

Review

The Role and Regulatory Mechanism of Methionine Sulfoxide Reductase (Msr) in the Process of Chilling Injury of Fruits and Vegetables: A Review

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Abstract: The failure to promptly eliminate excessive reactive oxygen species (ROS) leads to the oxidation of biological macromolecules such as proteins, which is a key factor in chilling injury (CI) in harvested fruits and vegetables. Methionine sulfoxide reductase (Msr) is a class of redox proteins that reduce methionine sulfoxide (MetSO) in oxidized proteins back to methionine (Met), thereby restoring protein function. In recent years, the role of Msr in protecting fruits and vegetables from CI has attracted increasing research interest. This review summarizes the classification, distribution, and subcellular localization of Msr in plants and examines its roles and regulatory mechanisms in mitigating CI. The discussion focuses on postharvest CI, ROS dynamics, and Msr-related regulatory pathways. This review provides insights into improving plant quality and enhancing cold resistance through genetic engineering.

Keywords: chilling injury; Msr; postharvest; ROS



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1. Introduction

ROS is an unavoidable product in the metabolism of plants [1]. The production and clearance of ROS in organisms maintain a dynamic balance, and appropriate levels of ROS play important physiological functions in organisms, such as signaling [2,3] and resistance to pathogenic bacteria [4]. Although there are ROS scavenging systems in organisms, under certain stress conditions, especially under low-temperature stress conditions, the accumulation of ROS exceeds their ability [5]. At this time, high concentrations of ROS will attack biological macromolecules, causing changes in their structure and function, thereby accelerating the aging and deterioration of cells and organisms [6,7]. To counteract this oxidative stress, organisms have evolved oxidative repair mechanisms to restore the functionality of oxidized proteins and other macromolecules [8,9]. One such mechanism involves methionine (Met), a sulfur-containing amino acid that is particularly susceptible to oxidation.

The oxidation of methionine residues in proteins leads to structural and functional alterations [8,9]. When oxidized, Met forms two methionine sulfoxide isomers, Met-S-SO and Met-R-SO, both of which can further oxidize to methionine sulfone (MetO₂) [10]. Notably, Met-SO can be reduced back to methionine by methionine sulfoxide reductases (Msr), restoring the protein's function. In contrast, MetO₂ is irreversibly oxidized and cannot be repaired [11]. At present, according to the different reducing substrates, Msr in plants is divided into MsrA and MsrB, with MsrA specifically reducing Met-S-SO to Met and predominantly localized in the cytoplasm, while MsrB specifically reduces Met-R-SO to Met and is mainly found in mitochondria and chloroplasts [12,13].

Numerous studies have demonstrated that Msr plays a critical role in mitigating cold stress in plants, a process mediated by various signaling molecules, including ROS [14], transcription factors (TFs) [15], kinases [16], and plant hormones [17,18]. Therefore, this paper reviews the role and regulatory mechanisms of Msr in the context of postharvest CI in plants, aiming to provide a theoretical foundation for further research in this field.

2. Msr in Plants

2.1. Classification and Distribution of Msr

Msr belongs to the oxidoreductase protein family, which is categorized into three subfamilies based on substrate specificity and phylogenetic clustering: MsrA, MsrB, and fMsr [19]. MsrA and MsrB are found in both prokaryotes and eukaryotes, whereas fMsr is restricted to prokaryotes and a limited number of single-celled eukaryotes. Among them, MsrA was the first methionine sulfoxide reductase to be discovered [20]. Early research on Msr focused primarily on animals and *Escherichia coli*. However, as research progressed, it was discovered that plants possess significantly more Msr variants than mammals [13,21]. For instance, mice have only four *Msr* genes [22], while *Arabidopsis thaliana* contains fourteen *Msr* genes [23], which has drawn considerable interest from researchers. Over the past decade, Msr has been identified and studied in various plants, including bananas [24], tobacco [25], peppers [26], tomatoes [27], soybeans [28], papayas [29], wheat [30], corn [31], and strawberries [32].

The classification of MsrA and MsrB in plants is based on two key criteria: function and evolutionary relationships. The functional classification considers the number of cysteine residues, which influences the enzyme's catalytic mechanism and redox activity [33]. Meanwhile, the evolutionary classification groups MsrA and MsrB are based on their phylogenetic relationships, reflecting their divergence and conservation across different plant species [34]. Clarifying these classifications helps to better understand their structural and functional diversity in plants. When discussing the first classification, it is necessary to examine cysteine (Cys). Cys plays a pivotal role in Msr due to its reducing properties [35,36]. As shown in Figure 1, the distribution of Cys residues is largely conserved among different MsrA enzymes, with two located at the N-terminus (CysA and CysB) and two at the C-terminus (CysC and CysD). CysA, the catalytic residue, is positioned within the conserved sequence F[A/G]AGCFW[G/R]VELA, where "GCFW" is a hallmark motif for identifying MsrA. CysB, also at the N-terminus, is conserved but not essential for catalysis. The C-terminal cysteines, CysC and CysD, are located within the highly conserved motif KGC[N/A/K]DPI[R/N]CYG, where they form a disulfide loop in Msr. The number of Cys residues involved in the reduction process varies among MsrA enzymes, which can be classified into three categories: (1) enzymes containing three conserved Cys residues, two of which participate in the MsrA catalytic process, a characteristic observed in most plants and *Escherichia coli* [37]; (2) enzymes with two conserved Cys residues, one of which functions as a reducing MsrA, as exemplified by *Mycobacterium tuberculosis* [38]; and (3) MsrA enzymes

possessing two conserved Cys residues but lacking reducing Cys residues within their sequences, as seen in the genus *Synechocystis* [20].

