Hydrogen Sulfide: A Gaseous Molecule in Postharvest Freshness

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Hydrogen sulfide (H₂S), as a signaling molecule, is involved in the regulation of growth and development in plants. Recent studies have indicated that H₂S also plays important roles in regulating postharvest senescence of horticultural products. The focus of this review is to summarize the synthesis of H₂S in plants and its potential roles in alleviating the senescence of cut flowers, fruits, and vegetables during postharvest storage. During postharvest of horticultural products, H₂S could scavenge reactive oxygen species via promoting the activity of antioxidant enzymes, thereby, sustaining the integrity of the membrane. In fruits, H₂S effectively enhanced the tolerance of chilling by increasing the content of proline and polyphenol compounds. During postharvest storage of perishable fruits and vegetables, H₂S significantly alleviated decay, which was caused by fungi by inhibiting the growth of fungal spores. Moreover, H₂S interacted with other molecules synergistically (NO) or antagonistically (ethylene) to alleviate senescence of horticultural products. At the transcriptional level, H₂S regulated the expression of senescence-related genes, which were related to degradation of proteins and chlorophyll, to delay the senescence of horticultural products. Thus, H₂S does not only possess positive antioxidant and antifungal properties, but also significantly regulates the senescence-related gene during postharvest of horticultural products. Future studies of H₂S in postharvest storage should focus on its molecular mechanism in the posttranslational modifications of proteins as well as its safety attributes in treated fruits and vegetables.

Keywords: hydrogen sulfide (H₂S), chilling injury, antioxidant system, antifungal, interactions, senescence-related genes

INTRODUCTION

Hydrogen sulfide (H₂S), a colorless gas with an odor of rotten eggs, is a new gaseous signaling molecule that regulates physiological processes in plants (Li et al., 2016b). Recently, many investigations have suggested that H₂S is involved in various growth and development processes in plants including germination (Liu and Lal, 2015), lateral and adventitious root formation (Lin et al., 2012; Jia et al., 2015), stomatal movement (Scuffi et al., 2014; Papanatsiou et al., 2015; Jin and Pei, 2016), and photosynthesis (Duan et al., 2015). In addition, the roles of H₂S in regulating plant responses to abiotic stress including drought stress (Chen et al., 2016; Jin et al., 2017), osmotic stress (Khan et al., 2017), salt stress (Lai et al., 2014), chilling stress (Fu et al., 2013), and heavy metal stress (Ali et al., 2015; Fang et al., 2017) were reported. Under abiotic stress, some researchers indicated that H₂S could ameliorate the quality and nutrients of horticultural products such as Capsicum annuum L. (Kaya et al., 2018), Brassica napus L. (Qian et al., 2014), and Brassica pekinensis (Lour.) Rupr. cv. Kasumi F1 (Reich et al., 2016). In addition, a number of
studies showed that H$_2$S played an important role in delaying senescence of horticultural products during postharvest storage with examples in kiwifruits (Zhu et al., 2014), daylily (Liu et al., 2017), and cut flowers (Zhang et al., 2011). Recently, there were reviews that discussed H$_2$S as a signal molecule or a versatile regulator in plant response to abiotic stress (Guo et al., 2016; Li et al., 2016b). However, its role in the postharvest life of horticultural products has not yet been summarized in a published review. Therefore, the main aim of this review is to summarize the importance roles of H$_2$S in the postharvest life of horticultural products. This review concentrates on the mechanisms by which H$_2$S is involved in maintaining the postharvest freshness such as by regulating antioxidant system, enhancing chilling tolerance, and inhibiting fungi growth. The interaction of H$_2$S with other molecules and the regulation of senescence-related genes during postharvest storage process have also been discussed.

