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A Strategic Gasotransmitter in Fruit Vegetables: Molecular Mechanisms, Stress Tolerance and Application Protocols of Hydrogen Sulfide

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ABSTRACT

Hydrogen sulfide (H_2S) has recently been redefined in plant biology, evolving from a perceived metabolic toxicant to a versatile gasotransmitter and key signaling molecule. This review provides a systematic analysis of H_2S biosynthesis pathways, signal transduction mechanisms, and its intricate cross-talk with phytohormones in fruiting vegetables. Evidence demonstrates that H_2S orchestrates a profound reprogramming of cellular activity through protein persulfidation-a key post-translational modification that enhances antioxidant defenses and bolsters plant resilience against major abiotic stresses, including drought, salinity, heavy metal toxicity, and temperature fluctuations. Beyond stress tolerance, exogenous H_2S applications play a decisive role in optimizing fruit development and quality. They positively modulate critical parameters such as the sugar-acid balance, antioxidant capacity, and pigment accumulation, while significantly extending postharvest shelf life by antagonizing ethylene-mediated senescence. The successful application of H_2S as a biostimulant is governed by the hormesis principle: beneficial physiological responses are achieved at micromolar concentrations, whereas exceeding specific thresholds leads to phytotoxicity. Proven methodologies-including seed priming, foliar spraying, and root drenching—demonstrate significant potential to enhance yield and quality across vegetable species. However, field efficacy remains contingent upon donor compound stability and environmental interactions. Integrating H_2S signaling into agricultural practice presents a strategic avenue for advancing sustainable production and food security. Future research should focus on the following priorities: (1) elucidating the interactive networks between H_2S and other gasotransmitters and hormones, (2) employing gene-editing technologies (e.g., CRISPR/Cas9) to fine-tune endogenous H_2S biosynthesis for targeted crop improvement, and (3) developing and standardizing robust, field-ready application protocols for commercial adoption.

Sebzelerde Stratejik Bir Gazotransmiter: Hidrojen Sülfürün Moleküler Mekanizmaları, Stres Toleransı ve Uygulama Protokolleri

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ÖZET

Hidrojen sülfür (H_2S), son yıllarda bitki biyolojisinde yalnızca toksik bir gaz değil, aynı zamanda çok yönlü bir gazotransmiter olarak tanımlanmıştır. Bu derleme, sebzelerde H_2S'nin biyosentez yollarını, sinyal iletim mekanizmalarını ve hormonlarla kurduğu çapraz etkileşimleri sistematik biçimde incelemektedir. Bulgular, H_2S'nin protein persülfidasyonu yoluyla enzim aktivitelerini yeniden programladığını, antioksidan savunmayı güçlendirdiğini ve abiyotik stres koşullarında (kuraklık, tuzluluk, ağır metal toksisitesi, sıcaklık dalgalanmaları) bitki dayanıklılığını artırdığını göstermektedir. Ayrıca H_2S uygulamalarının meyve gelişimi, kalite parametreleri (şeker-asit dengesi, antioksidan kapasite, renk oluşumu) ve hasat sonrası raf ömrünü belirgin şekilde iyileştirdiği ortaya

Biyostimülatör

konmuştur. Uygulama protokollerinin sentezi, hormesis ilkesine dayalı dozaj optimizasyonunun kritik olduğunu göstermektedir: düşük konsantrasyonlarda biyostimülatör etki sağlanırken, eşik değerlerin aşılması fitotoksisiteye yol açmaktadır. Tohum priming, yaprak spreyi, kök uygulamaları ve hasat sonrası fümigasyon gibi yöntemler, farklı sebze türlerinde başarıyla uygulanmış ve verim ile kaliteyi artırmıştır. Bununla birlikte, saha koşullarında donör bileşiklerin stabilitesi, çevresel faktörler ve güvenlik protokolleri uygulama başarısını doğrudan etkilemektedir. Hidrojen sülfürün sebzelerde stratejik bir biyostimülatör olarak kullanımı, sürdürülebilir tarım ve gıda güvenliği açısından önemli fırsatlar sunmaktadır. Gelecekteki araştırmalar şu konulara öncelik vermelidir: (1) H_2S ile diğer gazotransmiterler ve hormonlar arasındaki etkileşimli ağların aydınlatılması, (2) hedefli bitki iyileştirmesi için endojen H_2S biyosentezini hassas bir şekilde ayarlamak amacıyla gen düzenleme teknolojilerinin (örneğin, CRISPR/Cas9) kullanılması ve (3) ticari kullanım için sağlam, sahada kullanıma hazır uygulama protokollerinin geliştirilmesi ve standartlaştırılması.

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1.INTRODUCTION

Fruiting vegetables, particularly those in the Solanaceae (e.g., tomato, pepper, eggplant) and Cucurbitaceae (e.g., cucumber, zucchini, melon, watermelon) families, are cornerstone crops for the global agricultural economy and human nutrition. According to the Food and Agriculture Organization of the United Nations (FAO, 2023), these crops rank among the highest in production value and cultivated area. They are indispensable for a healthy diet due to their rich content of vitamins (A, C), essential minerals, dietary fiber, and bioactive functional compounds such as lycopene, carotenoids, and flavonoids (da Silva Dias, 2022).