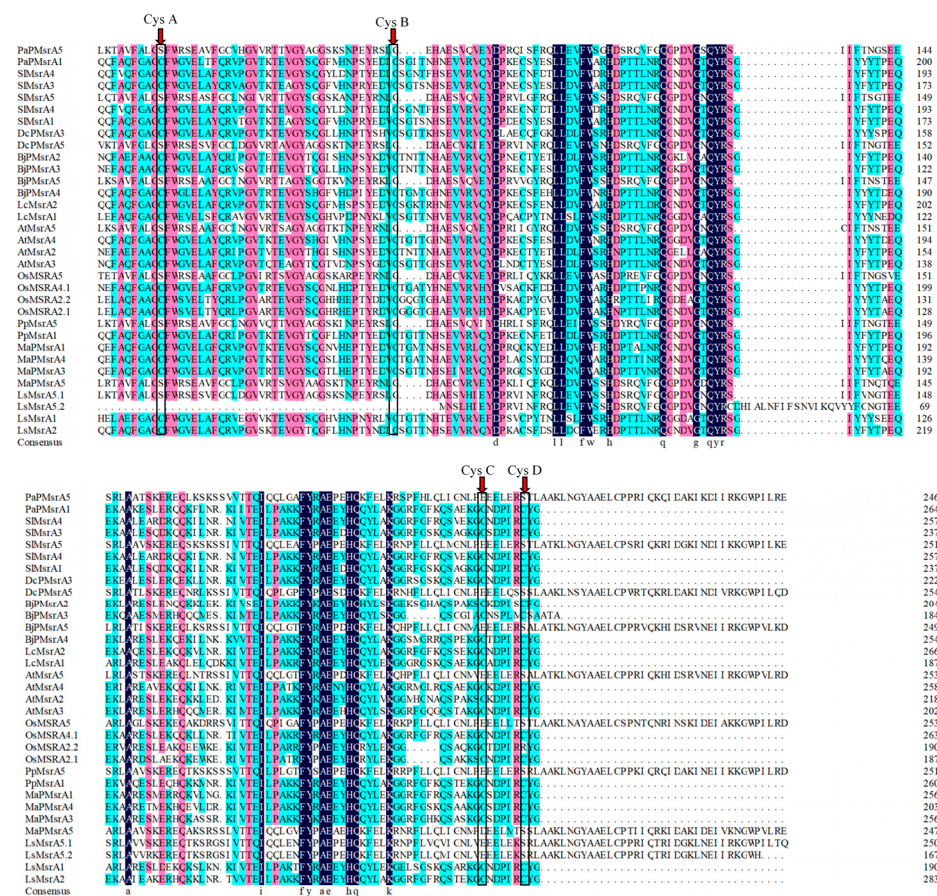


Figure 1. Multiple sequence alignment of *MsrA* genes in plants (Sequence information is detailed in Appendix A). Note: Black represents 100% homology, red represents 80~100%, blue represents 60~80%, and colorless represents less than 60%.

As shown in Figure 2, the *MsrB* sequences exhibit high homology, with most containing two “CxxC” motifs and two conserved cysteine residues. However, the number of reducing cysteines varies among *MsrB* variants, which can be classified into two categories based on this number: (1) *MsrB* containing one reducing Cys in the sequence, such as *MsrB* in most plants [39] and (2) *MsrB* not containing reducing Cys in the sequence, such as *MsrB* of *Arabidopsis* [40].

Another classification method is based on sequence homology [41]. Although both *MsrA* and *MsrB* can reduce MetSO, they exhibit no significant sequence homology between the two subfamilies. For example, the homology between *MsrA* sequences is 44.08% and between *MsrB* sequences is 44.62%, while the homology between *MsrA* and *MsrB* sequences is only 26.77%. Sequence alignment has revealed that *MsrA* variants can be grouped into two subpopulations (α and β) based on a rootless phylogenetic tree (Figure 3). The first subgroup (β) consists of *MsrA5*, while the second subgroup (α) includes all other *MsrA* proteins. It has also been reported that *MSRA5* exhibits significant differences in sequence homology compared with other *MSRA* proteins, as well as notable differences in the number of exons [9]. Similarly, *MsrB* is divided into two subgroups (α and β). The first subgroup (α) consists of *MsrB1*, while the second subgroup (β) includes all other *MsrB* proteins.

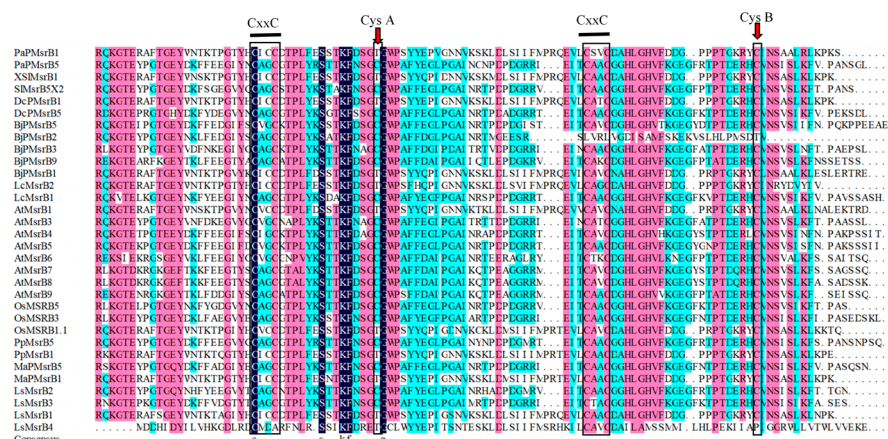


Figure 2. Multiple sequence alignment of *MsrB* genes in plants (sequence information is detailed in Appendix A). Note: Black represents 100% homology, red represents 80–100%, blue represents 60–80%, and colorless represents less than 60%.

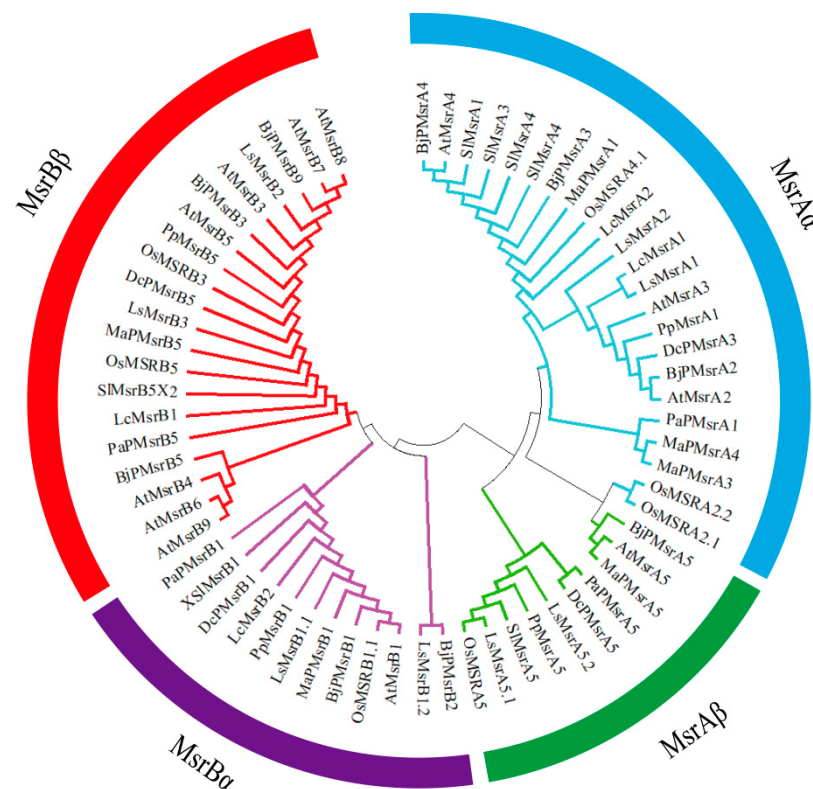


Figure 3. Evolutionary tree of *Msr* genes in plants (sequence information is detailed in Appendix A).

2.2. Subcellular Localization of *Msr*

In plants, *Msr* is distributed across various organelles [42]. *MsrA* is localized in the nucleus, mitochondria, chloroplast, cytoplasm, and endoplasmic reticulum, while *MsrB* is found in the nucleus, cytoplasm, chloroplast, and endoplasmic reticulum. Additionally, the subcellular localization of *MsrA* and *MsrB* is predominantly concentrated in the nucleus and chloroplasts (Figure 4) [33]. This diverse distribution of *Msr* proteins in plants enables them to play a crucial role in plant growth, development, and stress resistance [9,34].