**GENERATION OF H$_2$S IN PLANTS**

In higher plants, H$_2$S emission was first observed by DeCormis in 1968 (Rennenberg, 1989). Subsequently, Wilson et al. (1978) found that many higher plants including pumpkin, cucumber, cantaloupe, corn, and soybean could release H$_2$S dependent on light. The emission of H$_2$S in leaf tissue of cucumber was reported by Sekiya et al. (1982). Until now, there have been six pathways through which H$_2$S is generated in higher plants, and these could be summarized as follows: plants reduce sulfate to sulfide and incorporate it into organic metabolites. Before reduction, sulfate is activated by adenylation to form adenosine 50-phosphosulfate (APS), which is catalyzed by ATP sulfurylase (ATPS). In the plastids, APS is first reduced to sulfite by ferredoxin-dependent sulfite reductase (SIR) (Takahashi et al., 2011; Figure 1A). Finally, sulfite is incorporated into the amino acid skeleton of O-acetylserin (OAS) by O-acetylserine thiol lyase (OAS-TL) to form cysteine, and its reverse reaction could release H$_2$S (Li, 2015). Among these, OAS is a product from serine, which is catalyzed by serine acetyltransferase (SAT). Harrington and Smith (1980) first reported that the degradation of L-cysteine yielded H$_2$S, pyruvate, and NH$_4^+$ in tobacco cells. Subsequently, some researchers found that the L-cysteine was catalyzed by L-cysteine desulphhydrase (L-CDes) to form H$_2$S in other higher plants (Sekiya et al., 1982; Rennenberg, 1983; Xie et al., 2013). In addition, L-CDes also catalyzed the formation of L-alanine and elemental sulfur from L-cysteine. Then, the elemental sulfur could be reduced to H$_2$S if a reductant was present (Papenbrock et al., 2007; Figure 1A). Two genes, AtNFS1 and AtNFS2, which encoded NiS-like cysteine desulfurase have been identified in Arabidopsis, catalyzing cysteine to form H$_2$S (Léon et al., 2002). Whereas, Nagasawa et al. (1985, 1988) indicated that D-cysteine was decomposed into H$_2$S by D-cysteine desulphydrase (D-CDes) in Escherichia coli and Pseudomonas putida. The D-CDes was isolated from Arabidopsis thaliana and it could catalyze D-cysteine to release H$_2$S (Riemenschneider et al., 2005). However, L-CDes and D-CDes were different in substrates, enzymatic inhibitors, and subcellular localization (Guo et al., 2016). Besides, the β-cyanoalanine synthase (CAS) catalyzed L-cysteine and cyanide to form H$_2$S and β-cyanoalanine (Hatzfeld et al., 2000). Jost et al. (2000) found the three genes (CYS-C1, CYS-D1, and CYS-D2), which encoded CAS in Arabidopsis (Figure 1A). Therefore, H$_2$S was released from L-cysteine in the presence of hydrogen cyanide, which was catalyzed by CAS in plants. The H$_2$S, especially endogenous H$_2$S, which acts as a signaling molecule, can move freely from one plant cell to another. Thus, endogenous H$_2$S may play important roles in plants.

**REGULATORY ROLES OF H$_2$S IN ANTIMICROBIAL SYSTEM DURING HARVESTED STORAGE**

Reactive oxygen species (ROS) caused by oxidative damage could accelerate senescence and ripening of horticultural products during postharvest storage. Recent investigations suggested that H$_2$S could delay the senescence and ripening of horticultural products by alleviating the oxidative damage caused during postharvest storage. During postharvest of cut flowers, exogenous H$_2$S could delay senescence of cut flowers by decreasing ROS-induced oxidant damage. During postharvest of fruits, Hu et al. (2012) indicated that H$_2$S did not only improve the activities of CAT and POD, but also increased activities of APX and glutathione reductase (GR) during strawberry postharvest storage. Furthermore, H$_2$S could delay senescence of cut flowers by decreasing ROS-induced oxidant damage. During postharvest of vegetables, Hu et al. (2015) reported that the postharvest senescence of water spinach was alleviated by H$_2$S. In this process, H$_2$S improved antioxidant capacity and sustained the energy status, which decreased the degree of leaf yellowing of water spinach. The redox balance in the senescence of daylily was promoted by H$_2$S, which mainly reduced the overaccumulation of ROS via increasing the activity of CAT, APX, and SOD (Li et al., 2017; Table 1). In addition, Zeng et al. (2014a) suggested that H$_2$S could regulate phenolic
metabolism to alleviate browning of fresh-cut lotus root slices, and the role of \( \text{H}_2\text{S} \) in alleviating enzymatic browning was through inhibiting the activity of polyphenol oxidase (PPO) during postharvest storage. Thus, \( \text{H}_2\text{S} \) acted as a gaseous regulator to increase the activities of antioxidant enzymes to affect the accumulation of ROS. As mentioned earlier, \( \text{H}_2\text{S} \) alleviated the damage of lipid peroxidation and delayed the postharvest senescence of cut flowers, fruits, and vegetables. However, the detailed mechanism of \( \text{H}_2\text{S} \) regulating the activity of antioxidant enzymes still needs further research in order to be well understood.