However, the growth and development of these strategic species are highly sensitive to abiotic stresses intensified by climate change. Drought and high-temperature anomalies during the critical phases of flowering and fruit set reduce pollen viability, leading to substantial yield losses (Rouphael and Colla, 2020). Soil salinity causes osmotic imbalance and ion toxicity, while heavy metal accumulation and low-temperature stress further threaten sustainable production worldwide (Zhao et al., 2022).

In this context, the discovery of signaling molecules that coordinate plant responses to environmental change has been a revolutionary step for sustainable agriculture. Hydrogen sulfide (H_2S), long perceived merely as a toxic byproduct, is now defined alongside nitric oxide (NO) and carbon monoxide (CO) as one of the three fundamental gasotransmitters in plants (Corpas and Palma, 2020; Zhang et al., 2020). Produced endogenously at micromolar levels, H_2S regulates enzyme activity and signaling through protein persulfidation. It triggers antioxidant defense by managing reactive oxygen species (ROS) buildup, optimizes stomatal movements, and enhances stress tolerance by interacting with hormonal networks (Aroca et al., 2018; Zhang et al., 2021; Huang and Xie, 2023).

Research on fruiting vegetables specifically shows that exogenous H_2S applications not only bolster stress tolerance, but also optimize fruit quality parameters like the sugar-acid balance, increase the accumulation of functional components such as lycopene and vitamin C, and significantly extend postharvest shelf life (Zhong et al., 2021; Tayal et al., 2022). Therefore, hydrogen sulfide holds dual strategic potential for sustainable farming: as a growth-promoting biostimulant and as a protective agent that reduces postharvest losses.

This review synthesizes current scientific knowledge to explain how hydrogen sulfide (H_2S) is produced, how it regulates proteins via persulfidation, and how it activates protective responses against environmental stresses like drought and salinity in fruiting vegetables such as fruiting vegetables, particularly tomato, pepper, eggplant, cucumber, melon, watermelon, and related cucurbit crops. Furthermore, it provides concrete application recommendations to translate this knowledge into agricultural practice for improving yield and quality. Thus, this work aims to both contribute to scientific understanding and offer a roadmap for innovative H_2S-based solutions for the agricultural sector.

2. H_2S BIOSYNTHESIS, SIGNALING, AND HORMONAL NETWORKS IN FRUITING VEGETABLES

Cellular hydrogen sulfide (H_2S) homeostasis in plants is maintained by a delicate equilibrium between its biosynthetic production and metabolic consumption. As an integral component of sulfur metabolism, this gasotransmitter is synthesized across distinct cellular compartments-primarily the cytosol, chloroplasts, and mitochondria-and is dynamically regulated in response to developmental cues and environmental stimuli (Hancock and Whiteman, 2014; Li et al., 2016). In fruiting vegetables, the precise orchestration of H_2S biosynthesis, its downstream signaling cascades, and its intricate cross-talk with phytohormone networks are fundamental determinants of both abiotic stress tolerance and fruit quality traits (Corpas et al., 2022). The interplay between these enzymatic pathways and the ensuing molecular signaling events is summarized in Figure 1.

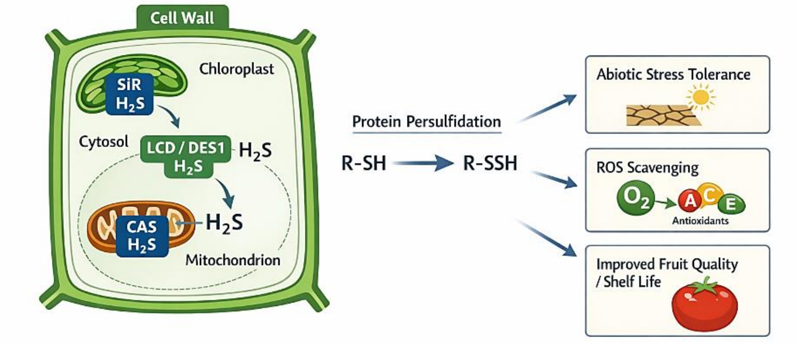

Figure 1. Integrative overview of H_2S biosynthesis, protein persulfidation mechanism, and downstream physiological responses in fruiting vegetables

2.1. Endogenous H_2O Biosynthesis Pathways and Enzymatic Regulation

In fruiting vegetables, endogenous hydrogen sulfide (H_2S) production is not a static process but a dynamically regulated metabolic response mediated by several compartmentalized enzymatic systems. This gasotransmitter, integral to sulfur metabolism, is synthesized across multiple cellular organelles and fine-tuned according to developmental phases and environmental signals (Hancock and Whiteman, 2014; Li et al., 2016). The principal pathways for H_2S generation are closely tied to sulfur assimilation and the detoxification of nitrogenous byproducts.

The key enzymatic players in this process include L-cysteine desulfhydrase (LCD) and D-cysteine desulfhydrase (DCD), which catalyze the degradation of L- and D-cysteine into H_2S, ammonia, and pyruvate within the cytosol. In chloroplasts, sulfite reductase (SiR) plays a dual role by reducing sulfite to H_2S, thereby facilitating the synthesis of sulfur-containing amino acids. Another critical route involves β-cyanoalanine synthase (CAS) in mitochondria, which links cyanide detoxification directly to H_2S production. The coordinated activity of these pathways is fundamental for regulating stress tolerance and fruit quality in fruiting vegetables (Corpas et al., 2022).