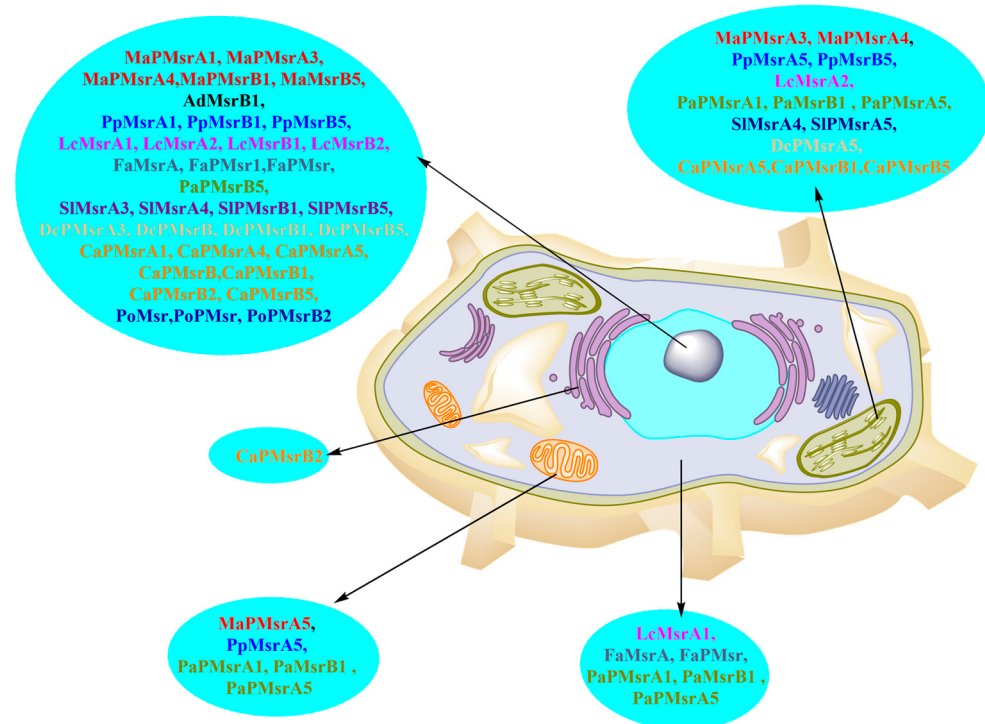


Figure 4. Subcellular localization of *Msr* genes in plants (sequence information is detailed in Appendix A, and subcellular localization is predicted in <http://www.csbio.sjtu.edu.cn/bioinf/Cell-PLoc/>, accessed on 3 January 2025).

3. Role of *Msr* in Response to Chilling Stress

3.1. Postharvest CI of Fruits and Vegetables

Fruits and vegetables continue to undergo active metabolic processes during postharvest storage, leading to changes in color, texture, flavor, aroma, and nutrient content [15,43,44]. Low-temperature storage can slow these metabolic activities, helping to preserve the quality of harvested produce and extend its storage and transportation life [45,46]. However, not all fruits and vegetables tolerate cold storage well. Some are prone to chilling injury (CI), a physiological disorder that occurs when sensitive produce is exposed to temperatures below their optimal range but above freezing. CI can lead to symptoms such as surface pitting, discoloration, uneven ripening, and off-flavors, ultimately causing quality deterioration and economic losses. Many tropical and subtropical fruits, including bananas [47], mangoes [48], papayas [49], guavas [50], lychees [18], pineapples [51], and green peppers [52], are particularly susceptible to CI during low-temperature storage and transportation.

Temperature is a critical factor influencing the postharvest storage quality and shelf life of fruits and vegetables [53]. CI occurs when low-temperature stress damages tissues at temperatures above freezing, disrupting cellular structures and physiological functions [5]. The symptoms of CI vary across different fruits and vegetables and can be categorized as follows:

1. Surface deformities: dimpled plaques or pitted lesions appear on the epidermis of fruits and vegetables such as apples [54] and sweet potatoes [55].
2. Water-soaked lesions: thin-skinned fruits and vegetables, including tomatoes [56], cucumbers [57], and bell peppers [58], often develop translucent, water-stained spots.
3. Discoloration and browning: CI-induced browning may occur on the surface or beneath the skin, affecting fruits such as bananas [59], mangoes [60], pears [61], peaches [62], and pineapples [63].

4. Ripening abnormalities: fruits such as bananas [59], mangoes [60], and peaches [62] may fail to ripen properly and lose some of their aromatic compounds.
5. Severe tissue breakdown: in advanced cases, CI leads to extensive tissue damage. For example, cold-damaged olive fruit develops a sunken, wrinkled surface with brown discoloration in both the skin and flesh [64].

Figure 5 illustrates specific CI symptoms in various fruits and vegetables.

