Hydrogen sulfide in horticulture: Emerging roles in the Era of climate change

Faisal Zulfiqar*[1] and John T. Hancock[2]

[1]Institute of Horticultural Sciences, Faculty of Agriculture, University of Agriculture Faisalabad, Pakistan.
[2]Department of Applied Sciences, University of the West of England, Bristol, UK.

*Correspondence:

Faisal Zulfiqar
Institute of Horticultural Sciences,
Faculty of Agriculture,
University of Agriculture Faisalabad, Pakistan
ch.faisal.zulfiqar@gmail.com
https://orcid.org/0000-0001-5428-5695

Short title: Hydrogen sulfide and abiotic stresses in horticulture

Highlights

Hydrogen sulfide (H_2S) is an endogenous molecule having vital roles in cell signaling pathways

Climate change may cause many environmental stresses, including drought, temperature, heavy metals and salt stress, whilst H_2S may mediate responses

H_2S regulates enzyme activities and gene expressions for the alteration in the cellular activities

In horticulture, H_2S also mitigates oxidative stress during post-harvest

H_2S is mooted as a focus for future agricultural treatments for better food security, especially during future climate changes

Abstract

Future climate change will present many plants with environmental challenges, including extreme temperatures and drought. Hydrogen sulfide (H_2S) has emerged as an important signal transmitting molecule in plants, especially important in many stress responses and it is known to regulate numerous physiological and developmental processes. Being recently suggested as a signaling molecule, research exploring the regulatory functions is continuously progressing regarding the role of H_2S in plant science, agriculture and horticulture. Biosynthesis of H_2S occurs in different cellular compartments from where it can freely translocate via membranes to where needed or be excluded where not required. H_2S interacts with related signaling molecules which together mediate stress tolerance against a plethora of harsh conditions. The H_2S induced tolerance against stresses occurs via regulation of antioxidants activities, endogenous levels of GSH, osmoregulator accumulation, cell signaling proteins, and stress-related gene expression. Overall this efficiently eliminates excessive reactive oxygen species (ROS) and maintains the intracellular redox balance. The current review summarizes the recent progress on H_2S or H_2S donor-mediated abiotic stress tolerance with special reference to climate change and horticulture crops, pre- and post-harvest. Elucidating the role of H_2S in cell signaling pathways may open new horizons towards understanding how exogenous treatments with H_2S in horticulture plants may aid in the

tolerance to stress, especially as environmental conditions change, and can secure better crop yields and avoid post-harvest losses.

Keywords: antioxidants; climate change; hydrogen sulfide; nitric oxide; plant stress; reactive oxygen species; oxidative damage

1. Introduction

There seems to be little doubt that the world has an ongoing climate change crisis, and this is only likely to get worse (Nolan et al., 2018). One of the main causes of such climate change is thought to be anthropogenic activities, which are not likely to cease in the near future. Therefore, ways to mitigate against its effects are increasingly important to find, and here it is suggested that treatments based on hydrogen sulfide (H_2S) may be useful.

Industrialization has increased the global carbon dioxide (CO_2) level from 270 to 401 μL L^{-1} within the duration of approximately 200 years. Along with this change, the global temperature has also risen by 0.85°C, having most obvious effects near the poles (IPPC, 2013). It is expected, extrapolated from greenhouse gas scenarios, that CO_2 levels and global temperatures will rise by at least 700 μL L^{-1} and 4°C, respectively, by the end of this century (IPCC, 2013). Furthermore, there will be a regional scale shift in the normal precipitation regimes resulting in extremes of dry and wet conditions due to intensification in the hydrological cycle (Medvigy and Beaulieu, 2012). These climatic changes are associated with the increase in greenhouse gases such as nitrogen oxides (NOx), CO_2, methane (CH_4) and ozone (O_3) (Min et al., 2011; Pall et al., 2011).

Under the scenario of growing climate fluctuations, there is a continuous threat for plants due to their sessile nature, as they are more prone to adverse environmental conditions. Events such as higher average and maximum temperatures, drought or flooding stress, beyond their physiological and adaptation limits (Pall et al., 2011; Shaw and Etterson, 2012), are likely to have an impact. In this regard, how plants adapt to climate fluctuations is one of the hot research topics globally. Although the tolerance range varies among plants, and many have evolved physiological plasticity to withstand stressful environments, the predicted severity of climate change could be so high that it can beat the tolerance ranges even in the plastic genotypes (Anderson et al., 2012). Such alteration are having profound impacts on the functioning of plants, having a significant influence on their food production capacity. Thus, there is a continuous need to boost the crop potential to cope with the climatic fluctuations stress. In this regard, understanding the potential for physiological changes under climate change scenario is a key challenge that must be met for achieving the target of food security under climate change induced harsh environmental conditions. Additionally, biotic stress, together with these increasing abiotic stresses, further increases the challenge of food security research to search for the novel strategies regarding the introduction of climate resilient crops to meet the food demands of continuously increasing population (Dhankher and Foyer, 2018; Zulfiqar et al., 2020). Many abiotic stress conditions such as drought or flooding, and the presence of harmful chemicals such as heavy metals and salt, are likely to be increased as the climate changes (Table 1). Therefore, it is timely to focus on plant physiological and signaling pathways which respond to environmental stress conditions.

Environmental stress responses in plants are often mediated by the generation of reactive oxygen species (ROS), including the superoxide anion ($O_2^{\bullet -}$), hydrogen peroxide (H_2O_2), and the hydroxyl radical ($\cdot OH$) (Cassia et al., 2018). There are several ROS sources in the different cellular compartments, such as the NADPH oxidases (RBOHs) and electron leakage from mitochondria and chloroplasts, as well as peroxidase- dependent ROS production in the apoplast (Mittler, 2017; Chapman et al., 2019). ROS, especially H_2O_2 (Černý et al., 2018), are needed by the plants at very low concentrations to perform intracellular signal transduction processes. However, their excessive production inhibits plant root growth. Stress conditions induce drastic increases in the production of ROS, with what has been dubbed an oxidative burst leading to oxidative stress. This can lead to the inactivation of crucial enzyme activities, protein degradation, alteration in gene expression and various metabolic pathways, resulting in overall cellular damage (Foyer, 2018; Singh et al., 2019). Plants have evolved several mechanisms to cope with the excessive ROS production, oxidative imbalance or for maintaining cell redox homeostasis. One of these mechanisms is a multifaceted and efficient antioxidant system comprising of enzymatic (eg superoxide dismutase and catalase) and non-enzymatic (e.g. glutathione, ascorbic acid, phenolics and proline) components which play crucial roles in sensing, elimination, detoxification or neutralizing toxic levels of ROS (Liebthal et al., 2018).

Acquisition of tolerance against oxidative damage via regulating antioxidant activities comprises signal crosstalk among vital signaling molecules including growth regulators and signaling proteins, such as kinases and phosphatases. Of the molecules with which ROS interact, gaseous signaling molecules, commonly known as gasotransmitters are particularly important owing to their vital roles. These include nitric oxide (NO) (León et al., 2020), hydrogen sulfide (H_2S) (Hancock, 2019), ethylene (C_2H_4) (Merchante et al., 2013), carbon monoxide (CO) (Wang and Liao, 2016) and methane (CH_4) (Li et al., 2019). Among the gasotransmitters (Wang, 2010), H_2S has recently gained momentum to be considered as a signaling molecule (Lisjak et al., 2013) since its recognition as a vital biomolecule, having potential for regulation of important cellular processes including plant development and stress tolerance (Hancock, 2019a). It is reported to be involved in signal transduction cascades, and therefore can alter cellular activity. It is a water soluble (partially), inorganic, colorless and rotten egg smelling gaseous molecule. It is generated endogenously but is inherently toxic, being a potent inhibitor of mitochondrial cytochrome oxidase (Complex IV), for example (Cooper and Brown, 2008). Despite this, it is now known to be instrumental in signaling events in a range of organisms including plants (Ma et al., 2019). In recent years, extensive research reports have revealed that H_2S plays a vital role in plant growth and development including seed germination, root organogenesis, stomatal movement (Ma et al., 2019), and photosynthesis (Chen et al., 2011). Besides this, H_2S is reported to be involved in the defense strategies against a diverse range of harsh environmental conditions (e.g., salinity, drought, heavy metal stress etc.) via crosstalk with other plant regulators, gene expression regulation and protein posttranslational modifications, the latter primarily through persulfidation of cysteine residues (Aroca et al., 2018; Jia et al., 2018). Furthermore, H_2S can act as a strong inducer of different cellular osmolytes, enzymatic and non-enzymatic antioxidants, and cell signaling proteins (e.g. mitogen activated protein kinases). H_2S leads to increases in cellular GSH (de Kok et al., 1985) and hence protects intracellular redox, and plant cell health (Figure 1). H_2S is produced by plant cells, but also can shift into plant cells from one to other cell, so can arrive or leave cells. Due to its small size and being uncharged it is easily diffusible through hydrophobic membranes (plasma membrane or membranes of organelles) without the aid of transport proteins such as aquaporins (Mathai et al., 2009). As shown in Figure 1, once in the cell, as well as potentially increasing glutathione (de Kok et al., 1985), H_2S can interact with NO metabolism, for example through the creation of nitrosothiol (HSNO) (Whiteman et al., 2006), and alter ROS metabolism, for example through alterations of antioxidant levels (Kaya et al., 2018), or through altering ROS synthesis (Christou et al., 2013). Often such alterations of cellular activity will lead to alterations of gene expression (Christou et al., 2013), perhaps through the action of microRNAs (Shen et al., 2013). Therefore, H_2S might have both short-term and long-term effects in plant cells.

