2015). Except for JA-Ile, JAZ is also influenced by other effectors, such as receptors of SA-NPRs and GAs associated DELLA proteins (Howe, Major, and Koo 2018). Different phytohormones have mutual effects and form signal integration and molecular crosstalk (Figure 1) (Kazan 2015).

SA plays a vital role in withstanding a broad range of pathogens and reactions to various biotic stresses. After infected by pathogens, SA is involved in massive procedures from basal and resistance gene-regulated defence to systemic acquired resistance (SAR) (Lu, Greenberg, and Holuigue 2016). Genetic evidence shows that SA binds to receptors, which are adaptors of Cullin 3-based E3 ubiquitin ligase, and then relieves inhibition of repressor on SA-response genes to acquire SAR and attract expressions of pathogenesis-related (PR) genes (Lu, Greenberg, and Holuigue 2016; Taiz and Zeiger 2015; Yan and Dong 2014).

Both of endogenous or exogenous SA can regulate defensive processes. After SA perceives, the nonexpressor of PR genes (NPRs; a family of ankyrin-repeat proteins acting as SA transducers), especially NPR3 and NPR4 are triggered through cell redox reactions (Saleh et al. 2015). Then conjugation of NPR3 and/or NPR4 to SA combines with E3 ubiquitin ligase, leading to degradation of NPR1 and removing inhibition on NIM1-INTERACTING (NIMIN) proteins and transcription factors, including activators (e.g., TGA3) and repressors (e.g., WRKY70) to defence genes (Saleh et al. 2015; Yan and Dong 2014). More precisely, NPR3 and NPR4 regulate the degradation of NPR1 under high and low concentrations of SA correspondingly. Through the antagonism combination, activation and degradation of NPR1, immune responses can be modulated.

With the *npr1* mutant, there are still NPR1-independent pathways by activating the immediate early gene AtWhy1 which contains PB promoter element to PR-10 gene

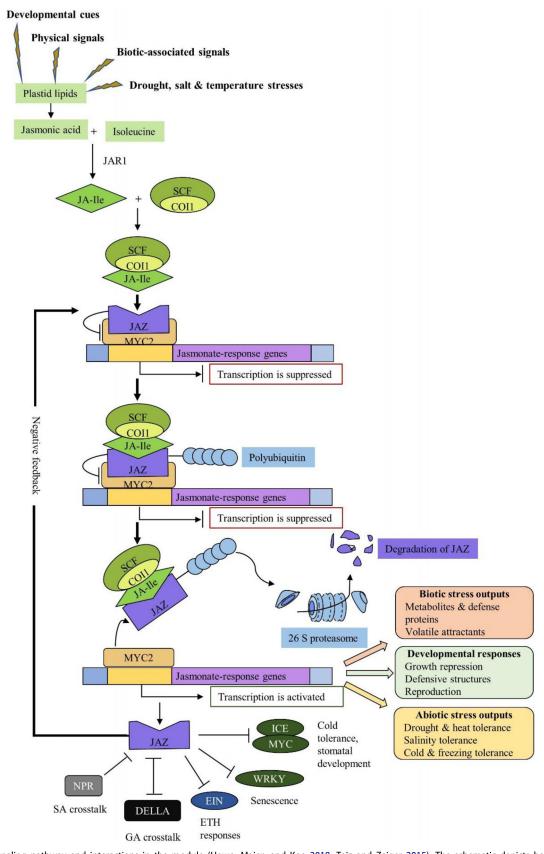


Figure 1. JAs signaling pathway and interactions in the module (Howe, Major, and Koo 2018; Taiz and Zeiger 2015). The schematic depicts how JAs stimulates defence genes translations and trigger defensive responses. Inductive signals are recognized by receptors at the surface of the cell and elicit synthesis of JA-lle under the participation of JAR1 through binding JAs to isoleucine. JAZ proteins are sequent degraded via conjugation of JA-lle to SCF^{COI1} and polyubiquitination of 26 S proteasome. Suppressions of transcription factors, like MYC, are removed and JA response genes are activated to produce various physiological responses during growth, development, senescence and tolerance to biotic and abiotic stresses. In the bottom of the figure, there are some jasmonate-regulate activities. Both of SA-associated NPRs proteins and GA-associated DELLA proteins will modulate JAZ functions. Jasmonate outputs are executed by tremendous transcription factors. Different transcription factor family is colored in different colors. bHLH factors colored in green occupy a prominent position in the JA signaling pathway. MYC can combine with ICE to resist cold or freezing stimuli while WRKY is involved in senescence. ETH responses can be controlled by EINs. JAZ proteins also have negative feedback to JA-lle.