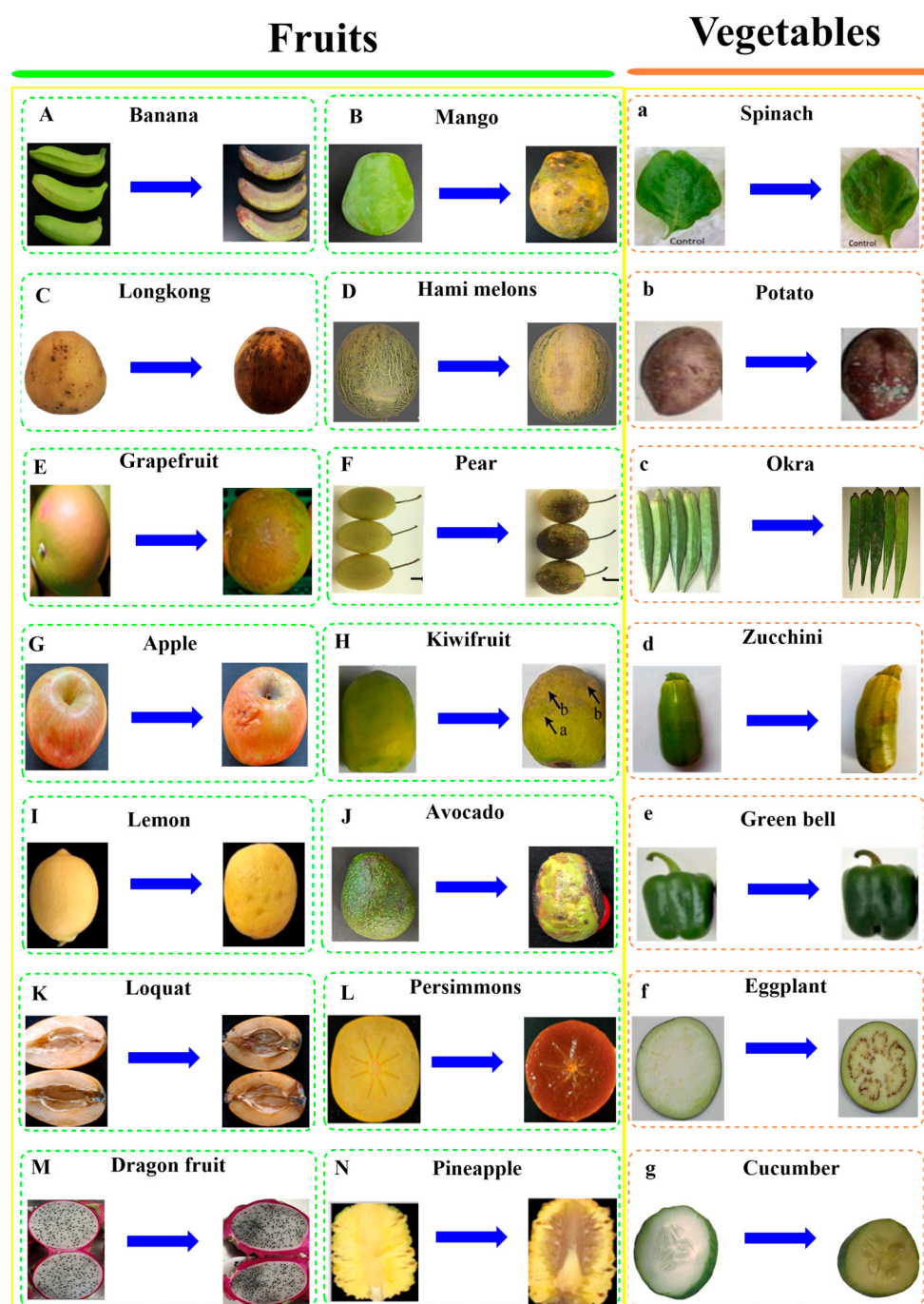


Figure 5. Symptoms of postharvest CI of fruits and vegetables ((A) banana [59]; (B) mango [60]; (C) longkong [29]; (D) Hami melons [65]; (E) grapefruit [66]; (F) pear [61]; (G) apple [54]; (H) kiwifruit [67]; (I) lemon [68]; (J) avocado [69]; (K) loquat [70]; (L) persimmons [52]; (M) dragon fruit [71]; (N) pineapple [63]; (a) spinach [72]; (b) potato [55]; (c) okra [17]; (d) zucchini; (e) green bell [58]; (f) eggplant [73]; (g) cucumber [57]).

3.2. ROS and CI of Fruits and Vegetables

3.2.1. Definition, Types, and Production of ROS

ROS refer to oxygen-containing derivatives or intermediate products generated during metabolic processes in biological systems involving oxygen [1]. ROS exhibit a significantly higher oxidative capacity compared with O_2 [4]. ROS are inevitable byproducts of aerobic metabolism, as continuous electron transfer occurs within organisms [2]. During this process, a small fraction of O_2 , either absorbed or internally produced, undergoes gradual oxidation, resulting in the formation of ROS [3].

ROS include hydrogen peroxide (H_2O_2) and hydroxyl radicals ($\cdot OH$), along with superoxide anions ($O_2^{\cdot -}$) and singlet oxygen (1O_2) [3]. Among these, H_2O_2 and 1O_2 are classified as non-radical oxygen-containing molecules, while $O_2^{\cdot -}$ and $\cdot OH$ are categorized as oxygen radicals. Among ROS, the $O_2^{\cdot -}$ is the earliest generated species in the oxidative metabolism of O_2 in plants. It is considered a precursor to other ROS, as it undergoes further reactions to form H_2O_2 and $\cdot OH$ [1]. Specifically, $O_2^{\cdot -}$ is produced when O_2 accepts a single electron, initiating a cascade of ROS formation [3]. 1O_2 is produced when ground-state oxygen absorbs energy, exciting the unpaired electrons in its outer orbital [3]. This energy is typically supplied by photons, making the generation of singlet oxygen primarily occur in the photosystem II (PSII) of plant chloroplast [3,74]. Beyond these four primary types, ROS also include hydrogen peroxy radicals ($HO_2\cdot$), nitric oxide (NO), and lipid peroxidation products (LPOs). Regardless of their specific form, all ROS share the characteristic of being highly reactive oxygen derivatives [1,75,76].

The $O_2^{\cdot -}$ formed in the cell is not stable and is rapidly catalyzed by SOD to form H_2O_2 , so H_2O_2 is produced almost everywhere $O_2^{\cdot -}$ is produced [77]. The H_2O_2 can be produced by electron transport chains (ETCs) and photorespiration in plant cell chloroplasts, mitochondria, endoplasmic reticula, and plasma membranes under normal or stressful conditions (such as drought, low temperature, ultraviolet radiation, strong light, etc.) [4]. The H_2O_2 has a long range of action relative to other ROS. Compared with H_2O_2 and 1O_2 , $\cdot OH$ exhibits stronger oxidative properties. Due to their short half-life and high reactivity, $\cdot OH$ causes substantial damage to plant cells, especially at their sites of production. This damage primarily occurs through hydrogen extraction from organic molecules, oxidative decomposition of amino acids, and addition reactions with benzene ring-containing molecules [74].

3.2.2. Mechanism of ROS Causing Postharvest CI of Fruits and Vegetables

Under normal postharvest storage conditions, the production and removal of ROS in cells remain relatively balanced, as illustrated in pathways ① and ② in Figure 6 [1]. A moderately low-temperature environment can further reduce ROS production in postharvest vegetables, likely due to the inhibition of respiratory metabolism by low temperatures [78,79]. However, when the storage temperature drops excessively, vegetables experience low-temperature stress, disrupting the balance between ROS production and degradation (ROS production in pathway ① significantly exceeds ROS degradation in pathway ②) [52]. This imbalance leads to excessive ROS accumulation, which can damage cellular components [64].

Excess ROS damage DNA, RNA, proteins, membrane lipids, and polysaccharides, leading to accelerated lipid peroxidation. These processes ultimately disrupt the structure and function of cell membranes, causing further physiological damage [3]. Compared with other macromolecules, protein oxidation is more prevalent, accounting for 68% [2]. ROS can attack proteins directly or indirectly, leading to structural alterations and a partial or complete loss of biological activity [3,75]. Among them, the direct modification includes the oxidation of sulfur-containing groups, the peroxidation of amino acid residues, the

glycinylation of glutaten, and the formation of disulfide bonds [76]. Indirect modification mainly refers to the combination of protein with fatty acid peroxidation cleavage products to form carbonylated proteins [4]. These actions will destroy the original structure of the protein [4,75].

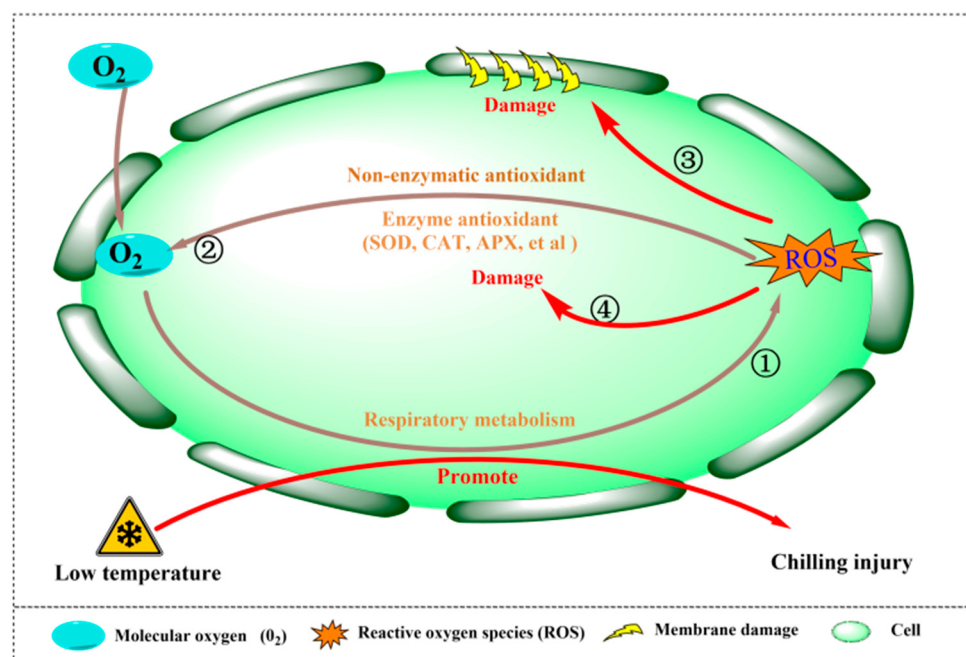


Figure 6. Mechanism of ROS causing chilling injury in fruits and vegetables under low-temperature stress.

