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Review

Advances in application of small molecule compounds for extending the shelf life of perishable horticultural products: A review

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ABSTRACT

Most of the horticultural products are highly perishable and reducing their postharvest losses is extremely important. There is a worldwide trend to explore new alternatives to increase shelf life and postharvest quality of horticultural products. This review discusses the use of gaseous and some other low molecular mass compounds as a feasible way to maintain quality and prolong shelf life of rapidly deteriorating horticultural products during postharvest stage. These compounds including nitric oxide (NO), carbon monoxide (CO), hydrogen sulfide (H_2S), hydrogen peroxide (H_2O_2), hydrogen gas (H_2), carbon dioxide (CO_2) and chlorine dioxide (ClO_2) could delay horticultural products senescence through different mechanisms such as suppressing respiration rate, inhibiting ethylene biosynthesis, delaying browning and regulating activity of antioxidant enzymes. The review also summarizes the interaction between these molecules and ethylene during horticultural products senescence process. Additionally, NO may cross talk with H_2O_2 or H_2S to promote the quality and prolong the postharvest life of perishable fruits and vegetables. Those compounds regulate the expression of genes during senescence, including ethylene biosynthesis related genes, lipoxygenase gene, cysteine protease gene and chlorophyll degradation related genes. Because of the obvious benefits of these compounds to postharvest freshness of fresh-cut flowers, fruits and vegetables, this area has been and will continue to be one of the priorities of horticultural research in the future.

1. Introduction

In recent times, customers pay more attention to the nutritional value and original quality of harvested horticultural products. Eating quality or ornamental value of horticultural products is largely dependent on preservation technology. Therefore, the application of new techniques to improve the postharvest quality of fresh-cut flowers, vegetables and fruits is urgently needed. Browning and other discolorations, tissue softening, surface dehydration, development of off-odours, water loss, as well as microbial spoilage are some of the common symptoms associated with deteriorating horticultural products (Rojas-Graü et al., 2009).

Many different kinds of molecules transmit information between the cells of multicellular organisms. These molecules are produced by signaling cells and subsequently bind to receptors in target cells, acts as ligands and chemical signals that travel to the target cells to coordinate responses (Jablonka, 1994). Over the past decade, the role of signaling molecules, such as nitric oxide (NO), hydrogen peroxide (H_2O_2), carbon monoxide (CO), hydrogen sulfide (H_2S) and hydrogen gas (H_2), have been extensively studied for their wide biological applications. A large number of papers on CO and H_2S were published during the last century, but these studies were related mostly to toxicological and environmental concerns (Wang, 2014). Gradually, it is also becoming clear that signaling molecule could regulate a variety of biological processes both in animals and plants. They are involved in numerous mammalian physiological processes, including the maintenance of blood pressure, relaxation of smooth muscle, inhibition of platelet aggregation and contraction of gastrointestines (Kovacic and Somanathan, 2011). In plants, those small molecules compounds have been linked to a range of physiological and developmental processes including endogenous ethylene biosynthesis, seed germination, root growth, stomatal closure, fruits and flower senescence. In addition, small molecule compounds are also involved in plants response to multiple environmental stresses, such as salinity, drought, heat stress and metal stress (Wang and Liao, 2016). The role of various signaling factors in plants responses to abiotic stresses is well studied through

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investigating their involvement in the regulation of the physiological processes. In recent years, it was shown that treatments with some low molecular mass compounds can extend the postharvest life of horticultural crops by regulating a variety of growth and developmental processes and through improving the resistance to abiotic and biotic stressful impacts (Guo et al., 2015).

Ripening of horticultural products is a complex and genetically programmed process that results in numerous physiological, biochemical, and structural changes. As influenced by endogenous and environmental factors, these changes are the result of the coordinated activation of multiple transcription regulatory and biochemical pathways. Flowers, fruits and vegetables are classified as climacteric or non-climacteric according to their ripening pattern, presence of a burst in respiration, and ethylene production during postharvest. In climacteric produce, ripening process is associated with increasing ethylene production and respiration. Small molecule compounds inhibit ethylene signal transduction pathway, thus, resulting in decreasing ethylene biosynthesis. However, in non-climacteric produce, ethylene plays a secondary role and signals that trigger most of the ripening pathways are unknown (Ghidelli and Perez-Gago, 2016). Thus, small molecule compounds may be beneficial in activation or inhibition of certain metabolic pathways during postharvest life of horticultural products.

The innovative use of molecules is indispensable for maintaining freshness and safety of fresh-cut flowers, fruits and vegetables and its significance in the horticulture industry cannot be over-emphasized. A few studies have demonstrated the effectiveness of these compounds when applied to different horticultural commodities (Soegiarto and Wills, 2004). But the postharvest life of cut flowers, fruits and vegetables is still being largely explored to better keep fresh by enhancing the nutritional value and original sensory quality. This review discusses the recent advances in the innovative use of small molecule compounds to maintain freshness and prolong postharvest life of horticultural products. An overview of studies on small molecule compounds cross-talk and the regulation of the expression of genes associated with senescence during postharvest life of horticultural products is also discussed.

2. Effect of small molecule compounds on postharvest quality of horticultural products

2.1. Nitric oxide (NO)

NO, a highly reactive signaling molecule, has been linked to a range of physiological and developmental processes including endogenous ethylene biosynthesis, chlorophyll production, root growth, fluid loss, and in fruits and flower development (Qiao and Fan, 2008). Postharvest application of NO has been shown to effectively extend postharvest life of a range of flowers, fruits and vegetables by inhibiting the emission of ethylene (Liao et al., 2013).