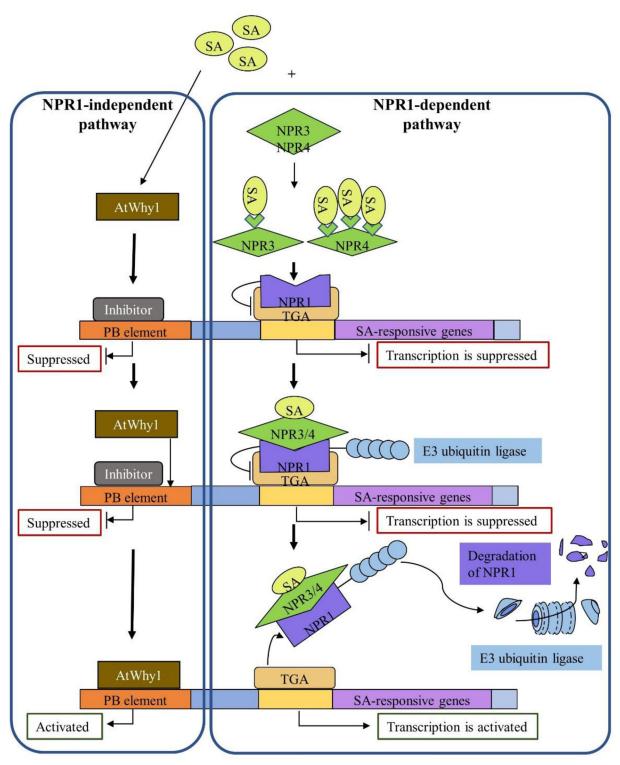


Figure 2. SA signaling pathways (Fu et al. 2012; Lu 2009; Taiz and Zeiger 2015; Uquillas et al. 2004). The scheme describes the SA-mediated defence network which is mainly comprised of NPR1-independent pathway and NPR1-dependent pathway. For NPR1-dependent pathway, after perceived SA, NPR3 and NPR4 act as SA receptors at low and high SA concentration respectively. Then the complex combines with Cullin 3-based E3 ubiquitin ligase and lead to degradation of NPR1 through removing inhibition on TGA, the activator of SA-responsive genes. For NPR1-independent pathway, SA stimulates expression of AtWhy1 which relieves suppression on PB element which is the elicitor of defence responses and SAR.

(Uquillas et al. 2004). Besides, compared with the NPR1-dependent pathway, NPR1-independent pathway does not need to biosynthesize novo protein firstly in the activation of *AtWhy1* (Desveaux et al. 2004). Even so, NPR1 is indispensable in the SA defence signaling networks including the NPR1-dependent pathway and NPR1-independent pathway.

Because NPR1 can be placed both in upstream and downstream of immunity responses in the SA signaling network, the global pathway of SA is interconnected and complicated. However, there are some other pathway remained to be determined (Figure 2) (Uquillas et al. 2004; Yan and Dong 2014).

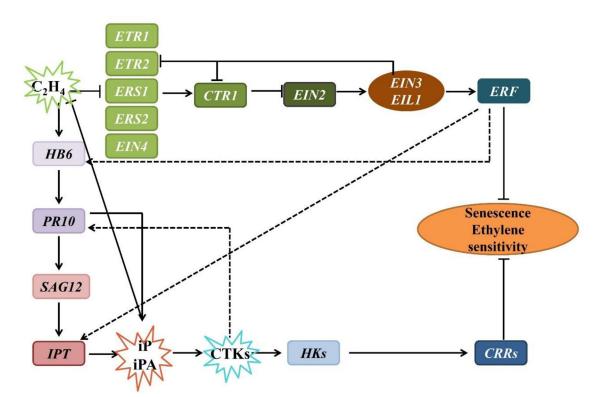


Figure 3. The signaling network between CTKs and ETH (Lines with small bar mean negative regulation, the solid arrow means positive regulation and the dotted arrow represents possible regulation.) (Khaskheli et al. 2018; Ma et al. 2018). The figure exhibits details of ethylene regulation in plants senescence while at the bottom of the picture shows particulars of ethylene modulating CTKs and how CTKs dealing with senescence. The ethylene-responsive factor can upregulate expression of CTKs biosynthesis gene *IPT* and nucleotide-binding module *HB6-PR10*, eventually, increases the concentration of CTKs in plants. Bioactive precursors of CTKs include iP and iPA, both of which are repressors of ETH biosynthesis. Receptors and regulators of CTKs can inhibit senescence and ethylene sensitivity.

2.2. Inhibiting the expression and/or sensitivity of senescence-related phytohormones

Senescence is a process occurring in all fruit and vegetables after harvest. The regulations of senescence by phytohormones include both promoting and inhibiting factors. ETH and ABA are promoting factors, which can accelerate senescence process, while CTK and GAs are inhibiting factors, which can retard ageing through suppressing biosynthesis and/or sensitivity of senescence-related phytohormones (Ma et al. 2018). Therefore, CTK or GAs pathways are useful for extending the shelf life in post harvested produce (Miret, Munne-Bosch, and Dijkwel 2018).

CTK may repress the production of ETH through bioactive derivative N^6 -(Δ^2 -isopentenyl)-adenine (iP), and isopentenyl adenosine (iPA), and/or decrease the sensitivity of ETH by cytokinin response regulators (CRRs) (Khaskheli et al. 2018). However, the interconnected networks between CTK and ETH, or other senescence-associated compounds have not been totally revealed, only potential pathways are available.