The CI of harvested vegetables caused by low-temperature storage is generally attributed to two key mechanisms. First, low temperatures disrupt the normal respiration of harvested vegetables, resulting in the accumulation of ROS (pathway ①: stimulation of ROS enrichment). Excess ROS oxidizes lipids and proteins in cell membranes, resulting in structural damage and accelerating cell senescence (pathway ③). Second, the accumulation of ROS can oxidize antioxidant enzymes. This oxidation reduces the ROS-scavenging efficiency of these enzymes, further exacerbating ROS accumulation (pathway ④) [44].

3.2.3. Repair Mechanism of Msr After Protein Oxidation in Fruits and Vegetables

Met is a sulfur-containing amino acid, and its sulfur atoms are highly prone to oxidation, making it one of the most oxidized amino acids in proteins [15]. Oxidation of the chiral sulfur atoms in Met produces two diastereomers, Met-S-SO and Met-R-SO, which typically exist in equal amounts (Figure 7) [31]. MetSO can further undergo oxidation to form MetO₂ [80]. Oxidation of methionine in proteins alters their structure and function. In organisms, MetSO can be reduced back to Met by Msr, thereby restoring the function of the oxidized protein [80]. MsrA specifically catalyzes the reduction of Met-S-SO to Met, while MsrB catalyzes the reduction of Met-R-SO to Met [80]. Additionally, in 2007, researchers identified a new enzyme in *Escherichia coli*, termed fRMsr, which efficiently catalyzes the reduction of free Met-R-SO [81,82]. However, fMsr is primarily found in prokaryotes and certain lower eukaryotes and has not yet been identified in plants, resulting in a lack of research on its presence and function in plant systems [82,83].

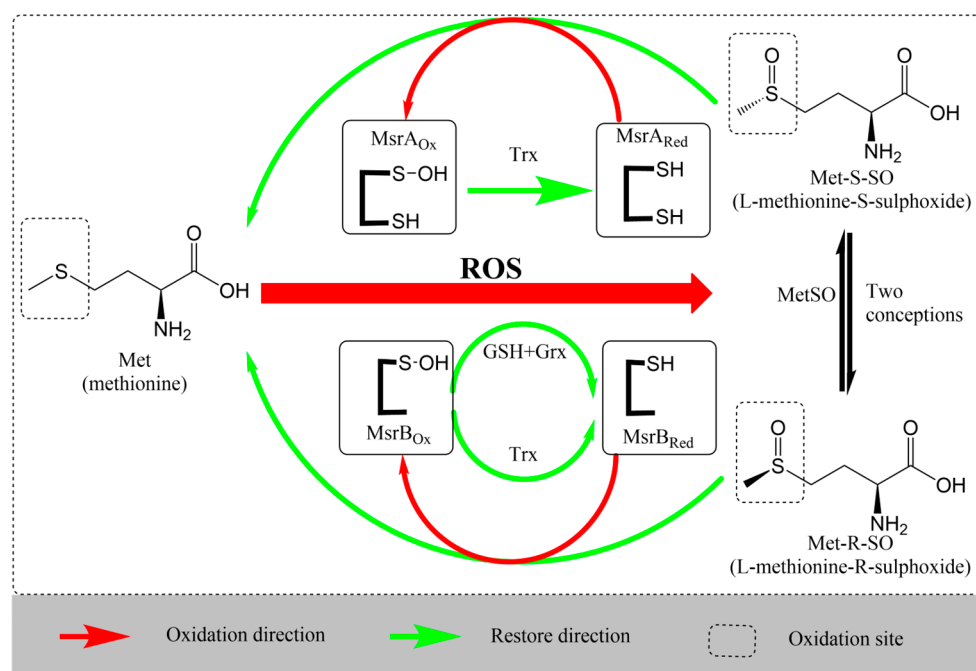


Figure 7. Repair mechanisms of Msr in plants.

Because Met in plants is oxidized to form racemic isomers of MetSO, the synergistic action of MsrA and MsrB is required to repair the oxidized Met [83]. Both MsrA and MsrB can reduce free Met as well as protein-bound Met, while fMsr is specific to free Met [84]. After repairing the oxidized protein, the Msr enzymes themselves are oxidized (transitioning from MsrRed to MsrOX). The thioredoxin (Trx) system and glutaredoxin (Grx) are necessary to reconvert MsrOX back to MsrRed. Specifically, MsrAOX is reduced by the Trx system alone to form MsrRed, while MsrBOX can be reduced by either the Trx system or the GSH + Grx system to form MsrRed [26,85].

4. Regulation of Msr Genes

4.1. Upstream Regulatory Mechanisms of Msr

The Msrs in plants are regulated by various factors, including environmental influences [86], plant hormones [15], and transcription factors [15,39]. Stress has been shown to induce the expression of multiple Msr in fruits and vegetables, which helps to eliminate excess ROS and plays a crucial role in regulating resistance to abiotic stress [8]. For example, the expression levels of *SIMsrA* and *PoMsrA* were significantly increased in tomato seedlings and oyster mushrooms treated with mannitol and sodium chloride to simulate drought and high salt stress [86]. Additionally, *SIMsrB2* enhances drought resistance by repairing catalase to scavenge ROS, further highlighting the role of Msr in drought stress response [86]. Extreme temperatures are another key environmental factor influencing the growth and quality of fruit and vegetable crops [87]. Msr also plays a crucial role in plants' response to low-temperature stress. For instance, when passion fruit was stored at 4 °C, 7 °C, and 10 °C, the peel of fruit stored at 4 °C exhibited a higher CI index compared with those stored at 7 °C and 10 °C. Additionally, the relative expression level of MsrA was significantly elevated in the 4 °C storage group compared with the other two groups (unpublished laboratory data). Yan et al. [24] reported that hyperoxia treatment accelerates the senescence of postharvest bananas, with the expression of *MaMsrB2* increasing under hyperoxia, suggesting that *MaMsrB2* may play a role in responding to hyperoxia stress.

The regulation of Msr by plant hormones is complex, with some hormones significantly increasing Msr expression while others inhibit it. For example, the expression of

SIMsrA in tomato seedlings was significantly increased in response to exogenous salicylic acid (SA) treatment, suggesting that *SIMsrA* may be involved in SA-mediated disease resistance in tomato seedlings [88,89]. Additionally, inositol 1,4,5-triphosphate (IP3) [90] and γ -aminobutyric acid (GABA) [52] have been shown to increase the expression of *Msr*, enhancing antioxidant capacity. Conversely, some hormones can regulate the growth of fruit and vegetable crops by inhibiting *Msr* expression. For instance, exogenous application of auxin (e.g., naphthalene acetic acid) inhibits the expression of *FaPMsr* in strawberries [32]. In peppers, the expression of *CaMsrB2* was significantly downregulated in response to SA, methyl jasmonate (MeJA), and ethylene treatments, accelerating ROS accumulation and triggering hypersensitive responses (HRs) at the disease site, indicating that *CaMsrB2* actively responds to defense signals [91].

