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Review

Effects of hydrogen sulfide on postharvest physiology of fruits and vegetables: An overview

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A R T I C L E I N F O

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A B S T R A C T

Hydrogen sulfide (H_2S) is a flammable, colorless and hazardous gas. Initially it was considered as an environment toxic gas; but, after its endogenous production discovery in plants, a wide variety of functions have been found associated with H_2S. H_2S plays an imperative role in the modulation of ripening and quality changes in various fruits and vegetables by regulating certain physiological aspects such as respiration, ethylene biosynthesis, color metabolism, enzymatic browning, softening, chilling injury and postharvest decay during storage. H_2S also acts as a signaling molecule to combat against oxidative stress by scavenging reactive oxygen species (ROS) due to up-regulation of antioxidative enzymes activities. Reduced membrane permeability, inhibited lipid peroxidation, up-regulation of antioxidant activities and inhibition of ROS production eventually leads to reduced senescence having conserved quality with extended shelf or cold storage life of H_2S treated fruits and vegetables. Potential of H_2S in delaying ripening and reducing senescence of fruits and vegetables is generally accepted. However, it may be worth considering the commercial H_2S application as a strategy of conserving external color, retarding senescence and reducing various physiological storage disorders of fruits and vegetables with acceptable consumer quality in the future. This review summarizes the possible role and mechanism of H_2S in prolonging storage life and conserving the quality attributes of fruit and vegetable crops during shelf or low temperature storage.

1. Introduction

H_2S is a flammable, colorless and hazardous gas. It has a very strong odor of ‘rotten egg’ (Lloyd, 2006). Due to implication of H_2S in numerous mass extinctions, its toxicity has been proved for about 300 years (Kump et al., 2005). In the last decade, most of the literature only focused on the environmental toxicology of H_2S (Beauchamp et al., 1984; Koch and Erskine, 2001). Indeed, the exposure of H_2S, at the higher rates is considered highly toxic to all of the mammalian species. Nevertheless, after the endogenous H_2S production discovery in the mammalian cell, a large number of different physiological functions have been ascribed to this gas. However, in the recent years, H_2S has been included to carbon monoxide and nitric oxide as a newly classified group of the biologically active gases called as gaso-mediators and gasotransmitters owing to their ability to control large number of imperative physiological responses in plants and animals (Wang, 2003). Similar to carbon monoxide and nitric oxide, H_2S is known as third leading signaling molecule (Wang, 2012). Being a potent reductive substance, H_2S can directly and efficiently scavenge various ROS including hydrogen peroxide, superoxide, hypochlorite and peroxynitrite (Geng et al., 2004; Whiteman et al., 2004; Mitsuhashi et al., 2006).

H_2S also acts as an imperative antioxidative signaling molecule to

Abbreviations: AA, amino acids; APX, ascorbate peroxidase; ATP, adenosine triphosphate; ADP, adenosine diphosphate; AMP, adenosine monophosphate; CCO, cytochrome c oxidase; CAT, catalase; CI, chilling injury; CS, cysteine synthase; DCD, D-cysteine desulfhydrase; EL, electrolyte leakage; DPPH, 2,2-diphenyl-1-picrylhydrazyl; EGase, endo-β-1,4-glucanase; FRAP, Ferric ion reducing antioxidant power; GR, glutathione reductase; H_2S, hydrogen sulfide; LCD, L-cysteine desulfhydrase; CAS, cyanoalanine synthase; OAS, *O*-acetylserine; MDA, malondiladehyde; NaHS, sodium hydrosulfide; LOX, lipoxygenase; POD, peroxidase; PPO, polyphenol oxidase; PAL, phenylalanine ammonia lyase; PG, polygalacturonase; PME, pectin methylesterase; ROS, reactive oxygen species; SiR, sulfite reductase; SDH, succinate dehydrogenase; SSC, soluble solid contents; TA, titratable acidity

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combat against the abiotic stress by reducing the levels of ROS and promoting antioxidative enzymes activities (Christou et al., 2013). It has been reported that H_2S play an imperative role in the postharvest physiology of various fruits and vegetables by regulating their ripening related aspects such as color changes, chilling injury, respiration, ethylene biosynthesis, enzymatic browning, softening and postharvest decay during storage (Hu et al., 2014b; Fu et al., 2013; Sun et al., 2015). Moreover, H_2S has also been found to act as an important antioxidant to conserve the postharvest quality of fruits and vegetables by enhancing the activities of antioxidative enzymes (Hu et al., 2012). H_2S also has antibrowning ability. It has been reported that the postharvest treatment with H_2S enhanced antioxidative activities, alleviated the oxidative damage and eventually inhibited browning of the fresh-cut slices of lotus roots (Sun et al., 2015). Likewise, H_2S also has antifungal effect. H_2S fumigation efficiently inhibited growth of *Aspergillus niger*, *Penicillium expansum, Rhizopus oryzae* and *Saccharomyces cerevisiae* on apple, kiwifruit, mandarins, tomato, pear and sweet orange proposing that H_2S can be utilized as a potential fungicide during postharvest storage (Hu et al., 2014b; Fu et al., 2014). So, it can be said that the role of H_2S might be a widespread event in the different processes such as oxidative stress alleviation, senescence inhibition, control of postharvest pathological infections and storage life extension of fruits and vegetables. To elucidate the possible roles of H_2S in extending storage life and maintaining quality of fruits and vegetables, its underpinning molecular and physiological mechanisms need to be reviewed. So, this review summarizes the possible role of H_2S in different postharvest physiological aspects of fruit and vegetable crops during shelf or cold storage.