Under the influence of stress, H_2S can act as a quality enhancer and nutrient of horticultural crops such as *Capsicum annum* (Kaya et al., 2018). Furthermore, a growing body of research also reveals that H_2S possesses the potential to delay senescence of various horticultural products during postharvest storage (Hu et al., 2015; Li et al., 2016; Aghdam et al., 2018a; Geng et al., 2019).

In the quest for sustainable horticulture crop production, in the face of future changes in climatic conditions (Tirado et al., 2010), here is discussed the possible roles of H_2S in horticultural crops. Focusing on the current knowledge on H_2S in horticulture sector, the regulation of physiological mechanisms, oxidative stress and abiotic stress are addressed. The discussion also focuses the mechanisms of responses to exogenous fumigation or applications of H_2S donor (sodium hydrosulfide (NaHS)) related to horticultural crops. Other review papers in this area includes: (Fotopoulos et al., 2015; Huo et al., 2018; Gong et al. 2018; Corpas and Palma, 2020; Xuan et al. 2020).

2. H_2S application to plants

If treatments based in H_2S are to be used in the environment to mitigate against climate change, the application of any relevant bio-active molecules has to be both beneficial and safe. It is known that gaseous H_2S is a toxin to many organisms owing to its inhibition of mitochondrial activity (Cooper and Brown, 2008). However, owing to its vital roles in plant key physiological processes, as well its potential as a therapeutic for human disease (Powell et al., 2018), different contemporary methods have been developed to deliver H_2S, including to plants (Hancock, 2019b). The easiest method to apply H_2S is as a gas, but outside of the laboratory this becomes impractical, especially on safety grounds as non-plant organisms may be affected, including humans (Rubright et al., 2017). Therefore, a range of donor molecules have been employed to deliver H_2S. Many experiments use sodium hydrosulfide (NaHS), or sodium sulfide (Na_2S) as H_2S donors, but these release H_2S very rapidly in solution and therefore give a short, not-sustained burst, and are not physiological. Much of the H_2S would be rapidly lost to the atmosphere and such compounds would have limited use in the environment. To overcome this, compounds such as GYY4137 have been developed (Li et al., 2009) that release H_2S at a much slower rate. Such compounds would give a longer treatment of plants in the environment, and may therefore may be a better option for agricultural use Further compounds have been developed too, which will release H_2S at particular intracellular locations. One such donor is the molecule AP39, which targets the mitochondria (Karwi et al., 2017). Although at present limited in their use, such compounds will be extremely useful for the delivery of H_2S to plant tissues in the future, especially in a laboratory or under controlled conditions (such as in a glasshouse). However, as well as the direct toxicity of H_2S to the environment (and to people in the vicinity of its use), donor compounds also leave behind a by-product, and often such residual molecules are also bioactive, and therefore any future widespread use would need to ensure that the safety of the treatment is considered, especially as by-products may enter environments not immediately treated, such as rivers and water courses.

3. H_2S production and its effects

At this stage, information regarding the exact endogenous production of H_2S in plant cells and its interaction of with other molecules is still scarce. However, it is thought that H_2S is primarily produced in subcellular compartments such as the chloroplast, cytosol, mitochondria and peroxisomes, which are linked with sulfur metabolism (Goter et al., 2015; Hancock and Whiteman, 2016; Corpas et al. 2019). Among these, chloroplast is thought to be a major production site of H_2S due to reduction of sulfite into sulfide via a chloroplast specific catalyst sulfite reductase during the sulfate assimilation pathway. Besides this, H_2S can be produced in the cytosol through the action of L-cysteine desulfhydrase (LCD) (García-Mata, and Lamattina, 2010; Corpas and Palma, 2020), with the accompanying formation of ammonia and pyruvate. While in mitochondria, H_2S can be produced via the action of β-cyanoalanine synthase, which catalyzes the conversion of cyanide to β-cyanoalanine at the cost of cysteine (Gotor et al., 2019). In a recent study with Arabidopsis, Corpas et al. (2019) reported the existence of H_2S in the peroxismomes. Furthermore, the expression of plant cellular proteins (L-cysteine desulfurase such as O-acetylserine thiol lyase (OAS-TL) and Nifs-like proteins) in different cellular organelles also possess the production potential of H_2S (Gotor et al., 2019). Besides its production in these organelles, H_2S due to its highly lipophilic nature, can easily translocate in the lipid bilayer of cell membranes (Cuevasanta et al., 2017) so may arrive from the cell’s environment, which may include anthropogenic activity, such as the petroleum industry (Habeeb et al., 2017) Additionally, the exposure to different environmental conditions and interactions with nitric oxide and plant hormones induces the production of H_2S in plant tissues (Fang et al., 2017; Jia et al., 2018). Alternatively NO may remove H_2S from cells. For example, H_2S and NO can react together to create the nitrosothiol, HSNO (Whiteman et al., 2006). This molecule is not inert and therefore the reaction of NO and H_2S potentially creates a new bio-active molecule which can partake in the cell signaling events in plant cells, as previously suggested for animal cells (Whiteman et al., 2006).

H_2S and photosynthesis

The relationship between the photosynthetic rate of plants and climate change is complex. On the one hand the photosynthetic activity of plants has an immensely important role in the sequestration of carbon (Raven and Carley, 2006), so removing

CO_2 from the atmosphere and potentially reducing the effects of anthropogenic activity. On the other hand, as environmental conditions change, plants may be exposed to increased or decreased amount of light (brightness or duration) and light levels will have a profound effect on photosynthetic activity (Rascher and Nedbal, 2006) as well as potentially causing a stress to plant cells (Reddy and Raghavendra, 2006).

An increase of photosynthetic activity may depend on the activity of ribulose-1, 5-bisphosphate carboxylase (RuBISCO). So increasing the RuBISCO activity is immensely important for enhancing photosynthesis. Exogenous NaHS, and hence H_2S, enhanced photosynthesis via elevating chloroplast biogenesis, endogenous H_2S concentration, RuBISCO enzyme activity, thiol redox modification and photosynthetic enzyme expression (Chen et al., 2011). Under stress condition such as overnight frost and day high light that negatively effect photosynthesis, foliar application of NaHS resulted in an improved photosynthetic response, including inhibition of CO_2 assimilation, a lower accumulation of hydrogen peroxide as well as lower photoinhibition, and a higher nonphotochemical quenching (Joshi et al. 2020). Further, it was reported that H_2S application can alleviate the degradation of chlorophyll, carotenoids and reduce the photoinhibition of PSII and PSI via promoting the electron transfer from QA to QB on PSII acceptor side under low temperature stress (Tang et al., 2020). Such increases in photosynthetic potential may enhance plant growth, increasing carbon sequestration as well as increasing crops, and hence H_2S may be useful as a treatment to mediate such effects.

H_2S and post-harvest of horticultural produce

As climate change has a greater impact on the world and the production of food for a growing population (Cohen, 2005) will become more important, getting crops to the table will be critical. As part of this, the need for better transportation and storage of crops will be vital. Treatment with H_2S gas or H_2S-based molecules may be part of a suite of strategies to ensure post-harvest management of crops is improved.

Information regarding endogenous H_2S metabolism in horticulture produce is limited and not well understood. Even so, increasing research evidence demonstrate that H_2S significantly influences the post-harvest of horticultural produce. In a recent study it was reported that endogenous H_2S content in sweet pepper fruits was upregulated during ripening (Muñoz-Vargas et al., 2018). In peach fruit during cold storage H_2S content is regulated by NO, for modulating the chilling injury response (Geng et al., 2019). ATP normally decreases under senescence or stress occurring during post-harvest storage and hence adversely affects post-harvest longevity (Aghdam et al., 2018a). H_2S application maintains this intracellular energy, ie ATP, via increasing related enzymes, such as H^+-ATPase or Ca^{2+}-ATPase, during post-harvest and helps in increasing post-harvest life of horticultural produce (Hu et al., 2015; Li et al., 2016). Maintenance of freshness, as depicted by the green color, especially in leafy vegetables during post-harvest, is critical to fetch good prices with consumer satisfaction, vital factor to allow some producers and suppliers to financially survive (Wognum et al., 2010) Application of NaHS (and hence H_2S) to cut broccoli during post-harvest regulated chlorophyll gene expression and thus slowed senescence leading to a longer shelf life compared to an untreated control (Li et al., 2015). Another factor affecting the post-harvest life of horticulture produce is the maintenance of cell structure. In kiwi fruit, application of H_2S delayed the ripening and senescence via regulating the cell-wall degrading enzyme genes and ethylene signal transduction pathway genes (Lin et al., 2020). Oxidative stress, as a result of excessive ROS production during post-harvest storage, is detrimental for horticulture produce. Various research reports have demonstrated that H_2S aids in lowering ROS via improving the activities of antioxidants (Zhang et al., 2011; Zheng et al., 2016; Ge et al., 2017; Ul Ubeed et al., 2017; Aghdam et al., 2018b; Liu et al., 2019; Mukhrjee et al., 2019), and may have effects through the maintenance of GSH (de Kok et al., 1985).

Clearly enhanced post-storage has massive commercial potential, as movement of crops around the globe is such an important aspect of today's society. However, the produce has to remain safe and desirable. H_2S is both toxic and smelly, so clearly work needs to be carried out to make sure there are no undesirable after effects. However, other redox compounds, such as nitric oxide (Huang et al., 2020; Qi et al., 2020; Zhang et al., 2020), have been mooted as useful for controlling post-harvest conditions, and therefore it is possible that H_2S-based compounds may be useful, perhaps at lower concentrations, as part of a suite of molecules used in food storage in the future. As climate changes and land use alters the movement of crop produce may become more important, and new strategies and formulations may be needed to be developed, with H_2S being part of this.