From a molecular breeding standpoint, these enzymatic pathways represent promising targets for genetic enhancement. Natural variation in the expression and catalytic efficiency of LCD and DCD genes among cultivars correlates with differing stress resilience. Harnessing the allelic diversity of these biosynthesis genes could enable the development of varieties with intrinsically elevated H_2S production, thereby conferring “built-in” resilience to environmental stresses and reducing dependence on exogenous chemical treatments.

The specific characteristics, substrates, and cellular localizations of these core enzymes, essential for maintaining cellular redox and sulfur homeostasis, are summarized in Table 1.

Table 1. Key enzymes involved in H_2S biosynthesis, their cellular localizations, and physiological significance in fruiting vegetables

Enzyme	Cellular Localization	Primary Biochemical Function	Significance in Cultivation & Breeding
L-Cysteine Desulfhydrase (LCD)	Cytosol	Catalyzes the degradation of L-cysteine into H_2S, NH_3, and pyruvate.	The dominant source of H_2S for regulating **fruit ripening** and **stress signaling** (Corpas et al., 2022).
D-Cysteine Desulfhydrase (DCD)	Cytosol	Catalyzes the degradation of D-cysteine.	Works synergistically with LCD to maintain **sulfur homeostasis** (Hancock and Whiteman, 2014).
Sulfite Reductase (SiR)	Chloroplast	Reduces sulfite (SO_3^{2-}) to H_2S.	Contributes to sulfur assimilation and the synthesis of sulfur-containing metabolites required for photosynthetic function.
β-Cyanoalanine Synthase (CAS)	Mitochondria	Detoxifies cyanide while simultaneously producing H_2S.	Enhances **mitochondrial respiration** and provides protection during **seed germination**.
Desulfhydrase 1 (DES1)	Cytosol / Organelles	Catalyzes cysteine desulfuration.	A key regulator of **stomatal closure** and **ABA-mediated drought tolerance** (Li et al., 2016).

Note: The activity and regulation of these enzymatic pathways represent potential selection markers for breeding climate-resilient vegetable cultivars with enhanced endogenous stress tolerance.

Recent studies emphasize that the manipulation of endogenous H_2S levels through genome editing (e.g., overexpression of LCD genes) significantly enhances the stress-adaptive capacity of Solanaceous crops, providing a robust genetic tool for modern horticulture.

2.2. Core Signaling Mechanisms: Persulfidation and Molecular Players

The most specific and well-characterized mechanism of H_2S action is protein persulfidation (S-sulfhydration). This post-translational modification involves the conversion of a cysteine residue's thiol group (-SH) into a persulfide group (-SSH), leading to profound changes in the protein's conformation, stability, and catalytic activity (Aroca et al., 2018; Huang and Xie, 2023).

Recent comprehensive persulfidation profiling in sweet pepper (*Capsicum annum*) fruits quantified this widespread modulation, revealing that 891 distinct proteins undergo persulfidation during ripening (Muñoz-Vargas et al., 2024). The principal functional outcomes of this extensive protein network modification are:

- **Activation of Metabolic Enzymes:** Persulfidation activates enzymes, like leucine aminopeptidase (LAP), promoting amino acid recycling and nitrogen remobilization.
- **Inhibition of Senescence Pathways:** By persulfidating and inhibiting key enzymes in the ethylene biosynthesis pathway (ACS and ACO), H_2S effectively suppresses ethylene production, thereby delaying fruit senescence and extending marketable life (Zhong et al., 2021).
- **Enhancement of Antioxidant Defense:** The persulfidation of core antioxidant enzymes, including ascorbate peroxidase (APX), catalase (CAT), and glutathione reductase (GR), significantly boosts their activity, enhancing the plant's tolerance to oxidative stress (Zhang et al., 2021).

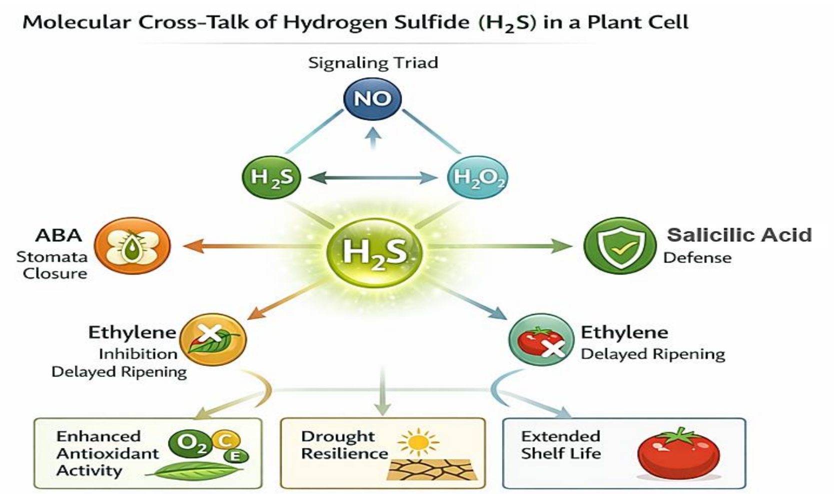

Figure 2. Schematic representation of H_2S cross-talk with phytohormones and other gasotransmitters in modulating stress responses and fruit quality

2.3. Crosstalk with ROS, NO, and Hormones

The H_2S-NO-ROS Interplay: H_2S forms a crucial "signaling triad" with NO and ROS (notably hydrogen peroxide, H_2O_2). This synergy is fundamental for maintaining redox homeostasis. H_2S works with NO to amplify the antioxidant defense system, while simultaneously regulating NADPH oxidase activity to ensure controlled, signaling-competent ROS production under stress (Zhang et al., 2021; Corpas et al., 2022).