**INVolvement of \( \text{H}_2\text{S} \) in PostHarvest Chilling Stress**

Cold storage is widely used to delay senescence and ripening of fruits during postharvest handling. However, storage at low
non-freezing temperatures causes chilling stresses for fruits like banana (Luo et al., 2015) and peach (Cao et al., 2018), which are extremely sensitive to chilling injury. Chilling injury not only retards shelf life, but also reduces quality of fruits in the postharvest storage process. In recent years, some researchers reported that H$_2$S could alleviate chilling injury, which is caused by the low temperature, during postharvest storage. Luo et al. (2015) found that H$_2$S fumigation could alleviate chilling injury of harvested banana by promoting the antioxidant capacity and increasing the content of proline. During that process, the activities of antioxidant enzymes like SOD, CAT, and APX were increased by H$_2$S, for these to scavenge ROS (Table 1). Aghdam et al. (2018) also found that H$_2$S could regulate the activities of antioxidant enzymes to sustain the lower malondialdehyde (MDA), ameliorating chilling injury of hawthorn fruit. It showed that H$_2$S could increase the activity of antioxidant enzymes to decrease the membrane lipid peroxidation, so as to sustain the high tolerance for chilling. In parallel, the content of polyphenol increased in H$_2$S treatment, and this was because the activity of phenylalanine ammonia lyase was increased, while the activity of PPO was decreased by H$_2$S (Luo et al., 2015). Furthermore, proline content was also elevated by H$_2$S, which resulted from the increase of the activity of 1-pyrroline-5-carboxylate synthetase and the decrease of activity of proline dehydrogenase. Proline, as an osmotic substance, could maintain the high cytosolic concentration of the cell to increase the ice point. This indicates that H$_2$S could directly or indirectly alleviate chilling injury by increasing the content of proline. Li et al. (2016a) suggested that H$_2$S could improve the tolerance of banana to chilling injury by promoting the activities of the energy metabolism-related enzymes such as H$^+$-ATPase, Ca$^{2+}$-ATPase, cytochrome C oxidase, and succinate dehydrogenase. In addition, the quality of bananas such as firmness was also sustained by H$_2$S under chilling condition (Li et al., 2016a; Table 1). Thus, H$_2$S seemly regulated the content of osmotic substances, sustaining the tolerance to chilling stress. Taken together, it could be seen that the tolerance to chilling injury of fruits was promoted by H$_2$S, which sustained the integrity of the membrane and maintained sufficient energy via regulating activities of enzymes and content of osmotic substances.

**TABLE 1 | Effects of hydrogen sulfide on postharvest senescence of horticultural products.**

| H$_2$S-involved | Plant species | H$_2$S-mediated effect | Reference |
|-----------------|--------------|-----------------------|-----------|
| Antioxidant system | Cut flowers: Erigeron annuus and Saik matsuana | Increasing the activities of CAT, POD, and APX; Extending vase life of cut flowers | Zhang et al., 2011 |
| | Fragaria × ananassa | Improving the activities of CAT, POD, APX, and QR; Decreasing the activity of LOX; Prolonging postharvest shelf life of strawberry | Hu et al., 2012 |
| | Actinidia deliciosa | Increasing the activities capacity; Alleviating senescence and tissue softening of kiwifruit | Gao et al., 2013 |
| | Nelumbo nucifera | Regulating phenolic metabolism; Alleviating browning of fresh-cut lotus | Sun et al., 2015 |
| | Ipomoea aquatica | Improving antioxidant capacity; Delaying senescence of water spinach | Hu et al., 2015 |
| | Vitis vinifera | Reducing the accumulation of MDA, H$_2$O$_2$, and O$_2$$^-$$^-$; Alleviating postharvest senescence and decrease of firmness of grape | Ni et al., 2016 |
| | Hemerocallis fulva | Increasing activities of antioxidant enzymes; Alleviating senescence of daylily | Liu et al., 2017 |
| Chilling resistance | Musa spp. | Increasing the content of proline; Alleviating chilling injury of banana | Luo et al., 2015 |
| | Musa spp. | Promoting the activity of the energy metabolism-related enzymes; Alleviating chilling development | Cao et al., 2018 |
| | Crataegus pinnatifida | Regulating the activities of antioxidant enzyme; Promoting chilling injury of hawthorn | Aghdam et al., 2018 |
| Antifungal | Fruits: Malus domestica, Actinidia deliciosa, Pyrus bretschneideri Rehd. | Inhibiting the colony growth of A. niger and P. italicum; Decreasing the postharvest decay of fruits | Fu et al., 2014 |
| | Pyrus pyrifolia | Inhibiting the growth of A. niger and P. expansum; Prolonging the shelf life of fresh-cut pear | Hu et al., 2014b |
| | Ipomoea batatas L. | Inhibiting the growth of fungal pathogens; Inhibiting the senescence and decay of fresh-cut sweet potato | Tang et al., 2014 |
| | Prunus persica L. | Inhibiting the spore germination rate, mycelial development diameter, and pathogenicity; Alleviating the brown rot of peach | Wu et al., 2018 |