Additionally, Skelly found that the transcription factors NOR and NAC regulate the transcriptional activity of *SIMsrA* and *SIMsrB2* by binding to the TATA box in their promoters. This activation enhances their expression and promotes fruit ripening [92]. During the postharvest storage of kiwifruit, ethylene induces the expression of *AdMsrB1* by activating the transcription factors *AdNAC2* and *AdNAC72* [93].

Beyond its regulatory role in hormone signaling and stress response, *Msr* also influences fruit ripening and senescence by modulating enzymatic activity and protein redox states (Figure 8).

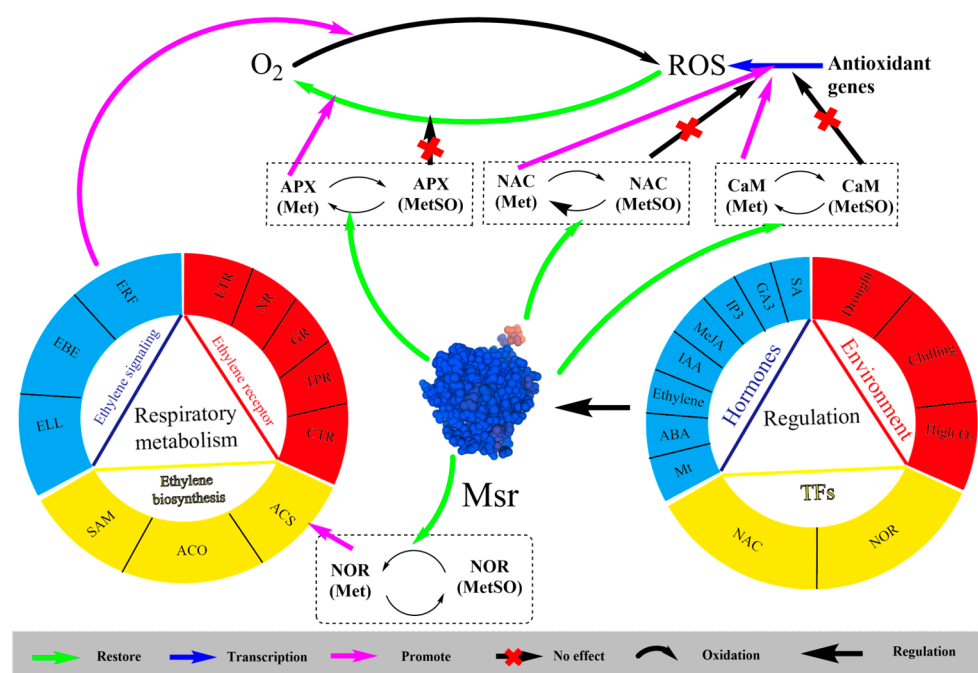


Figure 8. Regulatory mechanisms of *Msr* in plants.

4.2. Substrate Protein of *Msr*

Msr can also indirectly regulate the ripening and senescence of fruits and vegetables through various mechanisms, such as enzymatic systems and redox modification of proteins [24]. APX and Cat are key antioxidant enzymes in plant systems, participating in a variety of developmental processes and stress responses by scavenging ROS and regulating ROS levels [21]. In bananas, *MaMsrB2* was found to reduce MetSO in *MaAPX1*, restoring *MaAPX1* activity and thereby regulating the ripening and senescence of the fruit [16]. In addition, Jiang et al. [94] demonstrated that *MaMsrA7* repairs the methionine sulfoxide in *MaCaM1*, thereby enhancing the transcription of *MaCaM1*-mediated genes involved in the antioxidant response in fruits.

MsrS can be interregulated through transcription factors associated with maturation and participate in response to various stresses. For example, in tomatoes, studies have shown that SIMsrA effectively repairs the oxidative damage of the transcription factor NOR [95]. This repair reverses the reduction in the transcriptional activity of genes related to respiratory metabolism, which is caused by NOR sulfoxide, thereby inhibiting the production of ROS [93].

4.3. Msr-Mediated Regulation of CI in Postharvest Fruits and Vegetables

The study found that the occurrence of CI was effectively mitigated in certain fruits and vegetables when pretreated after harvest with substances such as ABA [96], nitric oxide (NO) [97,98], and 1-MCP [52]. Additionally, these treatments were found to regulate the expression of Msr [9,46]. These results suggest that Msrs play a crucial role in delaying the onset of CI in treated fruits and vegetables.

4.3.1. Msr Mediates the Regulation of NO Inhibition of CI in Postharvest Fruits and Vegetables

The occurrence of CI during low-temperature storage has been significantly delayed by NO treatment in various fruits and vegetables, including oranges [99], kiwifruits [100], peaches [90], bananas [101], plums [102], loquats [103], longkongs [29], bamboo shoots [104], and Hami melons [97]. Over the past few decades, the inhibitory effects of NO on CI have been primarily attributed to its role in enhancing antioxidant capacity, maintaining high energy charge, and reducing lipid peroxidation [97,99,105]. For instance, in bananas, NO treatment improves cold tolerance and preserves storage quality by activating energy metabolism-related enzymes and sustaining a high-energy status during refrigeration [101]. Furthermore, NO enhances fruit quality by inducing antioxidant responses and mitigating lipid peroxidation, thereby delaying CI onset [29]. Recent studies have demonstrated a direct link between NO and Msr regulation in CI mitigation. Jiang et al. showed that NO mitigates oxidative damage in fruits by increasing the expression of Msr genes and proteins, which helps delay CI. Additionally, Jiang et al. [94] revealed that Msr contributes to CI resistance by regulating ROS metabolism, energy homeostasis, and lipid oxidation through the redox modulation of Cam.

4.3.2. Msr Mediates the Regulation of MeJA Inhibition of CI in Postharvest Fruits and Vegetables

MeJA treatment has been shown to significantly delay the onset of CI in various fruits and vegetables, including mango [106], tomato [107], cowpea [108], loquat [109], banana [87], and pineapple [63]. Over the past few decades, the mechanisms underlying MeJA-mediated CI inhibition have been extensively explored, focusing on glucose metabolism [107], antioxidant capacity [108], cell wall metabolism [110], and arginine metabolism [111]. For example, MeJA treatment enhances the cold tolerance of tomato fruits by modulating sugar metabolism, promoting starch degradation and sucrose accumulation while inhibiting excessive increases in glucose and fructose levels [107]. Similarly, Zhang et al. [111] demonstrated that MeJA participates in arginine metabolism by upregulating the mRNA expression and enzymatic activities of arginase, arginine decarboxylase, and ornithine aminotransferase, leading to increased accumulation of free putrescine and proline, thereby improving the cold tolerance of cherry tomatoes during postharvest storage. More recently, Min et al. [44] found that MeJA treatment upregulates the expression of SIMsrB5 in tomatoes, which is associated with a significant reduction in CI. Conversely, silencing SIMsrB5 not only increased CI incidence in tomato fruits by 52.17% but also weakened the protective effects of MeJA against CI. These findings suggest that Msr plays

a crucial role in mitigating CI in postharvest fruits and vegetables, likely by contributing to MeJA-mediated stress responses.