Hormonal Regulation: H_2S fine-tunes the action of major phytohormones:

Abscisic Acid (ABA): H_2S acts as a key downstream component of ABA signaling, promoting stomatal closure and drought tolerance by regulating S-type anion channels and modulating the OST1 kinase via persulfidation (Hancock and Whiteman, 2014; Aroca et al., 2018).

Ethylene: H_2S acts as an ethylene antagonist, delaying fruit senescence and extending postharvest shelf life by directly suppressing the expression and activity of ethylene biosynthetic genes (ACS and ACO) (Zhong et al., 2021; Zhao et al., 2022).

Auxin: H_2S influences lateral root development by affecting the distribution and activity of auxin transporters, thereby enhancing root system architecture and nutrient uptake (Hancock and Whiteman, 2018).

Breeding Implication: From a horticultural perspective, deciphering this cross-talk is essential for developing resilient, high-efficiency cultivars. Selecting genotypes with optimized H_2S -ABA sensitivity can yield drought-tolerant varieties with superior water-use efficiency. Simultaneously, harnessing the H_2S-ethylene antagonism can lead to genotypes with naturally extended shelf life, reducing postharvest losses.

3. H_2S AS A BIOSTIMULANT AND PROTECTIVE AGENT UNDER ABIOTIC STRESS

Abiotic stress factors—including drought, salinity, heavy metal toxicity, and temperature fluctuations—represent formidable challenges for fruiting vegetables, capable of disrupting cellular homeostasis and reducing photosynthetic efficiency, can cause substantial yield losses, in some cases exceeding 50% depending on crop species, stress intensity, and developmental stage. (Zhang et al., 2021). Under these conditions, hydrogen sulfide (H_2S) functions dually as a key signaling molecule and a potent biostimulant, activating the plant's defense mechanisms across multiple physiological levels.

3.1. Drought Stress and Regulation of Water Relations

Drought stress exerts devastating effects, particularly during the critical phases of flowering and fruit set. H_2S mitigates water loss by precisely regulating stomatal movements and osmotic balance.

Stomatal Movements: H_2S is a crucial component of the abscisic acid (ABA) signaling pathway. It modulates the Open Stomata 1 (OST1) kinase via persulfidation, which in turn activates S-type anion channels in guard cells, leading to stomatal closure and reduced transpiration (Aroca et al., 2018). In tomato (*Solanum lycopersicum*), exogenous application of sodium hydrosulfide (NaHS, a common H_2S donor) has been shown to reduce transpiration rates by 25-30%, thereby maintaining leaf water potential under drought (Li et al., 2022).

Osmotic Adjustment: Beyond stomatal control, H_2S promotes the accumulation of osmo-protectants such as proline. In pepper seedlings, H_2S treatment enhances the expression of proline biosynthesis genes, notably Δ^1-pyrroline-5-carboxylate synthetase (P5CS), which is vital for protecting cell membrane integrity and preventing electrolyte leakage under osmotic stress (Song et al., 2024).

3.2. Salt Stress and Regulation of Ion Homeostasis

Salinity stress, primarily through NaCl, imposes ion toxicity and osmotic imbalance on vegetable crops, severely hindering growth and development. Hydrogen sulfide (H_2S) provides multi-faceted protection by regulating ionic balance and bolstering cellular defense systems.

Ion Homeostasis: H_2S is crucial for maintaining a favorable cytosolic Na^+/K^+ ratio. It achieves this by enhancing the activity of key membrane transporters: the plasma membrane H^+-ATPase and the Salt Overly Sensitive 1 (SOS1) Na^+/H^+ antiporter. This coordinated action facilitates the extrusion of excess Na^+ ions and the retention of K^+ ions, thereby preventing ionic toxicity (Raju and Prasad, 2021). Practical applications in eggplant and tomato have demonstrated that treatment with 40 µM NaHS effectively reduces Na^+ accumulation in roots (Raju and Prasad, 2023).

Photosynthetic and Antioxidant Defense: Salinity often impairs photosynthesis by degrading chlorophyll and reducing stomatal conductance. H_2S protects the photosynthetic apparatus, notably the Oxygen-Evolving Complex (OEC) of Photosystem II, helping to sustain photosynthetic efficiency. Concurrently, H_2S activates a robust antioxidant defense:

- It increases the activity of key enzymes like superoxide dismutase (SOD) and peroxidase (POD), which reduces lipid peroxidation (as indicated by lower malondialdehyde - MDA levels) (Raju and Prasad, 2021).
- It promotes the accumulation of non-enzymatic antioxidants such as glutathione (GSH) and ascorbic acid (AsA), which directly neutralize salt-induced reactive oxygen species, like superoxide radicals and hydrogen peroxide (H_2O_2) (Corpas et al., 2022).

3.3. Heavy Metal Stress and Detoxification Mechanisms

The contamination of agricultural soils with heavy metals-such as cadmium (Cd), lead (Pb), and chromium (Cr)-poses a severe threat to the metabolic integrity of fruiting vegetables and food safety. H_2S serves as a critical mediator in detoxification by orchestrating a multi-pronged defense strategy.