2. H_2S production and metabolism

The H_2S endogenous metabolism consists of its biosynthesis and breakdown in various crop plants (Fig. 1). The synthesis of H_2S is comprised of D-cysteine desulfhydrase (DCD), L-cysteine desulfhydrase (LCD), cyanoalanine synthase (CAS), sulfite reductase (SiR) and cysteine synthase (CS) biosynthetic pathways (Rausch and Wachter, 2005). The enzyme LCD leads to L-cysteine degradation eventually resulting in the production of H_2S, ammonia gas, and pyruvate that persists in nucleus, cytoplasm, and the mitochondrial cells. DCD degrades D-cysteine to produce H_2S in the mitochondria. The SO_3^{+2} ions are reduced in the presence of SiR enzyme to biosynthesize H_2S with ferredoxin donor of the electron in the chloroplasts. In the mitochondria and cytoplasm of the plant cells, CAS converts L-cysteine and cyanide into H_2S and cyanuric acid. The CS catalyzes *O*-acetylserine (OAS) and H_2S to produce cysteine in chloroplast, cytoplasm, and mitochondria. These reversible reactions can generate H_2S. Under CS action, excessive H_2S may leads to reduction of protein/polypeptides or cysteine comprising cysteine except the emission of gas. The H_2S-releasing and cysteine-degrading enzymes have been categorized in various conditions (Papenbrock et al., 2007). So, depending upon the conditions, balance between biosynthesis and degradation of the endogenous H_2S, the homeostasis of H_2S is critical for adaptation of various fruits and vegetables to chilling or oxidative stress during postharvest life (Hu et al., 2014a; Luo et al., 2015).

3. Effects of H_2S on postharvest physiology of fruits and vegetables

3.1. Effect of H_2S on intracellular energy

Due to higher water contents, fresh fruits and vegetables are perishable in nature. Higher perishability makes them prone to quantitative and qualitative losses due to various biotic (diseases) and abiotic (chilling injury and other physiological disorders) stresses (Aghdam and Fard, 2017; Cao et al., 2014; Zhang et al., 2017). Intracellular energy in the form of adenosine triphosphate (ATP) reduces under certain stresses or senescence process during postharvest storage. Reduced intracellular energy ultimately leads to decreased storage potential (Pan et al., 2017; Aghdam et al., 2018a). Therefore, warranting adequate energy might be considered a suitable scheme for delaying senescence of fresh fruits and vegetables, which may lead to prolonged postharvest storage life with conserved overall quality (Aghdam et al., 2018a). H_2S fumigation of water spinach (*Ipomoea aquatic*) resulted in higher energy change with maintained levels of ATP, ADP and AMP that was beneficial in

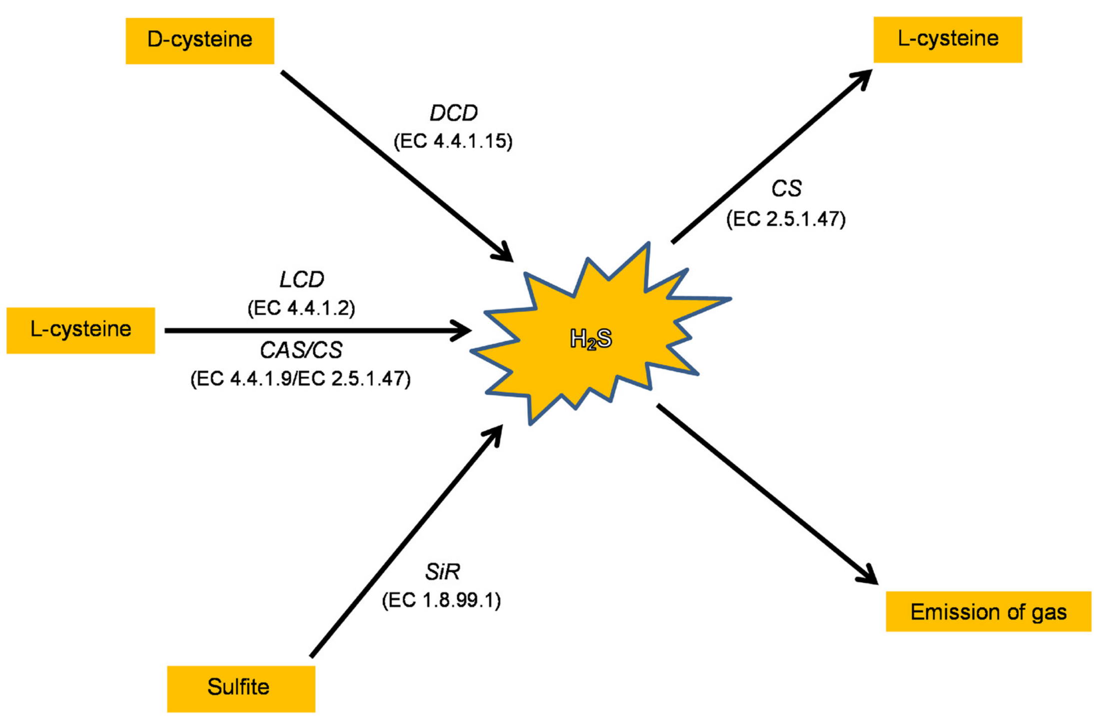

Fig. 1. Production and metabolism of hydrogen sulfide (H_2S) in plants. DCD, D-cysteine desulfhydrase; LCD, L-cysteine desulfhydrase; CAS, cyanoalanine synthase; CS, cysteine synthase; SiR, sulfite reductase. Modified from He et al. (2018).