H_2S and drought/osmotic stress

As climate change has increasing effects on the environment in many areas of the globe, weather patterns will change with precipitation altering (Dore, 2005). On this background, some areas will become wetter and some drier, so plants may have to be able to survive, or adapt to both floods (Hirabayashi et al., 2013) and drought (Strzepek et al. 2010). This will, of course, have a major impact on agricultural practices when this happens. Therefore, treatments to help mitigate these effects are needed. Along with other strategies, such as the use of NO-based compounds (Tian and Lei, 2006), H_2S-based treatments may be a useful adjunct for consideration in the future (Table 1).

Sensitivity of horticultural crops to osmotic/drought stress has been considered as a major hindrance towards achieving the target of increased production efficiency (Kopta et al., 2020). On the other hand, low rainfall and high evaporation rates due to elevated temperature associated with climate change, is predicted to increase the drought stress severity. Thus, under osmotic or drought stress, there can be a dramatic decline in the horticulture production (Zulfiqar et al., 2019). Additionally, if coinciding with the crop sensitive stage of development, drought not only lowers the yield but also affects the quality of horticulture produce. Plants have adaptation to survive under unfavorable conditions such as drought stress and the first reaction towards drought stress is stomatal closure as a way to reduce transpirational water loss that allows plant to retain sufficient amount of water for the regulation of key physiological processes.

H_2S acts upstream or downstream of NO signaling cascades, depending on processes such as stomatal closure or in response to abiotic stress (Corpas et al., 2019). The role of H_2S as a stomatal control agent is still under debate. For instance under some instances H_2S may cause stomatal opening but closure in other conditions (Garcia-Mata and Lamattina, 2010; Lisjak et al., 2010; 2011; Hou et al., 2013; Jin et al., 2013; Papanatsiou et al., 2015). In another report, it has been shown that H_2S short-term exposure induced stomatal closure while long term caused enhanced stomatal apertures and the H_2S impact was mediated by 8-mercapto-cGMP (Honda et al., 2015) cGMP was thought to be a downstream mediator of NO effects in plants, but this has recently been thrown into doubt (Astier et al., 2019), and therefore its role in mediating H_2S effects should also be thrown into doubt.

NaHS, and hence H_2S, treated plants maintain higher relative water content under drought stress than control plants (Chen et al., 2016). NaHS as an exogenous H_2S donor application to spinach plants grown under drought stress imparted drought tolerance via increasing proline, polyamine and endogenous H_2S biosynthesis (Chen et al., 2016). Further, it was reported that several genes related to soluble sugars, polyamines, aquaporin (*SoPIP1;2*), choline monooxygenase (*SoCMO*) and betaine aldehyde dehydrogenase (*SoBADH*) were upregulated following H_2S application under drought stress (Chen et al., 2016). NaHS treated plants also showed decreases in MDA and H_2O_2 content, leading to a reduction in drought-induced oxidative stress (Chen et al., 2016). Shi et al. (2013) reported enhanced tolerance against salt, osmotic and low temperature stress in Bermuda grass following treatment with H_2S. They concluded that H_2S decreased oxidative stress via increasing both enzymatic and non-enzymatic antioxidants, together with an increase in osmolytes. In citrus plants, Ziogas et al. (2014) used a proteomic approach to evaluate the H_2S induced drought tolerance. They observed regulation of different proteins, especially *S*-nitrosated proteins and photosynthesis related proteins, following H_2S treatment.

Therefore, the control of water movements in plants may be a suitable target for H_2S modulation of physiological responses when crops are being grown in suboptimal conditions. As discussed above, H_2S-based formulations and treatments may need to be combined with the action of other molecules, and once again, NO-based signaling may be an interesting adjunct to any sulfur-based compounds.

H_2S and salt stress

Salt (i.e. NaCl) stress has an adverse impact on horticultural crops and thus decreases plant growth and productivity (Safdar et al., 2019; Zelm et al., 2020). Climate change may alter land use and hence agriculture may be affected by higher salt levels, especially in coastal regions (Hadley, 2009). Recent work, discussed below, suggests that H_2S may be part of the suite of cellular responses to elevated salt and hence may be a useful focus for future agricultural interventions (Table 1).

In cucumber plants, exogenous H_2S application induced salt tolerance via regulating Na^+/K^+ balance, regulating the H_2S endogenous level, and enhancing antioxidant activities (Jiang et al., 2019). Kaya et al. (2019) demonstrated that the melatonin induced salt and iron deficiency tolerance in pepper plants was via increasing H_2S and the activities of other antioxidants. In cabbage plants, application of NaHS increased tolerance to salt stress through elevating the antioxidant activities and improving processes involved in glutathione homeostasis and the enzymes related to AsA-GSH cycle (Montesinos-Pereira et al., 2020).

In another study, Christou et al. (2013) reported NaHS induced both salt stress tolerance and non-ionic osmotic stress tolerance in strawberry plants. They observed increases in the activities of antioxidants and maintenance of high ascorbate and glutathione redox states, thus minimization of oxidative and nitrosative stress (the latter being from increased NO accumulation (Corpas et al., 2007)). Additionally, quantitative real-time RT-PCR gene expression analysis revealed that H_2S plays a vital role in the regulation of antioxidants, transcription factors (e.g. dehydration-responsive element binding factor), ascorbate and glutathione biosynthesis, and salt overly sensitive (SOS) pathway genes (Christou et al. 2013). Application of NO and H_2S donors to tomato plants alleviated the oxidative damage induced by NaCl toxicity (da Silva et al., 2018). The authors also suggest that H_2S acts downstream of NO in this signaling cascade.

It is clear, therefore, that the generation and accumulation of H_2S has an influence on stress-induced signaling pathways in response to high NaCl, and can help mitigate the effects of high salt (Table 1).

H_2S and temperature stress

Climate change has long been dubbed global warming (Leiserowitz et al., 2019), mainly because the average temperature of Earth is increasing. However, many areas are seeing extreme temperature changes, both warming and cooling, and as such, agriculture in many global regions may be affected. As with the other stress conditions discussed here, there will be a future need to put in place mitigating regimes, and H_2S-based compounds may have a part to play in combating future novel temperature changes.

Being sessile organisms, plants have to endure the temperature that their surrounding environment dictates and often this is not ambient (Bita and Gerats, 2013). H_2S has been suggested to play a vital role in the induction of tolerance to both low and high temperatures in several horticultural crops. For instance, in a recent study, Tang et al. (2020) evaluated the influence of exogenous applied H_2S and hypotaurine (a H_2S scavenger) on blueberry seedlings for their role in low temperature stress tolerance. They observed improvement in tolerance following application of H_2S (supplied as NaHS) via regulating leaf gas exchange, reducing the photoinhibition of PSII and PSI and increasing proline content. They also measured oxidative stress indicators, H_2O_2 and MDA, and found that these reduced following H_2S application, while hypotaurine aggravated the negative effects of low temperature stress. In another study, Zhang et al. (2020) reported exogenous applied NaHS induced enhanced chilling tolerance in cucumber seedlings. The authors reported crosstalk between H_2S and indole acetic acid (IAA) in low temperature stress responses, as an enhancement of the activity of flavin monooxygenase (FMO) and relative expression of FMO-like proteins (*YUCCA2*), which in turn elevated endogenous IAA. The elevated IAA production decreased the low temperature stress-induced electrolyte leakage (EL) and ROS accumulation, and increased the gene expression and enzyme activities related to photosynthesis. The authors concluded that IAA acts as a downstream signaling molecule involved in the H_2S-induced low temperature tolerance in cucumber (Zhang et al., 2020). Liu et al. (2020) reported enhanced low temperature stress tolerance in response to H_2S. In the same study H_2S enhanced Cucurbitacin C (CuC), a triterpenoid secondary metabolite, that enhanced stress tolerance but it imparted a bitter taste in H_2S treated cucumber (not a desired feature for commercial production).

On the other hand, H_2S has also been demonstrated to be a relieving agent against the high temperature stress that can be lethal to horticultural crops, a factor predicted to increase in view of climate change. In a study on strawberry grown under high temperature stress, pretreatment with H_2S – in the form of NaHS – was found to lower oxidative damage and induce heat shock defense. It was concluded that H_2S induced heat resistance was mediated by the upregulation of antioxidants, aquaporins and heat shock protein genes and by preserving ascorbate/glutathione homeostasis (Christou et al., 2014).

Work such as this shows that there is potential for H_2S-based treatments to be used to mitigate against temperature changes, either too high or too low, which may be seen in the future as climate changes become more significant (Table 1).

H_2S and nutritional stress

Horticulture crops are very sensitive to nutritional toxicity or deficiency and they often have to tolerate conditions where nutritional excess or shortages prevails. Climate change will increase atmospheric CO_2, but may also alter nutrient availability through effects on the microbiotic interactions of plants (Table 1).

Exogenous application of NaHS reduced oxidative stress in cucumber plants grown under nitrate stress condition (Qi et al., 2019). The ROS level decreased while antioxidants' activities increased via mitogen-activated protein kinase/nitric oxide (MAPK/NO) signaling and upregulation of CsNMAPK transcript levels in the roots of stressed cucumber following H_2S application (Qi et al., 2019). In tomato plants, application of H_2S improved germination under nitrate stress via improving the activities of antioxidants (Li et al., 2015). Kaya and Ashraf (2019) suggested that iron deficiency induced chlorosis was alleviated by NaHS and the oxidative stress decreased, so improving the health of the plants.

The relationship between plants, their microbiotic environment, and nutrient availability, with a view to how H_2S may mediate effects, should be a focus of future work.

H_2S and heavy metal tolerance

Although climate change may be caused by anthropogenic activity (Trenberth et al., 2015), the manner in which societies use land may change as a result (Ouyang *et al*. 2018). One of the consequences of industrialization and altered land use is that the bioavailability of heavy metals will increase, and numerous heavy metals, such as copper, lead, zine, cadmium and mercury are known to cause stress in plants (Ghori et al., 2019). As this becomes an increasing problem, mitigating regimes will need to be considered, and again, H_2S-based compounds may have a place to play.