Homeobox protein 6 (*HB6*) and pathogenesis-associated PR10 family gene (*PR10*) acts as a nucleotide-binding site and is a regulatory module in the ethylene pathway. Endogenous CTK content can be increased by hydrolyzing *HB6-PR10* complex into isoprenoid CTKs with ribonuclease (RNase) participation (Sakakibara 2006). This regulation module can also motivate the expression of the senescence-related gene *SAG12* (a marker of senescence delaying and ethylene desensitivity). Both *PR10* and *SAG12* are involved

in RNase activities. *SAG12* is an indispensable gene in the biosynthesis of CTK, which can upregulate the isopentenyl transferase gene (*IPT*) as well as *HB6-PR10* (Ma et al. 2018; Wu et al. 2017). Moreover, CTK treatment can enhance *PR10* expression in horticultural products (Wu et al. 2017).

iP, iPA and CTKs trans-zeatin are activators of the CTK pathway. iPA is an efficient repressor of ethylene synthesis in immature and mature crops. Furthermore, Apetala 2/ ethylene-responsive factor (AP2/ERF) gene, ERF113, plays a crucial role in boosting expressions of HB6-PR10 module and CTK biosynthesis genes, such as IPT5 and IPT8. Meanwhile, silenced ERF113 leads to a decrease of CTK receptors histidine kinase (HK) 2&3 (HK2 & HK3) and CRR3/5/8 and eventually suppress the expression of CTK (Khaskheli et al. 2018). On the other hand, ERF gene family are also pivotal responders in the ethylene pathway. Some act as senescence accelerators and play positive roles in volatile biosynthesis and others have functions in retarding ethylene-induced senescence through CTK (Figure 3) (Khaskheli et al. 2018; Ma et al. 2018).

Although there are many applications of GAs in preservation, the mechanisms of regulation at the molecular and gene-level are not clear. Several hypotheses have been proposed to explain the function of GAs in extending the shelf life of fresh products. It was suggested that GAs would repress biosynthesis and expression of ethylene to prolong the lifespan of products. Specifically, exogenous GA₃ can upregulate transcriptions of *1-aminocyclopropane-1-carboxylate synthase-1* (ACS1) and *1-aminocyclopropane-1-carboxylate*

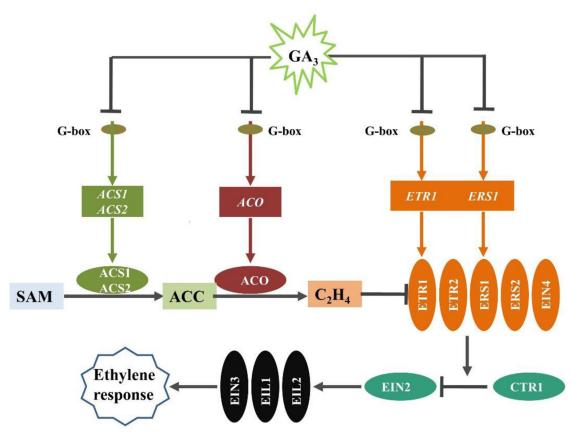


Figure 4. The signaling network between GAs and ETH (Kashyap and Banu 2019). This module shows that exogenous GAs will repress transcription of ethylene synthases and oxidase including ACS and ACO. Both of them are indispensable enzymes in biosynthesis ETH from SAM. As a result, GAs reduce the output of ethylene in plants, slower ripening process and extend shelf life. Moreover, GAs can also impede transcription of ethylene receptors, especially ETR1 and ERS1, both of which are stimulators of CTR1, the negative regulator of ethylene response. Upregulation of CTR1 and downregulation of ETR1 as well as ERS1 will greatly impact ETH perception. Consequently, application of GAs will impede biosynthesis and expression of ethylene.

synthase-2 (ACS2) (Kashyap and Banu 2019). Both ACS1 and ACS2 are two of the key genes encoding the biosynthesis of ethylene. Ethylene response-1 (ETR1) and ethylene response sensor-1 (ERS1) are vital activators belonging to constitutive triple response-1 (CTR1). In ethylene expression, CTR1 will hinder another subfamily of receptors comprising ethylene insensitive 3 (EIN3), ethylene insensitive 3-like-1 (EIL1), and ethylene insensitive 3-like-2 (EIL2). Upregulations of ACS1 and ACS2 would stimulate ethylene production, while an increase in ETR1 and ERS1 would suppress the expression of ethylene. Hence, the application of GA3 can prolong shelf life through ETH biosynthesis and signaling pathway (Figure 4).

In *Arabidopsis thaliana*, GA interacts with the receptors - gibberellin-insensitive dwarf 1 (*GID1*) and forms a combined substance, GID1-GA. GID1-GA is associated with proteolysis of aspartic acid-glutamic acid-leucine-leucine-alanine (DELLA), which can upregulate transcripts of *XERICO*, acting as zinc finger factor of RING-H2 (Ariizumi et al. 2013). The level of *XERICO* shows a positive effect on ABA biosynthesis (Ko, Yang, and Han 2006). Adding GA decreases GID1-GA-DELLA complex formation, repressing the expression of *XERICO*, and downregulating ABA production (Golldack et al. 2014). The evidence proves that the application of GAs and CTK may influence biosynthesis and expression of senescence-related phytohormones in fruit and vegetables.