Chelation, Sequestration, and Enhanced Barrier Function: H_2S promotes the synthesis of phytochelatins and metallothioneins, which chelate toxic metal ions and facilitate their sequestration into vacuoles, thereby reducing cytosolic concentrations (Arif et al., 2021; Corpas et al., 2022). Additionally, H_2S application strengthens the physical root barrier by enhancing processes like lignification and suberization, which limit the initial uptake and vascular transport of metals into the shoot system.

Protection of Photosynthetic Integrity and Redox Homeostasis: Heavy metals induce severe oxidative stress and disrupt photosynthesis. H_2S provides a dual-layer defens:

- **Photosynthetic Protection:** H_2S application prevents chlorophyll degradation and safeguards the efficiency of Photosystem II (PSII), helping to maintain photosynthetic capacity under metal stress (Arif et al., 2021).
- **Antioxidant System Activation:** H_2S mitigates metal-induced oxidative bursts by upregulating the ascorbate-glutathione (AsA-GSH) cycle. It stimulates key enzymes such as glutathione reductase (GR) and dehydroascorbate reductase (DHAR), which are essential for preserving cellular redox homeostasis during prolonged exposure (Siddiqui et al., 2021).

3.4. Temperature Stress (High and Low Temperature)

Temperature fluctuations represent a critical threat to the reproductive success of fruiting vegetables, directly impacting pollen viability, fertilization, and fruit set. Hydrogen sulfide (H_2S) serves as a vital molecular buffer against both chilling and heat-induced injuries.

Cold Stress: In cucumber (*Cucumis sativus*), H_2S signaling activates the CsARF5-CsDREB3 gene module. This transcriptional reprogramming enhances freezing tolerance by stabilizing cell membrane integrity and preventing electrolyte leakage during sudden temperature drops (Zhang et al., 2021).

Heat Stress: In tomato, H_2S enhances thermotolerance by inducing the expression of heat shock proteins (HSPs). These molecular chaperones prevent protein denaturation and maintain cellular protein homeostasis, which is vital for improving pollen germination and preventing flower abscission under heat stress (Li et al., 2022).

These findings demonstrate that H_2S undertakes critical regulatory roles across a wide spectrum of abiotic conditions. The physiological outcomes and application specifics across different vegetable species are systematically summarized in Table 2.

Table 2. Key mechanisms of action and application examples of H_2S under abiotic stress conditions in fruiting vegetables

Stress Factor	Core Mechanism	Application Example	Outcome	Reference
Drought	Stomatal control, ABA crosstalk	Tomato (NaHS foliar spray)	Reduced water loss, prevention of oxidative damage	Raju and Prasad, 2021
Salinity	Na^+/K^+ homeostasis, SOS1 activation	Eggplant (40 µM NaHS)	Prevention of ion toxicity	Raju and Prasad, 2023
Heavy Metal	Phytochelatin synthesis & chelation	Pepper (under Cd stress)	Preservation of photosynthetic apparatus	Arif et al., 2021
Cold	CsDREB3 activation, membrane stability	Cucumber (100 µM NaHS)	Increased freezing resistance	Li et al., 2024
Heat	HSP induction, protein stabilization	Tomato (NaHS application)	Preservation of pollen viability	Zhang et al., 2020

4. EFFECTS OF H_2S ON FRUIT QUALITY, YIELD, AND POSTHARVEST PHYSIOLOGY

Hydrogen sulfide (H_2S) plays a decisive role not only in vegetative growth but also in reproductive development, fruit quality, and postharvest durability. This gasotransmitter enhances the economic and nutritional value of vegetable production across a broad physiological spectrum-from pollen viability to final shelf life.

4.1. Effects on Plant Development, Flowering, and Yield Components

H_2S serves as a potent biostimulant that positively influences plant architecture and the robust development of reproductive organs. In key fruiting vegetables like tomato and pepper, exogenous H_2S application has been shown to shorten the flowering period, improve pollen germination rates, and significantly increase the overall fruit set.

A critical mechanism underlying these yield improvements is the prevention of premature organ abscission. H_2S delays flower and fruit abscission by modulating endogenous ethylene signaling and maintaining cellular redox homeostasis. By suppressing ethylene biosynthesis peaks in the abscission zone, H_2S ensures higher flower retention, directly translating into increased yield potential per plant (Ma et al., 2021). Furthermore, the enhancement of biomass accumulation during flowering provides the necessary metabolic reserves to support subsequent fruit expansion, thereby improving both fruit size and number.

4.2. Enhancement of Fruit Quality Traits and Nutritional Value

Fruit quality is a multidimensional parameter critical for consumer preference, marketability, and nutritional impact. Exogenous H_2S applications provide significant improvements in the organoleptic and functional profiles of fruiting vegetables.

Sugar-Acid Balance: The taste profile of vegetables like tomato is largely governed by the sugar-to-acid ratio. H_2S application has been shown to increase the concentrations of soluble sugars-specifically fructose and glucose-while simultaneously maintaining an optimal balance of organic acids. This metabolic fine-tuning enhances the overall flavor profile and palatability of the produce (Zhang et al., 2023).

Antioxidant Capacity and Functional Quality: H_2S acts as a metabolic trigger, promoting the accumulation of high-value secondary metabolites. It significantly elevates the levels of ascorbic acid (Vitamin C), lycopene, and total phenolics. These compounds not only increase the fruit's nutritional density but also enhance its functional quality as a source of dietary antioxidants (Ziogas et al., 2018; Siddiqui et al., 2023).