Valivand et al. (2019a) suggested that H_2S was involved in the acquisition of the relief from nickel ions ($Ni(NO_3)_2$) stress via seed priming with H_2S and Ca^{2+} in zucchini seedlings. Whilst in another study, Valivand et al. (2019b) confirmed that H_2S either alone or in combination with Ca^{2+} imparts nickel ($Ni(NO_3)_2$) tolerance in zucchini seedlings.

In pepper, NaHS could alleviate the oxidative stress caused by high zinc ($ZnSO_4.7H_2O$) stress (Kaya et al., 2018), while endogenous level of H_2S, proline and antioxidants activities increased and electrolyte leakage, H_2O_2 and MDA was decreased. Arsenate ($Na_2HAsO_4.7H_2O$) stress in pea seedlings was alleviated by NaHS, with restoration of redox status of the ascorbate and glutathione pools together with the reduction of ROS (Singh et al., 2015). In chromium ($K_2Cr_2O_7$) stress, NaHS increased the activities of antioxidants and restricted the uptake of chromium ions in stressed cauliflower seedlings (Ahmad et al., 2019). Recently, lead (provided in the form of lead acetate [Pb($CH_3COO)_2\cdot 3H_2O$/PbAc] treatment of cauliflower led to inhibition in seed germination and seedling growth due to oxidative stress. However, the negative effects were alleviated by the application of NaHS (Chen et al., 2018). Expression of antioxidative enzymes and metallothioneins was noted to be important in the H_2S effects observed on the cadmium/zinc hyperaccumulator *Solanum nigrum*. Exogenous NaHS decreased free cytosolic Zn^{2+} content in roots, altered antioxidant activities and decreased toxic ROS (Liu et al., 2016).

Heavy metal stress is one which is only likely to increase as human activity escalates, exacerbated by climate change, and therefore the exploration of H_2S-mediated treatments may be important.

4. Conclusion and the future use of H_2S treatments

Regardless whether climate change is because of anthropogenic activity or the result of natural causes (Trenberth et al., 2015), there is little doubt that weather conditions are altering around the globe. Along with higher average temperatures and more extreme temperature fluctuations, this may have other consequences such as more flooding, increased drought conditions, and greater risk of salt and heavy metal stress. Therefore, there is a growing and urgent need to find treatments of plants, particularly those instrumental to agriculture and horticulture, which may mitigate against these more harsh growing conditions. Some plants may be able to adapt, whilst other may not. Although there is a growing body of work in this area (Raza et al., 2019), it is mooted here that H_2S-based treatments may have a place to play, even if they are only an adjunct to other regimes.

H_2S is a novel gasotransmitter, playing vital roles plant sulfur metabolism and sulfur-based signaling, through redox interactions with other signals (Hancock and Whiteman, 2014) and particularly through the protein post-translational modification persulfidation (Aroca et al., 2018; Jia et al., 2018). H_2S has been proposed to regulate various plant developmental processes from seed germination to post-harvest in horticulture. Importantly here, it is known to mitigate the negative impact of environmental stresses such as drought, temperature extremes, salinity, and heavy metal etc. and their associated oxidative stress (Hancock, 2019a) (Figure 2: Table 1).

Therefore, the role of H_2S in enhancing the stress tolerance of plants in the face of global climate change is immensely important. Exogenous application of H_2S seems a promising approach to help mitigate the food security problem, especially under climatic fluctuations inducing environmental stresses. The approach could further extend to promote seed germination via seed priming with H_2S and plant development of horticultural crops. The impact of exogenous pre-harvest applications on post-harvest storage is also an unexplored area needing future research attention. H_2S-based protocols could also be used as promising tools to prevent post-harvest diseases and extending longevity during storage of horticultural produce. Furthermore, the impact on nutritional quality of horticulture produce needs to be explored.

H_2S application methods are being developed in the medical arena, with the creation of such H_2S donors as GYY4137 and Ap39 (Karwi et al., 2017). A similar approach in agriculture-based research would enable treatments for plants to be developed which would be more effective than presently available, and be easy and cheap to apply. Most evidence related to post-harvest are based on NaHS treatments, which is certainly not suitable for the food industry and therefore it is one of the main challenges of this field is to find a way to supply H_2S in order to increase both crop production and post-harvest crop quality. Simply spraying H_2S gas onto plants in the environment is not feasible, especially for safety reasons, but also for societal concerns – it is extremely smelly. However, H_2S-donor-based treatments may be feasible if able to be made and delivered in a financially sustainable manner, perhaps in controlled conditions, where plants are grown under glass. Furthermore, using a H_2S-based method of stress mitigation as an adjunct to other treatments, perhaps other redox-based treatments such as those based on NO signaling, may be a preferred way forward. However, H_2S, like NO, has been seen to have numerous effects in cells, and work will need to be done not only on how multiple treatments may interfere with each other, but also on investigating whether using H_2S-based treatments for one stress does not have adverse effects under a different stress. For example, if using such a regime for alleviating heavy metal stress, it will be important that it does not adversely affect the transpiration of plants, as both physiological systems are impacted by intracellular H_2S accumulation.

Clearly, there is much to learn about how H_2S integrates into cell signaling pathways, and how it mitigates against plant stress, and with the changing global climate there is much potential here to develop H_2S-based treatments. With the future food requirements set to increase substantially with the human population (Zulfiqar et al., 2019), H_2S-based protocols may be part of a suite of solutions which could be adopted more widely in agricultural practice.

References

Aghdam, M.S., Jannatizadeh, A., Luo, Z., Paliyath, G., 2018a. Ensuring sufficient intracellular ATP supplying and friendly extracellular ATP signaling attenuates stresses, delays senescence and maintains quality in horticultural crops during postharvest life. Trends Food Sci. Technol. 76, 67-81.

Aghdam, M.S., Mahmoudi, R., Razavi, F., Rabiei, V., Soleimani, A., 2018b. Hydrogen sulfide treatment confers chilling tolerance in hawthorn fruit during cold storage by triggering endogenous H_2S accumulation, enhancing antioxidant enzymes activity and promoting phenols accumulation. Sci Hortic. 238, 264-271.

Ahmad, R., Ali, S., Rizwan, M., Dawood, M., Farid, M., Hussain, A., Wijaya, L., Alyemeni, M. N., Ahmad, P., 2019. Hydrogen sulfide alleviates chromium stress on cauliflower by restricting its uptake and enhancing antioxidative system. Physiol. Plant. 168, 289-300.

Al Ubeed, H.M.S., Wills, R.B.H., Bowyer, M.C., Vuong, Q.V., Golding, J.B., 2017. Interaction of exogenous hydrogen sulphide and ethylene on senescence of green leafy vegetables. Postharvest Biol. Technol. 133, 81-87.

Anderson, J.T., Inouye, D.W., McKinney, A.M., Colautti, R.I., Mitchell-Olds, T., 2012. Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. Proc. Biol. Sci. 279, 3843–3852.

Aroca, A., Gotor, C., Romero, L.C., 2018. Hydrogen sulfide signaling in plants: emerging roles of protein persulfidation. Frontiers in Plant Science 9, 1369.

Asseng, S., Ewert, F., Martre, P. et al., 2015. Rising temperatures reduce global wheat production. Nature Clim Change. 5, 143–147. https://doi.org/10.1038/nclimate2470

Astier, J., Mounier, A., Santolini, J., Jeandroz, S., Wendehenne, D., 2019. The evolution of nitric oxide signalling diverges between animal and green lineages. J. Exp. Bot. 70, 4355-4364.

Bita, C.E., Gerats, T., 2013. Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops. Front. Plant Sci. 4, 273.

Cassia R, Nocioni M, Correa-Aragunde N, Lamattina L., 2018. Climate change and the impact of greenhouse gasses: CO2 and NO, friends and foes of plant oxidative stress. Front. Plant Sci. 9, 273.

Černý, M., Habánová, H., Berka, M., Luklova, M., Brzobohatý, B. 2018. Hydrogen peroxide: its role in plant biology and crosstalk with signalling networks. Int. J. Mol. Sci. 19, 2812.

Chapman, J.M., Muhlemann, J.K., Gayomba, S.R., Muday, G.K., 2019. RBOH-dependent ROS synthesis and ROS scavenging by plant specialized metabolites to modulate plant development and stress responses. Chem. Res. Toxicol. 32, 370-396.

Chen, J., Shang, Y.T., Wang, W.H., Chen, X.Y., He, E.M., Zheng, H.L., Shangguan, Z., 2016. Hydrogen sulfide-mediated polyamines and sugar changes are involved in hydrogen sulfide-induced drought tolerance in *Spinacia oleracea* seedlings. Front. Plant Sci. 7, 1173.

Chen, J., Wu, F.H., Wang, W.H., Zheng, C.J., Lin, G.H., Dong, X.J., He, J.X., Pei, Z.M., Zheng, H.L., 2011. Hydrogen sulphide enhances photosynthesis through promoting chloroplast biogenesis, photosynthetic enzyme expression, and thiol redox modification in *Spinacia oleracea* seedlings. J. Exp. Bot. 62, 4481-4493.

Chen, Z., Yang, B., Hao, Z., Zhu, J., Zhang, Y., Xu, T., 2018. Exogenous hydrogen sulfide ameliorates seed germination and seedling growth of cauliflower under lead stress and its antioxidant role. J. Plant Growth Regul. 37, 5-15.

Christou, A., Filippou, P., Manganaris, G.A., Fotopoulos, V., 2014. Sodium hydrosulfide induces systemic thermotolerance to strawberry plants through transcriptional regulation of heat shock proteins and aquaporin. BMC Plant Biol. 14, 42.