2.3. Stimulating activities of antioxidant enzymes

During harvesting and preservation, reactive oxygen species (ROS) and free radicals may be induced badly (Figure 5). These superfluous metabolites can shorten the shelf life of fresh products because of the oxidation, inactivating enzymes and decomposing membranes (Jajic, Sarna, and Strzalka 2015). Exogenous phytohormones can eliminate these negative derivatives by activating accumulation of antioxidants enzymes or metabolites, like superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), glutathione peroxidase (GSH-Px), ascorbic acid (AsA), β -carotene and glutathione (GSH) (Birben et al. 2012; Jajic, Sarna, and Strzalka 2015).

Hydrogen peroxide (H₂O₂) is the most stable ROS, which can transport readily between membranes (Jajic, Sarna, and Strzalka 2015). Singlet oxygen acts as a critical signal in activating related stress-responses and H₂O₂ triggers the main damages. The singlet oxygen originates from electron transport chain (ETC), respiration and some redox reactions, which is reduced as hydroperoxyl radical (HO₂) and H₂O₂ when interacting with SOD, and H₂O₂ is reduced as H₂O under the participation of NADPH by CAT, AsA, GSH, etc (Figure 5). Consequently, elimination of ROS can not only protect nucleotides, proteins, and lipids, from oxidative damage but also consume NADPH to impair respiration activities (Kasote et al. 2015). Therefore, activating antioxidant enzymes result in relieving oxidative stress and maintaining a higher level of metabolites.

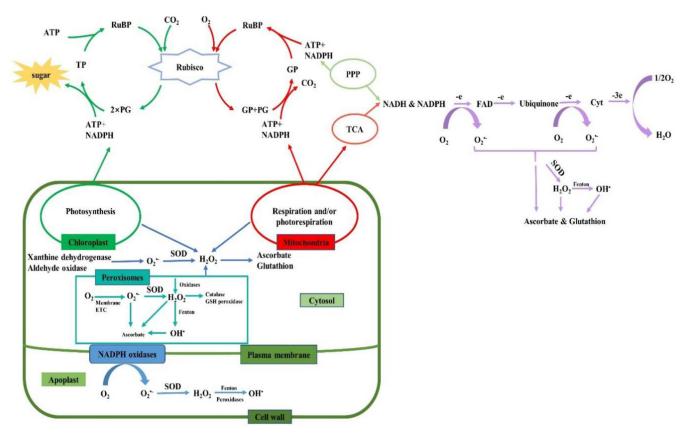


Figure 5. Antioxidant activities and related physiological activities in plants cells (Jajic, Sarna, and Strzalka 2015; Kasote et al. 2015). The figure represents antioxidant activities in the cell. Generally, oxidation substances derive from oxygen and are turned into ROS during diverse physiologic activities like respiration, photosynthesis and photorespiration in various places containing membrane, apoplast, cytosol, chloroplast and mitochondria. These ROS could be scavenged and/or transformed by reductive components and oxidoreductases. For example, superoxide anion free radical $(O_2 \bullet^-)$ evolves into H_2O_2 under the participation of SOD and finally eliminated by CAT, ascorbate and glutathione. H₂O₂ can also be transformed into hydroxyl radical (OH•) through Fenton reaction or peroxidase and eventually scavenged by ascorbate and glutathione. Not insignificant, NADPH and NADH are indispensable in ROS elimination. Meanwhile, they are products of Kreb's cycle (TCA) and glycolysis pathway (PPP) and substrates of Rubisco cycle. Hence, enhancing activities of antioxidant enzymes and reductive substances may release cells from ROS damage and influence respiration and photosynthesis.

2.4. Regulating the integrity of plasma membrane

Containing double lipid bilayer and proteins embedded inside, the plasma membrane is a complex and prerequisite organization associated with many physiological processes and cell defence (Gronnier et al. 2018). The integrity of the plasma membrane refers to structure completeness and function perfection, which is important in defending biotic and antibiotic stresses.

Exogenous phytohormones are reported to enhance defence capability to extend shelf life through manipulating the integrity of the plasma membrane. One possibility is to apply phytohormones, like BR, to upregulate membrane protein genes including Remorins family protein (REM), abscisic stress ripening-like protein (ASR), temperature-induced lipocalin protein (TIL), and typeII SK2 dehydrin (TSD) (Li et al. 2012). REM proteins are considered as membrane skeleton proteins and responsive to environmental stimuli and signal transduction. ASR plays as signal transductor in cold conditions, which scatters in the whole cell. TIL proteins usually act as harmful molecules scavengers on the surface receptors of the plasma membrane with hydrophobic ligands including fatty acids, steroids, odorants, etc. TSD proteins are a group of stress proteins maintaining membrane stabilization and activating antioxidative capabilities (Zhang and Tian 2010).