Color Development and Pigment Regulation: The visual appeal of fruiting vegetables is determined by precise pigment biosynthesis. H_2S slows chlorophyll degradation (degreening) while systematically regulating carotenoid biosynthesis to ensure uniform and attractive coloration. This dual effect on pigment dynamics has been confirmed in high-value crops like strawberry and tomato, where H_2S ensures a more controlled and stable color transition during ripening (Chen et al., 2024).

4.3. Postharvest Durability and Shelf Life Extension

Postharvest losses remain one of the most significant economic challenges in the global vegetable supply chain. Hydrogen sulfide (H_2S) has emerged as a revolutionary “anti-senescence” molecule, offering a non-toxic and effective strategy to extend the marketable life of perishable produce through multiple physiological pathways.

Cell Wall Protection: H_2S significantly delays fruit softening by inhibiting the activity of key cell wall-degrading enzymes, such as pectin methylesterase (PME) and polygalacturonase (PG). This action preserves the integrity of the middle lamella, ensuring fruits retain their firmness during transport and storage.

Ethylene Antagonism: A hallmark of H_2S action is its ability to antagonize ethylene-mediated ripening. By suppressing the expression of 1-aminocyclopropane-1-carboxylic acid synthase (ACS) and oxidase (ACO) genes, H_2S prevents the climacteric respiratory peak and slows down excessive ripening processes (Zhong et al., 2021).

Decay Control and Pathogen Defense: H_2S fumigation serves as a dual-action defense mechanism. It exerts direct fungicidal effects on common postharvest pathogens, like *Botrytis cinerea* and *Rhizopus stolonifer*, while simultaneously priming the plant’s innate immunity by activating pathogenesis-related (PR) proteins (Tang et al., 2014).

The practical implications of these mechanisms, including specific application methods and the resulting shelf-life extensions across various species, are systematically summarized in Table 3.

Table 3. Effects of H_2S applications on fruit quality and shelf life in fruit vegetables

Vegetable	Application Method	Primary Outcome	Shelf-Life Extension	Expected Effect	Reference
Tomato	1.0 mM NaHS (fumigation)	Delayed softening, lycopene preservation	+5-7 days	↑ Antioxidant capacity	Zhong et al., 2021
Pepper	0.5 mM NaHS (spray)	Reduced water loss, chlorophyll retention	+4-6 days	↑ Photosynthetic efficiency	Muñoz-Vargas et al., 2024
Eggplant	1.0 mM NaHS (dipping)	Prevention of browning	+3-5 days	↓ PPO activity	Tang et al., 2014
Cucumber	0.2 mM NaHS (fumigation)	Reduced chilling injury	+4 days	↑ Membrane stability	Li et al., 2024
Squash	0.5 mM NaHS (spray)	Delayed yellowing, reduced water loss	+3-4 days	↑ Chlorophyll preservation	Zhang et al., 2020

5. APPLICATION PROTOCOLS, DOSAGE, AND SAFETY MEASURES: A SCIENCE-BASED GUIDE FOR VEGETABLES

The efficacy of hydrogen sulfide (H_2S) in horticultural systems is governed by the principle of hormesis. This pharmacological phenomenon dictates that while H_2S acts as a potent stimulator of metabolic and defensive processes at low (micromolar) concentrations, it can exhibit phytotoxic effects if a specific concentration threshold is exceeded (Li et al., 2016). Consequently, the practical success of H_2S in fruiting vegetable production hinges on a precise synthesis of donor selection, phenological timing, and a methodology tailored to the specific target tissue (Zhao et al., 2022).

5.1. Seed Preparation and Seedling Stage Strategies (Priming)

Seed priming with H_2S donors is a strategic intervention that activates the plant’s endogenous defense systems at the earliest stages of development, effectively establishing a “stress memory” (priming effect) that enhances resilience throughout the plant’s life cycle.

Dosage and Efficacy: Research indicates that priming treatments using a 50-100 µM NaHS solution are optimal for high-value crops like tomato and pepper. These concentrations not only enhance synchronized germination rates but also significantly bolster the seedlings' resilience to salinity and osmotic stress during early establishment (Raju and Prasad, 2021).

Biochemical Mechanism: At the molecular level, H_2S facilitates the persulfidation of key metabolic enzymes, such as α-amylase, which are responsible for mobilizing stored nutrient reserves in the endosperm. This accelerated nutrient turnover ensures more robust and uniform seedling emergence under suboptimal environmental conditions.

5.2. Foliar and Root Applications During Vegetative and Reproductive Stages

The method of H_2S delivery must be carefully selected based on the phenological stage of the crop and the target physiological response. Both foliar and root-targeted applications offer distinct advantages.

Foliar Spray: For fruiting vegetables, the optimized exogenous dose generally falls within the range of 50-200 µM NaHS. Due to the high volatility of H_2S and its rapid metabolic degradation, maintaining an effective concentration requires repeated applications at 5-7 day intervals. This approach is particularly effective for triggering rapid antioxidant responses in leaves and stabilizing the photosynthetic apparatus under sudden stress events (Zhang et al., 2021; Siddiqui et al., 2023).

Root Drenching (Soil Drench): This method involves the direct application of H_2S donor solutions to the substrate, ensuring complete saturation of the rhizosphere. Root drenching facilitates systemic signaling from the roots to the shoots. Since the soil matrix can buffer the active molecule, dosages for root applications are typically higher, reaching up to 500 µM to ensure sufficient uptake and systemic efficacy (Arif et al., 2021).