Christou, A., Manganaris, G. A., Papadopoulos, I., Fotopoulos, V., 2013. Hydrogen sulfide induces systemic tolerance to salinity and non-ionic osmotic stress in strawberry plants through modification of reactive species biosynthesis and transcriptional regulation of multiple defence pathways. J. Exp. Bot. 64, 1953-1966.

Christou, A., Manganaris, G.A., Papadopoulos, I., Fotopoulos, V., 2013. Hydrogen sulfide induces systemic tolerance to salinity and non-ionic osmotic stress in strawberry plants through modification of reactive species biosynthesis and transcriptional regulation of multiple defence pathways. J. Exp. Bot. 64, 1953-1966.

Cohen, J. E. 2005. Human population grows up. Sci. American, 293, 48-55.

Cooper, C.E., Brown, G.C., 2008. The inhibition of mitochondrial cytochrome oxidase by the gases carbon monoxide, nitric oxide, hydrogen cyanide and hydrogen sulfide: chemical mechanism and physiological significance. J. Bioenerg. Biomembr. 40, 533.

Corpas, F.J., Barroso, J.B., González-Gordo, S., Muñoz-Vargas, M.A., Palma, J.M., 2019. Hydrogen sulfide: A novel component in Arabidopsis peroxisomes which triggers catalase inhibition. J. Integr. Plant Biol. 61, 871-883.

Corpas, F.J., Del Rio, L.A., Barroso, J.B. 2007. Need of biomarkers of nitrosative stress in plants. Trends in Plant Science 12, 436-438.

Corpas, F.J., González-Gordo, S., Cañas, A., Palma, J.M., 2019. Nitric oxide and hydrogen sulfide in plants: which comes first?. J. Exp. Bot. 70, 4391-4404.

Corpas, F.J., Palma, J.M., 2020. H_2S signaling in plants and applications in agriculture. J. Adv. Res. 24, 131-137.

Cuevasanta, E., Möller, M.N., Alvarez, B., 2017. Biological chemistry of hydrogen sulfide and persulfides. Arch Biochem Biophys. 617, 9-25.

da Silva, C.J., Mollica, D.C.F., Vicente, M.H., Peres, L.E.P., Modolo, L.V., 2018. NO, hydrogen sulfide does not come first during tomato response to high salinity. Nitric Oxide 76, 164-173.

De Kok, J.L., Bosma, W., Maas, F.M., Kuiper, P.J.C., 1985. The effect of short-term H_2S fumigation on water-soluble sulphydryl and glutathione levels in spinach. Plant Cell Environ. 8, 189-194.

Dhankher, O.P., Foyer, C.H., 2018. Climate resilient crops for improving global food security and safety. Plant Cell Environ. 41, 877–884.

Dore, M.H. 2005. Climate change and changes in global precipitation patterns: what do we know?. Environ. Int. 31, 1167-1181.

Eva van, Zelm., Yanxia, Zhang., Christa, Testerink., 2020. Salt Tolerance Mechanisms of Plants. Annual Review of Plant Biology. 71:1, 403-433.

Fang, H., Liu, Z., Long, Y., Liang, Y., Jin, Z., Zhang, L., Liu, D., Li, H., Zhai, J., Pei, Y., 2017. The Ca2+/calmodulin2- binding transcription factor TGA3 elevates LCD expression and H2S production to bolster Cr^{6+} tolerance in Arabidopsis. Plant J. 91, 1038–1050.

Fotopoulos, V., Christou, A., Antoniou, C., Manganaris, G.A. 2015. Review article hydrogen sulphide: a versatile tool for the regulation of growth and defence responses in horticultural crops. J. Hortic. Sci. Biotechnol, 90, 227-234.

Foyer, C.H., 2018. Reactive oxygen species, oxidative signaling and the regulation of photosynthesis. Environ. Exp. Bot. 154, 134-142.

García-Mata, C., Lamattina, L., 2010. Hydrogen sulfide, a novel gasotransmitter involved in guard cell signalling. New Phytol. 188, 977-984.

García-Mata, C., Lamattina, L., 2010. Hydrogen sulphide, a novel gasotransmitter involved in guard cell signalling. New Phytol, 188, 977-984.

Ge, Y., Hu, K. D., Wang, S. S., Hu, L. Y., Chen, X. Y., Li, Y. H., Yang, Y., Yang, F., Zhang, H., 2017. Hydrogen sulfide alleviates postharvest ripening and senescence of banana by antagonizing the effect of ethylene. PLoS One, *12*, e0180113.

Geng, B., Huang, D., Zhu, S., 2019. Regulation of Hydrogen sulfide metabolism by nitric oxide inhibitors and the quality of peaches during cold storage. Antioxidants, 8, 401.

Ghori, N. H., Ghori, T., Hayat, M. Q., Imadi, S. R., Gul, A., Altay, V., Ozturk, M., 2019. Heavy metal stress and responses in plants. Int. J. Environ. Sci. Technol. 16, 1807-1828.

Gong, T., Li, C., Bian, B., Wu, Y., Dawuda, M.M., Liao, W., 2018. Advances in application of small molecule compounds for extending the shelf life of perishable horticultural products: a review. Sci. Hortic. 230, 25-34.

Gotor, C., García, I., Aroca, Á., Laureano-Marín, A. M., Arenas-Alfonseca, L., Jurado-Flores, A., Moreno, I., Romero, L.C., 2019. Signaling by hydrogen sulfide and cyanide through post-translational modification. J. Exp. Bot. 70, 4251-4265.

Gotor, C., Laureano-Marín, A.M., Moreno, I., Aroca, A., García, I., Romero, L.C., 2015. Signaling in the plant cytosol: Cysteine or sulfide? Amino Acids. 47: 2155–2164.

Habeeb, O.A., Kanthasamy, R., Ali, G.A., Sethupathi, S., Yunus, R.B.M., 2018. Hydrogen sulfide emission sources, regulations, and removal techniques: a review. Reviews in Chemical Engineering, 34, 837-854.

Hadley, D., 2009. Land use and the coastal zone. Land Use Policy. 26: S198-S203.

Hancock J.T., 2019b. Methods for the Addition of Redox Compounds. In: Hancock J., Conway M. (eds) Redox-Mediated Signal Transduction. Methods in Molecular Biology, vol 1990. Humana, New York, NY.

Hancock, J. T., Whiteman, M., 2018. Cellular redox environment and its influence on redox signalling molecules. React. Oxyg. Spec. 5, 78-85.

Hancock, J.T., 2019a. Hydrogen sulfide and environmental stresses. Environ. Exp. Bot. 161, 50-56.

Hancock, J.T., Whiteman, M. 2016. Hydrogen sulfide signaling: interactions with nitric oxide and reactive oxygen species. Annals New York Academy Sci. 1365, 5-14.

Hancock, J.T., Whiteman, M., 2014. Hydrogen sulfide and cell signaling: team player or referee? Plant Physiol. Biochem. 78, 37-42.

Hirabayashi, Y., Mahendran, R., Koirala, S., Konoshima, L., Yamazaki, D., Watanabe, S., Kanae, S. 2013. Global flood risk under climate change. Nat. Clim. Change. 3, 816-821.

Honda, K., Yamada, N., Yoshida, R., Ihara, H., Sawa, T., Akaike, T., Iwai, S., 2015. 8-Mercapto-cyclic GMP mediates hydrogen sulfide-induced stomatal closure in Arabidopsis. Plant Cell Physiol. 56, 1481-1489.

Hou, Z., Wang, L., Liu, J., Hou, L., Liu, X., 2013. Hydrogen sulfide regulates ethylene-induced stomatal closure in *Arabidopsis thaliana*. J Integr Plant Biol, 55, 277-289.

Huang, D., Tian, W., Feng, J., Zhu, S., 2020. Interaction between nitric oxide and storage temperature on sphingolipid metabolism of postharvest peach fruit. Plant Physiol Biochem. 151: 60-68.

Huo, J., Huang, D., Zhang, J., Fang, H., Wang, B., Wang, C., Liao, W., 2018. Hydrogen sulfide: a gaseous molecule in postharvest freshness. Front. Plant. Sci, 9, 1172.

IPCC., 2013. Climate Change 2013: The Physical Science Basis. Intergovernmental Panel on Climate Change, Cambridge, UK.

Jia, H., Chen, S., Liu, D., Liesche, J., Shi, C., Wang, J., Ren, M., Wang, X., Yang, J., Shi, W., Li, J., 2018. Ethylene induced hydrogen sulfide negatively regulates ethylene biosynthesis by persulfidation of ACO in tomato under osmotic stress. Front. Plant Sci. 9, 1517.

Jiang, J., Li, L., Yu, M., Hou, R., Ren, X., 2019. H_2S alleviates salinity stress in cucumber by maintaining the Na+/K+ balance and regulating H_2S metabolism and oxidative stress response. Front. Plant Sci. 10, 678.

Jin, Z., Xue, S., Luo, Y., Tian, B., Fang, H., Li, H., Pei, Y., 2013. Hydrogen sulfide interacting with abscisic acid in stomatal regulation responses to drought stress in Arabidopsis. Plant Physiol Biochem, 62, 41-46.

Joshi, N.C., Yadav, D., Ratner, K., Kamara, I., Aviv-Sharon, E., Irihimovitch, V., Charuvi, D., 2020. Sodium hydrosulfide priming improves the response of photosynthesis to overnight frost and day high light in avocado (*Persea americana* Mill, cv.‘Hass’). Physiol Plant, 168, 394-405.

Karwi, Q.G., Bornbaum, J., Boengler, K., Torregrossa, R., Whiteman, M., Wood, M.E., Schulz, R., Baxter, G.F., 2017. AP39, a mitochondria‐targeting hydrogen sulfide (H2S) donor, protects against myocardial reperfusion injury independently of salvage kinase signalling. Br. J. Pharmacol. 174, 287-301.