Another possibility is to apply phytohormones to alter the synthesis of fatty acids especially unsaturated fatty acids (UFAs). Linoleic acid and linolenic acid lead an increase in the double bond index and a reduction in phase transition temperature. In addition, membrane fluidity is improved with an increase in UFAs proportion and better adaption to environmental responses, such as resilience reduction and electrolyte permeability aggravation (Li et al. 2012).

3. Applications of phytohormones in postharvest storage

Figure 6 shows the publication profile of the six phytohormones introduced above during 2010-2020. A total of 175 articles were published in the past decade. Figure 6B exhibits the numbers and percentage of phytohormone applications in fruit and vegetables regarding different phytohormones and treatment modes. In the recent decade, SAs attract the majority of research interests, accounting for 48.0% of the total research papers. Single phytohormone treatment is the mainstream of applying phytohormones during postharvest storage (68.0%). These studies confirmed the advantages of phytohormones in postharvest storage of fruit and vegetables as summarized in Table 2, including

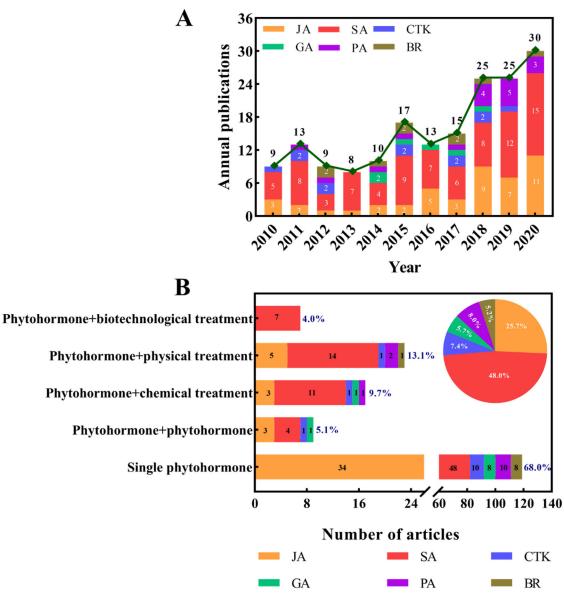


Figure 6. Publication profile concerning phytohormones during 2010-2020. (A) Numbers and types of annual publications. (B) Numbers and percentage of phytohormone applications regarding different phytohormones and treatment modes. JA: Jasmonates, SAs: Salicylic acids, CTK: Cytokinins, GAs: Gibberellins, PAs: Polyamines, and BRs: Brassinosteroids.

stimulating response to biotic stress, delaying senescence, enhancing antioxidant system and maintaining cell integrity.

3.1. Stimulating response to biotic stress

Table 2 summarizes the positive effects of phytohormones on prolonging the shelf life of fruit and vegetables. High cold resistance during the storage period is also observed after JAs or SAs treatments. For instance, Chen et al. (2019) proved that exogenous MeJA could alleviate chilling injury in peach fruit, and Glowacz et al. (2017) showed that 100 μmol/L MeJA and MeSA could sharply relieve chilling injury in 'Hass' avocados. Besides, different phytohormones are often applied together to achieve better preservation. SAs always combine with JAs to resist bacterial and retard chilling injury (Siboza, Bertling, and Odindo 2014).

Zhu et al. (2015) indicated that the infection rate was decreased significantly from 18.7% to 4% as compared with

the control in *Citrus unshiu*, which was treated with 5 mg/L 24-epibrassinolide (EBR) alone and stored for 50 days. '*Kyoho*' grapes were sprayed with 0.5% w/v burdock fructooligosaccharide (BFO) and stored at 25 °C for 24 h and it was found that SA-dependent pathway was triggered to defense diseases (Sun et al. 2013), while spermine treatment at 1.0 mmol/L could effectively inhibit the decay index of vegetable *Glycine max* (Song et al. 2015). These results show that single phytohormone has multiple functions, crosstalk, as well as mutual effects, which exists among different members.

3.2. Delaying senescence

Senescence is an inevitable physiological process for plants, which apparently influences the lifespan of the products after harvest. Therefore, it is a challenge for conventional methods to mitigate this adversity due to the ubiquitous endogenous ETH, ABA, etc, which are related to ripening