4.3.3. Msr Mediates the Regulation of GABA Inhibition of CI in Postharvest Fruits and Vegetables

Pre-storage treatment with γ -aminobutyric acid (GABA) has been shown to significantly delay the onset of CI in various fruits and vegetables, including peaches [112], anthurium cut flowers [113], papayas [114], star fruits [115], Chinese olive fruits [64], mangoes [116], blueberries [117], cucumbers [57], apples [118], mushrooms [119], and bananas [120]. In recent decades, the mechanisms underlying CI inhibition have been explored across various metabolic pathways [115]. For instance, Yang et al. [112] demonstrated that GABA treatment enhances the enzymatic antioxidant system and energy homeostasis in peach fruit, thereby improving its cold tolerance and significantly reducing CI incidence. Similarly, Khaliq et al. [114] investigated the effects of two GABA concentrations (1 mM and 5 mM) on papaya fruit quality during low-temperature storage (4 °C, 80–90% RH). Their findings revealed that GABA-treated fruits exhibited significantly higher proline levels, endogenous GABA accumulation, phenolic content, and total antioxidant activity compared with the control group. These results suggest that GABA enhances cold tolerance in papaya by reducing oxidative stress and strengthening the fruit's defense system, thereby effectively inhibiting CI. Additionally, Ge et al. [117] reported that GABA treatment increased total phenol and flavonoid accumulation in blueberries, extending shelf life and delaying senescence through the activation of key enzymes in phenylpropanoid metabolism, including phenylalanine ammonia-lyase, cinnamate-4-hydroxylase, 4-coumarate:CoA ligase, and polyphenol oxidase. More recently, Jiao et al. [121] investigated the effects of GABA treatment on the storage quality of peach fruit under low-temperature conditions. Their study demonstrated that GABA treatment activates the Msr-TrxR system by enhancing the gene expression and enzymatic activities of *MsrA*, *MsrB*, and *TrxR*, thereby maintaining high protein oxidative repair capacity and delaying CI progression in peach fruit.

4.3.4. Msr Mediates the Regulation of Melatonin Inhibition of CI in Postharvest Fruits and Vegetables

Fruits and vegetables such as kiwifruit [122], pineapple [123], guava [48], loquat fruit [124], cucumber [125], cherry tomato [126], sweet persimmon [52], pear [127], mango [128], and tomato [129] were treated with melatonin before storage, and the occurrence of CI during low-temperature storage was significantly delayed. In the past few decades, the mechanism of inhibition of CI has been generally elaborated from the perspective of ascorbic acid-glutathione cycle [126], antioxidant capacity [18], membrane lipid metabolism [130], proline metabolism [131], and phenolic metabolism [132]. For example, Madebo et al. showed that melatonin (MT) can improve the cold resistance of cucumber by regulating the metabolism of amines, proline and γ -aminobutyric acid and delay the occurrence of CI of cucumber fruit [125]. Liu et al. found that MT treatment could effectively inhibit the occurrence of CI and also proved that the enhancement of cold tolerance of pear fruit may be related to the regulation of proline, GABA, AsA, and soluble sugar metabolism [127]. Recently, Liu et al. [98] demonstrated that melatonin (MT) treatment enhances endogenous NO synthesis by upregulating protein oxidative repair-related genes (*LcMsrA1*, *LcMsrA2*, *LcMsrB1*, *LcMsrB2*, *LcTrx2*, and *LcNTR1*), thereby improving the cold tolerance of litchi fruit and delaying peel browning during low-temperature storage. Similarly, Xie et al. found that MT treatment upregulates gene expression of *LcMsr*, preserves protein repair and antioxidant capacity, and effectively mitigates browning in litchi under cold storage conditions [18].

4.3.5. Msr Mediates the Regulation of Gibberellin Inhibition of CI in Postharvest Fruits and Vegetables

Fruits and vegetables such as tomatoes [56] and peaches [90] were treated with gibberellin (GA3) before storage, and the occurrence of CI was significantly delayed during low-temperature storage. In the past few decades, the mechanism of inhibition of CI has been generally elaborated from the perspective of improving membrane lipid metabolism [133] and antioxidant capacity [134]. GA3 treatment regulates endogenous GA3 metabolism and enhances antioxidant capacity, which helps delay CI in postharvest fruits [56]. In small tomatoes, it was also found that the use of exogenous GA3 could regulate the metabolism of endogenous GA3, maintain the high antioxidant capacity of cherry tomatoes, and delay the increase of the CI index [135]. In addition to the internal regulation of endogenous GA3 metabolism, Jiao et al. recently found that exogenous GA3 treatment enhanced the expression level of *Msr*, maintained the high protein oxidative repair ability and cold tolerance of peach fruits, and delayed the occurrence of CI [133].

4.3.6. Potential Role of Msr in Brassinolide-Mediated CI Inhibition in Postharvest Fruits and Vegetables

Fruits and vegetables, including eggplant [136], sweet cherry [137], *Toona sinensis* Bud [138], peach [139], and tomato [140], have been treated with brassinolide prior to storage, significantly delaying the onset of CI during low-temperature storage. Over the past few decades, the mechanism by which brassinolide mitigates CI has been extensively elucidated through various metabolic pathways. For example, Gao et al. [139] demonstrated that brassinolide enhances cold resistance in peach fruit by maintaining high antioxidant capacity through the regulation of phenolic and proline anabolism, thereby delaying CI during low-temperature storage. More recently, Hu et al. [140] found that upregulating the expression of the endogenous brassinolide synthesis gene (*SICYP90B3*) effectively inhibits phospholipase activity, thereby preserving cell membrane integrity and enhancing cold tolerance in tomato fruits. However, it remains unreported whether *Msr* mediates the regulatory role of brassinolide in inhibiting CI in postharvest fruits and vegetables. Nevertheless, studies have shown that sulfur-oxidized proteins can mediate the response of brassinolide to low-temperature stress [141]. Trx has long been considered the most suitable electron donor for *Msr* in living organisms [142], highlighting the need for further investigation into whether *Msr* plays a role in brassinolide-induced CI inhibition in postharvest fruits and vegetables.

While *Msr*'s direct involvement in brassinolide-mediated CI inhibition remains unexplored, its role in oxidative stress regulation, membrane protection, protein repair, and hormonal crosstalk suggests multiple possible pathways. Further studies could focus on elucidating the interaction between *Msr* and brassinolide signaling components.

5. Conclusions

With the advancement and refinement of molecular biology techniques, including yeast two-hybrid assays and co-immunoprecipitation, numerous target proteins of *Msr* have been identified and validated. These targets include calmodulin, apolipoprotein, potassium ion channel proteins, and the Ffh protein in *Escherichia coli*. Considering *Msr*'s critical role in plant stress responses, future research should prioritize exploring its interactions with potential target proteins and elucidating the physiological and biochemical mechanisms underlying these regulatory processes.

Current technologies for preventing and controlling postharvest chilling injury in fruits and vegetables primarily involve physical methods, such as heat treatment, packaging, and UV irradiation, as well as chemical methods, including ethylene, 1-MCP, GA, calcium ions,

NO, melatonin, SA, MeJA, and polyamines. Given the critical role of Msr in regulating ROS, future research should investigate the role and mechanisms of Msr within these approaches.

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Appendix A

Table A1. Information on genes in the paper.