Kaya, C., Ashraf, M., 2019. The mechanism of hydrogen sulfide mitigation of iron deficiency-induced chlorosis in strawberry (*Fragaria*× *ananassa*) plants. Protoplasma, 256, 371-382.

Kaya, C., Ashraf, M., Akram, N.A., 2018. Hydrogen sulfide regulates the levels of key metabolites and antioxidant defense system to counteract oxidative stress in pepper (*Capsicum annuum* L.) plants exposed to high zinc regime. Environ. Sci. Pollution Res. 25, 12612-12618.

Kaya, C., Higgs, D., Ashraf, M., Alyemeni, M.N., Ahmad, P., 2019. Integrative roles of nitric oxide and hydrogen sulfide in melatonin‐induced tolerance of pepper (*Capsicum annuum* L.) plants to iron deficiency and salt stress alone or in combination. Physiol Plant. 168, 256-277.

Kopta, T., Sekara, A., Pokluda, R., Ferby, V., Caruso, G., 2020. Screening of chilli pepper genotypes as a source of capsaicinoids and antioxidants under conditions of simulated drought stress. Plants. 9, 364.

Leiserowitz, A., Maibach, E., Rosenthal, S., Kotcher, J., Bergquist, P., Gustafson, A., Ballew, M., Goldberg, M., 2019. Politics & Global Warming, November 2019. Yale University and George Mason University. New Haven, CT: Yale Program on Climate Change Communication.

León, J., Costa‐Broseta, Á., 2020. Present knowledge and controversies, deficiencies, and misconceptions on nitric oxide synthesis, sensing, and signaling in plants. Plant Cell Environ, 43, 1-15.

Li, D., Limwachiranon, J., Li, L., Du, R., Luo, Z., 2016. Involvement of energy metabolism to chilling tolerance induced by hydrogen sulfide in cold-stored banana fruit. Food Chem. 208, 272-278.

Li, L., Salto-Tellez, M., Tan, C.H., Whiteman, M., Moore, P. K., 2009. GYY4137, a novel hydrogen sulfide-releasing molecule, protects against endotoxic shock in the rat. Free Radic. Biol. Med. 47, 103-113.

Li, L., Wei, S., Shen, W., 2019. The role of methane in plant physiology: a review. Plant Cell Rep, 1-9.

Li, S., Yan, J.P., Yang, E., Bai, X.G., Long, J., Li, K.Z., Xu, H.N., 2015. Effects of exogenous H_2S on the germination of tomato seeds under nitrate stress. J. Hortic. Sci. Biotechnol. 90, 39-46.

Liebthal, M., Maynard, D., Dietz, K.J., 2018. Peroxiredoxins and redox signaling in plants. Antioxid. Redox Signal. 28, 609-624.

Lin, X., Yang, R., Dou, Y., Zhang, W., Du, H., Zhu, L., Chen, J., 2020. Transcriptome analysis reveals delaying of the ripening and cell wall degradation of kiwifruit by hydrogen sulfide. J. Sci. Food. Agric. 100, 2280-2287.

Lisjak, M., Teklic, T., Wilson, I. D., Whiteman, M., Hancock, J. T., 2013. Hydrogen sulfide: environmental factor or signalling molecule?. Plant Cell Environ, 36, 1607-1616.

Lisjak, M., Teklic, T., Wilson, I.D., Wood, M., Whiteman, M., Hancock, J.T., 2011. Hydrogen sulfide effects on stomatal apertures. Plant Signaling and Behavior 6, 1444-1446.

Liu, X., Chen, J., Wang, G.H., Wang, W.H., Shen, Z.J., Luo, M.R., Gao, G.F., Simon, M., Ghoto, K., Zheng, H.L., 2016. Hydrogen sulfide alleviates zinc toxicity by reducing zinc uptake and regulating genes expression of antioxidative enzymes and metallothioneins in roots of the cadmium/zinc hyperaccumulator *Solanum nigrum* L. Plant Soil. 400, 177-192.

Liu, Z., Li, Y., Cao, C., Liang, S., Ma, Y., Liu, X., Pei, Y., 2019. The role of H_2S in low temperature-induced cucurbitacin C increases in cucumber. Plant Mol. Biol. 99, 535-544.

Ma, Y., Zhang, W., Niu, J., Ren, Y., Zhang, F., 2019. Hydrogen sulfide may function downstream of hydrogen peroxide in salt stress-induced stomatal closure in *Vicia faba*. Funct. Plant Biol. 46, 136-145.

Mathai, J. C., Missner, A., Kügler, P., Saparov, S. M., Zeidel, M. L., Lee, J. K., Pohl, P., 2009. No facilitator required for membrane transport of hydrogen sulfide. Proc Natl Acad Sci, 106, 16633-16638.

Medvigy, D., Beaulieu, C., 2012. Trends in daily solar radiation and precipitation coefficients of variation since 1984. J. Clim. 25, 1330–1339.

Merchante, C., Alonso, J. M., Stepanova, A.N., 2013. Ethylene signaling: simple ligand, complex regulation. Curr. Opi. Plant. Biol, 16, 554-560.

Min, S.K., Zhang, X., Zwiers, F.W., Hegerl, G.C., 2011. Human contribution to more-intense precipitation extremes. Nature 470, 378–381.

Mittler R., 2017. ROS are good. Trends Plant Sci. 22, 11–19.

Montesinos-Pereira, D., de la Torre-González, A., Blasco, B., Ruiz, J. M., 2018. Hydrogen sulphide increase the tolerance to alkalinity stress in cabbage plants (*Brassica oleracea* L.'Bronco'). Sci. Hortic. 235, 349-356.

Mukherjee S., 2019. Recent advancements in the mechanism of nitric oxide signaling associated with hydrogen sulfide and melatonin crosstalk during ethylene-induced fruit ripening in plants. Nitric Oxide. 82:25-34.

Muñoz-Vargas, M.A., González-Gordo, S., Cañas, A., López-Jaramillo, J., Palma, J.M., Corpas, F.J., 2018. Endogenous hydrogen sulfide (H_2S) is up-regulated during sweet pepper (*Capsicum annuum* L.) fruit ripening. In vitro analysis shows that NADP-dependent isocitrate dehydrogenase (ICDH) activity is inhibited by H_2S and NO. Nitric Oxide 81, 36-45.

Nolan, C., Overpeck, J. T., Allen, J. R., Anderson, P. M., et al., 2018. Past and future global transformation of terrestrial ecosystems under climate change. Sci. 361, 920-923.

O'Gorman, P.A., 2015. Precipitation extremes under climate change. Curr. Clim. Change. Rep. 1, 49-59.

Ouyang, W., Wang, Y., Lin, C., He, M., Hao, F., Liu, H., Zhu, W., 2018. Heavy metal loss from agricultural watershed to aquatic system: A scientometrics review. Sci. Total Environ. 637, 208-220.

Pall, P., Aina, T., Stone, D.A., Stott, P.A., Nozawa, T., Hilberts, A.G., Lohmann, D., Allen MR., 2011. Anthropogenic greenhouse gas contribution to flood risk in England and Wales in autumn 2000. Nature 470, 382–385.

Papanatsiou, M., Scuffi, D., Blatt, M. R., García-Mata, C., 2015. Hydrogen sulfide regulates inward-rectifying K^+ channels in conjunction with stomatal closure. Plant Physiol, 168, 29-35.

Powell, C.R., Dillon, K.M., Matson, J.B., 2018. A review of hydrogen sulfide (H_2S) donors: Chemistry and potential therapeutic applications. Biochem. Pharmacol. 149, 110-123.

Qi, Q., Guo, Z., Liang, Y., Li, K., Xu, H., 2019. Hydrogen sulfide alleviates oxidative damage under excess nitrate stress through MAPK/NO signaling in cucumber. Plant Physiol. Biochem. 135, 1-8.

Qi, X., Ji, Z., Lin, C., Li, S., Liu, J., Kan, J., Zhang, M., Jin, C., Qian, C., 2020. Nitric oxide alleviates lignification and softening of water bamboo (*Zizania latifolia*) shoots during postharvest storage. Food Chem. 127416.

Rascher, U., Nedbal, L. 2006. Dynamics of photosynthesis in fluctuating light. Curr. Opin. Plant Biol, 9, 671-678.

Raven, J.A., Karley, A.J. 2006. Carbon sequestration: photosynthesis and subsequent processes. Current Biol, 16, R165-R167.

Raza, A., Razzaq, A., Mehmood, S. S., Zou, X., Zhang, X., Lv, Y., Xu, J., 2019. Impact of climate change on crops adaptation and strategies to tackle its outcome: A review. Plants, 8, 34.

Reddy A.R., Raghavendra A.S. 2006. PHOTOOXIDATIVE STRESS. In: Madhava Rao K., Raghavendra A., Janardhan Reddy K. (eds) Physiology and Molecular Biology of Stress Tolerance in Plants. Springer, Dordrecht

Rennenberg, H., 1984. The fate of excess sulfur in higher plants. Annu. Rev. Plant Biol. 35, 121-153.

Rubright, S. L.M., Pearce, L.L., Peterson, J., 2017. Environmental toxicology of hydrogen sulfide. Nitric oxide: biology and chemistry, 71, 1.

Safdar, H., Amin, A., Shafiq, Y., Ali, A., Yasin, R., Shoukat, A., Sarwar, M. I., 2019. A review: impact of salinity on plant growth. Nat Sci, 17, 34-40.

Sekiya, J., Schmidt, A., Wilson, L.G., Filner, P., 1982. Emission of hydrogen sulfide by leaf tissue in response to L-cysteine. Plant Physiol. 70, 430–436.

Shaw, R.G., Etterson, J.R., 2012. Rapid climate change and the rate of adaptation: insight from experimental quantitative genetics. New Phytol. 195, 752–765.