Phytohormones	Treatment mode	Materials	Preservation conditions	Type of application	Results	Reference
JAs	JA	Mangosteen	Immersed with 0.20 mM MeJA and	Enhancing	Delayed weight loss and pericarp hardening, well-maintained antioxidant activity, PPO	Mustafa et al. (2018)
	4 S + A1	Penner	Stored at 6°C for 12 d Treated with 0.05 mM Me1A and	antioxidant system Enhancing	activity and cold tolerance Inhibited seed browning and well-maintained of utamate sucrose and galacting	Sen et al. (2020)
			0.25 mM MeSA, stored at 2°C and	antioxidant system	ממת מינים מינים מו מינים וויים שני וויים שמינים מינים	(242)
	10 - Aleminal treatment	Cicimber	13°C With 85-90% RH for 25 d Treated with 0.01 mM MelA and	Enhancing	Inhibited H.O. appearation and anhanced CAT activity and page aspraceion	(3016)
			1.00 mM SNP, stored at 5 °C in the	antioxidant system	וווווסוגים ו207 פנובומנסון, מוס כוווומוגים כדו מנימיון מוס פנוב בארכננום	
	JA + physical treatment	Broccoli	Treated with ultrasound (20 min, 24 kHz,	Delaying senescence	Increased accumulation of 4-hydroxy glucobrassicin, glucoerucin, gluconas-turtiin,	Aghuilar-Camacho, Welti-
			amplitude 100 µm), and 1.15 mM		neoglucobrassicin, 3-O-caffeoylquinic acid, 1-sinapoyl-2-fer-ulolylgentiobiose,	Chanes, and Jacobo-
SAs	SA	Avocado	MeJA, and stored at 15 $^{\circ}$ C for 3 d Treated with 0.1 mM MeSA vapors and	Maintain cell integrity	and1,2,2-trisinapoy/gentiobiose Alleviated chilling iniury by altering the fatty acid content and composition	Velázquez (2019) Glowacz et al. (2017)
			stored at 2 °C for 21 d and 20 °C for 6-7 d			
	SA + JA	Pepper	Treated with 0.05 mM MeJA and	Enhancing	Inhibited seed browning, and well-maintained glutamate, sucrose, and galactinol	Seo et al. (2020)
			0.25 mM MeSA, stored at 2°C and 13°C with 85-90% RH for 25 d	antioxidant system		
	SA + chemical treatment	Bell pepper	Dripped in 0.5 g L ⁻¹ trisodium	Maintain cell integrity	Increased genes expression and content of key unsaturated fatty acids, and enhanced	Ge et al. (2020)
			phosphate for 20 min, sprayed with 0.20 mM SA for 10 h, and stored at 4 ± 1 °C with 80–85 % RH and 20 + 1 °C for 3 d		water retention	
	SA + physical treatment	Lemon	Dipped in 2 mM SA, waxed and stored at -0.5, 2 or 4.5 °C for 28 d and	Enhancing antioxidant system	Enhanced chilling tolerance, total phenolics and PAL activities, reduced membrane permeability, lipid peroxidation, POD and PPO activities	Siboza, Bertling, and Odindo (2014)
			23 °C for 7d	•		
	SA + biotechnological treatment	Strawberry	Treated with 1 × 108 CFU ml ^{−1} **Rhodotorula glutinis and 0.72 mM SA, incubated at 20 °C for 2 d or at 4 °C	Stimulating response to biotic stress	Increased the activity of POD and eta -1,3-glucanase, and inhibited spore germination of Rhizopus stolonifer,	Zhang et al. (2010)
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CTKs	J.	Broccoli	Dipped in 0.89 mM 6-BA for 1 min and	Enhancing antioxidant system	Reduced L^* value, MDA content, POD activities, maintained h° and chlorophyll and anhanced DPDH radical convencing SOD ADY and CAT activities	Xu et al. (2012)
	CTK + SA + chemical treatment	Broccoli		Delaying senescence	Inhibited accumulation of reactive oxygen, and delayed the degradation of chlorophyll	Guo, Chen, and Li (2018)
	CTK + physical treatment	Green asparagus	Immersed with 0.09 mM 6-BA, treated with ultrasound (20 min, 20 kHz), and crowd at 12+2°C for 10 d and	Enhancing antioxidant system	Ultrasound and 6-BA synergistically reduced shear fore, lignin and crude fiber, increased CAT, PPO, APX, and POD as well as inhibited PAL	Wei and Ye (2011)
GAs	GA	Mandarin	Sprayed with 0.06 mM GA ₃ and stored at 4 $^{\circ}$ C and 20 $^{\circ}$ C for 42 d	Delaying senescence	Enhanced cold tolerance through inducing transcriptions of ACS1, ACS2, ETR1 and ERS1	Kashyap and Banu (2019)
	GA + CTK	Banana	Treated with 0.07 mM CPPU and 0.07, 0.14, or 0.29 mM GA ₃ for 10 min, and stored at 23 ± 2 °C with 75-90% RH for 20 d	Delaying senescence	Delayed respiration peak and ethylene production, and well-maintained h^{o} , maximal chlorophyll fluorescence, soluble reducing sugars, ascorbic acid and total phenols	Huang et al. (2014)
	GA + chemical treatment	Peach	Treated with 2% CaCl ₂ and 1.44 mM GA ₃ for 15 min, and stored at 3±1 °C for	Maintain cell integrity	Controlled membrane permeability to alleviate chilling injury, inhibited respiration rate and PPO activity	Gang et al. (2015)
PAs	PA	Apricot	20 d with 90-95% RH Soaked with 1 mM putrescipe or	Fnhancing	Increased antioxidant enzyme activity and delayed ripening and chilling injury	Koushesh Saba. Arzani.
			spermidine and stored at 1°C for 21 d and 20°C for 2 d	antioxidant system		and Barzegar (2012)
	PA + chemical treatment	Pomegranate	Dipped in 2% CaCl ₂ and 2.00 mM spermidine, and stored at 2 °C for	Enhancing antioxidant system	Increased CAT and SOD activities, inhibited POD activities and enhanced chilling tolerance	Ramezanian and Rahemi (2011)
	PA + physical treatment	Mango	120 d as well as at 20°C for 3 d Dipped in 1% chitosan and 0.69 μΜ	Stimulating response to	Inhibited development of lesion area, induced ${\rm H}_2{\rm O}_2$ and phenolic compounds	Jongsri et al. (2017)
			spermidine, and stored at $25\pm2^{\circ}\text{C}$ for 9 d	biotic stress	production, and increased chitinase, eta -1,3-glucanase and POD activities	
BRs	BR	Mandarin	Soaked with 10.4 μ M 24-EBR and stored at 12-16 °C with 90-95% RH for 50 d	Stimulating response to biotic stress	Enhanced biotic stress tolerance and inhibited weight loss, increased H_2O_2 content, stress-responsive metabolites and expressions of stress-responsive genes	Zhu et al. (2015)
	BR + physical treatment	Green asparagus		Enhancing antioxidant system	Inhibited respiration rate, water loss, MDA production, electrolyte leakage and PAL activity, well-maintained ascorbic acid, total phenolics and DPPH radical-scavenging	Wu and Yang (2015)
			with 90-95% RH for 24 d		activity, and enhanced SOD, APX and CAI activities	