5.3. Postharvest Fumigation and Storage Protocols

In the postharvest phase, the gaseous nature of H_2S is leveraged through fumigation, allowing for rapid and uniform penetration into fruit tissues without direct liquid contact, which can sometimes encourage microbial growth.

Target-Specific Protocols:

- ✓ **Tomato (climacteric):** A concentration of 1.0 mM NaHS fumigation is established as a standard protocol for the effective suppression of ethylene biosynthesis and the preservation of fruit firmness (Zhong et al., 2021).
- ✓ **Pepper and Eggplant (non-climacteric)**: Lower concentrations around 0.5 mM NaHS are sufficient to preserve antioxidant capacity and significantly reduce weight loss due to transpiration (Zhong et al., 2021; Muñoz-Vargas et al., 2024).

Safety and Duration: To prevent potential phytotoxicity and ensure worker safety, fumigation should be conducted in airtight, controlled environments. Exposure is generally limited to short durations of 30-60 minutes, followed by adequate ventilation to remove residual gas (Zhao et al., 2022).

5.4. Environmental Factors Affecting Application Success

The transition of H_2S applications from controlled laboratory conditions to field environments presents unique challenges. A primary constraint is the inherent instability of common H_2S donors, such as NaHS and GYY4137, which are highly susceptible to rapid photodegradation and thermal decomposition.
To maximize donor stability and optimize plant uptake, foliar applications should ideally be conducted during the early morning hours when temperatures are lower and stomatal conductance is at its peak. This strategic timing ensures that H_2S molecules penetrate the leaf mesophyll effectively before midday heat accelerates gas volatilization (Siddiqui et al., 2023).

The strategic parameters for various application methods, including optimized dosage ranges and critical timings, are systematically summarized in Table 4.

Table 4. H_2S application types, dosages, and critical timings for fruiting vegetables

Application Type	Target Vegetable	Recommended Dosage	Critical Timing	Reference
Seed Priming	Tomato, Pepper	50-100 µM NaHS	24 hours before sowing	Raju and Prasad, 2021
Foliar Spray	Cucumber, Pepper	100 µM NaHS	Before stress onset, weekly repeat	Zhang et al., 2021; Siddiqui et al., 2023
Root Drenching	Eggplant	40-500 µM NaHS	During saline irrigation period	Arif et al., 2021; Raju and Prasad, 2023
Fumigation	Tomato (Postharvest)	1.0-2.0 mM NaHS	Immediately after harvest, 30-60 min	Tang et al., 2014; Zhong et al., 2021

6. DISCUSSION AND SECTORAL PERSPECTIVES

Hydrogen sulfide (H_2S) serves a dual function in fruiting vegetable systems, acting both as a sophisticated biochemical regulator and a versatile agricultural biostimulant. This section synthesizes the critical links between the physiological mechanisms of H_2S and their agronomic outcomes, identifies key knowledge gaps, and outlines a roadmap for sectoral integration.

6.1. Physiological Mechanisms and Agronomic Outcomes

The multifaceted influence of H_2S is primarily executed through protein persulfidation, a post-translational modification that reprograms enzyme activities to enhance cellular resilience (Aroca et al., 2018). This molecular reprogramming orchestrates antioxidant defenses and hormonal signaling to produce tangible field-level results.

- **Drought and Salinity:** By modulating the ABA-OST1 pathway and activating SOS1 transporters, H_2S optimizes water use efficiency and maintains ionic homeostasis (Raju and Prasad, 2021).
- **Heavy Metal Mitigation:** H_2S facilitates the synthesis of phytochelatins, ensuring the sequestration of metals like Cd and Pb, thereby preventing growth retardation and improving food safety (Arif et al., 2021).
- **Thermal Resilience:** Induction of CsDREB3 and Heat Shock Proteins (HSPs) provides a dual shield against cold and heat stress, respectively (Zhang et al., 2021; Li et al., 2022).
- **Postharvest Longevity:** Suppression of ethylene biosynthesis genes (ACS/ACO) and cell wall-degrading enzymes (PME/PG) directly translates into a significant extension of shelf life (Zhong et al., 2021; Zhao et al., 2022).

These physiological responses may contribute to agronomic benefits, although field validation remains necessary. The connections between specific mechanisms and outcomes are systematically summarized in Table 5.

Table 5. Links between H_2S physiological mechanisms and agronomic outcomes

Mechanism	Molecular Effect	Agronomic Outcome	Reference
ABA-OST1 modulation	Stomatal closure	Drought tolerance, water efficiency	Raju and Prasad, 2021
SOS1 activation	Na^+/K^+ homeostasis	Salinity tolerance	Raju and Prasad, 2023
Phytochelatin synthesis	Heavy metal chelation	Prevention of growth retardation	Arif et al., 2021
CsDREB3 / HSP induction	Gene expression regulation	Cold and heat stress tolerance	Li et al., 2024; Zhang et al., 2020
ACS/ACO inhibition	Ethylene suppression	Shelf-life extension	Gao et al., 2013; Tang et al., 2014
PME/PG suppression	Cell wall stabilization	Preservation of fruit firmness	Zhong et al., 2021