Shen, J., Xing, T., Yuan, H., Liu, Z., Jin, Z., Zhang, L., Pei, Y., 2013. Hydrogen sulfide improves drought tolerance in Arabidopsis thaliana by microRNA expressions. PloS one, 8, e77047.

Shi, H., Ye, T., Chan, Z., 2013. Exogenous application of hydrogen sulfide donor sodium hydrosulfide enhanced multiple abiotic stress tolerance in Bermuda grass (*Cynodon dactylon* (L). Pers.). Plant Physiol. Biochem. 71, 226-234.

Singh, S., Kumar, V., Kapoor, D., Kumar, S., Singh, S., Dhanjal, D.S., Datta, S., Samuel, J., Dey, P., Wang, S., Prasad, R., Sing, J., 2019. Revealing on hydrogen sulfide and nitric oxide signals co-ordination for plant growth under stress conditions. Physiol Plant. 168, 301–317.

Singh, V.P., Singh, S., Kumar, J., Prasad, S.M., 2015. Hydrogen sulfide alleviates toxic effects of arsenate in pea seedlings through up-regulation of the ascorbate–

glutathione cycle: possible involvement of nitric oxide. J. Plant Physiol. 181, 20-29.

Soares, J. C., Santos, C. S., Carvalho, S. M., Pintado, M.M., Vasconcelos, M.W., 2019. Preserving the nutritional quality of crop plants under a changing climate: importance and strategies. Plant. Soil. 443, 1-26.

Strzepek, K., Yohe, G., Neumann, J., Boehlert, B. 2010. Characterizing changes in drought risk for the United States from climate change. Environ. Res. Letters, 5, 044012.

Tang, X., An, B., Cao, D., Xu, R., Wang, S., Zhang, Z., Liu, X., Sun, X., 2020. Improving photosynthetic capacity, alleviating photosynthetic inhibition and oxidative stress under low temperature stress with exogenous hydrogen sulfide in blueberry seedlings. Front Plant Sci, 11.

Tang, X., An, B., Cao, D., Xu, R., Wang, S., Zhang, Z., Liu, X., Sun, X., 2020. Improving photosynthetic capacity, alleviating photosynthetic inhibition and oxidative stress under low temperature stress with exogenous hydrogen sulfide in blueberry seedlings. Front. Plant Sci. 11.

Tian, X., Lei, Y. 2006. Nitric oxide treatment alleviates drought stress in wheat seedlings. Biologia Plant. 50, 775-778.

Tirado, M.C., Clarke, R., Jaykus, L.A., McQuatters-Gollop, A., Frank, J.M., 2010. Climate change and food safety: A review. Food Res. Int. 43, 1745-1765.

Trenberth, K. E., Fasullo, J. T., Shepherd, T. G., 2015. Attribution of climate extreme events. Nat. Clim. Chang. 5, 725-730.

Valivand, M., Amooaghaie, R., Ahadi, A., 2019a. Seed priming with H_2S and Ca^{2+} trigger signal memory that induces cross-adaptation against nickel stress in zucchini seedlings. Plant Physiol. Biochem. 143, 286-298.

Valivand, M., Amooaghaie, R., Ahadi, A., 2019b. Interplay between hydrogen sulfide and calcium/calmodulin enhances systemic acquired acclimation and antioxidative defense against nickel toxicity in zucchini. Environ. Exp. Bot. 158, 40-50.

Wang, M., Liao, W., 2016. Carbon monoxide as a signaling molecule in plants. Front. Plant. Sci, 7, 572.

Wang, R., 2010. Hydrogen sulfide: the third gasotransmitter in biology and medicine. Antioxid. Redox Sign. 12, 1061-1064.

Whiteman, M., Li, L., Kostetski, I., Chu, S.H., Siau, J. L., Bhatia, M., Moore, P. K., 2006. Evidence for the formation of a novel nitrosothiol from the gaseous mediators nitric oxide and hydrogen sulphide. Biochemical and biophysical research communications, 343, 303-310.

Wilson, L.G., Bressan, R.A, Filner, P., 1978. Light-dependent emission of hydrogen sulfide from plants. Plant Physiol. 61, 184-189.

Wognum, P. N., Bremmers, H., Trienekens, J. H., van der Vorst, J. G., Bloemhof, J. M. 2011. Systems for sustainability and transparency of food supply chains–Current status and challenges. Advanced engineering informatics, 25, 65-76.

Xuan, L., Li, J., Wang, X., Wang, C., 2020. Crosstalk between Hydrogen Sulfide and Other Signal Molecules Regulates Plant Growth and Development. Int. J. Mol. Sci. 21, 4593.

Zhang, H., Hu, S.L., Zhang, Z.J., Hu, L.Y., Jiang, C.X., Wei, Z.J, Liu, J., Wang, H.L., Jiang, S.T., 2011. Hydrogen sulfide acts as a regulator of flower senescence in plants. Postharvest Biol. Technol. 60, 251-257.

Zhang, W., Cao, J., Fan, X., Jiang, W., 2020. Applications of nitric oxide and melatonin in improving postharvest fruit quality and the separate and crosstalk biochemical mechanisms. Trends. Food. Sci. Technol. 99: 531-541.

Zhang, X., W., Liu, F. J., Zhai, J., Bi, H.G., Ai, X.Z., 2020. Auxin acts as a downstream signaling molecule involved in hydrogen sulfide-induced chilling tolerance in cucumber. Planta. 251, 1-19.

Zheng, J.L., Hu, L.Y., Hu, K.D., Wu, J., Yang, F., Zhang, H., 2016. Hydrogen sulfide alleviates senescence of fresh-cut apple by regulating antioxidant defense system and senescence-related gene expression. HortSci. 51, 152-158.

Ziogas, V., Tanou, G., Belghazi, M., Filippou, P., Fotopoulos, V., Grigorios, D., Molassiotis, A., 2015. Roles of sodium hydrosulfide and sodium nitroprusside as priming molecules during drought acclimation in citrus plants. Plant. Mol. Biol. 89, 433-450.

Zulfiqar, F., Akram, N.A., Ashraf, M., 2020. Osmoprotection in plants under abiotic stresses: new insights into a classical phenomenon. Planta, 251, 3.

Zulfiqar, F., Casadesús, A., Brockman, H., Munné-Bosch, S., 2019. An overview of plant-based natural biostimulants for sustainable horticulture with a particular focus on moringa leaf extracts. Plant Sci. 110194.

Figure Legends

Figure 1: Some of the cellular effects of H_2S. H_2S may arrive from the outside of plant cells from a variety of means: from the environment; from other cells; or via treatments in agriculture. Endogenous H_2S can also be increased via the action of cellular biosynthetic pathways, perhaps in response to cellular stress. Accumulated H_2S may have a range of actions in cells. It can lead to increased glutathione (de Kok et al., 1985), and this, along with the fact that H_2S acts as part of a redox couple (Hancock and Whiteman, 2018), may alter intracellular redox. H_2S can interact with NO metabolism, for example through removal of NO in the creation of nitrosothiol (HSNO) (Whiteman et al., 2006), and alter ROS metabolism, for example through alterations of antioxidant levels (Kaya et al., 2018), or through altering ROS synthesis (Christou et al., 2013). H_2S, significantly, may cause persulfidation of proteins (Aroca et al., 2018; Jia et al., 2018), which can alter their activity. Often such alterations of cellular activity will lead to alterations of gene expression (Christou et al., 2013). Therefore, H_2S might have both short-term and long-term effects in plant cells, both of which may aid plants adapt to climate change.

Figure 2: Mechanisms by which H_2S may mitigate environmental stresses in plants. H_2S may aid to combat stress by several mechanisms, but often focused on altering ROS metabolism. Here, alterations of antioxidants, changes in signaling mechanisms, and altered protein activity through cysteine persulfidation (Aroca et al., 2018; Jia et al., 2018) may be important. Long-term effects may be modulated by alterations of secondary metabolites and gene expression