It has also been shown that NO extends vase life of some flowers as a signaling molecule. For example, the NO donor compound 2, 2′-(hydroxynitrosohydrazino)-bisethanamine (DETA/NO) exerted a positive effect on the longevity of cut flowers including snapdragon, delphinium, chrysanthemum, oriental lily and so on (Badiyan et al., 2004; Bowyer et al., 2003) (Table 1). Some studies have shown that the use of sodium nitroprussiate (SNP) as the NO donor also significantly extended the vase life and markedly increased fresh mass of cut carnation and rose flowers (Dhiman and Parkash, 2013; Liao et al., 2013; Zeng et al., 2011).

NO treatment increased the activities of superoxide dismutase (SOD), peroxidase (POD), catalase (CAT) and ascorbate peroxidase (APX) in carnation (Zeng et al., 2011), and decreased lipoxygenase (LOX) and proteas activity in Gladiolus (Dwivedi et al., 2016). Exogenous NO also decreased 1-aminocyclopro-pane-1-carboxylate oxidase (ACO) activity in rose flower (Liao et al., 2013). Besides, previous studies showed that thidiazuron (TDZ) is able to inhibit carotenoid degradation and retard chlorophyll degradation. Combined with SNP and TDZ decreased ethylene output by inhibiting 1-aminocyclopropane-1-carboxylic acid synthase (ACS) activity and reducing 1-aminocyclopropane-1-carboxylic acid (ACC) content during postharvest life of rose and lily (Kaviani and Mortazavi, 2013; Mortazavi et al., 2011). Thus, these results indicate that NO acts as a signal molecule during senescence in cut flowers by regulating ethylene production and enzymatic activity (Table 1).

NO is reported to delay fruit ripening through different mechanisms such as suppressing respiration rate (Singh et al., 2009), inhibiting ethylene biosynthesis (Wu et al., 2012), delaying pericarp browning (Duan et al., 2007), enhancing resistance to postharvest diseases and regulating the activity of enzymes (Lai et al., 2011) (Table 2). For example, endogenous NO accumulation significantly increased the activities of CAT, POD, APX and SOD in loquat fruit (Xu et al., 2012) and reduced the activities of phenolic-associated enzymes, phenylalanine ammonia lyase (PAL), POD and polyphenol oxidase (PPO) in longan fruit (Duan et al., 2007). NO treatments also promoted the activities of arginine decarboxylase (ADC), diamine oxidase (DAO), glutamate decarboxylase (GAD), ornithine aminotransferase (OAT), ornithine decarboxylase (ODC) and polyamine oxidase (PAO) in banana fruits (Wang et al., 2016). Moreover, NO effectively enhanced the resistance of tomato fruits against gray mold rot caused by *Botrytis cinerea* (Lai et al., 2011). In some species, however, NO is reported to have had negative effects. For example in kiwifruits, NO solution promoted the accumulation of ROS, accelerated peroxidation and diminished the activity of antioxidant enzymes (Zhu et al., 2008).

Reports have shown that NO fumigation alleviated chilling injury during fruits and vegetables storage. Postharvest NO fumigation delayed ripening and also alleviated chilling injury symptoms in ‘Amber Jewel’ plums (Singh et al., 2009). Postharvest application of NO alleviated chilling injury symptoms in a range of fresh-cut produce such as mango (Zaharah and Singh, 2011), banana (Wang et al., 2016) and loquat fruit (Xu et al., 2012) (Table 2). Most studies on postharvest response of horticultural products to NO application have been conducted using biochemical and physiological approaches. Detail mechanisms of the role of NO, particularly at the molecular level need to be investigated in future.

2.2. Hydrogen sulfide (H_2S)

H_2S is a gaseous mediator synthesized from cysteine by the enzymes cystathionine beta-synthase, cystathionine gamma-lyase, and 3-mercaptopyruvate sulfurtransferase (Szczesny et al., 2016). H_2S is an endogenous gaseous signaling molecule in animal systems. Recently, scientists have found that it may act as an important gaseous regulator involved in various processes in plants, including seed germination (Zhang et al., 2008), root organogenesis (Li et al., 2014a), stomatal closure (Garcia-Mata and Lamattina, 2010), and flower senescence (Zhang et al., 2011). In addition, H_2S is also involved in plant response to multiple environmental stresses, such as salinity, drought, heat stress and metal stress (Guo et al., 2015).

Several evidence have shown that H_2S is involved in the regulation of postharvest shelf life of horticultural products. Respiration rate and susceptibility to decay-causing pathogens are important factors that determine the postharvest deterioration in flowers, fruits and vegetables. H_2S fumigation treatment prolonged postharvest shelf life of strawberry fruits with the optimal concentration of H_2S donor NaHS (Hu et al., 2012). The prolonged postharvest shelf life could be due to the decreased respiratory intensity and susceptibility to decay-causing pathogens in NaHS-treated fruits, with inhibiting polygalacturonase (PG) activities. Fumigation with H_2S released from 0.8 mmol·L^{-1} NaHS solution significantly enhanced the endogenous H_2S content by increasing the activities of D-cysteine desulfhydrase (LCD) and L-cysteine desulfhydrase (DCD) (Hu et al., 2014c). Therefore, NaHS could delay the ripening rate of mulberry fruit and reduce the respiratory intensity.