Note: JAs: Jasmonates, SAs: Salicylic acids, CTKs: Cytokinins, GAs: Gibberellins, PAs: Polyamines, BRs: Brassinosteroids, MeJA: Methyl jasmonate, MeSA: Methyl salicylate, 6-BA: 6-benzylaminopurine (a kind of nitric oxide donor). ACS7: 1-aminocyclopropane-1-carboxylate synthase-1, ACS7: 1-aminocyclopropane-1-carboxylate synthase-1, ACS2: 1-aminocyclopropane-1-carboxylate synthase-2, ETR1: Ethylene response-1, ERS1: Ethylene response-1, ERS1: Ethylene response-1, APX: Ascorbate peroxidase, CAT: Catalase, DPPH: 1-diphenyl-2-picrylhydrazyl, H₂O₂: Hydrogen peroxide, MDA: Malondialdehyde, PAL: Phenylalanine ammonia lyase, POD: Peroxidase, PPO: Polyphenol oxidase, SOD: Superoxide dismutase. RH: Relative humidity.

and senescence. GAs and CTKs have been proved to have negative effects on biosynthesis and expression of these small molecules (Kashyap and Banu 2019; Liu et al. 2013). Hence, there have been widely practical usages of GAs and CTKs in extending the storage time of agricultural products, such as Citrus reticulata (Kashyap and Banu 2019), Olea europaea (Tsantili et al. 2002), and Brassica oleracea (Liu et al. 2013; Xu et al. 2012).

Kashyap and Banu (2019) showed that after employing GA₃, the regulation on ACO gene expression of fruit and vegetables slowed down to impede biosynthesis and sensitivity of ETH. Except for ethylene production, stress-responsive proteins and antioxidant enzymes like Fe-superoxide dismutase and ascorbate peroxidase were all retarded in CTK treated broccoli (Liu et al. 2011). These findings indicate that both GAs and CTKs indeed have antagonism toward senescence.

Besides, some phytohormones are reported to play a similar role in suppressing senescence. The CTK contents and cell integrity of green cabbage leaves were founded to increase after treated with ABA (Miret, Munne-Bosch, and Dijkwel 2018). The ripening process of plum fruit was effectively delayed after application of putrescine by lowering the weight loss, and increasing firmness, AsA and total phenolics (Davarynejad et al. 2015). PAs can slow down ripening by inhibiting ACC synthase and accumulation to reduce endogenous ethylene content and protect leaf chlorophyll from quenching.

3.3. Enhancing antioxidant system

Overdosage of oxidative compounds in agricultural products can lead to damage to quality and longevity. Therefore, enhancing antioxidant capacity is important for preserving fruit and vegetables. Many phytohormones have been demonstrated to play positive roles in stimulating antioxidative systems in fresh products, such as Vitis vinifera (L.) (Mirdehghan and Rahimi 2016; Sun et al. 2013), Prunus avium (Shafiq, Singh, and Khan 2013), Citrus sinensis (L.) (Habibi and Ramezanian 2017), *Prunus* armeniaca (Koushesh Saba, Arzani, and Barzegar 2012), Solanum lycopersicum var. cerasiforme (Wu, Lu, and Wang 2015), Glycine max (Song et al. 2018), Brassica oleracea var. italica (Xu et al. 2012), Cucurbita pepo var. cylindrica (Palma et al. 2015) and Cucumis sativus (Jia et al. 2018). Free radical scavenging activity and antioxidant enzyme activities are often used to represent antioxidant capabilities. Research evidences (Koushesh Saba, Arzani, and Barzegar 2012; Jia et al. 2018; Xu et al. 2012) show that different phytohormones can alter 1, 1-diphenyl-2-picrylhydrazyl (DPPH) concentration and antioxidative enzymes, including peroxidase (POD), catalase (CAT), superoxide dismutase (SOD), and ascorbate peroxidase (APX).