**INHIBITION OF FUNGAL GROWTH BY H$_2$S IN POSTHARVEST HORTICULTURAL PRODUCTS**

Generally, decay of some perishable horticultural products happens during storage and transportation. The main reason behind decay is the activity of plant fungal pathogens, which is usually promoted by wounds. In recent years, some research has found that H$_2$S, applied as a regulator or fungicide, could alleviate senescence and decay of postharvest horticultural products by inhibiting the growth of fungi. Fu et al. (2014) reported that exogenous H$_2$S (0.5 mM NaHS solution) effectively decreased the decay of fruits such as apple, kiwifruit, pear, sweet orange, mandarin, and tomato by inhibiting the colony...
growth of *Aspergillus niger* and *Penicillium italicum*, which mainly inhibited spore germination, germ tube elongation, and mycelial growth (Table 1). This was possible because H$_2$S induced the accumulation of ROS in *A. niger* by decreasing the activity of antioxidant enzymes including CAT and SOD (Figure 1B). Contrarily, the investigations in postharvest freshness of horticultural plants suggested that H$_2$S could scavenge ROS accumulation by promoting the activities of CAT, SOD, APX, and GR (Zhang et al., 2011; Hu et al., 2012; Liu et al., 2017). Fu et al. (2014) also attributed the different effects of H$_2$S on microbes and plants to their different tolerances to H$_2$S. Hence, the low level H$_2$S (0.5 mM NaHS solution) seemingly induced the accumulation of ROS in fungal in vivo by decreasing the activities of antioxidant enzymes, thereby, inhibiting the growth of fungi during storage (Figure 1B). However, the higher level H$_2$S generally was used as a fungicide to inhibit the growth and infection of fungi. Wu et al. (2018) demonstrated that the spore germination rate, mycelial development diameter, and pathogenicity of *Monilinia fructicola* were inhibited by H$_2$S, especially 50 mM NaHS solution for 2 h, which alleviated brown rot of peach fruit, caused by *M. fructicola*. Hu et al. (2014b) found that H$_2$S delayed the shelf life of fresh-cut slices of pear and alleviated rots by inhibiting the growth of *A. niger* and *Penicillium expansum* (Table 1). The inhibition of mycelium growth of *A. niger* and *P. expansum* on medium depended on the H$_2$S concentrations, which was found totally inhibited at 2 mM NaHS treatment. Moreover, H$_2$S also blocked the decrease of reducing sugar and soluble protein during postharvest storage of pear (Hu et al., 2014b). The role of H$_2$S in inhibiting senescence and decay of fresh-cut sweet potato during postharvest also depended on exogenous H$_2$S concentration, especially on the optimal concentration of 2 mM NaHS (Tang et al., 2014). Interestingly, H$_2$S alleviated the decay of sweet potato via inhibiting the growth of fungal pathogens including *Rhizopus nigricans*, *Mucor rouxianus*, and *Geotrichum candidum*, which were isolated from sweet potato tissue, which was infected by black or soft rot (Tang et al., 2014; Table 1). Consequently, H$_2$S (at the higher concentration) as a fungicide inhibited the growth and infection of fungi during postharvest storage. As mentioned earlier, the low level H$_2$S may be acts as a gaseous regulator to affect the accumulation of ROS, while it appeared it played the role of a fungicide at high concentrations. Furthermore, H$_2$S might simultaneously play both a regulator and fungicide role in inhibiting the growth and infection of fungi. Although H$_2$S could induce the ROS accumulation in vivo to inhibit fungal infection, its role in regulating the content of ROS has still not been extensively reported. Therefore, the detailed mechanisms of H$_2$S in the inhibition of the fungal community need to be studied.