6.2. Knowledge Gaps and Academic Debates

Despite intensive research, several challenges must be addressed to transition H_2S from experimental plots to widespread commercial adoption:

- **Hormetic Precision:** The biphasic nature of H_2S requires precise, species- and stage-specific dosage maps to avoid phytotoxicity and maximize benefits (Li et al., 2016).
- **Donor Innovation:** While NaHS is the academic standard, the development of advanced, slow-release donors (e.g., GYY4137) is crucial for stable performance under unpredictable field conditions (Aroca et al., 2020).
- **Molecular Networks:** The relationship of H_2S with other hormones (e.g., auxin, gibberellin) and its intricate crosstalk with ROS and NO signaling networks are not yet fully resolved (Corpas, 2019; Zhang et al., 2020).
- **Sectoral Adaptation and Regulation:** The development of practical, low-cost protocols for small-scale producers remains limited. Furthermore, defining safety limits and establishing a clear regulatory framework for H_2S use in food production is essential for consumer acceptance and sectoral integration (Tayal et al., 2022; Zhao et al., 2022).

6.3. Sectoral Perspectives and Implementation Pathways

The strategic potential of H_2S for sustainable agriculture and food security becomes concrete through targeted implementation:

- **Industrial Scale:** Controlled fumigation systems offer viable, scalable solutions for large-scale producers in shelf-life management and quality preservation (Zhao et al., 2022).
- **Small-Scale Production:** Studies demonstrate the cost-effectiveness of dipping and low-dose foliar applications, making them suitable for cooperatives and smallholder farmers (Tang et al., 2014; Muñoz-Vargas et al., 2024).
- **Food Safety and Sustainability:** H_2S applications could promote safer products by reducing reliance on synthetic pesticides, aligning with integrated pest management (IPM) principles and consumer demand for cleaner food (Zhao et al., 2022; Siddiqui et al., 2023).
- **Policy and Future Research:** Concerted efforts are needed from researchers, policymakers, and industry to standardize protocols, invest in donor technology, and conduct long-term field trials to fully realize the promise of H_2S in modern horticultural.

7. CONCLUSIONS AND RECOMMENDATIONS

In the production of fruiting vegetables, hydrogen sulfide (H_2S) has transcended its status as a metabolic byproduct to become a strategic biochemical regulator and a versatile agricultural biostimulant. The evidence synthesized in this review demonstrates that H_2S-mediated molecular pathways translate directly into superior agronomic outcomes, indicating potential contributions to sustainability and climate-resilient horticulture.

To advance the field, future research must adopt a systems-biology approach. Deepening the investigation into the complex cross-talk between H_2S and other gasotransmitters (e.g., NO, CO, H_2) and less-explored hormones (e.g., strigolactones, brassinosteroids) is essential for a holistic understanding of plant stress management. Furthermore, leveraging advanced gene-editing technologies like CRISPR/Cas9 to optimize endogenous H_2S biosynthesis pathways stands as a high-priority target for developing “smart vegetable varieties” capable of thriving in suboptimal environments (Corpas, 2019; Li, 2024).

From a practical standpoint, H_2S applications should be integrated into established frameworks such as Integrated Pest Management (IPM) and precision agriculture. Utilizing H_2S-based biostimulants to counteract climate-induced stressors-including erratic temperature fluctuations, water scarcity, and rising soil salinity-can significantly minimize yield gaps and contribute to global food security (Tayal et al., 2022).

The responsible adoption of H_2S technology necessitates a disciplined approach to safety and precision to avoid phytotoxicity and ensure occupational health:

- ✓ **Precise Dosage:** For foliar applications, concentrations should be carefully maintained near the 100 µM threshold to ensure efficacy without exceeding hormetic limits (Siddiqui et al., 2023).
- ✓ **Optimal Timing:** Applications must be synchronized with peak stomatal opening (early morning hours) to maximize absorption and minimize gaseous loss (Zhao et al., 2022).
- ✓ **Chemical Safety:** Strict adherence to safety protocols is mandatory when handling donors like NaHS; crucially, these compounds must never be mixed with acidic fertilizers to prevent the sudden, hazardous release of H_2S gas (Zhao et al., 2022).

The strategic outputs of H_2S research and targeted recommendations for key stakeholders are systematically presented in Table 6.

Table 6. Strategic outputs of H_2S research and application recommendations

Stakeholder	Focus Area	Strategic Recommendation	Expected Impact
Molecular Research / Academics	Investigating gasotransmitter & hormone cross-talk	Foster a holistic understanding of stress signaling networks.	Foundation for next-generation stress biology.
Genetic / Research Institutes	CRISPR/Cas9-mediated enhancement of H_2S biosynthesis	Develop genetically improved, stress-resilient cultivars.	"Smart" varieties with built-in climate adaptability.
Producers / Agronomists	Integration of H_2S into IPM & precision agriculture frameworks	Implement H_2S as a tool for climate-smart yield stabilization.	Reduced yield loss, lower chemical input, improved sustainability.
Agriculture Policymakers	Standardizing dosage limits, safety, and application protocols	Establish clear regulations to ensure food safety and worker health.	Safe, regulated, and scalable adoption of H_2S technology.

Source: *Synthesis based on Corpas (2019); Tayal et al. (2022); Zhao et al. (2022); Li et al. (2024).*

Conflict of Interest Declaration

There is no conflict of interest.

Researchers' Contribution Rate Declaration Summary

All authors contributed equally to the article.

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