When malondialdehyde (MDA) production is repressed by postharvest treatment, antioxidant enzymes like CAT, SOD and APX are activated but POD and polyphenol oxidase (PPO) are uncertain. For example, apricot treated with 1 mM PAs, the POD was enhanced and preferable quality

was maintained (Koushesh Saba, Arzani, and Barzegar 2012). For broccoli dipped with 200 mg/L 6-BA, the POD was reduced sharply and better freshness was kept (Xu et al. 2012). On the other hand, the dosages of the same phytohormone change with varieties. The concentrations of PAs vary from 0.8 mM in soya bean (Song et al. 2018) to 1 mM in apricot (Koushesh Saba, Arzani, and Barzegar 2012), 2 mM in blood orange (Habibi and Ramezanian 2017) and 4 mM in cucumber (Jia et al. 2018).

3.4. Maintaining cell integrity

The plasma membrane is the most effective exothecium barrier for cells. The shelf life of fresh products mainly depends on the stable fluidity of the plasma membrane (Aghdam and Bodbodak 2013). Cell integrity can protect plants from electrolyte leakage mediated by plasma membrane cation conductance that could finally result in lipid peroxidation and programmed cell death (Demidchik et al. 2014). Numerous studies (Aghdam and Bodbodak 2013; Glowacz et al. 2017; Li et al. 2012) have proved that diverse phytohormones including BR, SA, and JA are all involved in maintaining cell integrity of fresh products.

The integrity of a cell depends on well-maintained membrane fluidity and enhanced antioxidant activities. Fluidity is influenced by plasma membrane proteins containing phospholipase C (PLC) and phospholipase D (PLD), and lipoxygenase (LOX), and membrane phase transition temperature mediated by UFAs ratio. These proteins are founded to be downregulated while UFAs ratios are upregulated in products treated with phytohormones (Aghdam and Bodbodak 2013; Li et al. 2012). Except for proteins, fatty acids content and concentration are found to improve membrane integrity in 'Hass' avocados which were treated by MeJA and MeSA (Glowacz et al. 2017).

4. Future trends

Phytohormones are a range of metabolites that have various signaling or regulating functions, and thus are indispensable and prerequisite in plants. Previous studies have demonstrated that phytohormone plays positive roles in prolonging the shelf life of fruit and vegetables, showing great potential to be an alternative preservation technology.

Although many studies on phytohormone applications have shown that phytohormones have overall effects on the preservation of fruit and vegetables, commercial applications of the technology still face challenges, for example, unclarified mechanisms on human health. The US EPA has exempted residue limits of 24-epibrassinolide (24-EBR) and prohydrojasmon from foods and declared the nontoxicity of 6-BA as a plant growth regulator in agriculture, however, the effects of other phytohormones including GA to human health remain unclear. Thus phytohormones can be combined with other physical technologies such as edible coating or modified atmosphere packaging. Such a hurdle technology can extend the shelf life of agricultural products more



effectively and reduce the dosage of phytohormones, benefiting human health.

Some mechanisms that are not completely understood and new findings on differential recognitions constantly emerge. The physiological metabolic mechanism, regulation pathways and cascade responses have been investigated in previous studies. Present studies mostly focus on the regulation of phytohormones and signaling mechanisms under biotic and abiotic stresses, especially on preharvest treatments at the genetic level. Researches on postharvest mainly focus on their applications on common fruit and vegetables. Different phytohormones play differential roles in different species of plants and diverse periods of their lifespan. For extending shelf life, postharvest treatments are more effective than preharvest treatments. Consequently, more studies should be devoted to the mechanisms and pathways of physiology after harvest in the future. Additionally, the effects of diverse phytohormones cannot be separately considered as they always form a signal cross-network and work mutually. Much work on the cross-regulating network remains to be explored in future.

5. Conclusions

As a key regulator of plant physiology and biochemistry, phytohormones have attracted much attention in postharvest technology in recent years, and therefore many functions and modulation mechanisms have been investigated. Phytohormones can be used to extend shelf life of fruit and vegetables by enhancing translations and expressions of defence genes, suppressing biosynthesis and metabolism of senescence-related phytohormones, enhancing antioxidant enzyme activities and maintaining a high level of ROS scavengers, and sustaining the integrity of plasma membrane with synthesis manipulation of fatty acids and plasma membrane proteins. In addition, phytohormones generally form a signaling network and regulate mutually. Nevertheless, with continuous research efforts and progress leading to a better understanding of the mechanisms of phytohormones, it is expected that the technology should be widely applied to extend the shelf life of fresh products in the agricultural industry.

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