**INTERACTION OF H$_2$S AND OTHER MOLECULES IN POSTHARVEST SENESCENCE**

In recent studies, the synergistic or antagonistic roles of H$_2$S with other molecules in postharvest senescence of horticultural products were reported. Zhang et al. (2014) reported the synergistic role of H$_2$S and nitric oxide (NO) in alleviating decay and softening of strawberry. Cotreatment with H$_2$S (0.8 mM NaHS solution) and NO (5 µM SNP solution) significantly maintained the quality (crust color and firmness) of strawberry and also inhibited its respiration rate and decay. Moreover, H$_2$S was combined with NO to increase the activities of chitinase and beta-1,3-glucanase, which played vital roles in ameliorating damages caused by pathogen. The lower activities of pectin methylesterase (PME), polygalacturonase (PG), and endo-beta-1,4-glucanase (EGase) that were related to softening of fruits were sustained by cotreatment with H$_2$S and NO (Zhang et al., 2014). Based on these results, the authors concluded that the synergistic effect of H$_2$S and NO could significantly delay senescence and alleviate decay of fruits. However, the mechanism of synergistic effect between H$_2$S and NO on senescence of harvested produce has not been extensively reported. In another study, Al Ubeed et al. (2017) found that H$_2$S alleviated the senescence and postharvest deterioration of pak choy by inhibiting the ethylene generation and ethylene action during storage. 1-Methylcyclopropene (1-MCP), as a competitive inhibitor of the action of ethylene, could inhibit the production of endogenous ethylene. Al Ubeed et al. (2018) found that 1-MCP and H$_2$S were equally effective in inhibiting respiration and endogenous ethylene production when pak choy was stored in the absence of exogenous ethylene. H$_2$S also prolonged postharvest senescence and ripening of banana during storage via antagonizing the effect of ethylene (Ge et al., 2017). It is well known that the ripening and senescence of fruits would be accelerated by the generation of ethylene. This is because ethylene accelerates respiration and other biochemical processes such as increasing cell membrane permeability and organic transformation. Thus, H$_2$S, as a signaling molecule, significantly alleviates the senescence and ripening of fruits by interfering with ethylene synthesis during storage of horticultural products. Moreover, H$_2$S also regulated the expression of ethylene synthesis genes and ethylene receptor genes at the transcriptional level. During ripening and senescence of kiwifruit, the expression of genes including *AdSAM*, *AdACSI*, *AdACS2*, *AdACO2*, and *AdACO3*, which were related to ethylene synthesis, was inhibited by H$_2$S (Li et al., 2017; Figure 1B). However, during postharvest storage of a banana, H$_2$S upregulated the expression of ethylene receptor genes such as *MaETR*, *MaERS1*, and *MaERS2*, which were at lower levels of expression in the presence of ethylene (Ge et al., 2017; Figure 1B). It has been indicated that H$_2$S regulated the ethylene generation and its signal transduction at the transcriptional level. Higher levels of nutrients such as ascorbic acid, soluble protein, and reducing sugar were sustained by H$_2$S during the postharvest storage of kiwifruit (Li et al., 2017). H$_2$S also alleviated the yellowing and softening of banana peel, which was caused by ethylene and evidently decreased the activity of PG, which was involved in cell wall degradation (Ge et al., 2017). It can be deduced that H$_2$S does not only regulates generation and signal transduction of ethylene, but also alleviates the deterioration of quality caused by ethylene of physiological parameters. To sum up, the synergistic or antagonistic effects of H$_2$S with other molecules might play vital roles in the regulation of senescence and quality of harvested fruits and vegetables.
SENESCENCE-RELATED GENES REGULATED BY H$_2$S