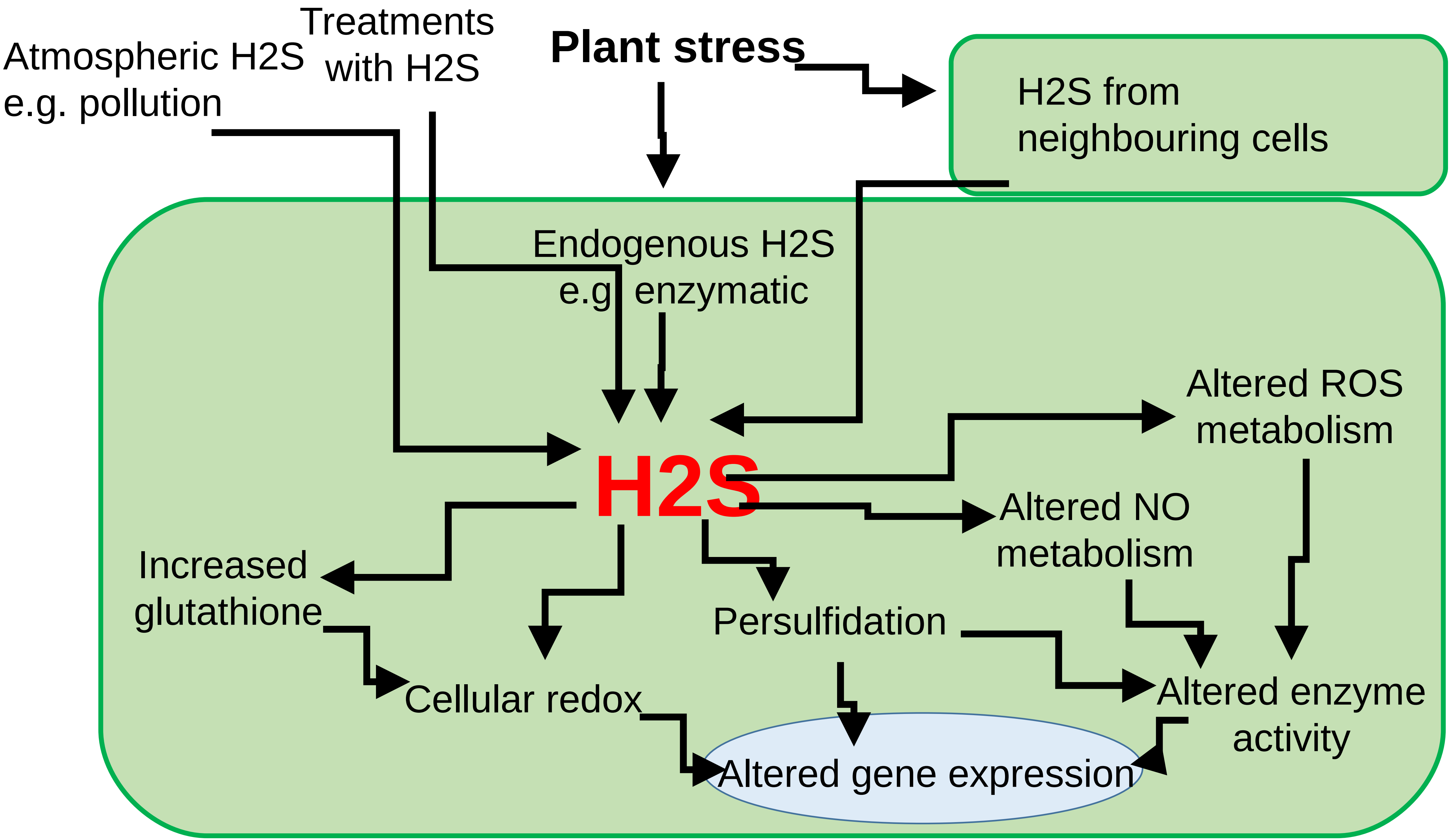
(Christou et al., 2013). Therefore a suite of responses mediated by H_2S will potentially enable cells to combat climate change.

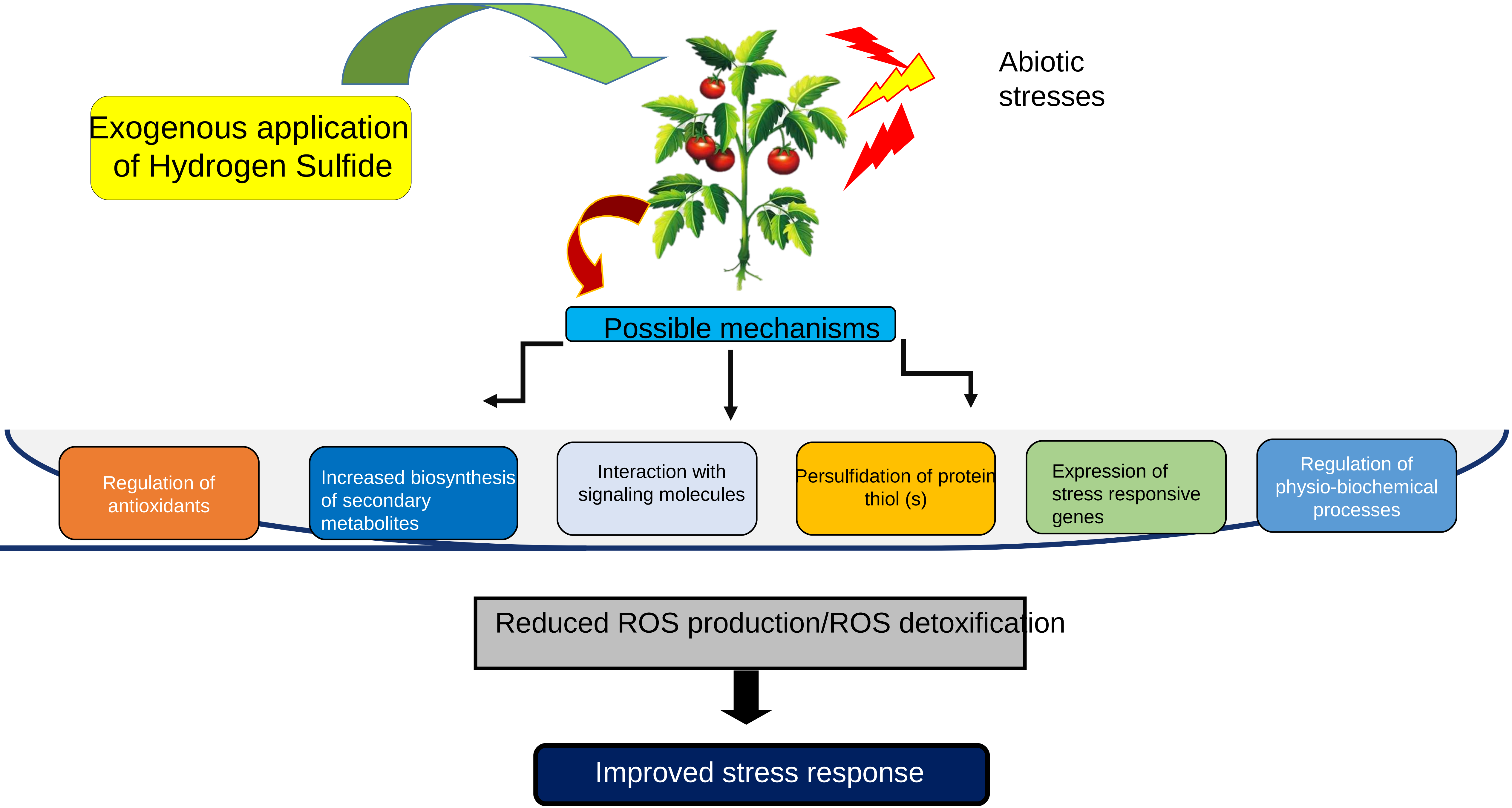
Table 1. Some examples of H_2S mediated alleviation of climate change related abiotic stresses in horticultural crops

Changes to environment because of climate change	Why climate change may have this effect	Mitigating effects of H_2S	References
Increased temperature	Climatic temperatures are rising and varying more substantially so high temperatures are likely (Asseng et al. 2014)	H_2S helps alleviates temp stress via upregulation of antioxidants, aquaporins and heat shock protein genes and by preserving ascorbate/glutathione homeostasis	Christou et al., 201
Cooling temperatures	Temperatures are likely to fluctuate more widely, including lower temperatures in some places (Chiang and Friedman, 2010)	H_2S helps alleviates chilling temperature stress via alleviating the degradation of chlorophyll and carotenoids and the photoinhibition of PSII and PSI by promoted the electron transfer from QA to QB on PSII acceptor side;	Tang et al., 2020 Zhang et al., 2020 Liu et al., 2020

		alleviate membrane peroxidation; enhancing osmoprotection compounds such as proline, scavenging oxidative stress and cross talk with phytohormones such as indole acetic acid and inducing molecular changes	
Heavy metal stress	Climate change may alter land use and therefore increase heavy metal bio-availability (Ouyang et al. 2018)	H_2S helps alleviates heavy metal stress via reducing H_2O_2 content, increasing the content of AsA and total thiols, osmolytes, and regulating antioxidant activities	Valivand et al. (2019a) Valivand et al. (2019b) Kaya et al., 2018 Singh et al. (2015) Ahmad et al. (2019 Chen et al. (2018) Liu et al. (2016)
Nutritional stress	Increase in eCO_2 as a climate change can increase the growth of plants demanding more nutrients that may cause nutritional starvation stress under low nutrient soil availability OR with climate change soil microbial communities deeply affected negatively affecting the nutrient realease from organic matter and nitrogen fixation (Soares et al. 2019)	H_2S helps alleviates nutritional stress via decreasing ROS accumulation and regulating antioxidant activities, upregulating CsNMAPK transcript level	Qi et al., 2019 Li et al. (2015) Kaya and Ashraf (2019)
Salt stress	Land use will alter with climate change, especially in coastal regions, meaning that salt stress may become a greater issue for plant growth (Hadley, 2009)	H_2S helps alleviates salt stress via alleviating the reduction in photosynthetic attributes, chlorophyll fluorescence and stomatal parameters. maintained Na^+ and K^+ homeostasis via regulation of the expression of PM H+-ATPase, SOS1 and SKOR at the transcriptional level under excess NaCl	Jiang et al. (2019) Kaya et al. (2019) Montesinos-Pereira et al., 2020 Christou et al. (2013) da Silva et al. (2018)

Drought stress and flooding	Climate change is likely to alter precipitation rates in many areas, either leading to drought conditions or flooding (O’Gorman, 2015)	H_2S helps alleviates drought/flooding stress via increasing water and osmotic potential; increasing osmoprotectants such as pro and GB, initiating biochemical changes such as soluble sugars (trehalose), polyamines and regulating several genes such as of aquaporins and of different proteins	Ziogas et al. (2014 Shi et al. (2013) Chen et al., 2016 Honda et al., 2015


Atmospheric H2S
e.g. pollution
Treatments
with H2S
Plant stress
H2S from
neighbouring cells
Endogenous H2S
e.g. enzymatic
H2S
Altered ROS
metabolism
Altered NO
metabolism
Increased
glutathione
Persulfidation
Cellular redox
Altered enzyme
activity
Altered gene expression



Exogenous application of Hydrogen Sulfide

Abiotic stresses

Possible mechanisms

Regulation of antioxidants

Increased biosynthesis of secondary metabolites

Interaction with signaling molecules

Persulfidation of protein thiol (s)

Expression of stress responsive genes

Regulation of physio-biochemical processes

Reduced ROS production/ROS detoxification

Improved stress response