Species	Gene	NCBI Reference Sequence (mRNA/Protein)
<i>Carica papaya</i> L.	<i>PaPMsrA5</i>	XM_022052179.1/ XP_021907871.1
	<i>PaPMsrA1</i>	XM_022049933.1/ XP_021905625.1
	<i>SlMsrA5</i>	NM_001320242.1/ NP_001307171.1
<i>Solanum lycopersicum</i> L.	<i>SlMsrA4</i>	NM_001321043.1/ NP_001307972.1
	<i>SlMsrA3</i>	NM_001320370.1/ NP_001307299.1
	<i>SlMsrA2</i>	JN102298.1/ AEN03272.1
	<i>SlMsrA1</i>	NM_001320202.1/ NP_001307131.1
<i>Daucus carota</i> var. <i>sativa</i> Hoffm.	<i>DcPMsrA3</i>	XM_017359291.2/ XP_017214780.1
	<i>DcPMsrA5</i>	XM_017399723.2/ XP_017255212.1
<i>Brassica juncea</i> (L.) Czern.	<i>BjPMsrA2</i>	XM_009124089.3/ XP_009122337.2
	<i>BjPMsrA3</i>	XM_009132743.3/ XP_009130991.2
	<i>BjPMsrA5</i>	XM_009114216.3/ XP_009112464.1
	<i>BjPMsrA4</i>	XM_009139249.3/ XP_009137497.1
	<i>LcMsrA1</i>	KY475577.1/ AQP31371.1
<i>Litchi chinensis</i> Sonn.	<i>LcMsrA2</i>	KY475578.1/ AQP31372.1
	<i>LcMsrB1</i>	KY475579.1/ AQP31373.1
	<i>LcMsrB2</i>	MH396620.1/ QBB68762.1

Table A1. Cont.

Species	Gene	NCBI Reference Sequence (mRNA/Protein)
<i>Arabidopsis thaliana</i> (L.) Heynh.	<i>AtMsrA5</i>	NM_127359.5/ NP_179394.1
	<i>AtMsrA4</i>	NM_118645.4/ NP_194243.1
	<i>AtMsrA2</i>	NM_120828.4/ NP_196363.1
	<i>AtMsrA3</i>	NM_120829.3/ NP_196364.1
	<i>AtMsrB1</i>	NM_104245.4/ NP_564640.2
	<i>AtMsrB2</i>	NM_001341518.1/ NP_001320026.1
	<i>AtMsrB3</i>	NM_116718.3/ NP_567271.1
	<i>AtMsrB4</i>	NM_116719.3/ NP_192390.1
	<i>AtMsrB5</i>	NM_116721.4/ NP_192392.1
	<i>AtMsrB6</i>	NM_116722.4/ NP_192393.2
	<i>AtMsrB7</i>	NM_118303.4/ NP_567637.1
	<i>AtMsrB8</i>	NM_118304.5/ NP_193915.1
<i>Oryza sativa</i> L.	<i>OsMsrA5</i>	NM_001419584.1/ NP_001406513.1
	<i>OsMsrA4.1</i>	XM_052278347.1/ XP_052134307.1
	<i>OsMsrA2.2</i>	XM_052297699.1/ XP_052153659.1
	<i>OsMsrA2.1</i>	NM_001419583.1/ NP_001406512.1
<i>Prunus persica</i> (L.) Batsch	<i>PpMsrA5</i>	XM_007227483.2/ XP_007227545.1
	<i>PpMsrA1</i>	XM_007218770.2/ XP_007218832.1
	<i>MaPMsrA1</i>	XM_009386413.3/ XP_009384688.2
<i>Musa acuminata</i> ‘(AAA)’	<i>MaPMsrA4</i>	XM_009383708.3/ XP_009381983.2
	<i>MaPMsrA3</i>	XM_009403708.3/ XP_009401983.2
	<i>MaPMsrA5</i>	XM_009394013.3/ XP_009392288.2
	<i>LsMsrA5.1</i>	Unpublished data
<i>Lactuca sativa</i> L.	<i>LsMsrA5.2</i>	Unpublished data
	<i>LsMsrA1</i>	Unpublished data
	<i>LsMsrA2</i>	Unpublished data
<i>Carica papaya</i> L.	<i>PaPMsrB1</i>	XM_022039393.1/ XP_021895085.1
	<i>PaPMsrB5</i>	XM_022034123.1/ XP_021889815.1

Table A1. Cont.

Species	Gene	NCBI Reference Sequence (mRNA/Protein)
<i>Solanum lycopersicum</i> L.	<i>SlMsrB1</i>	XM_004244256.5/ XP_004244304.3
	<i>SlPMsrB5</i>	XM_004229424.5/ XP_004229472.1
<i>Daucus carota</i> var. <i>sativa</i> Hoffm.	<i>DcPMsrB1</i>	XM_017394132.2/ XP_017249621.1
	<i>DcPMsrB5</i>	XM_017365040.2/ XP_017220529.1
	<i>BjPMsrB5</i>	XM_033286223.1/ XP_033142114.1
<i>Brassica juncea</i> (L.) Czern.	<i>BjPMsrB2</i>	XM_009122844.3/ XP_009121092.1
	<i>BjPMsrB3</i>	XM_009116296.3/ XP_009114544.1
	<i>BjPMsrB9</i>	XM_009110283.2/ XP_009108531.1
	<i>BjPMsrB1</i>	XM_009149339.3/ XP_009147587.1
<i>Litchi chinensis</i> Sonn.	<i>LcMsrB2</i>	MH396620.1/ QBB68762.1
	<i>LcMsrB1</i>	KY475579.1/ AQP31373.1
	<i>AtMsrB1</i>	NM_104245.4/ NP_564640.2
<i>Arabidopsis thaliana</i> (L.) Heynh.	<i>AtMsrB3</i>	NM_116718.3/ NP_567271.1
	<i>AtMsrB4</i>	NM_001340514.1/ NP_001329727.1
	<i>AtMsrB5</i>	NM_116721.4/ NP_192392.1
	<i>AtMsrB6</i>	NM_116722.4/ NP_192393.2
	<i>AtMsrB7</i>	NM_118303.4/ NP_567637.1
	<i>AtMsrB8</i>	NM_118304.5/ NP_193915.1
	<i>AtMsrB9</i>	NM_118305.3/ NP_567638.1
<i>Oryza sativa</i> L.	<i>OsMSRB1.1</i>	NM_001423988.1/ NP_001410917.1
	<i>OsMsrB3</i>	NM_001402525.1/ NP_001389454.1
	<i>OsMsrB5</i>	NM_001402157.1/ NP_001389086.1
<i>Prunus persica</i> (L.) Batsch	<i>PpMsrB5</i>	XM_020570828.1/ XP_020426417.1
	<i>PpMsrB1</i>	XM_007212038.2/ XP_007212100.1

Table A1. Cont.

Species	Gene	NCBI Reference Sequence (mRNA/Protein)
<i>Musa acuminata</i> ‘(AAA)’	<i>MaPMsrB5</i>	XM_009413902.3/ XP_009412177.2
	<i>MaPMsrB1</i>	XM_065153234.1/ XP_065009306.1
	<i>LsMsrB1</i>	Unpublished data
	<i>LsMsrB2</i>	Unpublished data
<i>Lactuca sativa</i> L.	<i>LsMsrB3</i>	Unpublished data
	<i>LsMsrB4</i>	Unpublished data

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