Postharvest senescence is a universally phenomenon for horticultural products, and this seriously affects the shelf life and quality of fruits and vegetables during storage. During senescence, the degradation of some proteins and chlorophyll occurs, and this is regulated by certain genes. The role of H$_2$S in regulating senescence-related genes during postharvest storage is discussed in this review. Li et al. (2014) indicated that the relative expressions of BoSGR, BoCLH2, BoPaO, and BoRCCR, which were related to chlorophyll degradation, were downregulated by H$_2$S during postharvest storage of broccoli. In the storage of broccoli, apart from BoSGR and BoRCCR, other chlorophyll degradation-related genes such as BoNYC, BoCLH1, and BoPPO were also downregulated by H$_2$S (Li et al., 2015). Thus, H$_2$S regulated the expression of chlorophyll degradation-related genes to inhibit degradation of chlorophyll, thereby, effectively alleviating the postharvest yellowing of broccoli. In addition, Li et al. (2015) showed that the expression of BoCP3 (cysteine protease gene) and BoLSC807 (aspartic protease gene) was inhibited by H$_2$S, suggesting that H$_2$S inhibited the degradation of proteins during the senescence process in broccoli. Meanwhile, H$_2$S cloud downregulate the expression of the LOX gene, BoLOX1, which catalyzed the hydroperoxidation of polyunsaturated fatty acids during senescence in broccoli (Li et al., 2014). The expressions of MdLOX2 and MdPPO (encoding PPO) were also downregulated by H$_2$S during storage of apples (Zheng et al., 2016). It can be deduced that H$_2$S delayed the senescence of fruits and vegetables by decreasing the expression of lipid peroxidation-related genes during postharvest storage. Generally, the genes that regulated the synthesis and signal transduction of ethylene were classified as senescence-related genes. Li et al. (2015) found that the expression of BoACS2 and BoACS3, which were key enzymes for ethylene generation, were downregulated by H$_2$S during broccoli postharvest storage. Meanwhile, the expressions of ethylene signal transduction genes, MdERS1 (ethylene response sensor 1) and MdETRI (ethylene receptor 1), were also inhibited by H$_2$S during the storage of apples (Zheng et al., 2016). Therefore, H$_2$S could inhibit the gene expression of ethylene generation and signal transduction, thereby, alleviating the senescence of postharvest horticultural products. Taken together, H$_2$S regulates the expression of senescence-related genes and delays the senescence of horticultural products during storage. However, the signaling transduction pathway of H$_2$S delaying senescence of horticultural products still has not been extensively reported.

CONCLUSION

Recently, a number of studies have suggested that H$_2$S played a significant role in maintaining the postharvest freshness of horticultural products. Presently, available reports have suggested that H$_2$S promotes postharvest life of horticultural products mainly by increasing the activity of antioxidant enzymes, alleviating chilling stress, inhibiting the growth of fungi, interacting with other molecules, and regulating senescence-related genes. Consequently, H$_2$S, as a gaseous regulator or signaling molecules, may regulate various physiological and biochemical processes during postharvest storage.

For now, the role of H$_2$S, in alleviating the senescence and decreasing quality, is mainly studied based on the antioxidant system and ethylene generation. However, the detailed mechanisms of H$_2$S, as a gaseous regulator to inhibit the growth of fungi and regulate activities of antioxidant enzymes, have not been reported. Meanwhile, the receptor proteins of H$_2$S regulating the senescence of plants have not been clearly reported at present. The interaction of H$_2$S with other molecules may exert significantly roles in the harvested storage of horticultural products, while its in-depth mechanisms have not been reported in detail until now. In addition, the safety of H$_2$S in the food chain, which is important to be considered in the consumption of fruits and vegetables, has also not been reported. Therefore, it is suggested that the future study of H$_2$S in postharvest storage should focus on its molecular mechanisms and its interaction with other molecules. Furthermore, the toxicity of its residues in treated fruits and vegetables should be paid more attention to in future studies.

AUTHOR CONTRIBUTIONS

WL provided the idea and revised the paper. JH prepared the manuscript. DH and JZ discussed the article structure. HF and BW finished the figures and tables. CW critically evaluated the manuscript. All the authors read and approved the submission of the manuscript.

FUNDING

This work was supported by the National Natural Science Foundation of China (Nos. 31560563 and 31160398) and Feitian Excellent Talents in Gansu China.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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